Revision of the *Aspicilia reptans* group in western North America, an important component of soil biocrusts

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Cover: Habitat for *Aspicilia reptans* at Juniper Beach Provincial Park, British Columbia, Canada, occurring on calcareous soil supporting a divirse community of biocrusts. Photo: J. Di Meglio.

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Type locality of *Aspicilia californica* var. *gigantea* in Klamath County, Oregon. During the wet season, partial submergence by standing water is common on these poorly drained basaltic flats. Photo: J. Di Meglio.

Habitat for *Aspicilia wyomingensis*. The species was abundant at this site. Wyoming: Fremont Co., W of Boysen Reservoir, just S of quarry, stony calcareous hilltop with sparse grasses and *Opuntia*, *McCune 37199*.

Abstract

Aspicilia in the broad sense is one of the most common and speciose genera of saxicolous lichens in the world. It is also a common genus in the biological soil crusts of arid and semi-arid parts of North America, as well as on other continents. Analysis of DNA sequences and morphology from *Aspicilia* in soil crusts revealed previously unrecognized species that are ecologically, geographically, morphologically, and genetically distinct. We describe six previously unrecognized species (*Aspicilia albonota, A. diploschistiformis, A. papilliformis, A. spicata, A. subcontinua,* and *A. wyomingensis*), supported by phylogenetic reconstruction from ITS and nuLSU sequence data. The combined ITS+LSU tree with 368 specimens (339 ITS, 145 LSU, including 177 new sequences) places these species in various genera that have been segregated from *Aspicilia*, but because of problems in generic delimitation, we adopted a broad genus concept and assigned all of the new species to *Aspicilia* for simplicity and practicality. Previous segregates from *Aspicilia* (*Agrestia, Aspiciliella, Aspilidea, Chlorangium, Circinaria, Lobothallia, Megaspora, Oxneriaria, Sagedia, Sphaerothallia,* and *Teuvoa*) were in some cases nested within each other, lacking statistical support, or polyphyletic. Recognition of these genera would require erection of additional new small genera to accommodate the sequenced species of *Aspicilia* s.l. that fall outside of those clades. The new species are mostly infertile, primarily terricolous, and are separable in most cases by a key to subtle differences in morphology, anatomy, and secondary chemistry. In many cases a thallus section viewed under the compound microscope along with thin-layer chromatography for aspicilin will help to identify species. Nevertheless, the plastic, substrate-coating morphology and common sterility present serious challenges to purely microscopic identification. In addition to recognizing these new species, we describe a new variety, *A. californica* var. *gigantea* from Oregon, allopatric with the typical variety, and having thalli about twice the size of typical *A. californica*. We hypothesize that the new variety has a polyploid origin. We synonymize *A. mansourii* described from Iran under *A. reptans* s.str., based on morphology, chemistry, and ITS sequences. *Aspicilia reptans* s.str. is thus new to Eurasia. The other new taxa are so far known only from western North America, with the exception of *A. wyomingensis*, which occurs in Spain, based on phylogenetic placement of a specimen with an ITS sequence. The Eurasian species *A. aspera* is tentatively confirmed for North America. Two additional new species are described, *A. maritima* and *A. supralittorea*, both from the Pacific coast of Oregon.

Keywords. Lichenized fungi, *Aspicilia albonota*, *Aspicilia aspera, Aspicilia californica* var. *gigantea, Aspicilia diploschistiformis, Aspicilia maritima, Aspicilia papilliformis, Aspicilia spicata, Aspicilia subcontinua, Aspicilia supralittorea, Aspicilia wyomingensis*, biological soil crust, *Circinaria*, Megasporaceae

Habitat for *Aspicilia filiformis* at Upper Table Rock, north of Medford, Oregon. Small thalli were entangled within the bryophyte mat over soil. Photo: J. Di Meglio.

Habitat for *Aspicilia hispida, A. reptans,* and *A. rogeri,* near Kremmling, Colorado. All three species were exceptionally abundant at this site. *Aspicilia hispida* was primarly found in areas devoid of vegetation and were partially sunken into the soil, forming robust and fertile thalli. Photo: J. Di Meglio.

Introduction

Aspicilia A. Massal. is one of the most common genera in the biological soil crusts of arid and semi-arid parts of North America, as well as on other continents. Because of the ecological significance of biocrusts (e.g., Belnap & Lange 2001; Rodríguez-Caballero et al. 2018), a strong taxonomic foundation is particularly critical. In recent decades, much taxonomic progress has been made on *Aspicilia* in the broad sense (Nordin et al. 2007, 2010, 2011; Owe-Larsson et al. 2007, 2011; Ren et al. 2018; Sohrabi et al. 2013; Zakeri et al. 2017, 2019a, 2019b) and terricolous species in particular (Rosentreter 1998; Sohrabi & Ahti 2010; Sohrabi et al. 2010a, 2010b, 2011a, 2012). Yet much remains to be done in this large and difficult genus.

The first recognition of crustose *Aspicilia* as a component of the North American biocrust was by Looman (1962, 1964), working in Saskatchewan and the northern Great Plains. As part of this work he described *Lecanora reptans* Looman. Now known as *Aspicilia reptans* (Looman) Wetmore, the species has been widely reported in western North America (e.g., McCune & Rosentreter 2007; Root et al. 2011); however, it was not included in the Sonoran Flora (Owe-Larsson et al. 2007). That treatment included only two terricolous crustose species, *A. glaucopsina* (Nyl.) Hue and *A. praecrenata* (Nyl.) Hue.

The taxonomy of *Aspicilia* in the western United States took another big step forward with the recognition of two prostrate fruticose species, *A. filiformis* Rosentr. and *A. californica* Rosentr. (Rosentreter 1998), which had previously been indiscriminately lumped under *A. reptans*. Although *A. californica* is endemic to California, *A. filiformis* has been recognized as a very common component of the biocrust throughout much of western North America (McCune & Rosentreter 2007; Owe-Larsson et al. 2007). Both *A. filiformis* and *A. reptans* frequent the Columbia Basin. For example, Root et al. (2011) reported *A. reptans* from 47 of 59 randomly selected plots and *A. filiformis* from 24 of 59 randomly selected plots. Clearly, these species are among the biocrust equivalents of the common epiphytes of our mountain forests, such as *Platismatia glauca* (L.) W.L. Culb. & C.F. Culb. and *Parmelia sulcata* Taylor.

Morphologically, *Aspicilia reptans* has always presented challenges due to its rather amorphous, plastic growth form. It almost seems to flow across various substrates, including mineral soil, organic matter, and pebbles, taking a bewildering variety of forms and colors, even over the span of a few centimeters, ranging from truly crustose-areolate to beaded strings or decumbent branching lobes, and varying from whitish to olive, gray, or brownish.

Although some of that variation in form clearly derives from its molding over the substrate, in other cases it is purely an expression of the lichen itself. Weber (1967) warned of the potential for extreme environmental plasticity in *Aspicilia.* He considered much of the morphological variation to be various expressions of a single species that he called *A. desertorum* (Kremp.) Mereschk. Although we now recognize that taxonomic conclusion as an oversimplification, the basic problem of environmental plasticity of form continues as a fundamental issue in this and many other groups of lichens, practically resolvable only by study of DNA sequences.

Materials and Methods

Preliminary sampling of terricolous *Aspicilia* revealed the fruticose species, such as *A. californica, A. filiformis, A. hispida* Mereschk., and *A. rogeri* Sohrabi (Sohrabi et al. 2011b), to have rather low variation in DNA sequences within species. But in *A. reptans* we immediately uncovered a surprisingly high level of variation, suggesting the presence of multiple species and stimulating this study: to resolve the taxonomy of *A. reptans* in the broad sense by collecting fresh material, sequencing it, and analyzing phylogenetic reconstructions in relation to morphology, anatomy, secondary substances, geographic distribution, and substrate.

We gathered both fresh specimens and herbarium material, then applied standard microscopy, chemical spot test methods, thin-layer chromatography (TLC), and DNA sequencing. We attempted to include material from throughout the western United States and southwestern Canada, though we sampled more heavily in the range where *Aspicilia reptans* is known to be frequent, from the northern Great Plains to the Columbia Basin and Snake River Plain. Because we had observed transitional forms growing on both rock and soil, we also sampled nearby saxicolous *Aspicilia*, to check for the possibility that terricolous specimens were identical to saxicolous species.

The type specimen of *Aspicilia reptans* had been reduced to crumbs due to lack of protection during shipping from Saskatchewan to its resting place at WIS and a subsequent loan to SRP. At SRP, Roger Rosentreter stabilized the remaining fragments before returning the specimen to WIS, but by then it was so fragmented that it interfered with forming a coherent picture of the morphology of the type. We therefore deemed it critical to resample in the vicinity of the type locality, even though the exact location is unknown. This effort resulted in a number of specimens from southern Saskatchewan and northern Montana that are consistent in form with the type specimen and had DNA sequences falling in a single clade. We therefore used those fresh specimens, along with similarity to the type specimen, as a basis for characterizing the "true" *A. reptans*.

Our sampling did not include terricolous material from southern California and the Channel Islands. This material has been reported as *A. praecrenata* and *A. glaucopsina* (Hasse 1898; Owe-Larsson et al. 2007) and is under active study by researchers in Uppsala.

For TLC we used the standard methods of Culberson (1972) as implemented by McCune (2017). We extracted fragments of selected specimens in acetone at room temperature, spotted on glass-backed silica gel plates (Merck 5554/7 Silica gel 60 F_{254}), and run in solvent systems A and C of Culberson (1972). To better detect fatty acids, after marking spots under UV light we submerged plates briefly in tap water, drained excess water off a corner, then gradually dried them on a lab bench, photographing and marking hydrophobic spots as they appeared. When completely dry, we lightly brushed plates with 10% H_2SO_4 and charred them in an oven at 100°C until our norstictic acid and atranorin controls showed their characteristic colors.

We studied apothecial anatomy and measurements with bright-field microscopy on freehand sections in water, with and without iodine (IKI). Apothecial sections were examined in both IKI and in IKI preceded by KOH and rinsing in 2% acetic acid (i.e., "K/I"). Because IKI and K/I reactions were similar, differing only in intensity, iodine reactions are reported simply as "I." Thallus sections, pycnidia, and apothecia were also studied under the compound microscope in water under polarized light (POL).

Ascospore and spermatia measurements were made photographically. Spores were photographed, cut and pasted onto a single canvas, then measured with the line tool in Adobe Photoshop with *View | Info* displayed. These raw values were converted to micrometers using a conversion factor calibrated from a stage micrometer. Comparison with previous ascospore measurements indicated no bias; however, we determined that because of refraction error one can misestimate spermatia widths when measured with an ocular micrometer. Size measurements were recorded for seven ascospores and spermatia when possible, then size ranges were combined across specimens.

DNA extraction and PCR amplification. We tried to obtain DNA sequences for all recently collected specimens available to us and that were similar in form to *Aspicilia reptans*. We chose to analyze nuclear

internal transcribed spacer (ITS) and large subunit (nuLSU) rDNA regions because of their general utility for species- and genus-level problems in *Lecanorales* and their previous use in *Aspicilia* (Ismayil et al. 2019; Nordin et al. 2007, 2010, 2011; Ren et al. 2018; Sohrabi et al. 2013; Zakeri et al. 2017).

For DNA isolation we selected a 1 mm^3 sample of thallus of each specimen. To reduce the amount of secondary metabolites, in most cases the sample was eluted in a 1.5 mL Eppendorf tube with one drop of 99.7% acetone for 30 minutes. The acetone was then removed via pipette and the remaining sample air dried for 10 minutes.

DNA was extracted with the REDExtract-N-Amp Plant PCR kit by Sigma-Aldrich. The procedure used was according to the manufacturer's instructions, except that one sixth of the suggested amount was used for each sample: 15 µL of extraction solution was added and incubated at 95°C for 10 minutes and finalized by adding 15 µL of dilution solution.

When unsuccessful with the previous method we used a larger sample FastDNA SPIN KIT (MP Biomedicals). The manufacturer's instructions were followed with the plant tissue CLS-VF and PPS cell lysis solutions used. In both cases DNA extracts were refrigerated at 4°C.

We had the highest PCR success rates as follows: We amplified ITS with primers ITS1F (Gardes & Bruns 1993) and ITS4 (White et al. 1990). The PCR master mix was 5 µL Dream Taq Green PCR Master Mix (2x; Thermo Scientific Inc.), 3 µL nuclease free H_2O, 0.5 µL ITS1F (10 µL stock solution + 90 µL nuclease free H_2O), and 0.5 µL ITS4 (10 µL stock solution + 90 µL nuclease free H_2O). Each PCR reaction had 9 µL master mix and 1 µL DNA extract. PCR reaction conditions were as follows: Initial denaturation at 94°C for 5 minutes, then 35 cycles of denaturation at 94°C for 30 seconds, annealing at 56°C for 45 seconds, and extension at 72°C for 1 minute 45 seconds, followed by an elongation cycle for 5 minutes at 72°C. An alternate method used an annealing temperature of 56.2°C.

Most nuLSU amplifications used the primer pair AL2R (Mangold et al. 2008) and LR6 or LR0R (Vilgalys & Hester 1990). The PCR master mix was the same as for ITS but with different primers. PCR reaction conditions were initial denaturation at 94°C for 3 minutes, then 36 cycles of denaturation at 94°C for 25 seconds, annealing at 54°C for 45 seconds, and extension at 72°C for 1 minute 45 seconds, followed by an elongation cycle for 7 minutes at 72°C. An alternate method used an initial denaturation of 95°C for 5 minutes, then 35 cycles of denaturation at 95°C for 1 minute, annealing at 56°C for 1 minute, and extension at 72°C for 1 minute 45 seconds, followed by an elongation cycle for 7 minutes at 72°C.

PCR products were viewed via gel electrophoresis and successful samples were then cleaned using ExoSAP-IT™ Affymetrix 78200. The recommended protocol was modified to use 3 µL PCR product and 1 µL ExoSAP-IT reagent. These were processed according to the manufacturer's protocol using thermocycler incubation at 37°C for 15 minutes followed by 80°C for 15 minutes. Cleaned PCR products were prepared for sequencing by combining 2.4 µL forward primer (as above), 7.7 µL nuclease free H_2O, and 1.9 µL ExoSAP-IT product, then sequenced with forward and reverse reads (Eurofins MWG Operon Inc.).

Geneious version 10.0.9 (http://www.geneious.com; Kearse et al. 2012) was used to check the quality of the raw sequences, align the two reads per sample, and generate a consensus sequence for phylogenetic analyses. We obtained 176 new sequences from 126 specimens, including 120 ITS sequences and 56 nuLSU sequences (**Table 1**).

Phylogenetic analyses. We compared our sequences with those in GenBank for ITS and nuLSU for *Aspicilia* and related genera to test for overlooked matches to existing taxa. We then constructed phylogenetic trees built from our sampling (**Table 1**) plus family-wide sampling for Megasporaceae from GenBank (**Appendix 1**). We subsampled within non-terricolous species that had disproportionately large numbers of records in GenBank, such as *Aspiciliella intermutans* (Nyl.) M. Choisy s.l. (Zakeri et al. 2019a). Whenever possible we selected specimens that had both ITS and nuLSU over those with results for just one locus. We also excluded a number of sequences that we could not align well with the other samples, including (DQ401560 through 64, DQ401566, DQ401571, and JQ797505). This resulted in a total of 339 sequences for ITS and 145 for nuLSU. Published nuLSU sequences were highly variable in length at the

3′ end and many contained an intron, so we trimmed the alignment to exclude this poorly represented region. Sequences were aligned initially with MAFFT in Geneious using default settings (auto algorithm selection, gap open penalty 1.53, offset 0.123), then adjusted manually. The ends of our new sequences were trimmed to match the annotated regions of those from GenBank, then concatenated into a single alignment with 368 specimens. The ITS alignment had 658 bases with 74.2% variable positions. The nuLSU alignment had 741 bases with 55.6% variable positions. The concatenated alignment is available through Dryad as a FASTA text file (https://doi.org/10.5061/dryad.tmpg4f4zs).

Phylogenetic trees were obtained by maximum likelihood analysis of the combined alignment using the GTR (general time-reversible) model with PhyML defaults, optimizing topology, length, and rate with an NNI search using PhyML 3.0 (Guindon et al. 2010). These maximum likelihood GTR+I+G models follow recommendations of Abadi et al. (2019). We chose *Megaspora* (Clauzade & Cl. Roux) Hafellner & V. Wirth as the outgroup, based on structures revealed by Nordin et al. (2010), Sohrabi et al. (2013), and Zakeri et al. (2017). Statistical support for branches was evaluated with the nonparametric Shimodaira–Hasegawa version of the approximate likelihood ratio test (aLRT-SH; Anisimova & Gascuel 2006; Anisimova et al. 2011). This method has been shown to be a robust branch support method (Anisimova et al. 2011) that is much faster than bootstrapping, an important consideration for this data set. Branch support for the hypothesis that the inferred branch is true can be interpreted as: support = 1 – false positive error rate. For example, 0.95 corresponds to a 5% false positive rate.

Table 1. Voucher information for the species sampled and the associated GenBank accession numbers for ITS and nuLSU. All new sequences are vouchered in osc unless otherwise specified. All specimens were terricolous unless otherwise indicated in the Comments column. Collection numbers preceded by "*(Stone)*" were assigned by D. Stone but collected by the persons indicated.

***Aspicilia* species**	**Location**	**Voucher**	**ITS**	**nuLSU**	**Comments**
albonota	USA: Oregon	*McCune 36793*	MZ536764		on basalt cobbles, iron stained; fertile; TLC: nil
albonota	USA: Washington	*McCune 38128*	MZ536783		type; TLC: nil
albonota?	USA: Washington	*McCune 38136*	MZ536784		on basalt; fertile
albonota	USA: Washington	*McCune 38139*	MZ536786		on pebble, fertile; TLC: nil
albonota?	USA: Idaho	*McCune 38166*	MZ536790		on rock
albonota?	USA: Oregon	*McCune 38192*	MZ536795		on basalt; fertile; TLC: nil
albonota?	USA: Montana	*McCune 38839*	MZ536805	MZ536873	on weakly HCl+ rock; areoles dark olive gray; ascospores 24–25 × 16 µm; spermatia 9–12 µm; TLC: nil; with *Farnoldia micropsis* and *Staurothele drummondii*
albonota	USA: Washington	*Rosentreter 17855* (SRP)	MZ536816	MZ536882	
albonota	USA: Idaho	*Rosentreter 18327* (SRP)	MZ536821	MZ536888	
albonota	USA: Washington	*Rosentreter (Stone) DC-rim-1*	MZ536831	MZ536897	
anglica	USA: Washington	*McCune 38144*	MZ536787		on basalt outcrops; thallus thick, gnarly, knobby, gray, similar but unrelated to *A. mastrucata*; TLC: norstictic acid
anglica	USA: Oregon	*McCune 38189*	MZ536794		on basalt outcrops; thallus thick, isidiate, gray
anglica	USA: Washington	*McCune 38230*	MZ536796	MZ536867	on basalt; thallus thick, isidiate, gray, K+ red; TLC: norstictic acid
aspera	Canada: British Columbia	*Di Meglio 311a*	MZ536746	MZ536854	on soil over rock with *311b*, *A.* cf. *elmorei*
aspera	USA: Montana	*McCune 35792*	MZ536760		
aspera	USA: Idaho	*Rosentreter 18317* (SRP)	MZ536820	MZ536887	with spicate lobe tips similar to *A. spicata*
berntii	USA: Alaska	*McCune 36300a*	MZ536762		on granitic shoreline rock; see McCune et al. (2020)
californica	USA: California	*Colwell 15–003*	MZ536717		thallus spottily K+ red
californica	USA: California	*Di Meglio 250*	MZ536723	MZ536841	
californica var. *gigantea*	USA: Oregon	*Di Meglio 495*	MZ536749	MZ536856	
californica var. *gigantea*	USA: Oregon	*Di Meglio 200*	MZ536718	MZ536837	
californica var. *gigantea*	USA: Oregon	*McCune 31794*	MZ536752		type
cinerea	USA: Montana	*McCune 38559*	MZ536800	MZ536870	thallus whitish gray; fertile but spores sparse; pycnidia not found
cinerea	USA: Montana	*McCune 38816*	MZ536804	MZ536872	on HCl+ rock; thallus whitish, margin zonate and vaguely lobate; ascospores 13–17 × 8–11 µm; spermatia 12–15 µm; TLC: norstictic acid
cyanescens	USA: Oregon	*McCune 37287*	MZ536772		thallus thinly areolate; spermatia filiform, about 22 µm

Table 1, cont.

***Aspicilia* species**	**Location**	**Voucher**	**ITS**	**nuLSU**	**Comments**
cyanescens	USA: Washington	*McCune 38068*	MZ536779	MZ536865	thallus continuous, smooth; ascospores 30–24 × 14–17 µm; spermatia filiform 17–21 µm
cyanescens	USA: Oregon	*McCune 38304*	MZ536798	MZ536868	on basalt; thallus brownish gray; epihymenium olive black, paraphyses submoniliform in water; spermatia not found; TLC: nil
diploschistiformis	USA: Idaho	*Rosentreter 18283* (SRP)	MZ536817	MZ536884	
diploschistiformis	USA: Idaho	*Rosentreter 18351* (SRP)	MZ536824	MZ536891	
diploschistiformis	USA: Idaho	*Rosentreter 18418* (SRP)	MZ536825	MZ536892	
diploschistiformis	USA: Idaho	*Rosentreter 19826* (SRP)	MZ536826		fertile portion possibly another *Aspicilia* species
diploschistiformis	USA: Idaho	*Rosentreter 19911* (SRP)	MZ536827	MZ536893	
diploschistiformis	USA: Oregon	*Stone 9228*	MZ536828		type
diploschistiformis	USA: Oregon	*Stone 9239*	MZ536829	MZ536895	
diploschistiformis	USA: Washington	*McCune 38137*	MZ536785		
diploschistiformis?	USA: Idaho	*McCune 38173*	MZ536791		on pebbles; in lithosol with sparse grasses; brownish areoles with whitish tops; spermatia 8–9.5 µm long; parasitized by *Stigmidium lendemeri*; TLC: nil
elmorei	USA: Wyoming	*McCune 37197*	MZ536770		algal layer type 2; ascospores 4/ascus, subspherical; spermatia 6.5–8.5 µm; TLC: aspicilin
cf. *epiglypta*	USA: Alaska	*McCune 34103*	MZ536754		as *A.* cf. *intermutans* in McCune et al. (2018); spermatia 15–20 µm; TLC: norstictic acid
filiformis	USA: Oregon	*Di Meglio 201*	MZ536719	MZ536838	
filiformis	USA: California	*Di Meglio 202*	MZ536720	MZ536839	
filiformis	USA: California	*Di Meglio 205*	MZ536722		
filiformis	USA: Washington	*Di Meglio 256*	MZ536726	MZ536842	
filiformis	USA: Washington	*Di Meglio 257*	MZ536727	MZ536843	
filiformis	USA: Oregon	*Di Meglio 274*	MZ536733		
filiformis	USA: Oregon	*McCune 32590*	MZ536753	MZ536858	
filiformis	USA: Washington	*McCune 38121*	MZ536782		
filiformis	USA: Idaho	*Rosentreter 17441* (SRP)	MZ536813	MZ536880	
filiformis	USA: Idaho	*Rosentreter 17552* (SRP)	MZ536814	MZ536881	
filiformis	USA: Idaho	*Rosentreter 18287* (SRP)	MZ536818	MZ536885	
hispida	Canada: Saskatchewan	*Di Meglio 272*		MZ536850	TLC: nil
hispida	USA: Colorado	*Di Meglio 304*	MZ536741		
hispida	USA: Idaho	*Di Meglio 307*	MZ536743		TLC: nil
hispida	USA: Colorado	*Di Meglio 310*	MZ536745		
hispida	USA: Montana	*McCune 35793*		MZ536861	
hispida	USA: Wyoming	*Perry 516*	MZ536810	MZ536876	
knudsenii	USA: Washington	*McCune 38056a*	MZ536778	MZ536864	on basalt; spermatia 6–8 µm; close to *A. albonota* but with norstictic acid

Table 1, cont.

***Aspicilia* species**	**Location**	**Voucher**	**ITS**	**nuLSU**	**Comments**
maritima	USA: California	*McCune 37589*	MZ536774		on ultramafic (peridotite) outcrops; mature asci not seen; spermatia 6–7 µm long; TLC: nil
maritima	USA: Oregon	*McCune 38648*	MZ536801		type; on basalt; ascospores and pycnidia not found; TLC: unknown near stictic acid
papilliformis	USA: Oregon	*McCune 34821*	MZ536756	MZ536859	
papilliformis	USA: Washington	*McCune 36744*	MZ536763		type
papilliformis	USA: California	*McCune 37575*	MZ536773		on rock; atypical in morphology and substrate
papilliformis	USA: Washington	*McCune 38052*	MZ536777		
papilliformis	USA: Washington	*McCune 38113*	MZ536781		
papilliformis	USA: Washington	*Rosentreter 17854* (SRP)	MZ536815	MZ536883	
papilliformis	USA: Idaho	*Rosentreter 18338* (SRP)	MZ536822	MZ536889	
papilliformis	USA: Washington	*Stone GLNE–1*	MZ536833		
phaea	USA: Montana	*Wheeler TW348* (herb. Wheeler)	MZ536835		unpublished Tim Wheeler sequence
reptans	USA: Oregon	*Di Meglio 203*	MZ536721	MZ536840	TLC: nil
reptans	Canada: Saskatchewan	*Di Meglio 261*	MZ536729	MZ536844	approximate topotype; with *Phaeorrhiza nimbosa* and *Collema tenax* group
reptans	Canada: Saskatchewan	*Di Meglio 262*	MZ536730	MZ536845	approximate topotype; with *Phaeophyscia constipata*, *Physconia muscigena*, and *Cladonia* squamules
reptans	Canada: Saskatchewan	*Di Meglio 263*	MZ536731	MZ536846	approximate topotype; TLC: aspicilin
reptans	Canada: Saskatchewan	*Di Meglio 264*		MZ536847	approximate topotype; pycnidia present; with *Collema tenax* group and *Phaeophyscia constipata*
reptans	USA: Montana	*Di Meglio 265*		MZ536848	
reptans	USA: Washington	*Di Meglio 270*	MZ536732	MZ536849	
reptans	USA: Oregon	*Di Meglio 275*	MZ536734		spermatia 8–9 µm long, hard to find
reptans	USA: New Mexico	*Di Meglio 487*	MZ536748		
reptans	USA: Colorado	*Di Meglio 284*	MZ536735		
reptans	USA: Colorado	*Di Meglio 285*		MZ536851	with *Xanthoparmelia camtschadalis* and *Physconia muscigena*
reptans	USA: Colorado	*Di Meglio 286*	MZ536736	MZ536852	
reptans	Canada: British Columbia	*Di Meglio 295*	MZ536738		TLC: aspicilin
reptans	USA: Colorado	*Di Meglio 303*	MZ536740		
reptans	USA: Colorado	*Di Meglio 287*	MZ536737	MZ536853	
reptans	USA: Montana	*McCune 35788*	MZ536761	MZ536861	
reptans	USA: Montana	*McCune 37157*	MZ536766		with cyanobacterium *Microcoleus vaginatus*
reptans	USA: Montana	*McCune 37111*		MZ536863	
rogeri	USA: Colorado	*Di Meglio 305*	MZ536742		TLC: nil
rogeri	USA: Colorado	*Di Meglio 309*	MZ536744		TLC: nil
rogeri	USA: Oregon	*McCune 34833*	MZ536757	MZ536860	TLC: unknown fatty acids
rogeri	USA: Idaho	*McCune 38174*	MZ536792		saxicolous, fertile
rogeri	USA: Colorado	*Smith, S.F. 0558*	MZ536750	MZ536894	

Table 1, cont.

***Aspicilia* species**	**Location**	**Voucher**	**ITS**	**nuLSU**	**Comments**
simoensis	USA: Oregon	*McCune 38315*	MZ536799	MZ536869	thallus dark gray with punctiform soralia; sterile; thallus section with K+ yellow diffusion
spicata	USA: Oregon	*Di Meglio 255*	MZ536725		on rock, transitional to crustose; TLC: nil
spicata	USA: Washington	*Hardman & Root (Stone) EGL1*	MZ536832	MZ536879	fertile; TLC: nil
spicata	USA: Washington	*Root & Smith (Stone) B1–15*	MZ536830	MZ536896	fertile; TLC: nil
spicata	USA: Washington	*Stone NC1–10*	MZ536834	MZ536898	type; TLC: nil
subcontinua	USA: California	*Di Meglio 253*	MZ536724		
subcontinua	USA: Washington	*Di Meglio 259*	MZ536728		
subcontinua	USA: Idaho	*McCune 38176*	MZ536793		
subcontinua	USA: Idaho	*Rosentreter 18307* (SRP)	MZ536819	MZ536885	
subcontinua	USA: Montana	*Wheeler 7421* (MONTU)	MZ536836		type; original ID *A. glaucopsina*; T. Wheeler DNA 344
supertegens	USA: Alaska	*McCune 35056*	MZ536758		on lakeshore rock (McCune et al. 2018); thallus whitish; ascospores about 2–26 × 15–16 µm; spermatia 20–22 µm; TLC: nil
supralittorea	USA: Oregon	*McCune 38048*	MZ536775		type; on supralittoral noncalcareous rock by ocean; TLC: stictic acid and trace norstictic acid
supralittorea	USA: Oregon	*McCune 38049*	MZ536776		on supralittoral noncalcareous rock by ocean; thallus light to dark gray, areolate; epihymenium blue green to blackish, POL–; paraphyses moniliform; mature spores not found; spermatia 10–13 µm long; thallus K+ red (norstictic acid crystals); TLC: stictic acid and trace norstictic acid
supralittorea	USA: Oregon	*McCune 38929*	MZ536807		on supralittoral noncalcareous rock by ocean; thallus light gray, areolate, thin to thick; epihymenium green black; ascospores broadly ellipsoid, 18–28 × 15–18 µm; cortex K–, medulla thallus K– to weakly K+ red; TLC: stictic acid with trace norstictic acid
supralittorea	USA: Oregon	*McCune 38932*	MZ536808		on supralittoral noncalcareous rock by ocean; thallus light gray, areolate, thin to thick; epihymenium green black; paraphyses moniliform; ascospores broadly ellipsoid, 16–19 × 12–13 µm; spermatia not found; thallus K+ red; TLC: stictic acid with norstictic acid (minor)
wyomingensis	USA: Idaho	*Di Meglio 300*	MZ536739		
wyomingensis	USA: Montana	*McCune 37169*	MZ536768		
wyomingensis	USA: Montana	*McCune 37170*	MZ536767		
wyomingensis	USA: Wyoming	*McCune 37196*	MZ536769		type
wyomingensis	USA: Wyoming	*McCune 37199*	MZ536771		
wyomingensis	USA: Wyoming	*Perry 595*	MZ536811	MZ536877	
wyomingensis	USA: Wyoming	*Perry 619*	MZ536812	MZ536878	

Table 1, cont.

***Aspicilia* species**	**Location**	**Voucher**	**ITS**	**nuLSU**	**Comments**
sp.	Canada: British Columbia	*Di Meglio 311b*	MZ536747	MZ536855	near *A. arida* or *A. elmorei*; on pebble; algal layer type 2; apothecia with swollen margins and pruinose disk; ascospores 23–27 × 20–23 µm, 4-6/ascus; thallus K-
sp.	USA: Alaska	*McCune 34206*	MZ536755		on HCl– rock; esorediate; sterile; TLC: nil
sp.	USA: Alaska	*McCune 35214*	MZ536759		as *A.* aff. *indissimilis* in McCune et al. (2020); on floodplain cobble; epihymenium olive black; spores 8/ascus, about 21 × 11 µm; TLC: nil
sp. (cf. *hoffmaniana*)	USA: Montana	*McCune 37138* (dupl. in UPS)	MZ536765		on calcareous sandstone; thallus white, papillate, sterile; TLC: nil
sp.	USA: Washington	*McCune 38091*	MZ536779	MZ536866	on basalt; epihymenium bright blue green; spermatia 10–12.5 µm long; TLC: unknown fatty acids
sp.	USA: Oregon	*McCune 38146*	MZ536789		on volcanic rock, dry subalpine; thallus verrucose-areolate, medium gray; apothecia subsessile; epihymenium green; paraphyses moniliform; spores 8/ascus, 21–26 × 11–16 µm; spermatia 14-17 µm long; thallus K–; TLC: unknown fatty acid Rf A3C2-3
sp.	USA: Oregon	*Kofranek 6884*	MZ536751	MZ536857	TLC: nil. See notes in "Unassigned Species"
sp.	USA: Wyoming	*Perry 501*	MZ536809	MZ536875	close to *A. aspera*; with short, spicate prothalline tips; also with crustose to 3D transition
sp.	USA: Idaho	*Rosentreter 18342* (SRP)	MZ536823	MZ536890	close to *A. aspera*; with crustose to 3D transition
sp. X	USA: Oregon	*McCune 38145*	MZ536788		thallus gray, areoles swollen; spores 18–23 × 13–16 µm; epihymenium green; TLC: nil
sp. X	USA: Montana	*McCune 38858*	MZ536806	MZ536874	on HCl– rock (argillite); some disks umbonate; epihymenium bright blue green; ascospores 24–30 × 15–19 µm; spermatia 18–23 µm; TLC: nil
sp. X	USA: Montana	*McCune 38790*	MZ536803	MZ536871	on HCl– rock (argillite); ascospores 22–25 × 15–18 µm; spermatia not found; TLC: nil
sp. Y	USA: Washington	*McCune 38238* (dupl. in UPS)	MZ536797		on basalt; areoles thick, crowded, contorted, whitish, esorediate; apothecia immature and degenerate; spermatia 15–18 µm; TLC: nil
sp. Y	USA: Oregon	*McCune 38723*	MZ536802		on basalt; TLC: nil

Results and Discussion

Character States

***Aspicilia reptans* group**. We refer to the "*Aspicilia reptans* group" as the terricolous *Aspicilia* in the broad sense (i.e., including *Circinaria* M. Choisy) that have a growth form intermediate between crustose and fruticose. The most characteristic thallus form, as in the type of *A. reptans* s.str., is prostrate, stringy with lumpy swellings, and both molded to the substrate and slightly elevated above it. This turned out to be an artificial group, expressed as specimens with rather similar morphologies occurring at very different places in phylogenetic trees.

In addition to the thallus characters described above, we found all species in this group to have the following characters: thallus with diffuse margins, corticate; cortex paraplectenchymatous, covered by an amorphous noncellular epicortex; parathecium hyaline; epihymenium olive green to brownish green, HCl+ green (1M HCl); hypothecium hyaline; ascospores broadly ellipsoid, hyaline, nonseptate; pycnidia immersed to slightly emergent, becoming compound, the walls hyaline, except often greenish near the ostiole; spermatia short to elongate rod shaped; photobiont a single-celled green alga (chlorococcoid).

Differentiating characters are summarized in **Table 2** and in species descriptions. Variations in character states are described below and illustrated in **Figures 1–6**.

Thallus form. Plasticity of thallus form is one of the biggest challenges in characterizing species in the *Aspicilia reptans* group. Thallus form varies considerably within species and even within individuals. The thallus form is, nevertheless, useful (**Table 2**). For example, *A. diploschistiformis* McCune & J. Di Meglio never has a beaded-stringy form, in contrast to most of the other species in this group.

Although many authors, including us, have used the word "squamulose" to describe thallus form in *Aspicilia*, we avoided that here for two reasons. First, squamules in the narrow sense of being discrete thallus units that are earlike or scalelike, as in *Psora* Hoffm. or *Hypocenomyce* M. Choisy, are rarely seen in *Aspicilia*. Second its broader use is so nonspecific as to be little use in separating species in the *Aspicilia reptans* group. We therefore used combinations of more specific descriptive terms, such as beaded-stringy, branched-lobate, areolate, warty, or compound warty. These terms are illustrated under species accounts below.

Pseudocyphellae. Presence, form, and position of pseudocyphellae are useful characters for separating some species in the *Aspicilia reptans* group (**Table 2**). In most cases they appear on the upper surface and edges of thallus units as whitish spots or short lines against a darker background (**Fig. 1**). They may, however, be obscured by heavy pruina. These whitish spots can be confirmed as pseudocyphellae by thin sectioning, where they usually appear as an upward eruption of the medulla through a gap in the cortex (**Fig. 1C, D**), with or without coating by an epicortex. In some species such as *A. reptans* s.str., they are laminal on the thallus units (**Fig. 1A**), while in other species (*A. albonota* McCune & J. Di Meglio) they are more often marginal or between areoles (**Fig. 1B**).

Pruina. Whitish pruina commonly occur on the upper surface of the thallus or the apothecial disk in *Aspicilia*. While notorious for its varied expression under different environmental conditions, including the availability of calcium carbonate in the substrate and insolation, pruinosity can be a useful character in *Aspicilia*. In some cases, pruina form discrete patches, in other cases a more diffuse coating (**Fig. 2**; **Table 2**). Moribund thallus parts that are whitish or grayish might be mistaken for pruina, but these lack the minutely crystalline texture of pruina.

Epicortex. We define the epicortex as the noncellular, nearly amorphous layer that covers the eucortex as viewed in thin sections of the thallus under the compound microscope. In the *Aspicilia reptans* group it varies from very thin and patchy to consistently thick, sometime up to 40 µm or more. Birefringent (POL+) crystals are often visible in the epicortex in the *Aspicilia reptans* group (**Fig. 3**). The thickness and appearance of this POL+ material varies greatly, from a very thin and discontinuous superficial

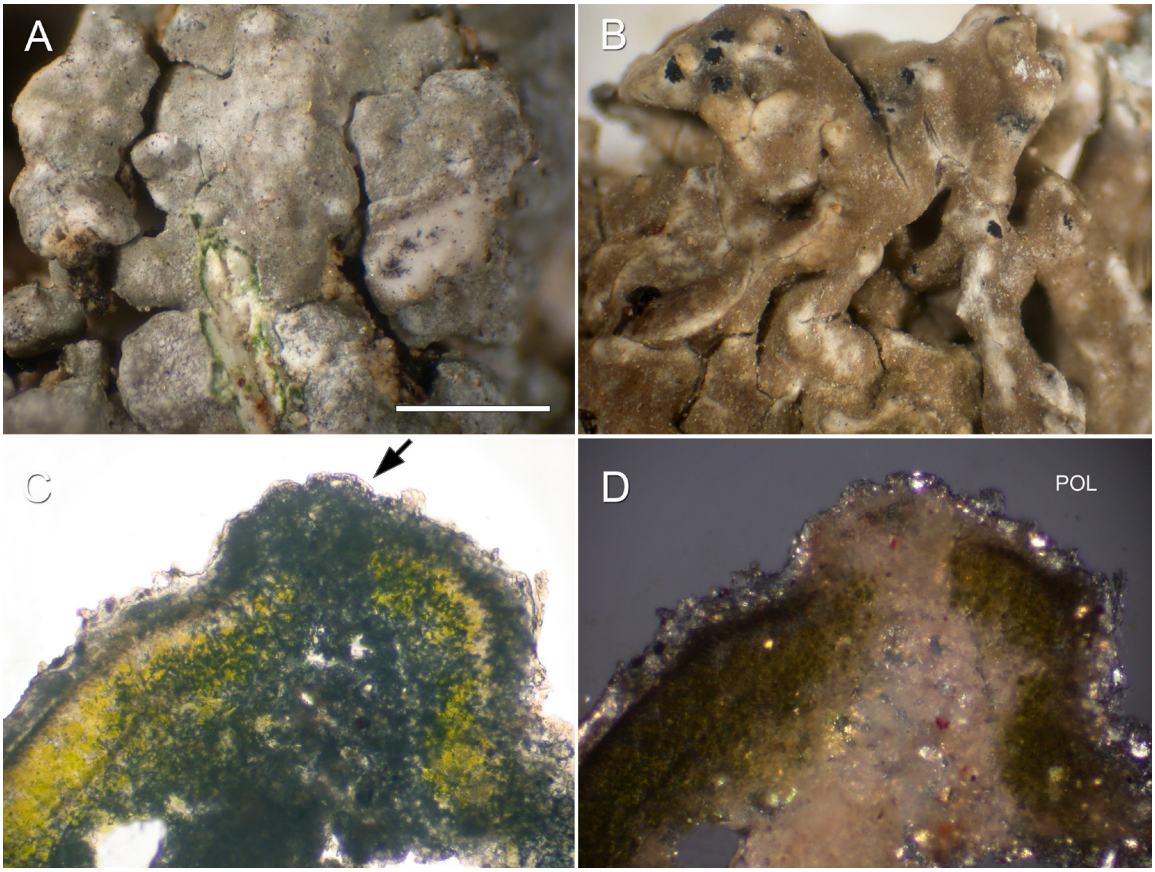

Figure 1. Presence and form of **pseudocyphellae**. — **A**. Pseudocyphellae as whitish spots on *Aspicilia reptans* s.str., *Di Meglio 263*. — **B**. Pseudocyphellae as short whitish lines and spots on *A. albonota, Rosentreter DC-rim-1.* — **C**. Pseudocyphella in section of thallus, *A. albonota*, *Rosentreter 18327*. — **D**. Same as C but under polarized light. Scale bar = 1 mm.

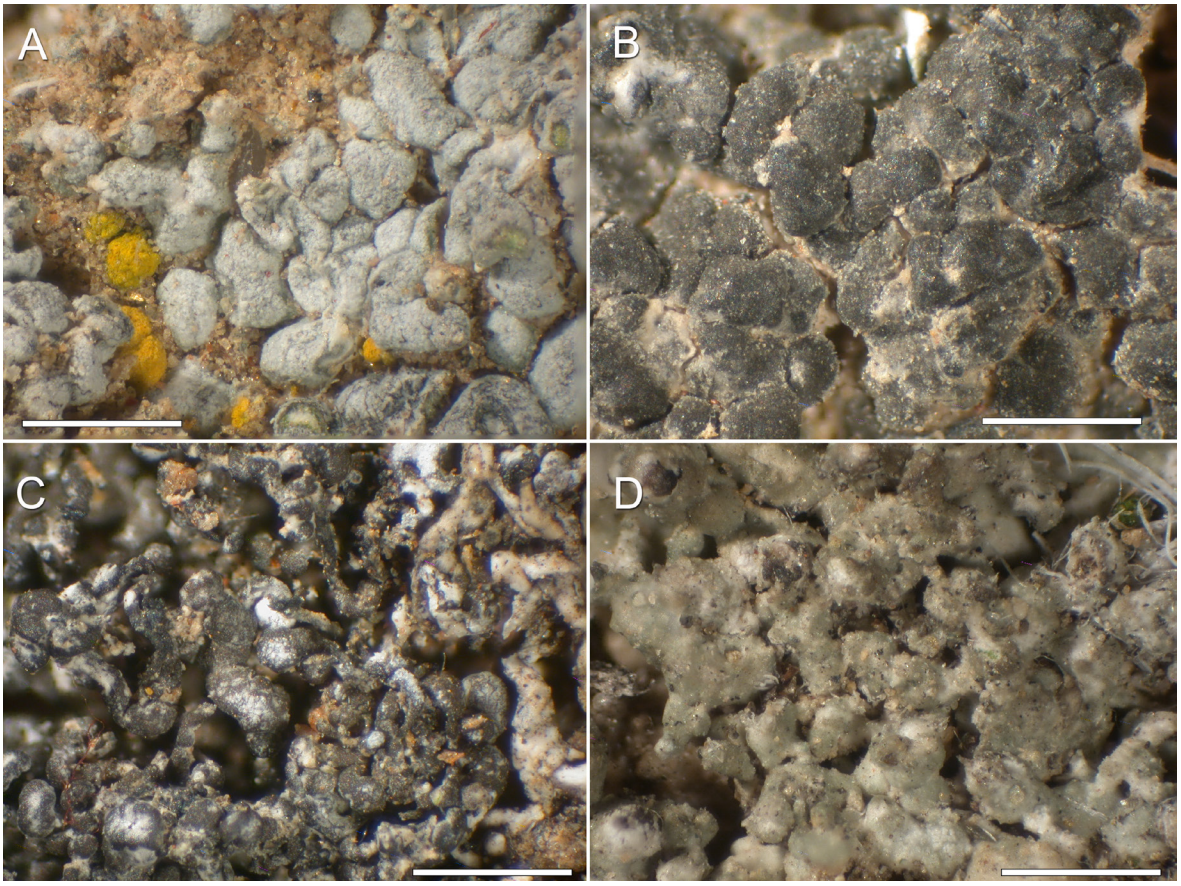

Figure 2. **Pruinosity**. — **A**. Upper surface diffusely pruinose, covering nearly the entire thallus, *Aspicilia diploschistiformis*, *Rosentreter 18418*. — **B**. Not pruinose, *A. albonota, Rosentreter 18327*. — **C**. Pruinose in discrete patches, *A. papilliformis, McCune 34821*. — **D**. Not pruinose but with whitish necrotic patches, *A. albonota, Rosentreter 17855*. Scale bar = 1 mm.

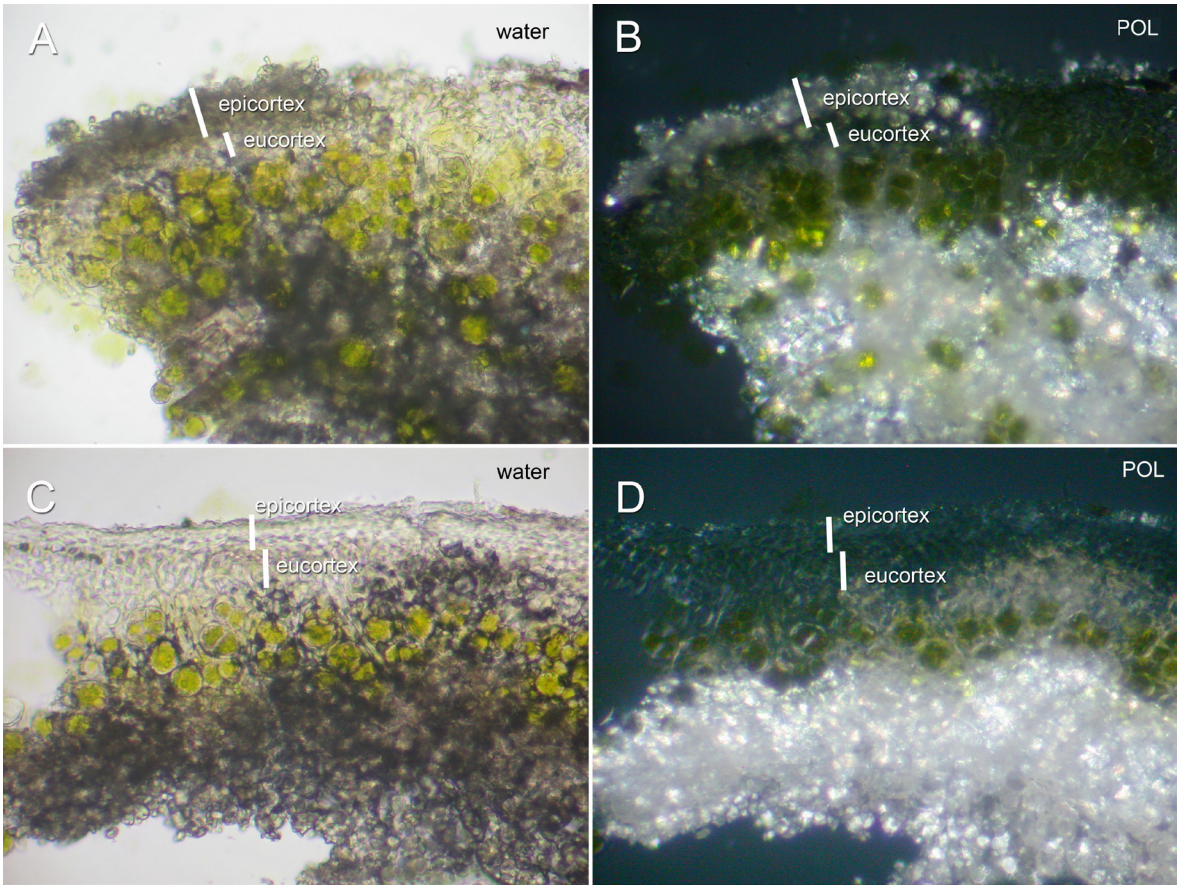

Figure 3. Presence and absence of crystals in the **epicortex and eucortex**. — **A and B**. *Aspicilia diploschistiformis*, *Rosentreter 18418*, epicortex with crystals, brightfield (A) and polarized light (B). — **C and D.** *A. reptans*, *Di Meglio 262*, epicortex with few or no crystals, brightfield (C) and polarized light (D).

layer that we interpret as scattered soil particles (**Fig. 3D**), to a thick layer of granular crystals that permeates the whole epicortex. To some extent, the POL reaction of the epicortex is correlated with pruina, because pruina are composed of crystalline materials, presumably calcium oxalate. On the other hand, while all pruinose lobes have a POL+ epicortex, epruinose lobes can also be POL+.

Eucortex. All terricolous *Aspicilia* that we have seen have a true upper cortex, or eucortex between the epicortex and the algal layer (**Fig. 3**). The eucortex in the *Aspicilia reptans* group is always paraplectenchymatous, of roundish to polygonal or slightly elongate cells, and hyaline throughout or brownish in the uppermost layers. In most cases this layer is more than 3 cells thick and distinct, but in some species, especially *A. diploschistiformis,* it is rather thin, often only 1–3 cells thick. In measuring the thickness of this layer we excluded intrusions of the cortex into the algal layer.

Algal layer and cortex. The contact between the eucortex and the algal layer (**Fig. 4; Table 2**) can be even (type 0), generally even but with frequent narrow intrusions of cortical cells (type 1), or lobate with frequent large indentations in the algal layer from the cortex (type 2). The intrusions in type 1 are typically formed by narrow groups of just a few hyphae, with cells isodiametric to somewhat elongate. Visualizing the contact between cortex and algal layer often improves by waiting 10 minutes after mounting a thin section in water on a slide, as air is replaced by water. The process can be accelerated by gently warming over a flame or by addition of KOH.

Prothallus. In many crustose lichens a prothallus is evident as a thin marginal zone of fungal hyphae often contrasting in color with the lichenized thallus. We have seen this only rarely in the *Aspicilia reptans* group, as a thin, whitish, fimbriate margin of the thallus at the contact with new substrate (e.g., in *A. aspera* (Mereschk.) Tomin).

More often in this group we have observed spicate prothalline lobe tips similar to those described by Sanders (1999) for *Aspicilia californica*: "Branches terminate in a darkly pigmented tip, which may be somewhat rounded like a blunt pencil point, or tapered, forked and spreading like the splayed tip of a used paintbrush. The tip sometimes adheres to other parts of the thallus, moss leaves, or particles of mineral substratum. It may then fan out into bands of fungal hyphae growing appressed to these surfaces." He contrasted this unusual form of expansion in fruticose lichens with the more usual developmental pattern of photobiont and fungal cells in fruticose lichens, with synchronous development in the branch tips as a "pseudomeristem" (Sanders 1999). He also contrasted these patterns with *A. hispida*, where darkly pigmented fungal tips can be produced from the cortex, without continuity to the bundle of parallel elongate cells in the medulla.

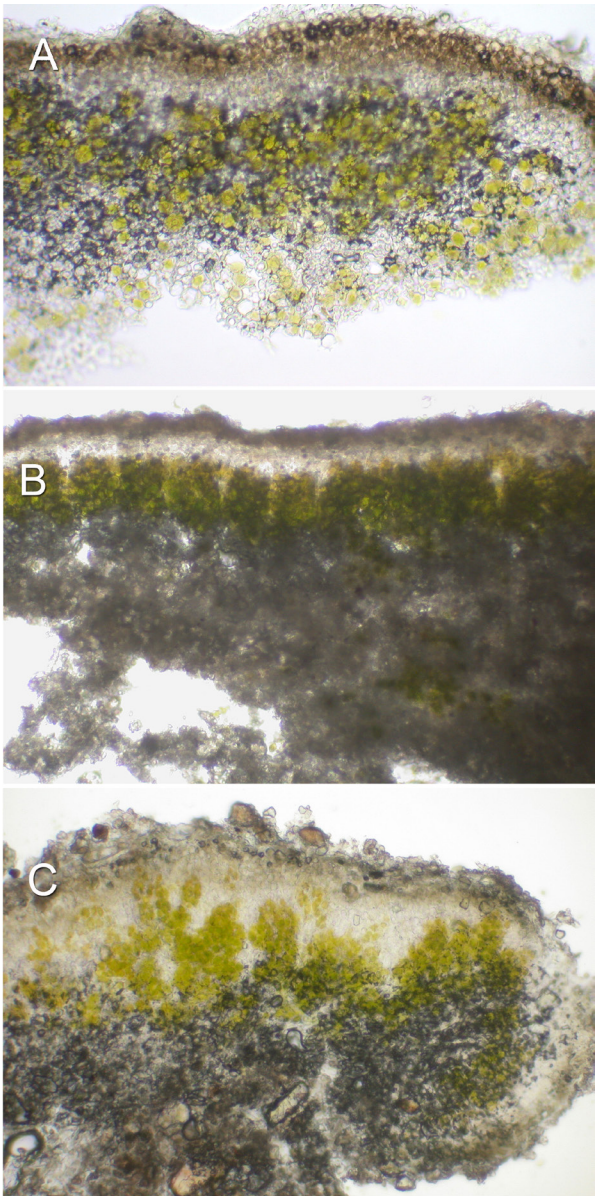

Figure 4. Variation in the presence and form of interruptions in the algal layer. — **A**. Even algal layer and cortex (type 0), *Aspicilia filiformis*, *Rosentreter 15683*. — **B**. Algal layer penetrated by narrow bundles of hyphae (type 1), *A. wyomingensis, Rosentreter 9257*. — **C**. Algal layer lobate (type 2), *Aspicilia* sp. near *A. aspera, Rosentreter 18342*.

We refer to these strictly fungal structures as "prothalline spicate tips." They are always present in *Aspicilia californica* and *A. filiformis*. We have also observed these in a number of species in the *A. reptans* group, but they are most frequent in *A. spicata* McCune & J. Di Meglio, a close relative of *A. californica* and *A. filiformis*, while being occasionally observed in other species, such as *A. aspera*. As reported by Sanders (1999), in *A. californica* these prothalline tips can also originate non-apically, produced laterally from thalline warts.

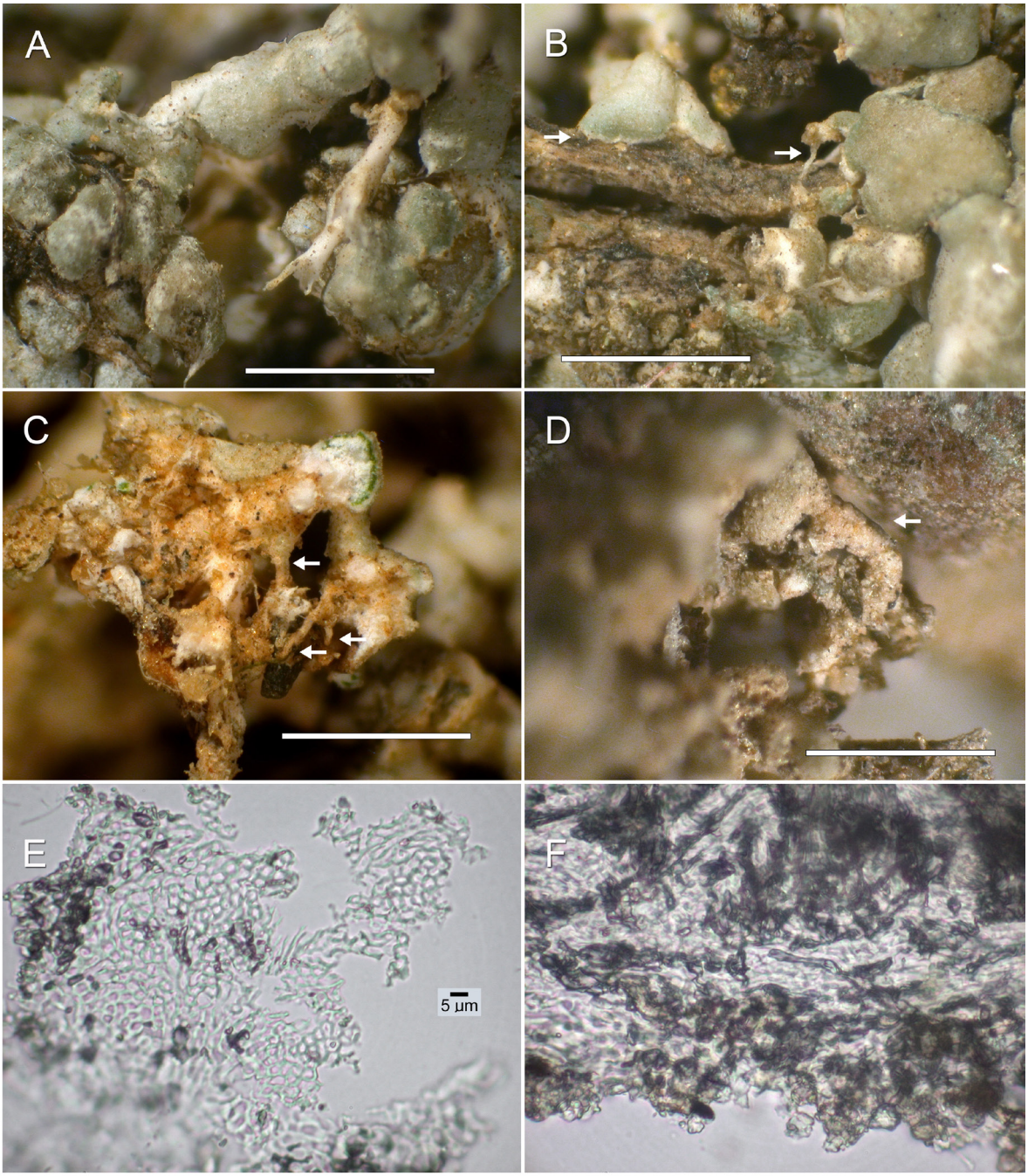

Figure 5. **Rhizomorphs**. — **A**. *Aspicilia reptans*, *Di Meglio 263*. — **B**. *A. reptans*, *McCune 35788*, showing slender rhizomorph extending from the thallus and attached to a fragment of plant detritus (see arrow on right). At the arrow on the left a thallus wart is closely molded to the same piece of detritus but with no visible prothallus or rhizomorph. — **C**. *A. wyomingensis*, *McCune 37196*; arrows point to rhizomorphs. — **D**. *A. aspera*, *Di Meglio 311a*. — **E**. *A. subcontinua*, *Di Meglio 253*, transverse section of rhizomorph. Note variation in orientation of the hyphae reflecting the twisted, ropy structure of the tissue. — **F**. *A. subcontinua*, *Di Meglio 253*, longitudinal section of rhizomorph. Scale bar for A–D = 1 mm.

Table 2. Substrate, morphology, and anatomy of terricolous *Aspicilia* in western North America. An asterisk (*) indicates the value is based on literature report(s) because the specimens were not seen by us. Substrate is primarily soil unless otherwise indicated.

Taxa	Substrate	Apothecia	Spermatia length, µm	Typical growth form	Thallus pruina	Pseudo-cyphellae	Algal layer continuity
A. albonota	rock or soil, noncalcareous or weakly calcareous	rare when on soil, common when on rock; aspicilioid	6–12(19)	areolate to compound warty or beaded-lobate	absent but sometimes whitish necrotic	present, whitish spots and short lines	type 0 or 1, with sparse, narrow intrusions from cortex
A. aspera	uncertain, calcareous in at least some cases	aspicilioid, with raised thalline margin; disk black, white-pruinose	12-17	cylindrical-lobate developing marginally from a continuous crust, sometimes with rounded or isidioid prothalline lobe tips	absent to patchy and thin	not seen	type 2, noticeably lobate and discontinuous
A. californica var. *californica*	noncalcareous	infrequent; erumpent to sessile, lecanorine; disk blackish, sometimes pruinose	not seen	decumbent to prostrate, narrow-lobed fruticose	absent	absent	type 0 or 1, with occasional narrow intrusions from cortex
A. californica var. *gigantea*	noncalcareous	adnate, lecanorine; disk brownish to black, epruinose	10–14	decumbent to prostrate, narrow-lobed fruticose	absent	absent	type 0 or 1
A. diploschistiformis	calcareous	uncommon; immersed, erumpent, or protruding	6–11	areolate to bullate-areolate, the areoles discrete or locally confluent	absent, sometimes present, chalky or scabrid in spots, especially over incipient apothecia and pycnidia	absent	type 0, continuous and even
A. filiformis	noncalcareous	occasional; erumpent to adnate, lecanorine; disk brown to black, sometimes pruinose	11–12(15)	decumbent to prostrate, narrow-lobed fruticose	absent	absent	type 0 or 1, with occasional narrow intrusions from cortex
*A. glaucopsina**	unknown	unknown	14–26*	unknown	unknown	unknown	unknown
A. hispida	calcareous	rare; erumpent to adnate, aspicilioid to lecanorine; disk pruinose	not seen	suberect to erect, fruticose, with spiky branch tips	absent	present, lateral, white	type 2, strongly lobate and discontinuous
A. papilliformis	noncalcareous	occasional; lecideine	10–15	bullate-areolate to papillate	usually heavily pruinose	absent	type 2, uneven, irregularly divided
*A. praecrenata**	noncalcareous	aspicilioid with crenulate white thalline margin	7–11(12)*	areolate to squamulose or continuous	absent	absent?	unknown

Table 2, cont.

Taxa	Substrate	Apothecia	Spermatia length, µm	Typical growth form	Thallus pruina	Pseudo-cyphellae	Algal layer continuity
A. reptans s.str.	calcareous	rare; aspicilioid to adnate	6–10	areolate to knobby, ±stringy in part	absent to patchy, sometimes extensive dull necrotic areas	present	type 1, narrow intrusions from cortex mostly 1–2 cells wide
A. rogeri	calcareous	rare	9–14	subspherical fruticose with stubby branch tips	absent	present, terminal, white	type 2, strongly lobate and discontinuous
A. spicata	noncalcareous	infrequent; aspicilioid to sessile and lecanorine	8–11	beaded-lobate often with spicate prothalline tips	present or absent	absent	type 1 with linear to triangular intrusions from cortex
A. subcontinua	noncalcareous	unknown	not seen	bullate- areolate or papillate from a subcontinuous base	absent	sparse to abundant	type 1, conical intrusions from cortex
A. wyomingensis	calcareous	unknown	6–12	areolate to knobby-areolate becoming branched and lobate	absent to commonly heavy	present but only visible where epruinose	type 1, narrow to broadly triangular intrusions from cortex

The prothalline lobe tips can also be warty or isidioid rather than spiky. These short, blunt prothalline tips were observed in North American specimens that we assigned to *A. aspera*. The cortical cells appear to proliferate, elongate, and darken, forming a distinct blackish bump on the thallus. As in *A. hispida*, this prothalline tissue appears to develop from the cortex. Note, however, that pycnidia in many species can appear similar and need to be distinguished by a thin section.

Rhizomorphs. Although seldom easily seen, most or all of the *A. reptans* group can form pale cream to tan rhizomorphs from the lower surface (**Fig. 5**). These are best seen where the substrate has been naturally eroded, exposing the lower surface of the thallus. In side view these rhizomorphs appear as slender, simple or branched stipes below thallus units. Rhizomorphs are usually difficult to reveal by dissection because of the fragility of the soil-hyphal matrix. Careful searching tends to destroy small specimens. For this reason, we have avoided using the presence of rhizomorphs as a character to distinguish species but include them in our species descriptions when we found them.

Rhizomorphs were noted in the original description of *Aspicilia reptans* by Looman (1962), who found "lower cortex white with sparse, short rhizinae." They were studied in detail in *Aspicilia* species by Sanders and Rico (1992) and Sanders (1999), where they were considered to have a "exploratory" role in growth of the thallus. In contrast to the muscicolous *A. crespiana* V.J. Rico studied by Sanders and Rico (1992), we did not observe an algal layer in rhizomorphs in the *A. reptans* group. We have, however, seen naked rhizomorphs with scattered beads of lichenized thallus, suggesting that the rhizomorphs may be the structure that generates the beaded-stringy appearance of *A. reptans* and related species.

Stipelike rhizomorphs were seen in *Aspicilia subcontinua* McCune & J. Di Meglio, as well as most other terricolous *Aspicila* species. Sometimes they are exposed from erosion of the substrate, but usually they are not apparent without excavating, which can be inconclusive. In the case of *A. subcontinua*, based on *Di Meglio 253*, cross sections and longitudinal sections show the rhizomorphs to be composed of a compact tissue of ± elongate cells that are ropelike and twisted in groups. In cross section some groups have roundish to polygonal cells (lumina 1.5–3.2 µm diameter, walls 0.9–1.3 µm thick) and some elongate cells (2–3:1). Interspersed among the groups and on the exterior of the rhizomorphs are POL+ strips that are dark gray to nearly opaque in thin section. Although the internal structure of the rhizomorphs appears similar to those of *Aspicilia crespiana* (Figs. 13 and 15 in Sanders & Rico 1992), we did not observe a cortex on the rhizomorphs.

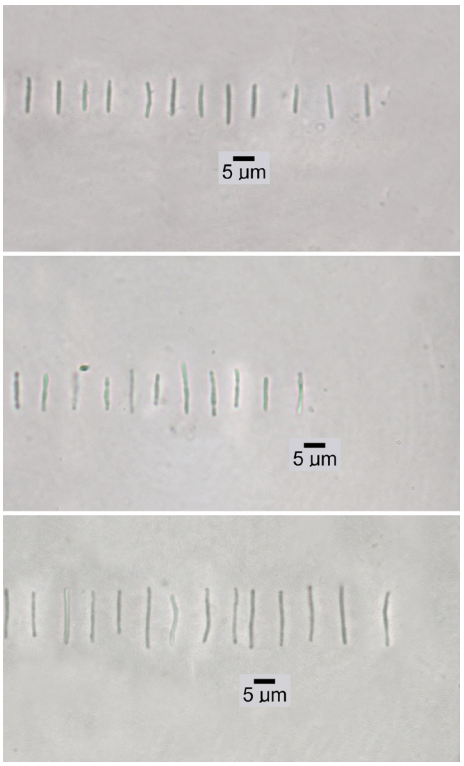

Figure 6. Spermatia, showing the range of lengths found in *Aspicilia reptans* and similar species. — **Top**. Short, *Aspicilia reptans*, *Di Meglio 262.* — **Center**. Medium short, *A. wyomingensis*, *McCune 37196*. — **Bottom.** Medium, *A. papilliformis*, *Rosentreter 17854*. Long spermatia (> 20 µm long) are characteristic of some *Aspicilia* species but were not found in the this terricolous group.

Spermatia. Nordin et al. (2010) and Owe-Larsson et al. (2007) gave considerable emphasis to spermatia length, not only in separating species of *Aspicilia*, but also in separating genera in the Megasporaceae. Their circumscription of *Circinaria* includes species with short spermatia (mostly < 10 µm long) while *Aspicilia* s.str. was considered to have long spermatia mostly 12–25 µm long. We have found length of spermatia (**Fig. 6, Table 2**) to be a useful character, consistent

within many clades. It can, however, be rather frustrating in practice, because pycnidia are commonly absent. When pycnidia are present, however, length of the spermatia is worth recording. Although the length of spermatia varies greatly among species in *Aspicilia*, the width of spermatia is so similar among species (mostly 0.7–1.1 μm) that we have not found the width of spermatia to be useful for identification.

Apothecia. Most species in the *Aspicilia reptans* group are routinely sterile, so apothecial characters are of limited practical utility in identification (**Table 2**). Even when apothecia are found they typically have poorly developed asci and spores. One notable exception is that *A. papilliformis* McCune & J. Di Meglio produces sessile lecideine apothecia, with no algae in the margin, while most species have aspicilioid apothecia, i.e., a disk surrounded by a level to raised thalline tissue, with a thin proper exciple (parathecium) embedded between the hymenium and surrounding thallus. In most species of *Aspicilia* multiple disks can be produced in a single thalline wart. When apothecia were found, all had greenish to olive brown or brownish epihymenium, the pigment intensifying in green with application of 1M HCl, as is typical for *Aspicilia*.

Lichen substances. We found only two diagnostic lichen substances for this group, aspicilin and norstictic acid (**Table 3**). Aspicilin is a fatty acid readily detectable by TLC on glass plates but not by spot tests. It occurs consistently in *A. reptans* and *A. wyomingensis* McCune & J. Di Meglio. Norstictic acid is readily detected both by TLC and by its P+ orange-red and K+ reddish reactions and K+ red needles forming under the compound scope. It occurs in *Aspicilia californica*.

Table 3. Lichen substances in terricolous *Aspicilia* in western North America. An asterisk (*) indicates that the record is based on literature report(s).

Taxa	nil	aspicilin[1]	unk. fatty acid Rf C5	unkown fatty acids Rf A6–7 C6–7	norstictic acid
A. albonota	yes	–	–	–	–
A. aspera	yes	–	±	–	–
A. californica var. *californica*	–	–	–	–	yes
A. californica var. *gigantea*	–	–	–	–	yes
A. diploschistiformis	yes	–	–	–	–
A. filiformis	yes	–	–	–	–
*A. glaucopsina**	yes	–	–	–	–
A. hispida	yes	–	–	–	–
A. papilliformis	yes	–	–	–	–
*A. praecrenata**	–	yes	–	–	–
A. reptans s.str.	–	yes	–	–	–
A. rogeri	usually	–	–	±	–
A. spicata	yes	–	–	–	–
A. subcontinua	yes	–	–	–	–
A. wyomingensis	–	yes	–	–	–

[1] includes an unknown fatty acid nearly identical in Rf to aspicilin in solvents A and C.

Phylogenetic Relationships

We found numerous supported clades that contained specimens that would have been named "*Aspicilia reptans*" under the existing taxonomy but fell in different parts of preliminary phylogenetic trees. Rather than being a single species complex, *A. reptans* as previously applied is clearly polyphyletic. Results from ITS data alone (**Fig. A2-1**) were largely concordant with those from the combined ITS+LSU tree (**Fig. 7**). In addition to the differences in ITS and nuLSU sequences, each of these clades differs from the others in morphology, anatomy, and substrate (**Table 2**), and to a lesser extent in secondary products (**Table 3**). To assign these to genera we intensified sampling throughout the Megasporaceae for our final phylogenetic reconstructions.

Generic placement

Although our purpose did not include a comprehensive evaluation of generic concepts within the Megasporaceae, naming new taxa forced us to evaluate the generic splits from *Aspicilia* and choose a genus for each new species. Definition of genera within and near *Aspicilia* has been challenging and as yet there seems to be little agreement among various workers (e.g., compare Nordin et al. 2010, Sohrabi et al. 2013, Kondratyuk et al. 2015, and Haji Moniri et al. 2017). Segregate genera include *Agrestia* J.W. Thomson*, Aspiciliella* M. Choisy*, Aspilidea* Hafellner*, Chlorangium* Rabenh.*, Circinaria, Lobothallia* (Clauzade & Cl. Roux) Hafellner, *Megaspora, Oxneriaria* S.Y. Kondr. & L. Lőkös*, Sagedia* A. Massal.*, Sphaerothallia* T. Nees, and *Teuvoa* Sohrabi & S.D. Leav. Topologies of phylogenetic trees differ considerably among authors, even using the same general methodologies, suggesting that taxon sampling may be influential. This idea is reinforced by somewhat different topology emerging with the addition of many North American specimens. In the combined ITS+nuLSU tree from our expanded taxon sampling we could identify the previously segregated genera as clades, but almost all of them are problematic, and numerous small, orphaned clades or individual species are left out (**Fig. 7**). Although taxonomic decisions on these genera clearly require more data than currently available, we nevertheless describe below the problematic placement of currently recognized segregates of *Aspicilia.* These problems support the retention of a broad genus concept at the present time.

Agrestia was monophyletic but unsupported and nested within *Circinaria* sensu Nordin et al. (2010) (**Fig. 7**). *Agrestia* would, however, become supported but still nested in *Circinaria* with the addition of *Circinaria* sp. 3 from Iran. ***Aspiciliella*** was supported as monophyletic and was not nested within the other segregate genera. As such it was the only nonproblematic segregate genus from *Aspicilia*. ***Aspilidea*** was represented by a single sequence of *A. myrinii*, which fell outside all of the other segregate genera from *Aspicilia* and was sister to a clade containing *Lobothallia*, *Teuvoa*, and *Aspicilia* sensu Nordin et al. (2010). ***Chlorangium*** was supported as monophyletic but was nested within *Circinaria*. ***Circinaria*** sensu Nordin et al. (2010) was monophyletic but unsupported; furthermore, it becomes paraphyletic with the recognition of *Agrestia, Chlorangium*, or *Sphaerothallia*. ***Lobothallia*** was polyphyletic, with one accession of *L. recedens* (Taylor) A. Nordin, Savić & Tibell and *L.* sp. from France separating from the other species and transitional to *Teuvoa*. ***Megaspora*** was monophyletic but unsupported, having two quite distinct subclades, one containing *M. cretacea* Gasparyan, Zakeri & Aptroot and *M. rimisorediata* Valadbeigi. The ***Oxneriaria*** clade (Haji Moniri et al. 2017) was unsupported and was nested within *Aspicilia* s.str. of Nordin et al. (2010). *Oxneriaria* was sister to *Sagedia*; together they form a supported subclade of *Aspicilia* s.str. Although *Aspicilia haeyrenii* (H. Magn.) Creveld has been assigned to *Oxneriaria,* it resolves outside of the well-supported *Oxneriaria* plus *Sagedia* clade. ***Sagedia*** was supported as monophyletic but was nested within *Aspicilia* s.str. ***Sphaerothallia***, represented by *S. esculenta* (Pall.) Eversm., was nested within *Circinaria*. ***Teuvoa*** was supported as monophyletic, but was nested within *Lobothallia*.

Comprehensive division of *Aspicilia* s.l. into the most widely accepted of these genera would appear to require erection of additional new small genera to accommodate the sequenced species of *Aspicilia* s.l. that fall outside of those clades (**Fig. 7**). In addition to the problems mentioned above, *A. maritima* occu-

pies an anomalous position outside the recognized segregates of *Aspicilia*, even though it has the appearance of a typical saxicolous *Aspicilia*. Furthermore, the existing generic splits of *Aspicilia* are frequently difficult to apply in routine identification, making it impossible to assign a genus without sequencing or knowing the species. A simple, practical, easily applied alternative that is completely faithful to the existing data is to adopt three genera, *Aspicilia* s.l., *Aspiciliella*, and *Megaspora*. We therefore took that approach and assigned all of the new species to *Aspicilia*. Whether or not a practical, comprehensive division of *Aspicilia* exists remains to be seen as future workers add more loci and improve taxon sampling.

Substrate Specificity

We sampled saxicolous *Aspicilia* species co-occurring with our terricolous specimens, to determine whether or not taxa could freely colonize various substrates. With exceptions, the terricolous species were generally faithful to that substrate and did not occur as extensive saxicolous individuals. Despite this generality, we frequently observed most of the terricolous species transgressing onto pebbles.

The most prominent exception was in *Aspicilia albonota*. About half the specimens were exclusively saxicolous, scattered throughout the *A. albonota* clade (**Fig. 7**). As discussed under that species, whether this represents substrate switching by a single species or substrate differences between close relatives cannot yet be decided. More sampling and additional loci are needed to answer the question. While some morphological similarities exist, such as the presence of short, linear pseudocyphellae along edges of areoles or lobes, the general appearance was so different between saxicolous and terricolous specimens as to make us question whether they should be considered the same species.

Other examples of substrate switching were rare. In one case (*McCune 38174*), *Aspicilia rogeri* was found covering loose pebbles, but was not seen in its typical fruticose vagrant form at that site. As a second example, *A. diploschistiformis* was found saxicolous on hard caliche fragments (*McCune 38137*).

We also found considerable specificity to calcareous substrates or not (**Table 2**). In the *A. reptans* morphological group, calciphiles included *A. diploschistiformis*, *A. reptans* s.str., and *A. wyomingensis*, while noncalciphiles were *A. papilliformis*, *A. spicata*, and *A. subcontinua*. Among the more clearly fruticose species, *A. hispida* and *A. rogeri* were strict calciphiles, while *A. californica* and *A. filiformis* were calcifuges.

Distributional Patterns

Most of the species formerly lumped under *Aspicilia reptans* have rather restricted distributions at a global scale, most being so far known only from western North America. One exception is *A. aspera*, a species that occurs in Eurasia and North America. A second probable exception is *A. reptans* s.str., which appears to be conspecific with *A. mansourii* Sohrabi from Iran. A third exception is *A. wyomingensis*, which occurs in Spain, based on a GenBank record previously assigned to another species; see *A. wyomingensis* for details.

Within western North America, *A. reptans* s.str. appears to be the most broadly distributed terricolous species, ranging from the northern Great Plains in southern Canada to the Columbia Basin and south to New Mexico (**Fig. 8**). The other species formerly included in *A. reptans* have more restricted distributions (**Figs. 9, 10**). For example, A. papilliformis frequents the rainshadow of the Cascade Range and semi-arid steppe of the Columbia Basin, while *A. wyomingensis* is most common east of the Continental Divide in Wyoming and Montana (**Fig. 10**).

Figure 7. (4 pages) Maximum likelihood phylogenetic tree from PhyML based on concatenated ITS and nuLSU. Approximate likelihood ratio test (aLRT-SH) support values over 0.80 are shown. Names include GenBank accession number when only one locus was used; cases with both loci include collector and collection number. New sequences are in **Table 1**. Pre-existing GenBank accessions are in **Appendix 1**. Segregate genera proposed by other authors are in colored boxes. Vertical bars indicate terricolous species that occur in western North America. Red asterisks (*) in the *A. albonota* clade indicate specimens on rock rather than soil.

Figure 7. (cont.)

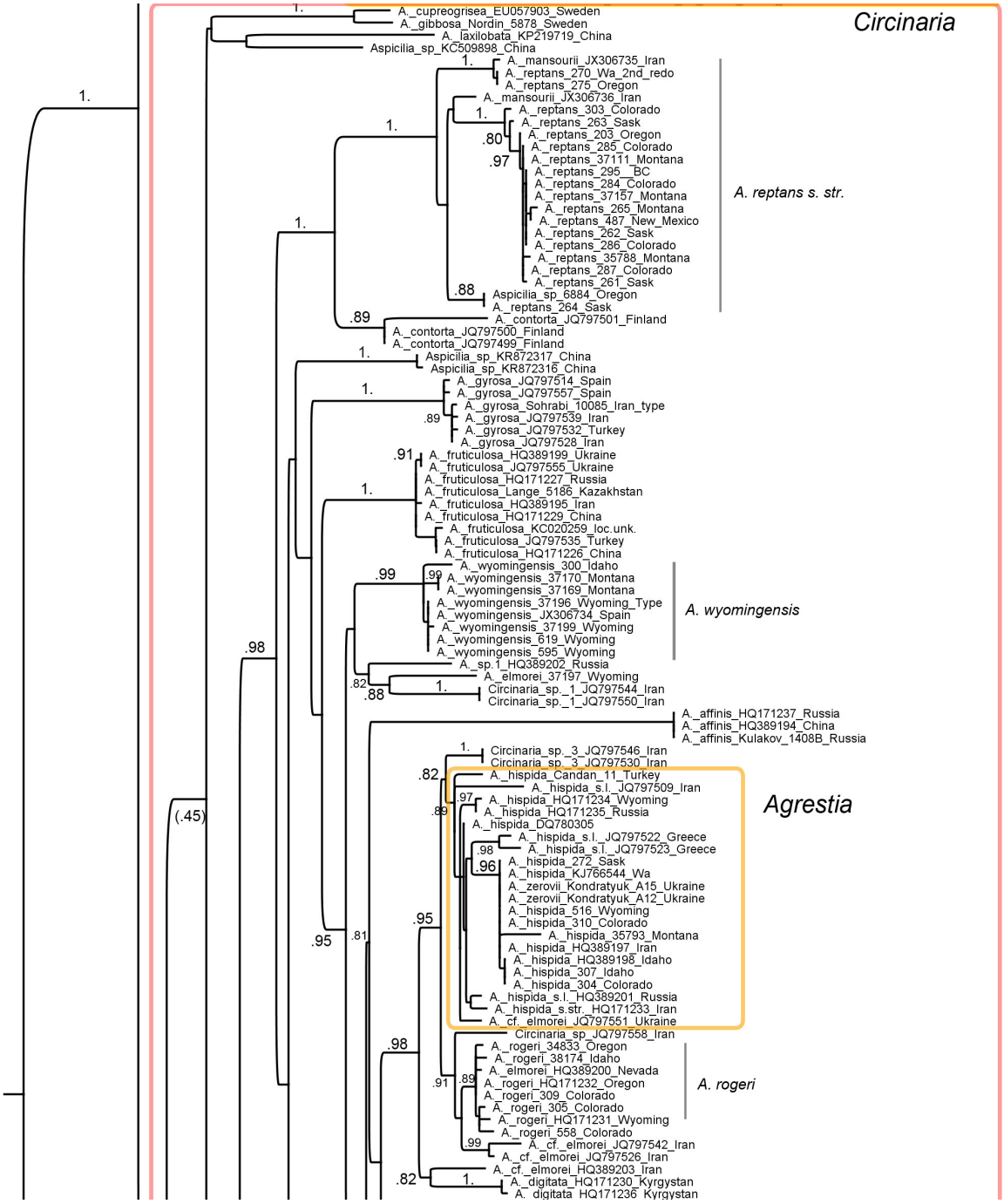

Figure 7. (cont.)

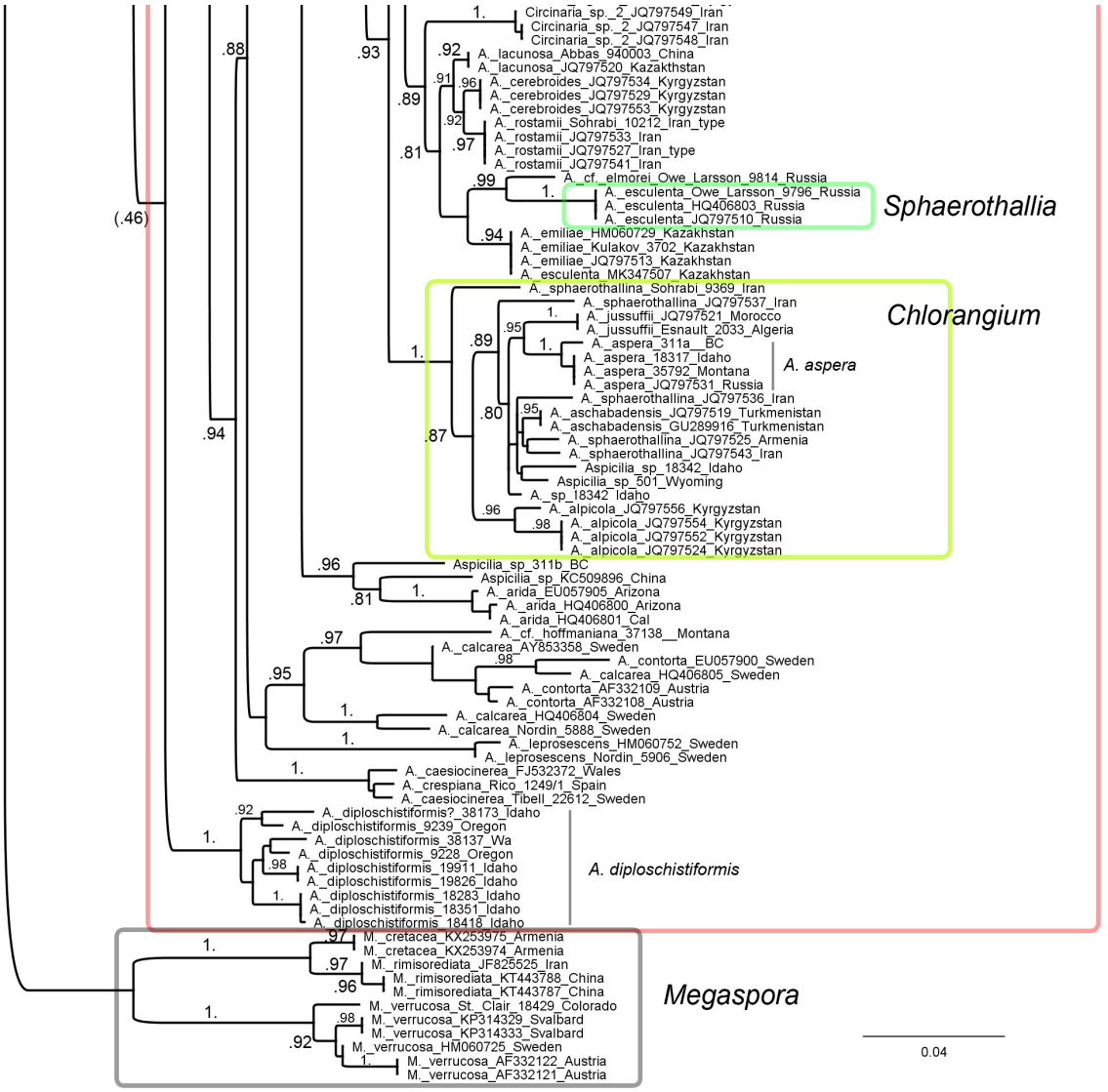

Figure 7. (concluded)

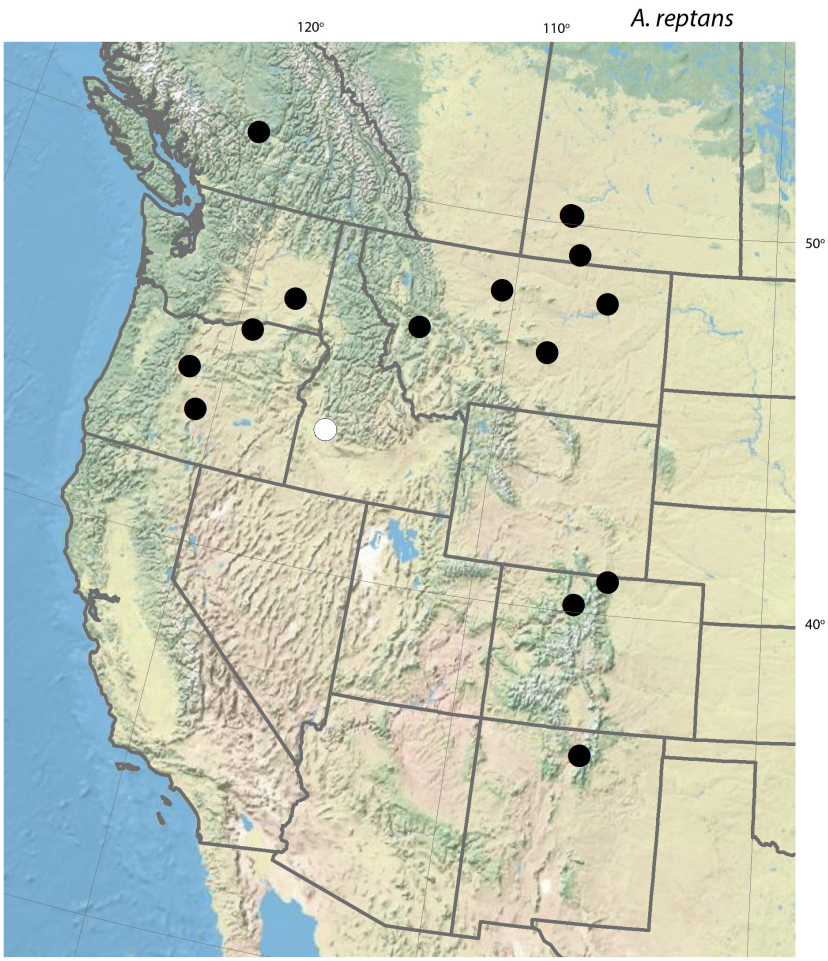

Figure 8. Distribution of sequenced specimens of *Aspicilia reptans* in North America. Black dots represent specimens that have been sequenced. White dots were assigned to species based on morphology and secondary chemistry.

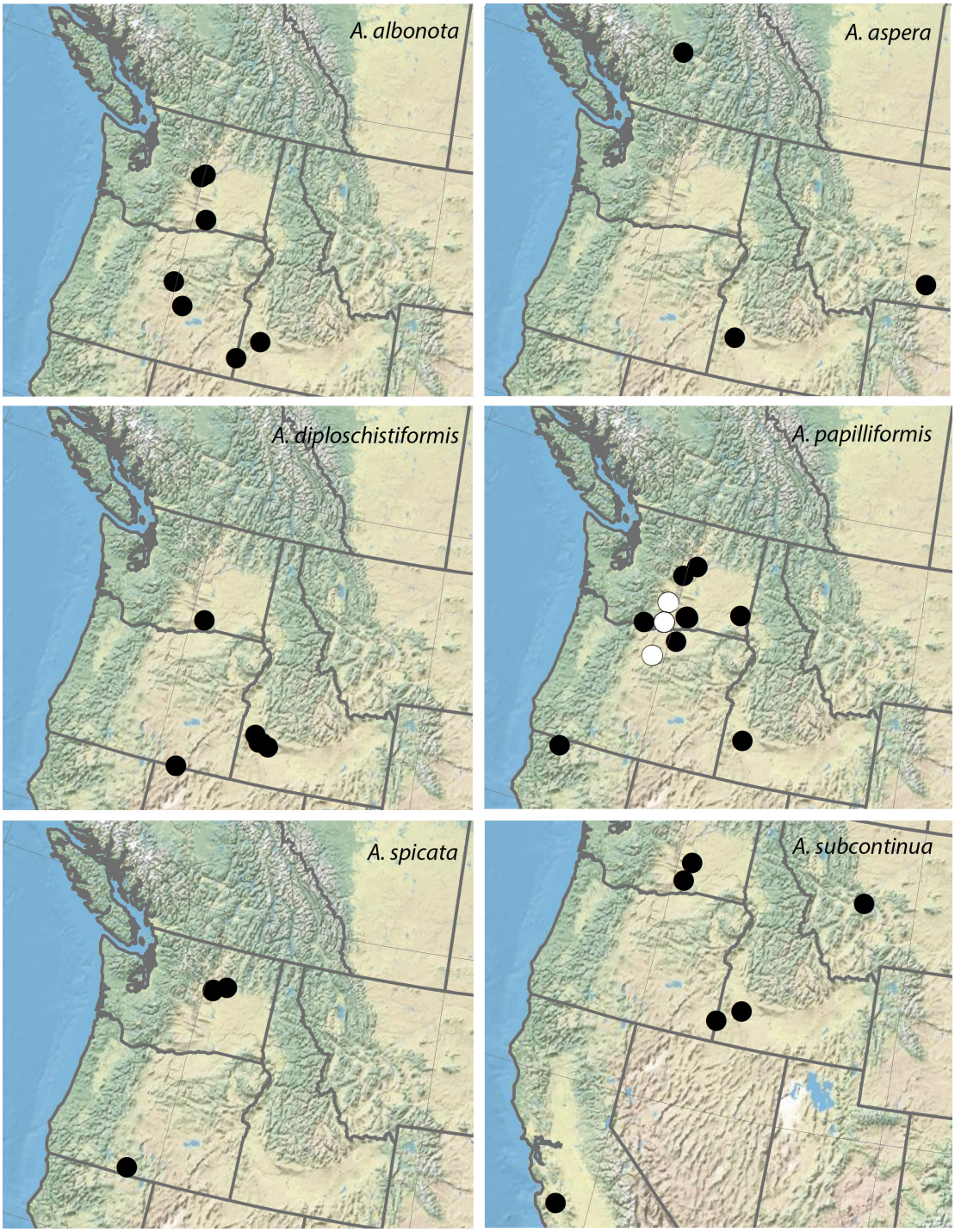

Figure 9. Distribution of *Aspicilia albonota, A. aspera, A. diploschistiformis, A. papilliformis, A. spicata*, and *A. subcontinua* in North America. Black dots represent specimens that have been sequenced. White dots were assigned to species based on morphology and secondary chemistry.

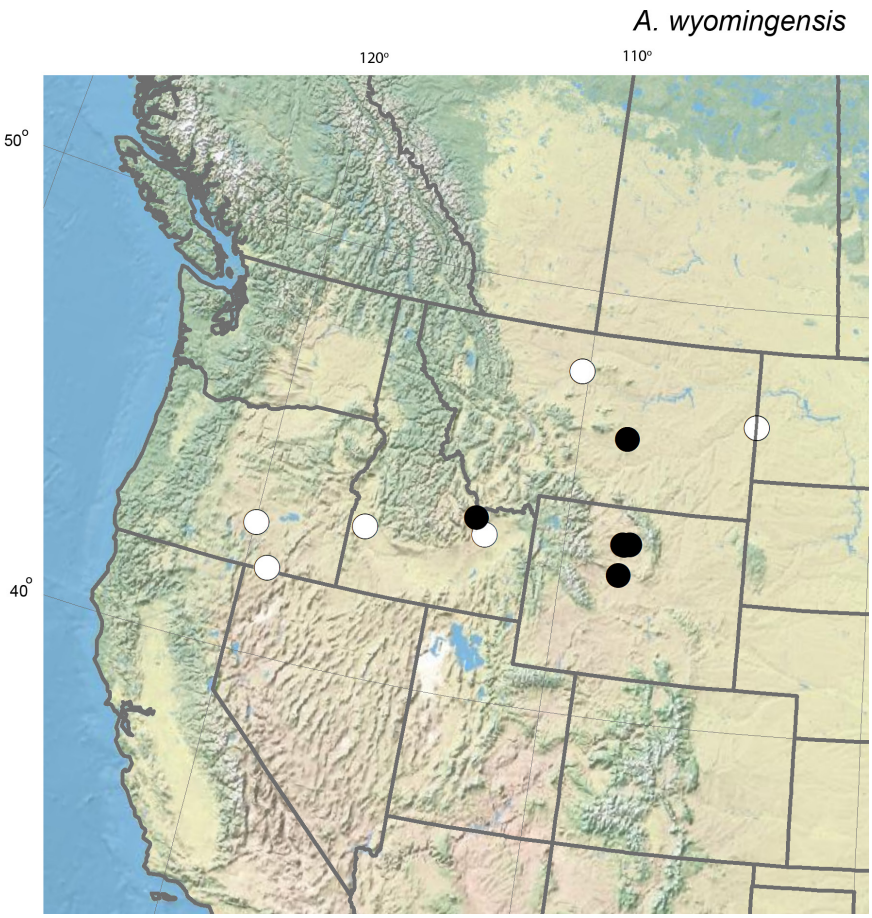

Figure 10. Distribution of *Aspicilia wyomingensis* in North America. Black dots represent specimens that have been sequenced. White dots were assigned to this species based on morphology and secondary chemistry.

The Species

This section contains full descriptions of species in the *Aspicilia reptans* group, but only brief descriptions for other terricolous *Aspicilia* from North America. All known terricolous *Aspicilia* in western North America, with the exception of southern California, are keyed after the descriptions.

Aspicilia albonota McCune & J. Di Meglio *sp. nov*. **Fig. 11**

MycoBank: MB839764 Barcode: MZ536783

Diagnosis. Thallus areolate to compound warty or beaded lobate, gray, olive gray, dark olive, or blackish green, with whitish spots and short lines (pseudocyphellae), particularly at contacts between areoles; apothecia aspicilioid; on soil, also on rock.

Type: U.S.A. **Washington**: Benton Co., Horse Heaven Hills, near junction of Dennis Road and Webber Canyon Road, 46.21689°N 119.43740°W, 245 m, low silty bluffs with old *Artemisia tridentata*, on soil, 9 June 2019, *McCune 38128* (holotype, OSC; isotype, WTU).

Description. Thallus usually occurring in small patches, most individuals < 3 cm diameter, medium gray, olive gray, dark greenish gray, or olive black, areolate, warty, compound warty, or beaded-lobate, in some cases with spicate lobe tips, protruding spikes of dense, blackish, sometimes white-tipped hyphae; vertical swellings and warts mostly 0.2–0.5 mm broad; pruina lacking but upper surface sometimes whitish necrotic; pseudocyphellae present, usually conspicuous as whitish spots and lines, which are flat, slightly raised, or in the crevices at the edges of areoles; epicortex (2)10–35(45) µm thick, mottled POL+ or with a thin superficial POL+ layer over a thicker primarily POL– layer; eucortex distinct, paraplectenchymatous, (12)15–40(57) µm thick, POL–, completely hyaline or more often brownish in the upper part; algal layer type 0, in some cases approaching type 1, mostly even but with sparse, narrow intrusions from the cortex; rhizomorphs not seen.

Apothecia rare when growing on soil. The following apothecial characters are based on a single fertile specimen on rock (*McCune 38192*). Apothecia 1–9 per areole, aspicilioid, the rim whitish; disk black, epruinose, to 0.8 mm in diameter; parathecium thin, hyaline throughout or greenish or olive brownish at the surface, only slightly expanded to the surface, I– , POL–; hymenium 120–155 µm tall, POL– , I+ blue, with occasional inclusions of sterile excipular tissue; epihymenium brownish to olive green or dark green, POL– or with very thin and discontinuous superficial POL+ layer; paraphyses submoniliform to moniliform, 2–3 µm at mid length, expanded to 4–6 µm on some tips; hypothecium hyaline, inspersed with oil drops, I+ blue; asci clavate, about 106 × 35 µm; ascospores 22–28 × 17–20 µm, median 26 × 18 µm; apothecial section K–; pycnidia immersed to partially exposed, with black ostiole, sometimes sunken in whitish raised pseudocyphellae and scabrid warts, becoming large and compound, in section greenish near the ostiole, otherwise hyaline; spermatia short-filiform, straight or slightly curved, mostly 6–12 × 0.7–1.1 µm, in one case (*Rosentreter DC-rim-1*) 10–19 µm × 0.5–0.7 µm.

***Chemistry*.** TLC: nil. Spot tests negative. Cortex and medulla I–. In one collection the medulla had aggregations of brownish crystals that were POL+ yellow and insoluble in K.

***Ecology and substrate*.** On soil, noncalcareous or weakly calcareous, also on noncalcareous pebbles and rock (basalt), usually at low elevations. Its shrub-steppe habitat is dominated by various shrubs, including *Atriplex confertifolia*, *Artemisia tridentata* ssp. *wyomingensis*, *Artemisia tridentata* ssp. *tridentata*, *Artemisia rigida,* and *Salvia dorrii*.

***Distribution*.** Columbia Plateau in central Washington to southern Oregon, east to the Snake River Plain of Idaho.

***Etymology*.** The epithet "*albonota*" refers to whitish (*albo*) distinguishing marks (*nota*) produced by pseudocyphellae in the form of dots and short lines.

Specimens examined (* = associated clade doubtfully assigned to this species). U.S.A. **Idaho**: Ada Co., Orchard training area, south of Bigfoot Butte, 43.18806°N 116.21573°W, 951 m, salt desert shrub habitat with shallow silty loam soils, with *Atriplex confertifolia, Picrothamnus desertorum, Poa secunda*, and *Ceratocephala testiculata*, 70-80% biological soil crust cover, on soil, 11 April 2014, *Rosentreter 18327*; Owyhee Co., southwest of Hemingway Butte, 43.308°N, 116.660°W, 853 m, 18 May 1994, *Rosentreter 8571* (SRP). **Montana**: Lake Co., Swan Range, Napa Ridge, 47.7908°N 113.7034°W, 2092 m, subalpine ridge with exposed rocky areas, on weakly calcareous rock, 25 July 2020, *McCune 38839**. **Oregon**: Crook Co., flats above N Fork Crooked River on Forest Route 150, 44.2958°N 120.0931°W, 1582 m, *Artemisia rigida – Poa sandbergii* steppe, June 2016, *McCune 36793*; Harney Co., stony flats east of Dry Mountain, near Beaver Slide Road, southern edge of Blue Mountains, 43.67485°N 119.52087°W, 1582 m, shrub steppe with scattered *Juniperus* and *Pinus ponderosa*, on rock (basalt), 21 June 2019, *McCune 38192**. **Washington**: Benton Co., Horse Heaven Hills, across gully from Dennis Road, 46.21437°N 119.43587°W, 286 m, steep, rocky lower slope with *Poa secunda* and *Salvia*, on rock (basalt), 9 June 2019, *McCune 38136**; on pebble, *McCune 38139*. Douglas Co., Rock Island Grade Wildflower Area, SE of Wenatchee, 47° 22.167′N 120° 4.664′W, 530 m, *Artemisia tridentata* ssp. *wyomingensis – Agropyron spicatum*, NW aspect, silt loam soil, on soil, 20 September 2013, *Rosentreter 17855*; north of Badger Mountain, 47.47908°N 119.91578°W, 650 m, *Artemisia rigida* with *Poa sandbergii* on clay loam soil, 22 September 2013, *Rosentreter DC-rim-1*.

Comments. As in most of the *A. reptans* group, the variation in thallus morphology can be vexing. Some specimens are simply areolate, while others become rough with compound warts and short lobes. In this case we are rescued by the consistent presence of pseudocyphellae in the form of whitish dots and short lines, often at contact points between areoles, and also at other places on the thallus. From the upper surface the cortex is not visibly broken at the white spots, but thin sections reveal that the eucortex is discontinuous underneath them (**Fig. 11**).

In the field with a hand lens, *A. albonota* on soil appears as a rough, warty crust of crowded areoles or warts, some of them confluent, and becoming greener than its common associates and other species in this group. Although the dark greenish hue is helpful in identification, it is less reliable than the presence of pseudocyphellae, as some specimens are more brownish or olive gray. Darker green individuals have a thinner cortex.

One of the most common dilemmas for species identification within the *A. reptans* group is separating *A. albonota* from *A. reptans*. Both are epruinose or nearly so and have similar internal structure. *Aspicilia reptans* is, however, a calciphile, while *A. albonota* is not. The calcareousness of the habitat is seldom specified on specimen labels, so look for well-known calciphilic associates on the sample, such as *Psora decipiens* and *Enchylium* (*Collema*) *tenax* group as a clue. TLC with glass plates for detecting the fatty acid aspicilin can also help to provide a more definite identification, because *A. reptans* always contains this substance, while *A. albonota* never does.

In one specimen we observed spiky blackish or white-tipped protrusions, apparently of prothallus similar to the black tips of *A. filiformis*, but in this case emerging from thalline warts.

We have seen four fertile specimens that fell in the *A. albonota* clade; all four were areolate forms growing directly on rock, four from the Columbia Basin (*McCune 36793, 38136, 38139, 38192*), and one from Montana (*McCune 38136*). The saxicolous specimens did not form a coherent subclade in the *A. albonota* clade (**Fig. 7**). ITS data showed minimal differences between saxicolous and terricolous specimens, despite a strong difference in appearance. All specimens, whether from rock or soil, are united by the white pseudocyphellae as described above. All of the saxicolous specimens were heavily fertile with crowded, black, irregularly shaped disks with white margins, often more than one per areole. The saxicolous specimens in the *A. albonota* clade might be mistaken for *A. knudsenii*, but that species is K+ red (norstictic acid). Indeed, if our identification of *McCune 38056a* as *A. knudsenii* is correct, then *A. albonota*, including the saxicolous specimens, is sister to *A. knudsenii*. More loci should be examined to test the hypothesis of whether the saxicolous and terricolous specimens in this clade represent different

species. More data are needed for *A. knudsenii* to resolve its relationship to *A. albonota* and the saxicolous form of that species.

Several specimens form a supported subclade that requires more study (*McCune 38136, 38192, 38839*, asterisked in specimen list). All were areolate-crustose forms growing directly on rock. We only tentatively assign these to *A. albonota*, as the closest relative and lacking a better name.

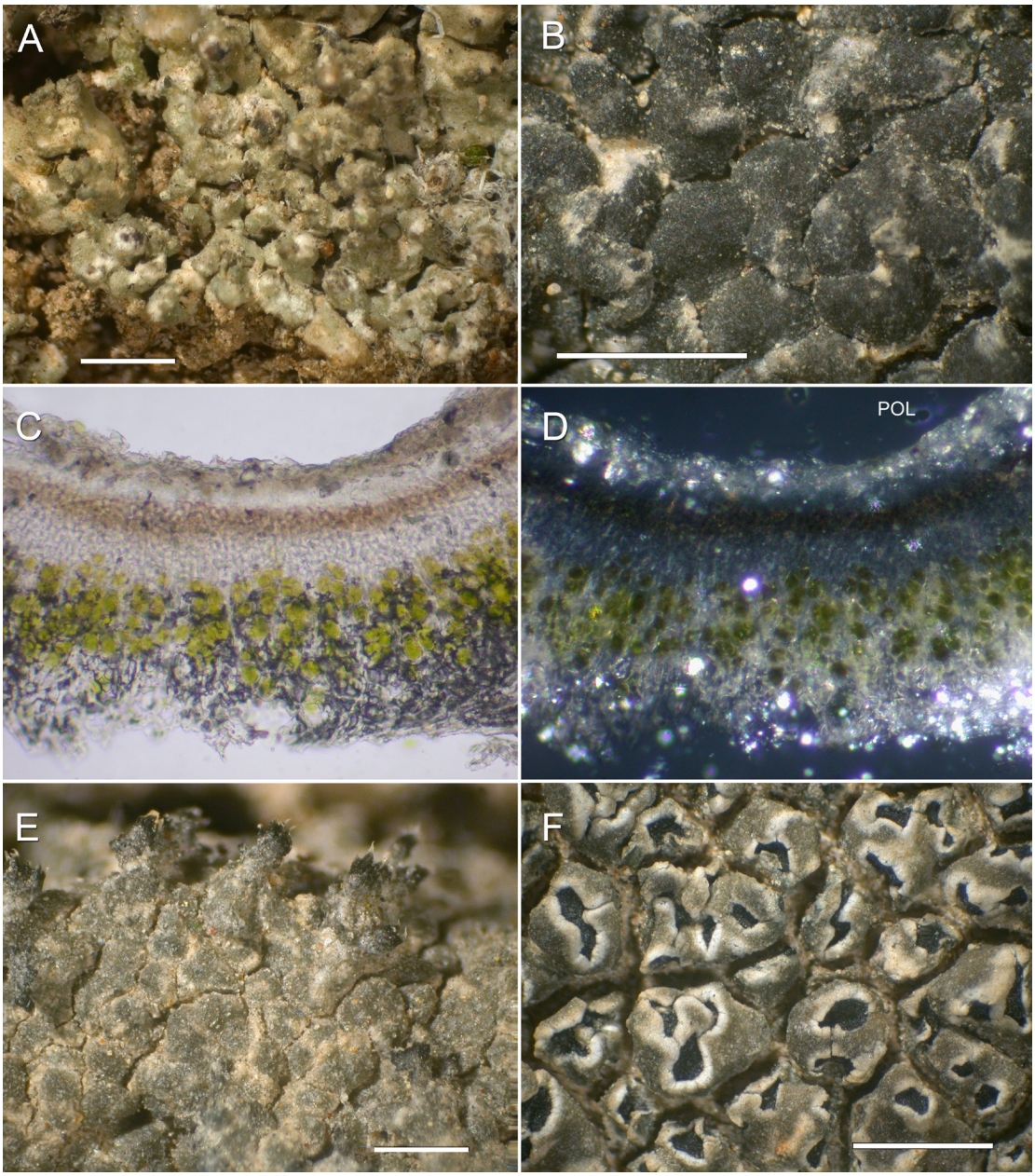

Figure 11. ***Aspicilia albonota***. — **A.** Habit, *Rosentreter 17855*. — **B.** Habit, *Rosentreter 18327*. — **C.** Thallus section, *Rosentreter DC-rim-1*. — **D.** Thallus section in polarized light, *Rosentreter DC-rim-1*. — **E.** Spicate lobe tips, *McCune 38128*. — **F.** Apothecia of saxicolous specimen, *McCune 38139.*

Aspicilia aspera (Mereschk.) Tomin, Handbook of the Lichens of the USSR 1: 198 (1971).
Fig. 12

Basionym: *Aspicilia desertorum* var*. aspera* Mereschk., Excursion lichénologique dans les steppes Kirghises (Mont Bogdo): 37 (1911).

Type: AZERBAIJAN, "In rupibus calcareis e gub. Baku in Caucaso," Lipsky in Elenkin, Lich. Fl. Ross. No. 24b (1893) (lectotype, designated by Sohrabi et al. (2012), le *L2017*; isolectotypes in h: *L2016*, *L 2018*).

Chlorangium asperum (Mereschk.) S.Y. Kondr., Gromakova & Khodos., Acta Botanica Hungarica 46 (2): 90 (2015); *Circinaria aspera* (Mereschk.) Sohrabi & Senkard., Mycological Progress 12: 265 (2012); *Sphaerothallia aspera* (Mereschk.) Follmann & A. Crespo, Anales del Instituto Botanico A.J. Cavanilles 31 (1): 330 (1974).

Description. This description is based on sequenced North American specimens that are affiliated with *A. aspera* from Asia. Thallus small, < 3 cm diameter; sometimes with both crustose and fruticose parts on a single individual, fruticose parts decumbent, cylindrical-lobate, marginally spreading by a continuous crust of knobby, confluent areoles, sometimes with a whitish prothallus at the edge of the crust, developing lobes from blackish prothalline warts or compound warts; lobes terete or subterete, irregularly branching, decumbent, mostly 0.3-1.0 mm diameter; transitional areas between crustose and fruticose parts are subareolate, but not forming discrete, separate areoles, rather with closely set bulges, often with whitish contacts between them; pruina lacking or lightly and patchily pruinose, but the crustose parts can be whitish, matte, rough, spongy-appearing; upper surface of the lobes pale olive gray, olive, tan, or mottled; upper surface of the marginal crust dark olive to whitish; pseudocyphellae not seen but crustose portions of the thallus sometimes with whitish markings between swellings; epicortex (12)15–30(50) µm thick, POL+ throughout or primarily at the surface, partly pock-marked and spongy in section; eucortex distinct, paraplectenchymatous, (15)20–30(62) µm thick, not including intrusions into the algal layer, POL–, brownish or greenish brown in the upper part, otherwise hyaline; algal layer type 2, noticeably lobate and discontinuous; medulla brightly POL+ except for ropy compact tissue in the central core of the lobes, this ropy tissue composed of thick-walled cells, the lumina about 2 µm in diameter, cells elongate and combined into groups that are twisted around each other, thus forming ropelike aggregations; these are embedded in a matrix of POL+ granular coated medullary cells; rhizomorphs sometimes present but difficult to expose.

Apothecia aspicilioid, with raised thalline margin; disk black, white-pruinose, to 1.5 mm diameter; epihymenium brownish olive, POL+; asci and ascospores not seen; pycnidia infrequent, erumpent, with whitish pruinose margin and black central spot or short lines, in section with hyaline walls except olive brownish around ostioles; spermatia 12–17 × 0.8–0.9 µm, median 15.3 × 0.8 µm.

Chemistry. TLC: nil, or with unidentified fatty acid Rf C5.

Ecology and substrate. With so few known locations in North America, it is difficult to generalize habitat requirements. So far, the species has been found in shrub steppe, on soil and on noncalcareous pebbles embedded in calcareous soil. In at least two cases a close associate was *Enchylium tenax*, an indicator of calcareous soils. Other associates include the mosses *Syntrichia caninervis* and *S. ruralis*.

Distribution. So far known from Idaho, Montana, Wyoming, and Russia.

Etymology. We presume that the epithet "*aspera*" refers to the rough thallus texture, as compared to the relatively smooth areolate texture of most *Aspicilia* species.

Specimens examined. CANADA: **British Columbia**: Cache Creek, east from Highway 1 to Juniper Beach Provincial Park access road, 50.78745°N 121.0742°W, 425 m, open *Artemisia* steppe on southeast slope, growing adjacent to and overtopping a crustose, fertile *Aspicilia* species, 9 July 2016, *Di Meglio 311a*. U.S.A. **Idaho**: Ada Co., Orchard Training Area, S of Bigfoot Butte, 43.18806°N 116.21573°W, 951

m, salt desert shrub habitat with shallow silty loam soils, with *Atriplex confertifolia, Picrothamnus desertorum, Poa secunda, Ceratocephala testiculata*, and 70-80% biological soil crust cover, 11 April 2014, *Rosentreter 18317;* Owyhee Co., Hemingway Butte, approximately 2 miles S of Highway 78, NW of Murphy, 43.3225°N 116.6396°W, 740 m, barren badland habitat with some *Atriplex* and *Artemisia spinescens*, on soil, 24 June 1991, *Rosentreter 6964* (SRP; with apothecia but no asci or spores; not confirmed with DNA sequence). **Montana**: Stillwater Co., rest area near Columbus on I-90, grassy hill, 45.60114°N 109.0654°W, 1110 m, 19 September 2014, *McCune 35792*.

Comments. The description is based on the three North American specimens that were demonstrated to have ITS sequences very similar to *A. aspera* from southwest Russia (*Owe-Larsson 9792*, H, Genbank JQ797531, from the Astrakhan Region of Russia). Because we have not studied authentic material of the species, and *A. aspera* has named varieties by Tomin and Oxner, this identification must be considered tentative. This is especially so, since Sohrabi et al. (2012) considered *A. aspera* to be primarily a crustose saxicolous species. The typical hand lens appearance of North American material is a low mat of terete or subterete lobes that appear to flow into a marginal crustose zone. In some collections the crustose part predominates. The continuous crustose portions of the thallus often have a spongy, porous texture contrasting with the smooth matte cortex of the terete lobes.

The prothalline lobe tips (also mentioned by Mereschkowsky [1911]) are more rounded or isidioid and non-spicate than those of *A. spicata, A. filiformis,* and *A. californica*. In longitudinal section these blackish warty lobe tips have dark brown to greenish cortical cells, are POL–, initially lack algae, and are elongate perpendicular to the surface of the thallus, forming a round-topped volcano of elongate dark brown to greenish hyphae grading to hyaline within (**Fig. 12**). We also sectioned some bulges that have the opposite structure: a thinner cortex as if the algal layer might erupt. We did not, however, see any developmental breaks in the cortex.

We have not yet found a sufficiently detailed description of the type material to allow us to evaluate similarities with the current material. Mereschkowsky (1911) described the species as follows: "The thallus is partly scaly (looks like deposits on the bottom of a kettle!), attached to a stone or to the ground, partly free, in the form of flat cakes. The surface of the humpy (uneven, hilly) thallus is covered in places, especially along the periphery, with extremely irregular prickly outgrowths, thorns, sometimes branchy isidia-like formations with a rough (scabrous) uneven surface. Apothecia are crater-like, rarely found. We found this in moderate numbers on Mount Bogdo in the Astrakhan province; one specimen was found in Crimea (Sevastopol, in the steppe)." We find this description sufficiently similar to our material to support the occurrence of *A. aspera* in North America. Mereschkowsky also noted that "in the exsiccata published by Elenkin under the name *Aspicilia alpino-desertorum* forma *foliacea*, there are two different lichens: the specimen under the letter *a* is the lichen named by Elenkin, but *b* is nothing more than *Aspicilia desertorum* var. *aspera,*" but we have not seen this specimen.

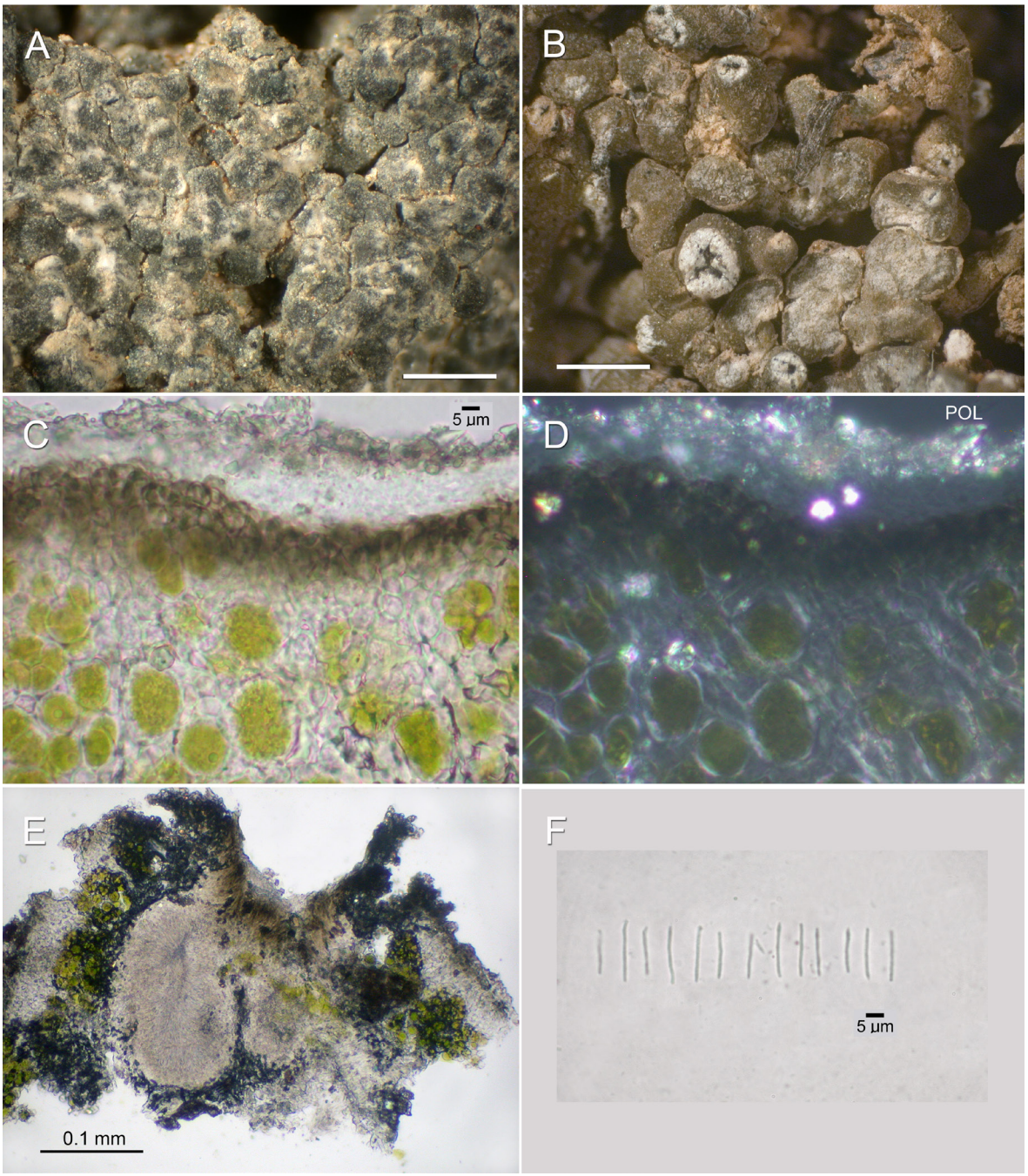

Figure 12. ***Aspicilia aspera***. — **A.** Habit, *Rosentreter 18317*. — **B.** Habit, with pycnidia, *Di Meglio 311a*. — **C.** Thallus section, *Rosentreter 18317*. — **D.** Thallus section in polarized light, *Rosentreter 18317*. — **E.** Thin section of pycnidium, *Di Meglio 311a*. — **F.** Spermatia, *Di Meglio 311a*.

Aspicilia californica Rosentr., Lichenogr. Thomsoniana, North American Lichenology in Honor of John W. Thomson (Ithaca): 165 (1998). **Fig. 13**

Type: U.S.A. California: San Benito Co., Pinnacles National Monument, east end of High Peaks Trail, chaparral habitat, on soil and organic matter, *Rosentreter 7241a* (holotype, SRP!; isotypes, WIS, BRY).

***Description for var.* californica.** See the previous descriptions in Rosentreter (1998) and Sanders (1999), supplemented here with characters that we used for other terricolous *Aspicilia* species. Thallus fruticose, in tangled prostrate patches, though crustose where in contact with pebbles, individuals usually < 1.5(2) cm diameter; main branches cylindrical to irregularly lumpy, mostly 0.2–0.7 mm wide, internodes to 5 mm long, branches tapering to filiform prothalline tips, the tips sharp or blunt, simple or sparingly dichotomously branched, blackish throughout or whitish at the very tips, not containing algae; branch tips free or appressed to the substrate; pruina lacking; upper surface mottled olive gray, gray, beige, and whitish, commonly mottled pale gray and pale olive brown; pseudocyphellae lacking; epicortex (2)5–12 µm thick, POL– or weakly POL+ in parts, I–; eucortex distinct, paraplectenchymatous, 12–24(30) µm thick, POL– or weakly POL+, brownish in the upper part, otherwise hyaline, I–; algal layer type 0 or 1, rather even but with occasional narrow intrusions from the cortex; medulla brightly POL+, with a prosoplectenchymatous core of elongate hyphae twisted into a ropy tissue, as in *A. filiformis*; rhizomorphs sometimes present, similar to prothalline tips.

Apothecia infrequent, erumpent to sessile, lecanorine, the thalline margin persistent, ± even, colored like the thallus or whitish gray, sometimes blacker than the thallus, containing algae, POL+ cloudy whitish in section; disk blackish, with or without white pruina, to 0.8 mm in diameter; parathecium thin, indistinct, hyaline POL– or with thin POL+ layer in the upper part; hymenium 79–97 µm tall, hyaline with yellowish deteriorated or abortive asci, widely scattered POL+ granules, I+ blue green; epihymenium light to dark brown, POL–, K–; paraphyses submoniliform near the tips, becoming more moniliform in K; hypothecium hyaline, with irregular POL– granules or oil drops, I+ strongly blue; mature asci and ascospores not seen; apothecial section K+ yellowish diffusion, sometimes forming red needle-like crystals; pycnidia and spermatia not seen.

***Chemistry*.** TLC: norstictic acid. Cortex and medulla K+ slowly red, P+ orange. The norstictic acid is quite unevenly distributed so that some branches can be almost completely K–, others with K– but K+ red spots, others K+ red throughout, including both cortex and medulla. Because of this variability it is worth checking multiple branches on specimens from California for the K reaction, the only character distinguishing it from *A. filiformis*.

***Ecology and substrate*.** On noncalcareous soil and plant detritus, partially on embedded pebbles, low-elevation valleys and foothills with Mediterranean climate.

***Distribution*.** The typical variety is so far known only from California, where it occurs from northern California south at least to Bakersfield, though not on the immediate coast, nor high in the mountains, nor east of the crest of the Sierra Nevada.

***Specimens examined*.** U.S.A. **California**: San Benito Co., San Benito Range, Pinnacles National Monument, wash along Chalone Creek, 36.483°N 121.167°W, 293 m, dry wash with noncalcareous gravel, June 1991, *McCune 19113*; near Highway 146, 36.48584°N 121.1667°W, 337 m, SW exposed hillside, with *Aesculus californica*, on mineral soil with granite gravel, 17 December 2014, *Di Meglio 250*; Tuolumne Co., 7.4 km NW of Mather Camp, on south rim of Tuolumne River, between Forest Service Road 1S26 and 1S02 (Mather Road), 37.86639°N 119.9389°W, 1325 m, annual grasses and forbs on andesitic and basaltic mudflow deposit, 19 April 2015, *Colwell 15-003*.

Comments. Together *Aspicilia filiformis, A. californica*, and *A. spicata* form the *A. filiformis* group (**Fig. 7).** *Aspicilia californica* contains norstictic acid, while the other two species do not; we take this as the sole reliable character for separation of *A. californica* and *A. filiformis*. The essentially identical morphology of *A. californica* and *A. filiformis* has been noted both in the original describing paper (Rosentreter

1998) and by Sanders (1999), who made detailed studies of their anatomy. Although Rosentreter (1998) also pointed out some subtle differences in appearance, it is not clear to what extent these are environmentally induced.

Our phylogenetic reconstruction does not support the separation of *A. californica* and *A. filiformis* in either the combined ITS+nuLSU tree (**Fig. 7**) or the ITS tree alone (**Fig. A2-1)**. At this time we refrain from recommending synonymy, given the distributional difference between the species: *A. filiformis* is frequent throughout western North America, while *A. californica* is restricted to California and extreme south-central Oregon. Additional loci are needed to clarify the structure within the *A. filiformis* group.

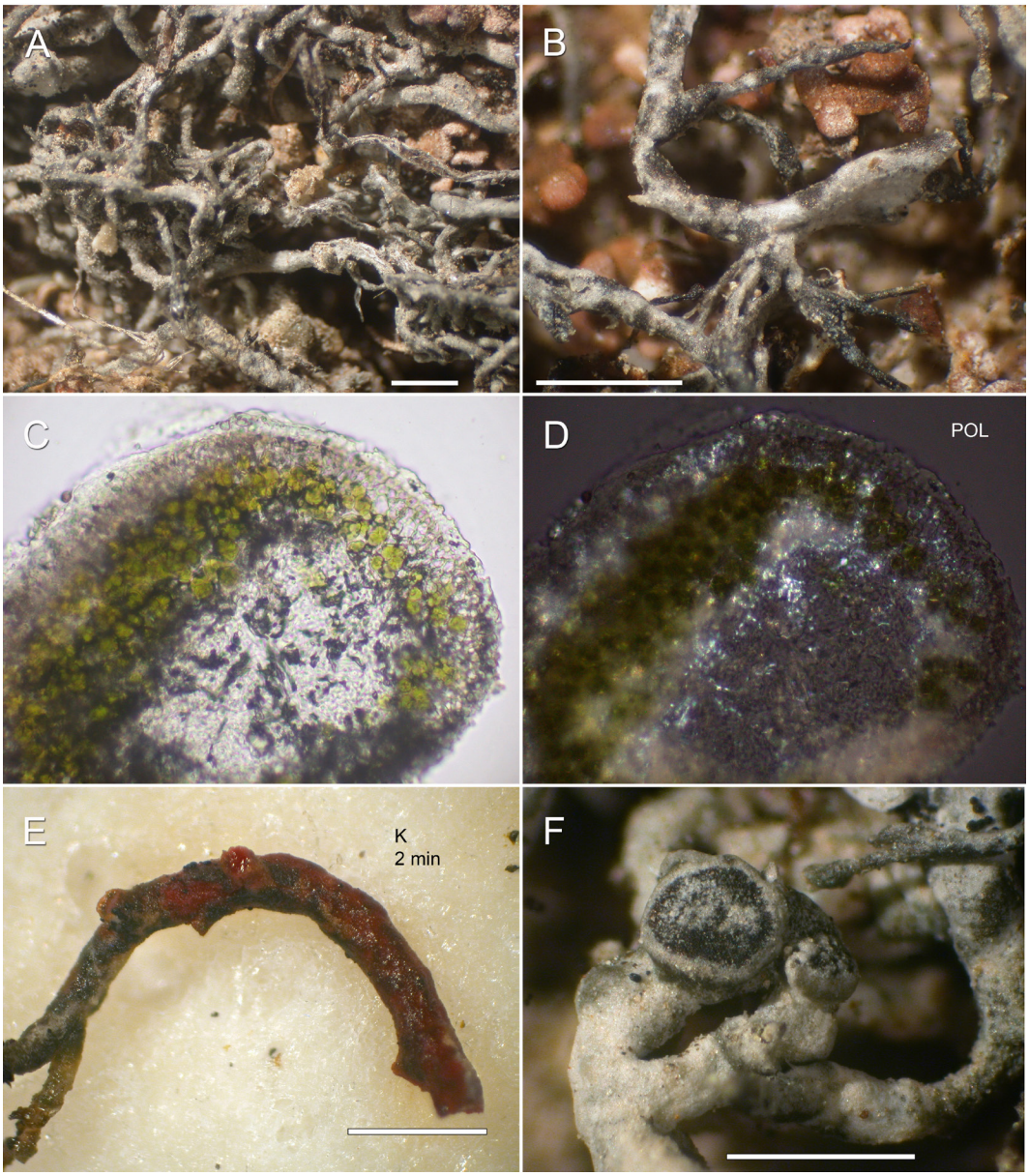

Figure 13. ***Aspicilia californica*** **var.** ***californica***. — **A.** Habit, *McCune 19113*. — **B.** Branches, *McCune 19113*. — **C.** Thallus section, *Di Meglio 250*. — **D.** Thallus section in polarized light, *Di Meglio 250*. — **E.** K test of branch after two minutes, *Di Meglio 250*. — **F.** Apothecia, *McCune 19113*.

Aspicilia californica var. *gigantea* McCune & J. Di Meglio *var. nov*. **Fig. 14**

MycoBank: MB839769 Barcode: MZ536752

Diagnosis. Similar to *Aspicilia californica* var. *californica* but more than twice as large in overall thallus size, branch diameter, and branch length.

Type: U.S.A. **Oregon**: Klamath Co., Cascade Range, just east of entrance to JWTR Travel Management Area and north of Highway 66, 42.12064°N 122.2108°W, 1251 m, stony, thin-soil basalt flats in large opening in conifer forest, on soil, 28 December 2011, *McCune 31794* (holotype, OSC; isotypes NY, SRP, UC, WTU).

Description. Thallus as in *A. californica* and *A. filiformis* except much larger, with longer, thicker branches, individuals often > 2 cm in diameter; branches (0.5)0.6–1.0(1.2) mm wide; internodes mostly 4–10 mm long; pseudocyphellae lacking; epicortex occludes, POL+ or weakly POL+, murky, 2–27 µm; eucortex weakly POL+ to distinctly POL+, 32–47 µm, brownish in upper part, otherwise hyaline, sometimes two layered with a grayish granular POL+ murky upper half and a brightly POL+ hyaline lower layer; algal layer type 0 or 1, weakly POL+; medulla partly paraplectenchymatous, weakly POL+ and partly prosoplectenchymatous and ropy, POL–.

Apothecia lecanorine (description based on *McCune 32606*), adnate; disk brownish to black, epruinose; amphithecial cortex distinct, POL+; amphithecial medulla with algae; epihymenium greenish brown, with superficial POL+ granules; hymenium 100–112 µm tall; parathecium hyaline, expanded at the surface; paraphyses submoniliform to moniliform at the tips; hypothecium hyaline, POL–; mature asci and spores not seen.

Pycnidia often numerous, prominent, bulging to subglobose swellings, their surface POL+, K+ yellow to red, in section forming K+ red needle-like crystals; spermatia short-filiform, 10.0–13.5 × 0.7–0.9 µm, median 11.4 × 0.8 µm.

***Chemistry*.** TLC: norstictic acid. Thallus K+ red, P+ orange-red.

***Ecology and substrate*.** On noncalcareous soil, poorly drained basalt flats with thin standing water at times, occurring with vagrant *Dermatocarpon*. We have seen the thalli partly submerged. These rocky openings are surrounded by mixed conifer forest and woodlands and are relatively dry in summer.

***Distribution*.** So far known from the southern Oregon Cascade Range, east of the crest.

***Etymology*.** The epithet "*gigantea*" refers to the large size as compared to the typical variety.

***Additional specimens examined*.** U.S.A. **Oregon**: Klamath Co., type locality (above), 31 May 2013, *Di Meglio 200*; *McCune 32606* (fertile, but mature asci and spores not seen); Fremont-Winema National Forest, east from Chiloquin, Sprague River Road, left on Lone Pine Road, right on FS 44, to FS 4464 to FS 4469059, 42.58528°N 121.3746°W, 1472 m, vernal pools with basal islands, surrounded by *Pinus contorta, P. ponderosa*, and bunchgrasses, 25 June 2020, *Di Meglio & D. Miller 495*.

Comments. Upon first finding this species in the field we were not even sure to what genus it belonged, it is so different in size from the closely related *A. californica* var. *californica* and *A. filiformis.*

Given the remarkable morphological difference between varieties and their essentially identical ITS regions, we hypothesize that the var. *gigantea* has a polyploid origin, given that polyploidy in plants is well known for producing gigantism. Polyploidy is known from ascomycetes (reviewed by Albertin and Marullo 2012) but has apparently never been demonstrated in lichenized ascomycetes. We suggest this variety as a target for such an investigation. Although pycnidia are common, apothecia are rare, and we have yet to find mature asci and spores.

Based on current known locations the two varieties are allopatric. The variety *californica* is known only from California and is rather frequent in a large area, while var. *gigantea* was found only in Oregon and is rare.

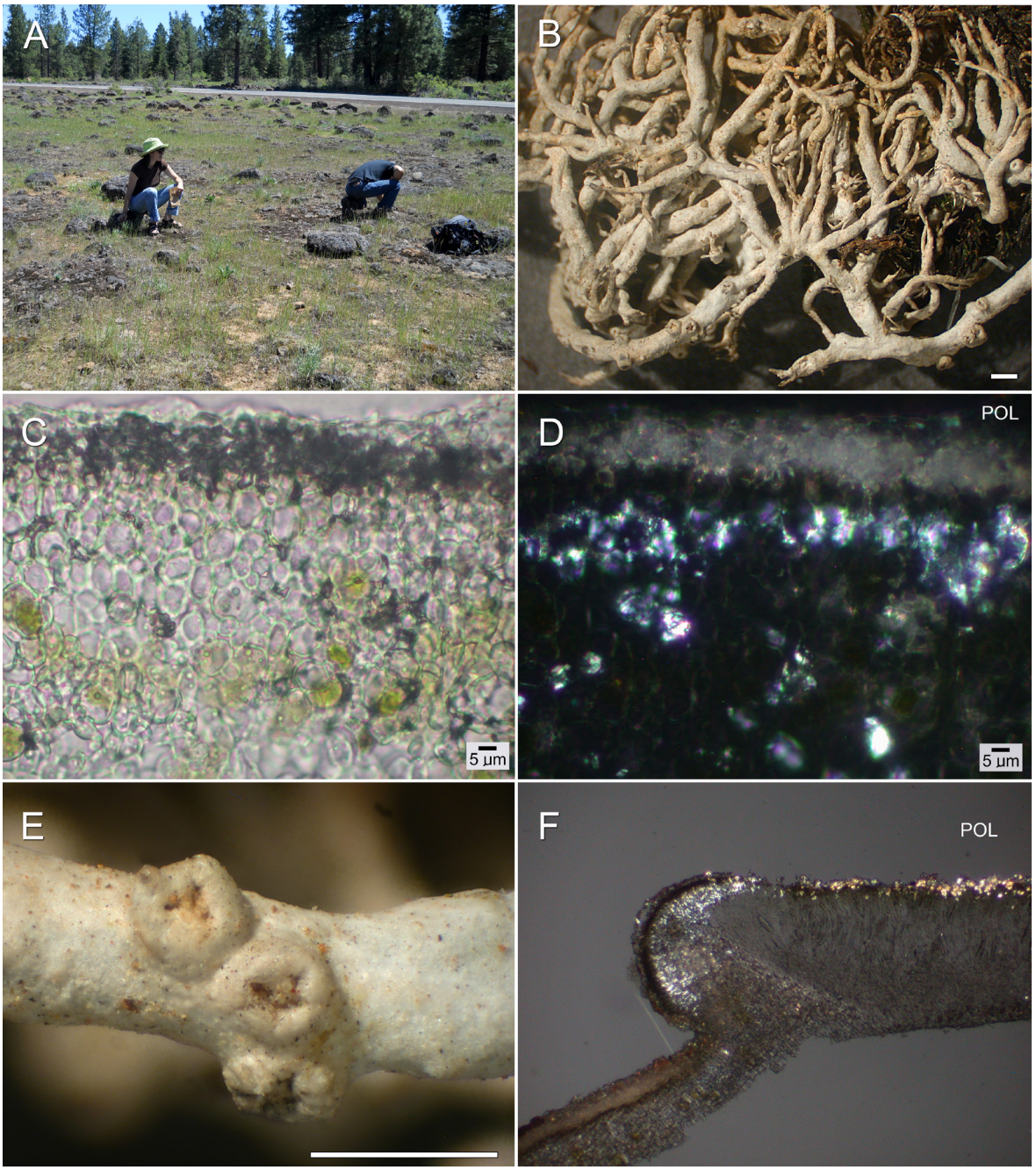

Figure 14. ***Aspicilia californica*** **var.** ***gigantea****.* — **A.** Type locality for the variety. — **B.** Branches, *McCune 31794*. — **C.** Thallus section, *McCune 31794*. — **D.** Thallus section in polarized light, *McCune 31794*. — **E.** Pycnidia, *McCune 31794*. — **F.** Apothecial section under polarized light, *McCune 32606*.

Aspicilia diploschistiformis McCune & J. Di Meglio *sp. nov*. **Fig. 15**

MycoBank: MB839765 Barcode: MZ536828

Diagnosis. Thallus areolate to bullate-areolate, lacking lobate, fruticose, or stringy parts; whitish, bluish gray, pale brownish gray, or pale olive gray; apothecia aspicilioid, erumpent, on soil, rarely on rock.

Type: U.S.A. **Oregon**: Harney Co., east of Adel, large unit of Hawksie-Walksie Research Natural Area, 42.005°N 119.135°W, approx. 1700 m, high desert with *Artemisia* and bunchgrass, large dry lakebed with fine soils, on soil, 25 June 2013, *D. Stone 9228* (fertile; holotype, osc).

Description. Thallus mostly < 5 cm diameter; field color white, grayish white, pale gray, pale brownish, or pale olive gray, the typical hand lens appearance white or grayish; thallus a monolayered, warty crust, not becoming lobate or imbricate, instead areolate to bullate-areolate, the areoles either discrete or locally confluent, becoming coarsely cracked at a large scale; vertical swellings mostly 0.3–1.2 mm broad, becoming thick and protruding as apothecia develop; pruina lacking or present, the surface subglossy or matte, sometimes with a whitish chalky texture, sometimes whitish scabrid over incipient apothecia and pycnidia; pseudocyphellae lacking, though cortex disintegrating over incipient apothecia; epicortex (0)10–40(60) µm thick, with coarse irregular POL+ granules throughout or in the upper half; eucortex distinct but the boundary with the algal layer diffuse, paraplectenchymatous, 7–20(30) µm thick, POL–, brownish in the upper part, otherwise hyaline; algal layer type 0, continuous; rhizomorphs present but difficult to expose by dissection, sometimes visible where the substrate has been eroded.

Apothecia uncommon, immersed, erumpent, or protruding, 1–2 per thalline wart, aspicilioid, the rim whitish, often paler than the adjoining cortex; disk black with variable white pruina, to 0.7 mm diameter; amphithecial cortex and algal layer similar in structure to the thallus; parathecium nearly hyaline, expanded toward the surface, I–, POL–; hypothecium hyaline, inspersed with oil drops; hymenium 125–150 µm tall, POL–, inspersed with oil drops; epihymenium greenish (yellower in K), with superficial irregular clumps of POL+ crystals; paraphyses 2–3 µm diameter, even to submoniliform near the tips in water, some expanded to about 5 µm near the tips, not much changed in K and the crystals persistent; mature asci and ascospores not seen, but one degenerate ascus contained about 6 spores, only one of which was measurable as 20 × 12.5 µm; apothecial section K–, I– except the amphithecial medulla I± weak violet; pycnidia infrequent (found on only one specimen), immersed, appearing as dark spots or short lines on thalline warts, becoming large and compound, the walls hyaline except olive green near the ostiole; spermatia narrow rod shaped, 6.4–10.3 × 0.8–1.0 µm, median 9.5 × 0.8 µm.

***Chemistry*.** TLC: nil. Spot tests negative.

***Ecology and substrate*.** On soil, also on caliche fragments, calciphilic, at low elevations on the Columbia Plateau (286 m) to middle elevations on the Snake River Plain, to at least 1700 m elevation in the extreme northern Great Basin of southern Oregon.

***Distribution*.** So far known from south-central Washington to southeast Oregon and the Snake River Plain of Idaho.

***Etymology*.** The epithet "*diploschistiformis*" refers to the similarity in the crustose appearance of the thallus to *Diploschistes muscorum*. Unlike most of the terricolous *Aspicilia*, *A. diploschistiformis* lacks fruticose, lobate, or stringy structures.

***Additional specimens examined*.** U.S.A. **Idaho**: Ada Co., Orchard Training Area, S of Bigfoot Butte, 43.19037°N 116.22116°W, 975 m, winterfat shrub steppe (*Krascheninnikovia lanata*), 17 April 2014, *Rosentreter 18351*; Orchard Training Area, Red Tie area, 43.30017°N 116.11750°W, 967 m, shrub steppe with *Artemisia tridentata* ssp. *wyomingensis* and *Poa secunda*, 8 April 2014, *Rosentreter 18283*; Orchard Training Area, 43.18806°N 116.21573°W, 967 m, *Poa secunda* steppe, 24 April 2014, *Rosentreter 18418*; NW of Initial Point, 8 miles south of Kuna, 43.37700°N 116.40760°W, *Poa secunda* steppe, 25 March 2017, *Rosentreter 19826*; Elmore Co., 7 miles SW of Mountain Home, N side of Highway 67, 43.10604°N

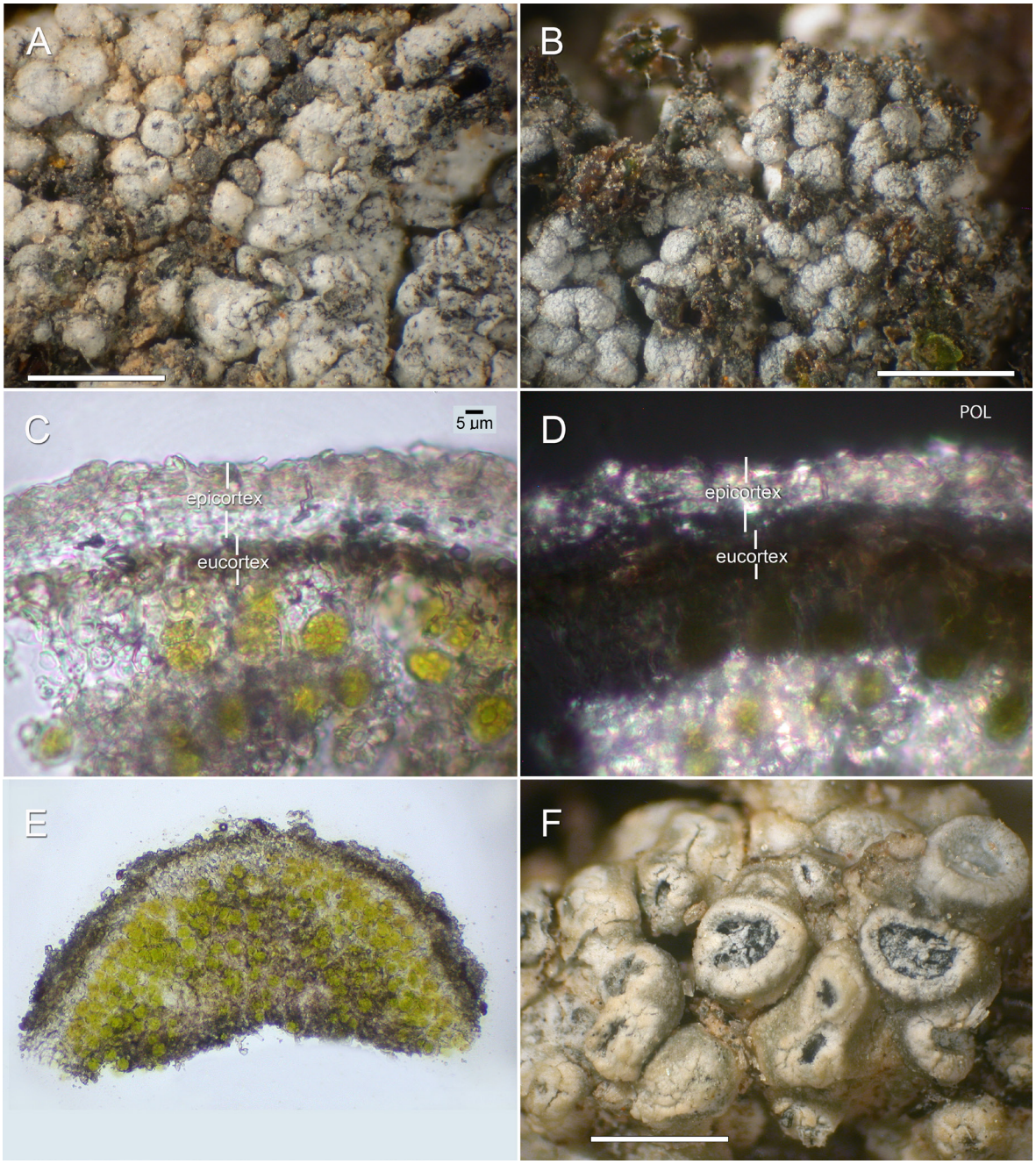

Figure 15. ***Aspicilia diploschistiformis***. — **A.** Habit, *Rosentreter 18418*. — **B.** Habit, *Rosentreter 18283*. — **C.** Thallus section, *Stone 9228* (type). — **D.** Thallus section in polarized light, *Stone 9228*. — **E.** Thallus section, *Rosentreter 18418*. — **F.** Apothecia, *Stone 9228*.

116.82228°W, 936 m, *Poa secunda* steppe, 15 April 2017, *Rosentreter 19911*. **Oregon**: Harney Co., east of Adel, large unit of Hawksie-Walksie Research Natural Area, 42.005°N 119.135°W, approx. 1700 m, high desert with *Artemisia* and bunchgrass, large dry lakebed with fine soils, on grass stubble and soil, 25 June 2013, *D. Stone 9239* (same as type locality). **Washington**: Benton Co., Horse Heaven Hills, across gully from Dennis Road, tributary to Webber Canyon, 46.21437°N 119.43587°W, 286 m, on caliche fragments, 9 June 2019, *McCune 38137*.

Comments. This species appears more like a soil-dwelling version of a typical crustose *Aspicila* than *A. reptans*. It is sister to a clade containing *A. reptans* and some pruinose calciphilic saxicolous species (*A. calcarea* and *A. contorta*).

Thin sections of the thallus are unique anatomically in having a very thin eucortex, only about 2–3 cells and typically 10–17 µm thick, but difficult to measure because it is indistinctly delimited from the algal layer. In contrast, all other species keyed here have a relatively thick and well-defined eucortex. In *Aspicilia diploschistiformis* the eucortex is usually thinner than the epicortex and the algal layer and is relatively even. Development of the epicortex is highly variable, but POL+ crystals are always present, contrasting with the POL– eucortex.

Characterizing the surface texture of the thallus is difficult, because of its variability. Although typical specimens have an epruinose subglossy pale gray, pale brownish, or pale olive gray surface, some specimens have a chalky-white appearance. The thallus does not, however, have the distinct white-pruinose patches of many other species, such as *A. papilliformis*. The apothecial disk is, however, distinctly pruinose, and the developing apothecia have a whitish scabrid appearance similar to pruina.

The type locality is the larger unit of Hawksie-Walksie Research Natural Area under jurisdiction of the Lakeview District of the Bureau of Land Management. This area has unusually high diversity of lichens and bryophytes in the soil crust, including the specific habitat for the type locality, an old lakebed (Stone & Hamill 2014).

Aspicilia filiformis Rosentr., Lichenographica Thomsoniana, North American Lichenology in Honor of John W. Thomson (Ithaca): 166 (1998). **Fig. 16**

Type: U.S.A. Oregon: Jefferson Co., The Island, 20 km northwest of Redmond, 730 m, with *Artemisia tridentata* subsp. *wyomingensis,* on soil, 28 March 1990, *Rosentreter 6521* (holotype, WIS; isotypes, ASU, BRY, CANL, COLO, OSU, SRP).

Brief Description. Thallus and apothecial morphology and anatomy similar to *A. californica*. Thallus fruticose, decumbent, pale olive brown to dark olive brown or grayish, often mottled whitish; epruinose; branches mostly 0.1–0.3 mm diameter, subcylindrical to irregular, internode length to about 2 mm; pseudocyphellae lacking; epicortex POL+ or POL–, 5–13 µm thick; eucortex fairly even in thickness, about 17–21 µm, POL–; algal layer type 0 or 1, with occasional narrow intrusions from cortex.

Apothecia occasional, initially erumpent, becoming adnate, lecanorine, the rim colored like the thallus; disk brown to black, whitish pruinose or bare, to 0.8 mm in diameter; exciple POL+, otherwise apothecial section POL–; amphithecial epicortex weakly POL+; parathecium dark olive brown at upper edge, hyaline within, POL–; epihymenium brown, POL–; paraphyses submoniliform; hypothecium hyaline; ascospores 16–21 × 10–13 µm, 6–8 per ascus; pycnidia infrequent, blackish, emergent; spermatia narrowly rod shaped, short-filiform, 11–12(15) × 0.8–0.9 µm.

***Chemistry*.** TLC: nil. Spot tests negative.

***Ecology and substrate*.** On noncalcareous soil and plant detritus, often attached to small pebbles, low to mid elevations, in a variety of steppe habitats, including grasslands and shrub steppe, rarely in dry alpine (2870 m in Pioneer Mountains, Montana).

***Distribution*.** California to B.C., inland to central Montana and Colorado, but most abundant on the

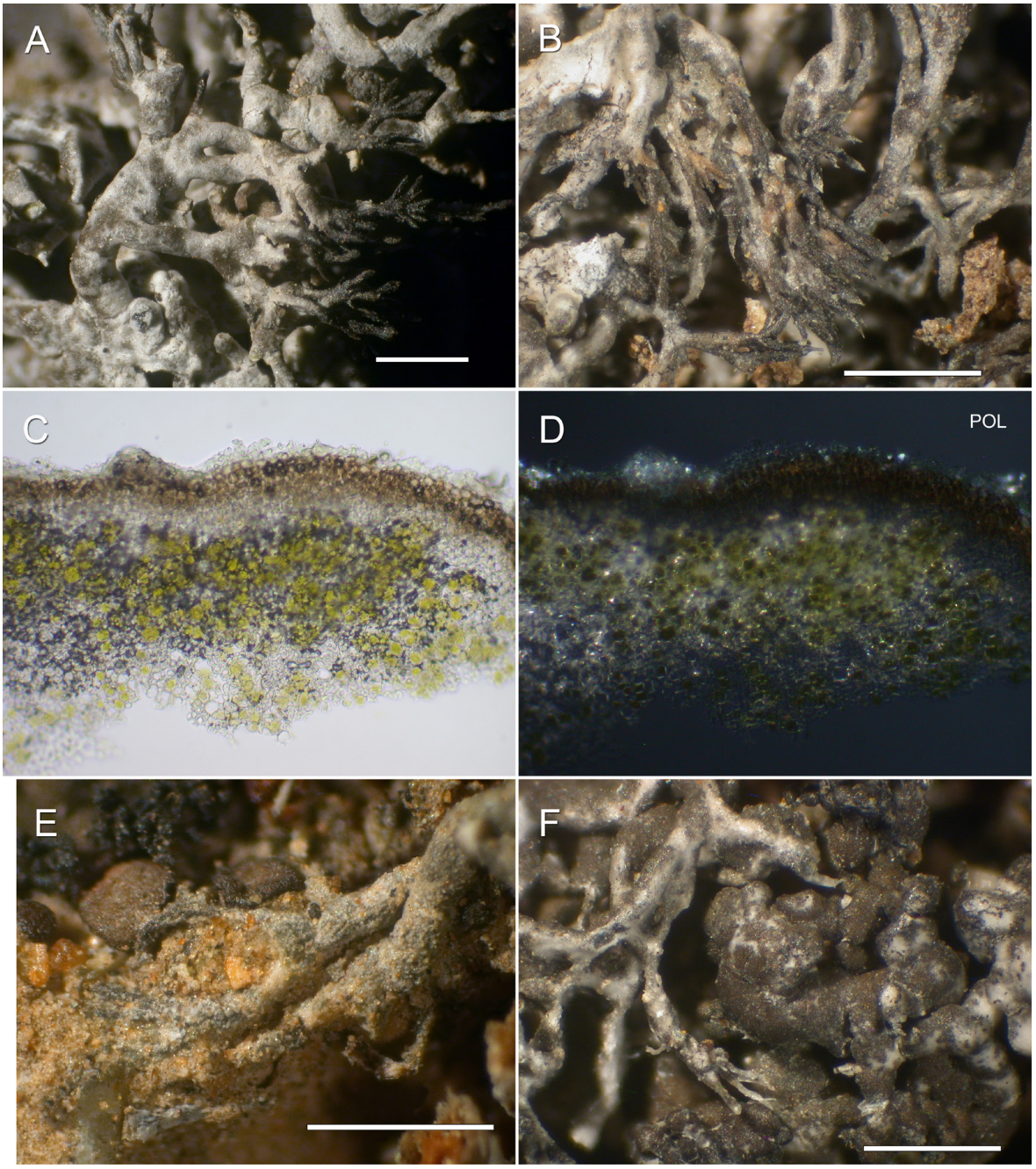

Figure 16. ***Aspicilia filiformis***. — **A.** Habit, *Di Meglio 202*. — **B.** Lobe tips free from substrate, *Rosentreter 15683*. — **C.** Thallus section, *Rosentreter 15683*. — **D.** Thallus section in polarized light, *Rosentreter 15683*. — **E.** Lobe tips appressed to substrate, *Di Meglio 202*. — **F.** Transition from crustose to fruticose thallus, *Rosentreter 15683*.

Columbia Plateau and Snake River Plain.

Selected specimens examined. U.S.A. **California**: San Luis Obispo Co., west from Taft on Highway 166 to Cable Corral Road, Forest Route 30S02, 35.1289°N 120.1156°W, 599 m, near exposed rock bluffs, on soil with detritus over rock, 25 September 2013, *Di Meglio 202, 205*. **Idaho**: Ada Co., Military Reserve Park, near archery range, NE part of Boise, *Purshia tridentata – Poa sandbergii*, overrun with *Bromus tectorum* and *Sitanion hystrix*, on soil, loamy sand, 8 June 1987, *Sharp 39c* (fertile, pycnidia); Red Tie site, 43.1811°N 116.0632°W, 953 m, June 2004, *Rosentreter 15683*; Elmore Co., 1.7 miles east on Old Highway 30 from Simco Road exit on I-84, 43.3300°N 115.9232°W, 1011 m, Wyoming sagebrush and bunchgrass, on hard soil in slickspots, 15 November 2012, *Rosentreter 17552*. **Montana**: Beaverhead Co., Pioneer Mountains, west slope Comet Mt., 45.46°N 113.03°W, 2870 m, alpine mats just above treeline, on soil and plant detritus, July 1993, *McCune 20950* (fertile; OSC, UPS, MONTU). **Oregon**: Deschutes Co., south of Highway 126 and east of Redmond Airport, *Juniperus – Artemisia* woodland, on soil, 44.2507°N 121.1132°W, 935 m, 22 April 2013, *McCune 32590*; Lake Co., Four Craters Wilderness Study Area near Christmas Valley, 43.36796°N 120.68763°W, 1368 m, low dry rangeland with bunchgrasses and *Juniperus* occidentalis, 2 September 2013, *Di Meglio 201*. **Washington**: Benton Co., Horse Heaven Hills, southwest of Benton City, 46.26038°N 119.5725°W, 259 m, flat bench with *Artemisia tridentata*, *Pseudoroegneria spicata*, and *Poa secunda*, 6 November 1998, *Ponzetti 1103* (fertile); Horse Heaven Hills, 0.5 km N of Chandler Butte, 46.25081°N 119.56339°W, 564 m, grassland, lithosol with *Poa secunda*, on soil and plant detritus, 8 June 2019, *McCune 38121*; Richland suburban fringe between the end of Evanslee Court and I-182, 46.24785°N 119.33042°W, 205 m, gentle slope with old *Artemisia tridentata* ssp. *tridentata*, 3 April 2015, *Di Meglio 256, 257, McCune 35795*; Klickitat Co., Cleveland Shrub Steppe Natural Area Preserve, stony flats with soil mounds, grassland (bunchgrasses and especially *Poa secunda*) with widely scattered *Pinus ponderosa*, 45.95816°N 120.3692°W, 945 m, 18 May 2019, *McCune 38086.*

Numerous additional specimens were cited by Rosentreter (1998).

Comments. Separation of *Aspicilia filiformis* and *A. californica* was not supported by either the combined ITS+nuLSU tree (**Fig. 7**) or the ITS tree alone (**Fig. A2-1)**. See further discussion under *A. californica*.

Aspicilia glaucopsina (Nyl.) Hue, Nouv. Arch. Mus. Hist. Nat., Paris, 5 sér. 2(1): 112 ([1910] 1912).

Basionym: *Lecanora glaucopsina* Nyl. in Hasse, Lichens of South California: 12 (1898).

Type: U.S.A. California: Santa Monica Range, Barton's Peak, *Hasse s.n.* (H-NYL).

Brief Description. Distinguished by an olive brown to gray green thallus, sometimes darkening to near black, continuous to areolate or squamulose thallus, epruinose, lacking aspicilin, long spermatia [14-24(26) × 0.8–1.0(1.3) µm according to Owe-Larsson et al. (2007)], and occurrence on soil, moss, *Selaginella*, or crumbling rock. The species is known fertile with 1–2(5) apothecia per areole and mostly 0.2–0.6 mm diameter, with a thalline margin that is concolorous with the thallus or whitish, and with spores 6-8 per ascus and (16)18–22(24) × 10–14(15) µm. The paraphyses are moniliform to submoniliform, with a green to olive or olive brown POL+ or POL– epihymenium. The species has been reported only from extreme southern California and Channel Islands (Owe-Larsson et al. 2007; see color photo; Knudsen 2007).

Comments. Two specimens from Riverside Co., California, have been sequenced by Owe-Larsson (*Knudsen 243*, *Owe-Larson 0906*). We have not studied this material, but it is currently under revision by Owe-Larsson and others. The type locality of "Barton's Peak" is unknown (Knudsen et al. 2008).

Aspicilia hispida Mereschk., Excurs. Lichénolog. Stepp. Kirghis.: 35 (1911). **Fig. 17**

Type: [RUSSIA], "ad terram argilloso-calcaream montis Bogdo prope lacu Baskuntschak in gub Astrachan," 50–120 m, 1910, *Mereschkowsky*, in Mereschkowsky, Lich. Ross. Exs. No. 34 (lectotype, designated by Sohrabi & Ahti (2010: 633), TU; isolectotypes, LE L1988, W).

Agrestia hispida (Mereschk.) J. W. Thomson in Hale, How To Know the Lichens: 182 (1969); comb. inval. according to Sohrabi & Ahti (2010); *Circinaria hispida* (Mereschk.) A. Nordin, Savić & Tibell, Mycologia 102(6): 1346 (2010).

Brief Description. Thallus mostly 1–4 cm diameter, olive, brownish, or bluish olive, suberect to erect fruticose, rarely with crustose parts; epruinose; branching irregular to dichotomous; branches mostly 0.3–1.0(1.5) mm diameter, short to elongate, tapered, with spiky tips, often delicate and easily fragmenting, not tipped with pseudocyphellae, which are instead scattered and lateral, conspicuous, white, roundish, flat to raised; epicortex 2–10 µm thick; eucortex hyaline, POL–, 25–60 µm thick, paraplectenchymatous, exclusive of elongate cells protruding into the algal layer; algal layer type 2, strongly lobate; central strand differentiated, prosoplectenchymatous, ropy, the cells elongate on the long axis of the branch, partly without crystals, partly with scattered POL+ clumps of crystals.

Apothecia rare, initially embedded in the branches, then erumpent, finally broadly sessile, aspicilioid to lecanorine, to 1 mm or more in diameter; disk dark but white-pruinose; amphithecium colored like the thallus but with a whitish excipular ring adjacent to the disk. Pycnidia and spermatia not seen.

***Chemistry*.** TLC: nil. Spot tests negative.

***Ecology and substrate*.** On calcareous soil in grasslands, shrub steppe, and open semi-arid woodlands at low to mid elevations.

***Distribution*.** Widespread, in North America from western Canada to Arizona, New Mexico, and California, but not west of the Cascade-Sierra axis; also in Eurasia and North Africa.

Comments. See additional illustrations in McCune and Geiser (2009: 28) and McCune and Rosentreter (2007: 53).

***Selected specimens examined*.** CANADA. **Saskatchewan**: Webb National Wildlife Area, 2 km NE of Webb, 50.19775°N 108.1501°W, 775 m, 11 August 2015, *Di Meglio 272*. U.S.A. **Colorado**: Grand Co., E side of Highway 40 N of Kremmling, 40.17284°N 106.4234°W, 2314 m, 12 August 2016, *Di Meglio 304, 306, 308, 310*. **Idaho**: Lemhi Co., Near O'Brien Gulch Road adjacent to Birch Creek, Lemhi Valley, 44.23445°N 112.9571°W, 1951 m, 16 August 2016, *Di Meglio 307*; Sinkhole Alley, 13 miles SE of Salmon, Idaho, near Kadletz Creek S of the road, 45.065°N 113.710°W, 1372 m, bentonite clay barrens, on soil, *Rosentreter 4518* (SRP, WIS). **Montana**: Stillwater Co., rest area near Columbus on I-90, 45.60114°N 109.0654°W, on grassy hill, 19 September 2014, *McCune 35793* (fertile). **Oregon**: Klamath Co., Gerber Reservoir Road, 1 mile from Gerber Reservoir, 42.20667°N 121.1443°W, 1507 m, *Di Meglio 268*. **Wyoming**: Big Horn Co., Kane Deer BLM exclosure, 24 km E of Lovell, 44.88917°N 108.0972°W, 1431 m, 15 May 2013, *Perry 516*.

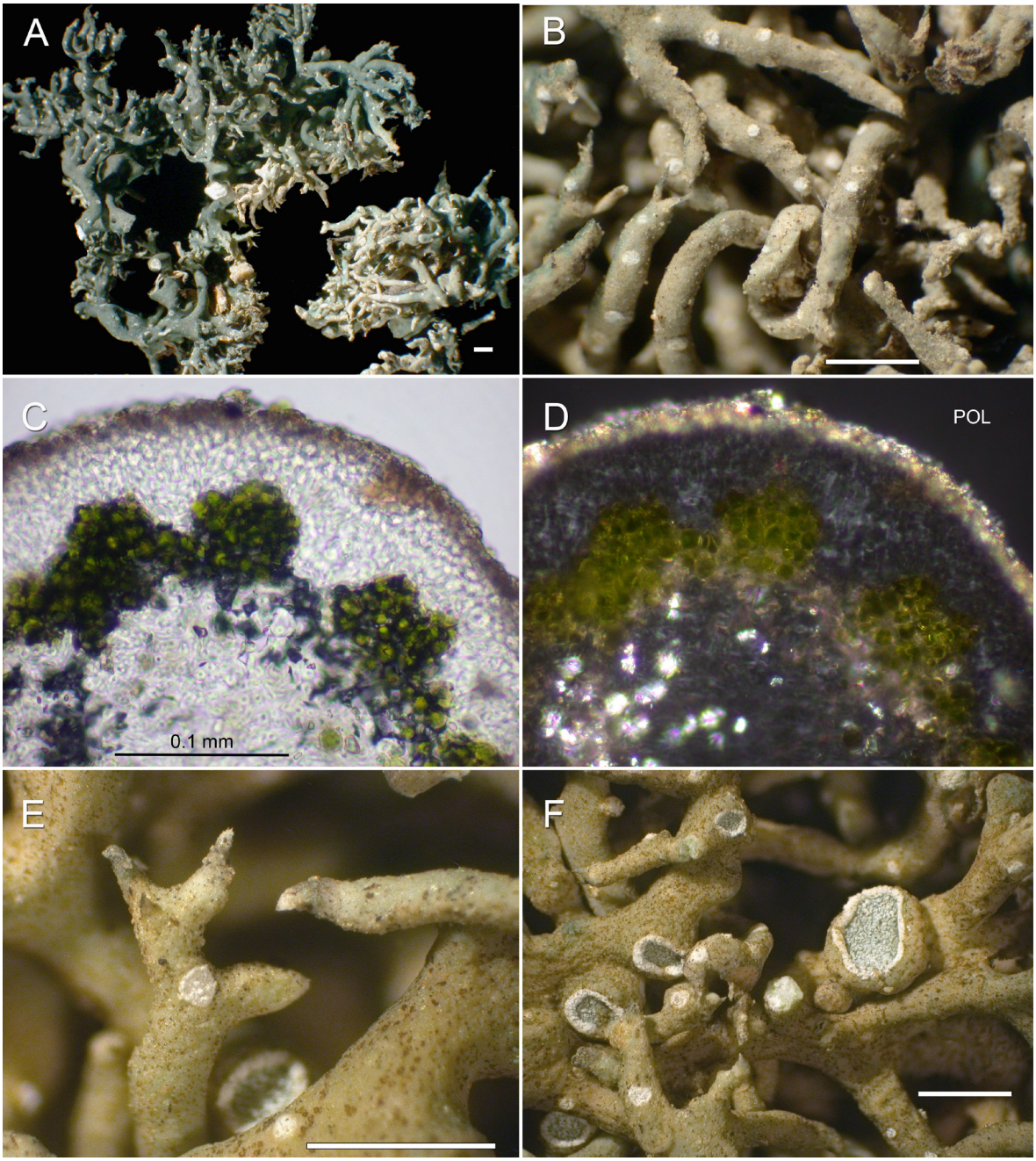

Figure 17. ***Aspicilia hispida***. — **A.** Habit, *Rosentreter 4518*. — **B.** Branches, *Rosentreter 4518*. — **C.** Thallus section, *McCune 35793*. — **D.** Thallus section in polarized light, *McCune 35793*. — **E.** Branch tips, *McCune 35793*. — **F.** Apothecia, *McCune 35793*.

Aspicilia papilliformis McCune & J. Di Meglio *sp. nov*. **Fig. 18**

MycoBank: MB839770 Barcode: MZ536763

Diagnosis. Thallus becoming bullate-areolate or papillate from a subcontinuous base, usually pruinose in patches or continuously so, bluish gray; apothecia sessile, with a proper margin, lacking thalline margin; spores 17–19(30) × 11–13 µm; on noncalcareous soil.

Type: U.S.A. **Washington**: Klickitat Co., Margerum Ranch above Klickitat, 45.8029°N 121.1575°W, 540 m, *Poa bulbosa* grassland and *Quercus garryana* savanna, on soil over rock (basalt), 20 May 2016, *McCune 36744* (fertile; holotype, OSC; isotype, UPS).

Description. Thallus often large, to over 10 cm diameter; field color bluish gray, the typical hand lens appearance of a dense mass of pruinose papillae; vertical swellings narrow (mostly 0.2–0.5 mm broad), high convex to papilla-like, becoming vertically elongate; pruina in discrete white patches or continuously pruinose over the whole thallus, epruinose healthy (non-necrotic) parts dark olive to olive black, but often with whitish necrotic mottles contrasting strongly with the dark olive cortex; pseudocyphellae lacking, although small pruinose spots can superficially look like pseudocyphellae; epicortex 5–15 µm thick, POL+ in pruinose parts; eucortex distinct, paraplectenchymatous, 22–33(42) µm thick, POL–; algal layer type 2, interrupted, uneven, irregularly divided by intrusions from the cortex; rhizomorphs common, thick and peglike or slender stipelike or spicate, cream, tan, or blackish, to > 1 mm long.

Apothecia occasional, sessile, lecideine, with a prominent black or whitish pruinose rim rather than the usual thalline margin, to 1.2 mm in diameter, the margin circular or wavy; disk black, concave to slightly convex; exciple edge blackish green or dark brown, hyaline to very pale brownish within, I–, POL– at the surface; exciple radiate, with roundish lumina becoming more angular toward the surface, becoming folded and mixed with the hymenium, with a POL+ noncellular nongranular hyaline coating about 3–10 µm thick; medullary part of exciple POL+ with grayish granules, lacking algae or with algae just at the base; hymenium 110–150 µm tall, POL–, sometimes with widely scattered POL+ flecks, otherwise not inspersed; epihymenium blue green or blackish green, not granular, K– or intensifying blue green; paraphyses submoniliform to moniliform near tips, more moniliform in K; hypothecium inspersed with oil droplets, hyaline to grayish; apothecial section K–; ascospores 17–25(30) × 11–16 µm.

Pycnidia with black tops that emerge slightly from the tops of the areoles; spermatia narrowly rod shaped, 10.4–14.5 × 0.6–0.8 µm.

***Chemistry*.** TLC: nil. Spot tests negative except thallus sometimes UV+ weakly yellowish.

***Ecology and substrate*.** On noncalcareous soil and plant detritus and those substrates over rock, or on crumbling rock, in grasslands and shrub steppe at low elevations.

***Distribution*.** So far known from the Columbia Basin of Washington, Oregon, and Idaho, with one outlying location in northern California. *Aspicilia papilliformis* is fairly common in central Washington to central Oregon and quite easy to find in the Horse Heaven Hills of south-central Washington.

***Etymology*.** The epithet "*papilliformis*" refers to the papillate thallus of this species, which is distinctive in comparison to other soil-dwelling *Aspicilia* in western North America.

***Specimens examined*.** U.S.A. **California**: Siskiyou Co., Sarah Totten Campground on Klamath River near old mine workings, *Pinus-Arctostaphylos* woodland, 41.68620°N 123.05109°W, 462 m, on friable schistose rock, 24 March 2018, *McCune 37575*. **Idaho**: Ada Co., Orchard Training Area, S of Bigfoot Butte, 43.18806°N 116.21573°W, 951 m, 11 April 2014, *Rosentreter 18338*. **Oregon**: Deschutes Co., below Steamboat Rock N of Redmond, 44.37175°N 121.27153°W, 813 m, 10 May 2020, *McCune 38728* (fertile); Grant Co., above John Day River and Lone Pine Campground E of Kimberly, 42.5028°N 119.6904°W, 625 m, June 2014, *McCune 34821*; Wasco Co., above John Day River, near badlands, 44.95075°N 120.49004°W, 398 m, May 2010, *McCune 30527*. **Washington**: Benton Co., Horse Heaven Hills, *Ponzetti 876, 877, 896*, *1221*, *1279*, *McCune 23925, 38113*; Douglas Co., Rock Island Grade Wildflower Area, 47° 22.167′N 120°

4.664′W, 530 m, 20 September 2013, *Rosentreter 17854*; N of Jameson Lake and S of Grimes Lake, N-facing slope in steep canyon, 47.72024°N 119.58884°W, 600 m, 21 September 2013, *Ponzetti GLNE-1*; Klickitat Co., Margerum Ranch, 45.8029°N 121.1575°W, 540 m, 20 May 2016, *McCune 36744* (fertile); Cleveland Shrub Steppe Natural Area Preserve, 45.95816°N 120.36925°W, 945 m, 18 May 2018, *McCune 38084, 38088* (fertile); Whitman Co., Wawawai Park above Snake River, 46.6390°N 117.3773°W, 265 m, 29 March 2019, *McCune 38052*; Yakima Co., W slope above orchard, BLM land, 46.52617°N 120.4123°W, 425 m, 14 May 2002, *Ponzetti 1597* (fertile).

Comments. This species is most closely related to *Aspicilia filiformis* and *A. subcontinua*, but is quite different in appearance from those. Indeed, it is one of the most easily recognized species in this group. In general *A. papilliformis* can be recognized in the field by the combination of bluish gray pruinose thallus, contrasting with cream-colored associates like *Diploschistes muscorum*, and areoles soon becoming bullate to papillose. If you are lucky enough to find the lecideine apothecia, this clinches the field determination. The species was previously referred to as "*Aspicilia* sp. (undescribed)" on p. 44 of McCune (2017), citing specimens from Horse Heaven Hills, Washington. We now have seen several fertile specimens from south-central Washington and central Oregon.

One specimen (*McCune 37575*) fell within the *Aspicilia papilliformis* clade but is an outlier geographically and morphologically. The only site for this species in California, it occurred on soft, friable schistose rock and appears intermediate between strictly crustose and *A. reptans* growth forms.

Aspicilia praecrenata (Nyl.) Hue, Nouv. Arch. Mus. Hist. Nat., Paris, 5 sér. 2(1): 115 ([1910] 1912).

Basionym: *Lecanora praecrenata* Nyl. in Hasse, Lichens of South California, ed. 2: 12 (1898).

Type: U.S.A. California: Santa Monica Range, Barton's Peak, on disintegrated granite and clay, *Hasse s.n.* (H-NYL 25559).

Brief Description. According to Owe-Larsson et al. (2007), the species is distinguished by a light buff to brownish areolate to squamulose thallus, epruinose (except for apothecial disk), presence of aspicilin, short spermatia [7–11(12) × 0.6–0.8(1.0) µm], and occurrence on noncalcareous soil and crumbling granite. The species is usually fertile, with 1–2(5) apothecia per areole, the apothecia mostly 0.3–0.9 mm diameter, aspicilioid, with a crenulate, white thalline margin, and spores 3–6 per ascus and (16)18–23(27) × 15–21 µm. The paraphyses are submoniliform, with an olive to olive brown or brown POL+ epihymenium. In North America, the species has been reported only from extreme southern California and Channel Islands (Owe-Larsson et al. 2007; see color photo). It also has been reported from South Australia by Kantvilas (2019).

Comments. More recent molecular study and revision by Owe-Larsson and colleagues is likely to modify this description. An unpublished ITS tree appeared sister to *A. diploschistiformis*. We have not studied this material.

The type location, "Barton's Peak", is apparently obscure (Knudsen et al. 2008).

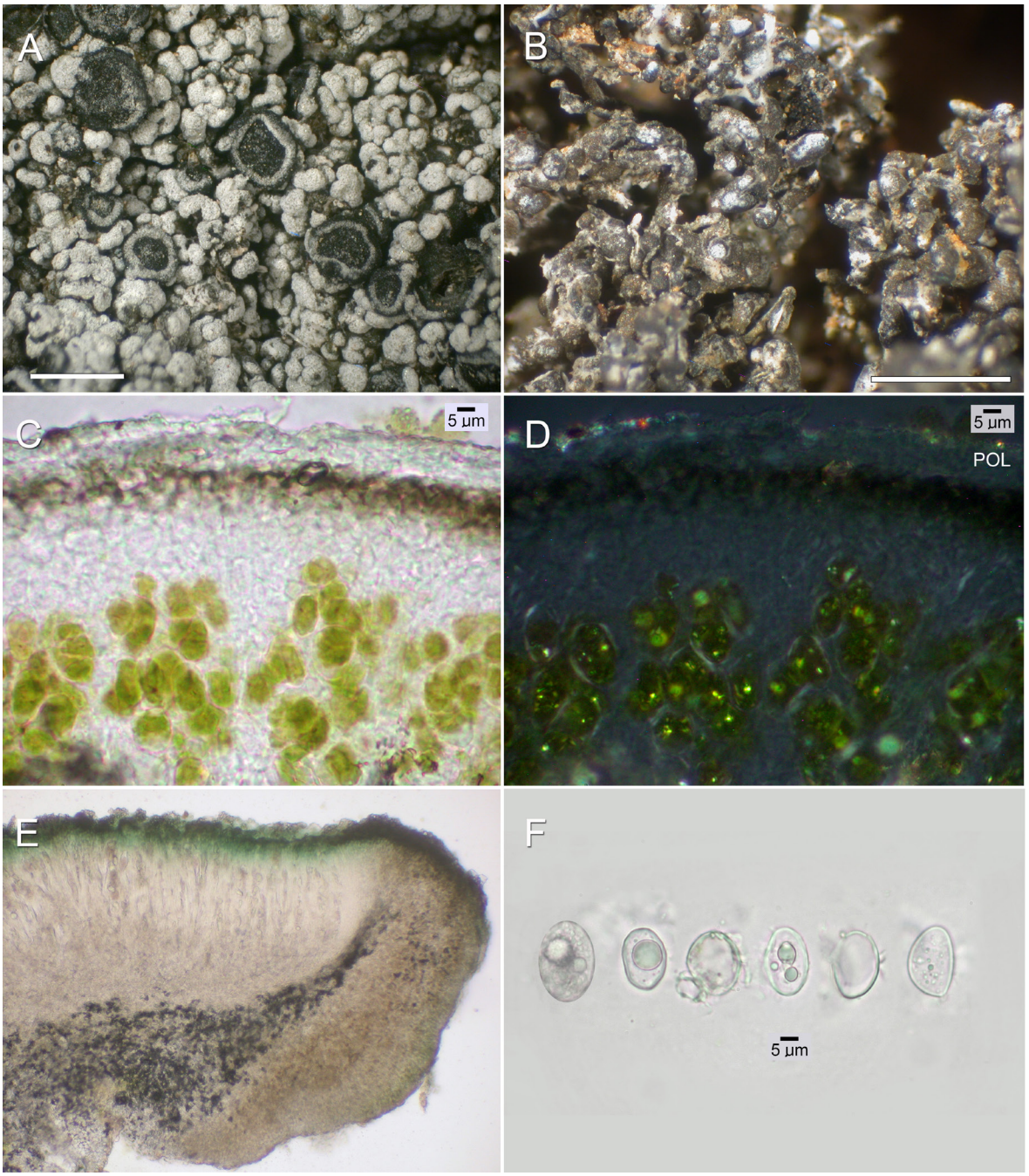

Figure 18. ***Aspicilia papilliformis***. — **A.** Habit, *McCune 38728*. **B.** Areoles and lobes, *McCune 34821*. **C— .** Thallus section, *McCune 34821*. — **D.** Thallus section in polarized light, *McCune 34821*. — **E.** Apothecial section, *McCune 38728*. — **F.** Ascospores, *McCune 38728*.

Aspicilia reptans (Looman) Wetmore, Mycotaxon 23: 243 (1985). **Fig. 19**

Basionym: *Lecanora reptans* Looman, Bryologist 65: 301 (1963).

Type: CANADA. Saskatchewan: Webb, near Swift Current, on soil in eroded grassland, elevation 2600 feet, 12 April 1959, *Looman 596114* (holotype, WIS!).

Aspicilia mansourii Sohrabi, Phytotaxa 18: 17 (2011); *Circinaria mansourii* (Sohrabi) Sohrabi, Lichenologist 45: 358 (2013).

Description. Thallus in small patches, most collections < 3 cm diameter, warty to beaded-lobate, usually with elongate lobes that are roundish in section or slightly compressed vertically, often anastomosing into a lumpy crust; vertical swellings coarsely warty or beaded, mostly 0.5–1.5 mm broad; pruina usually lacking, sometimes present in patches, but upper surface often with extensive whitish or grayish necrotic areas that are dull and resemble pruina; upper surface pale olive gray, bluish gray, pale olive tan, or grayish tan, sometimes with a distinct pale blue green-gray tone; pseudocyphellae present, appearing as whitish spots, often slightly raised, roundish, angular, or elongate; epicortex (0)2–13(15) µm thick, POL– throughout or more often with a thin superficial POL+ layer; eucortex distinct, paraplectenchymatous, (12)15–32(42) µm thick, POL–, often brownish in the upper part, otherwise hyaline; algal layer type 1, fairly even but with narrow intrusions 1–2 cells wide from the cortex or with more broadly triangular intrusions; rhizomorphs present but often inconspicuous, whitish or beige, produced at various places, in some cases extending from lobe tips to the substrate; medulla distinctly POL+.

Apothecia rare (but note that the type specimen is fertile), initially aspicilioid, becoming broadly adnate, with a thalline margin colored like the thallus or partially whitish; disk black, to 0.8 mm in diameter; to preserve the type we made no apothecial sections, so the following is based on Looman (1962): hymenium about 100 µm tall; epihymenium dark brownish, HCl+ green; paraphyses 2–3 µm broad, the upper cells moniliform and slightly expanded but not capitate; hypothecium hyaline; asci clavate; ascospores reportedly 2 per ascus and subspherical, about 10 µm diameter. However, unsigned notes with the specimen indicate spores 7.5–13 × 5–11 µm. Based on our observations in other *Aspicilia* species, these probably do not represent well developed asci and spores; apothecial section K–.

Pycnidia infrequent, forming thallus-colored bulges or irregular blackish eruptions, sometimes whitish pruinose, becoming compound, in section sometimes covered with dark brown or olive brown cells around the ostiole, but otherwise pycnidial wall hyaline and POL– throughout; spermatia narrowly rod shaped or short-filiform, 6.5–9.6 × 0.6–1.1 µm.

***Chemistry*.** TLC: aspicilin. Spot tests negative.

***Ecology and substrate*.** On calcareous soil and plant detritus and those substrates over rock, grasslands and shrub steppe at low elevations. Associates include *Cladonia pocillum*, the *Collema tenax* group, *Phaeophyscia constipata*, *Phaeorrhiza nimbosa*, *Physconia muscigena, Psora montana*, and *Xanthoparmelia camtschadalis*.

***Distribution*.** North America and Iran. In North America from the northern Great Plains and Rocky Mountains, from Saskatchewan south at least to Colorado and New Mexico, mainly east of the Continental Divide with scattered records to the west, including eastern Washington. In Iran from East Azerbaijan and Golestan Provinces.

***Etymology*.** We presume that the epithet "*reptans*" refers to the creeping lobes of the thallus.

***Specimens examined*.** CANADA. **British Columbia**: east from Cache Creek on Highway 1, Juniper Beach Provincial Park access road, 50.78745°N 108.07416°W, 425 m, open *Artemisia* steppe on SE slope towards Thompson River, with *Artemisia tridentata* subsp. *tridentata*, on fine silty soil, 8 July 2016, *Di Meglio 295*. **Saskatchewan**: North of Webb, 2 km on road 623 off Highway 1, 50.227831°N 108.21015°W, 765 m, 12 August 2015, *Di Meglio 261*; East of Webb, National Wildlife Area, 50.20609°N 108.12214°W, 751 m, prairie with glacial till and calcareous soil with limestone and granite gravel, 12 August 2015, *Di Meglio 263*; 50.19775°N, 108.15007°W, 775 m, road cut with native flora, fine grayish white calcareous

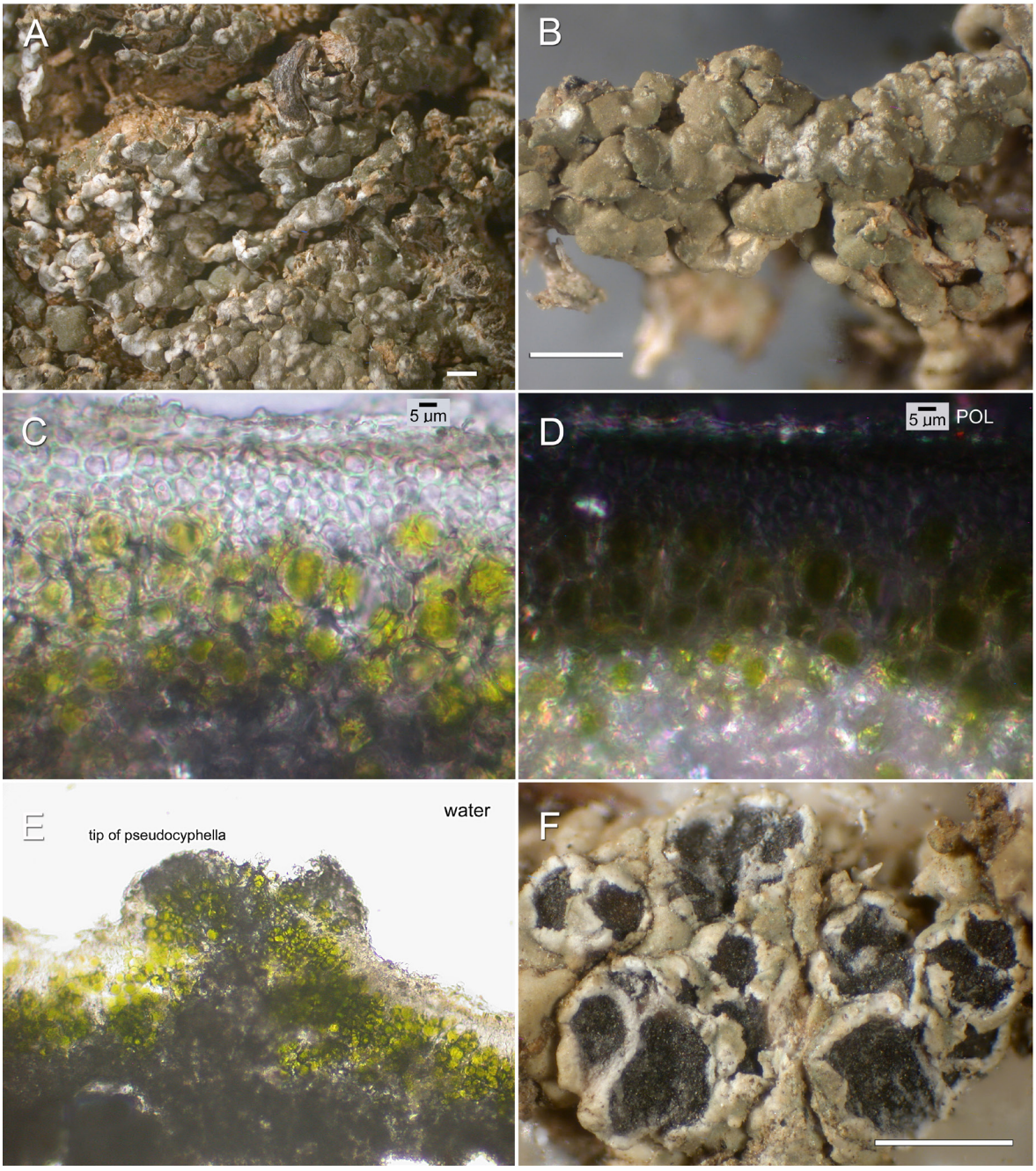

Figure 19. ***Aspicilia reptans***. — **A.** Habit, *Di Meglio 487*. **B.** Habit, *Di Meglio 262*. **C.** Thallus section, *Di Meglio 262*. — **D.** Thallus section in polarized light, *Di Meglio 262*. — **E.** Pseudocyphella in section, *Di Meglio 263*. — **F.** Apothecia, *Looman 596114* (type).

silty soil, 11 August 2015, *Di Meglio 262*; 70 mile Butte Trail, SE of Val Marie off of Highway 4, 49.20291°N 107.66294°W, 841 m, calcareous soil with coarse to fine gray shale and gypsum gravel, 10 August 2015, *Di Meglio 264*. U.S.A. **Colorado**: Larimer Co., 40.84118°N 105.33581°W, 1922 m, NW on Highway 287 from Livermore, on red mineral soil adjacent to sandstone cliffs, 5 April 2016, *Di Meglio 285*; 1979 m, *Di Meglio 287*. **Idaho**: Ada Co., Military Reserve Park just north of Boise, 792 m, on loamy silica sand, 23 April 1990, *Rosentreter 6685* (SRP). **Montana**: Chouteau Co., Highway 87, 48.02051°N 110.46015°W, 893 m, on soil, 13 August 2015, *Di Meglio 265*; McCone Co., just beyond south end of Fort Peck Dam, 46.56731°N 108.43480°W, 732 m, gravelly hill with small *Artemisia tridentata* and *Agropyron spicatum*, with calciphiles, on soil, August 2014, *McCune 35788*; Musselshell Co., Milton Ranch, flats south of ranch buildings, 48.0100°N 106.3888°W, 1070 m, infrequent in *Agropyron cristatum* plantings in prairie, 14 September 2016, *McCune 37157*. **New Mexico**: Taos Co., west side of Highway 86 SW from Taos, 36.32230°N 105.70528°W, 2135 m, high desert with *Pinus edulis, Opuntia*, and *Artemisia*, on soil, with *Xanthoparmelia wyomingica*, 22 September 2019, *Di Meglio 487*. **Oregon**: Deschutes Co., off of Dove Drive near Terrebonne, fringe of Crooked River National Grassland, 44.39705°N 121.2858°W, 842 m, *Juniperus occidentalis* - bunchgrass, undisturbed, 14 November 2016, *Di Meglio 275*; Lake Co., Four Craters Wilderness Study Area near Christmas Valley, 43.36796°N 120.68763°W, 1368 m, low bunchgrass with *Juniperus occidentalis*, 2 September 2013, *Di Meglio 203*. **Washington**: Adams Co., directly off Highway 26 on road berm, near fence line and in front of large basalt outcrop, 46.77192°N 118.11424°W, 340 m, 17 August 2015, *Di Meglio 270*.

Comments. The typical hand lens appearance of *Aspicilia reptans* in the narrow sense is of irregularly beaded-stringy, prostrate, anastomosing lobes. The color is quite variable, often similar to the substrate, with subtle tan, olive, bluish green, and gray tones. Although the upper surface lacks distinct pruina, one could be misled by whitish necrotic patches. Thin sections are distinguished by the bright POL+ medulla, while most *Aspicilia reptans* group species have a weak, murky POL+ medulla.

The description, illustrations, and ITS sequences of *A. mansourii* described from Iran fall within *A. reptans* s.str., thus we synonymize *A. mansourii* (*Circinaria mansourii*) under the earlier name *A. reptans*. Apparently *A. reptans* has not previously been reported from outside North America under that name. Sohrabi did not have the benefit of having DNA sequences from *A. reptans*, but briefly contrasted *A. mansourii* with *A. reptans*, stating that *A. reptans* lacked rhizomorphs and aspicilin (Lumbsch et al. 2011) . We found, however, that *A. reptans* frequently produces rhizomorphs and always produces aspicilin. The substrate and habitat described for *A. mansourii* are similar to those for *A. reptans*, both being calciphiles in open steppe.

Aspicilia rogeri Sohrabi, Bryologist 114(1): 182 (2011). **Fig. 20**

Type: U.S.A. Oregon: on calcareous soil in shrub steppe with *Artemisia*, *Rosentreter 16333* (holotype, SRP).

Circinaria rogeri (Sohrabi) Sohrabi, Mycol. Progr. 12(2): 265 (2012).

Brief description. Thallus fruticose, forming erect hemispherical to spherical cushions or knobby balls, dichotomously branched; epruinose; branches short, thick, terete, or subterete, about 0.5–1.5 mm diameter, erect, blunt, tipped with conspicuous white pseudocyphellae; epicortex 5–17 µm thick, weakly POL+; eucortex 30–50 µm thick, POL–; algal layer type 2, strongly lobate to discontinuous; central core of rather loose hydrophobic hyphae, POL+.

Apothecia rare, erumpent to broadly adnate, to 5 mm diameter, becoming compound, contorted, and folded, with a thick thalline margin; disk blackish, white-pruinose; algal layer in amphithecium strongly lobate; parathecium very thin; epihymenium olive black, with thin superficial POL+ layer; paraphyses moniliform near tips; hymenium about 130–140 µm; mature asci and spores not seen. Pycnidia developing beneath pseudocyphellae; spermatia 9.6–14.0 × 0.7–0.9 µm.

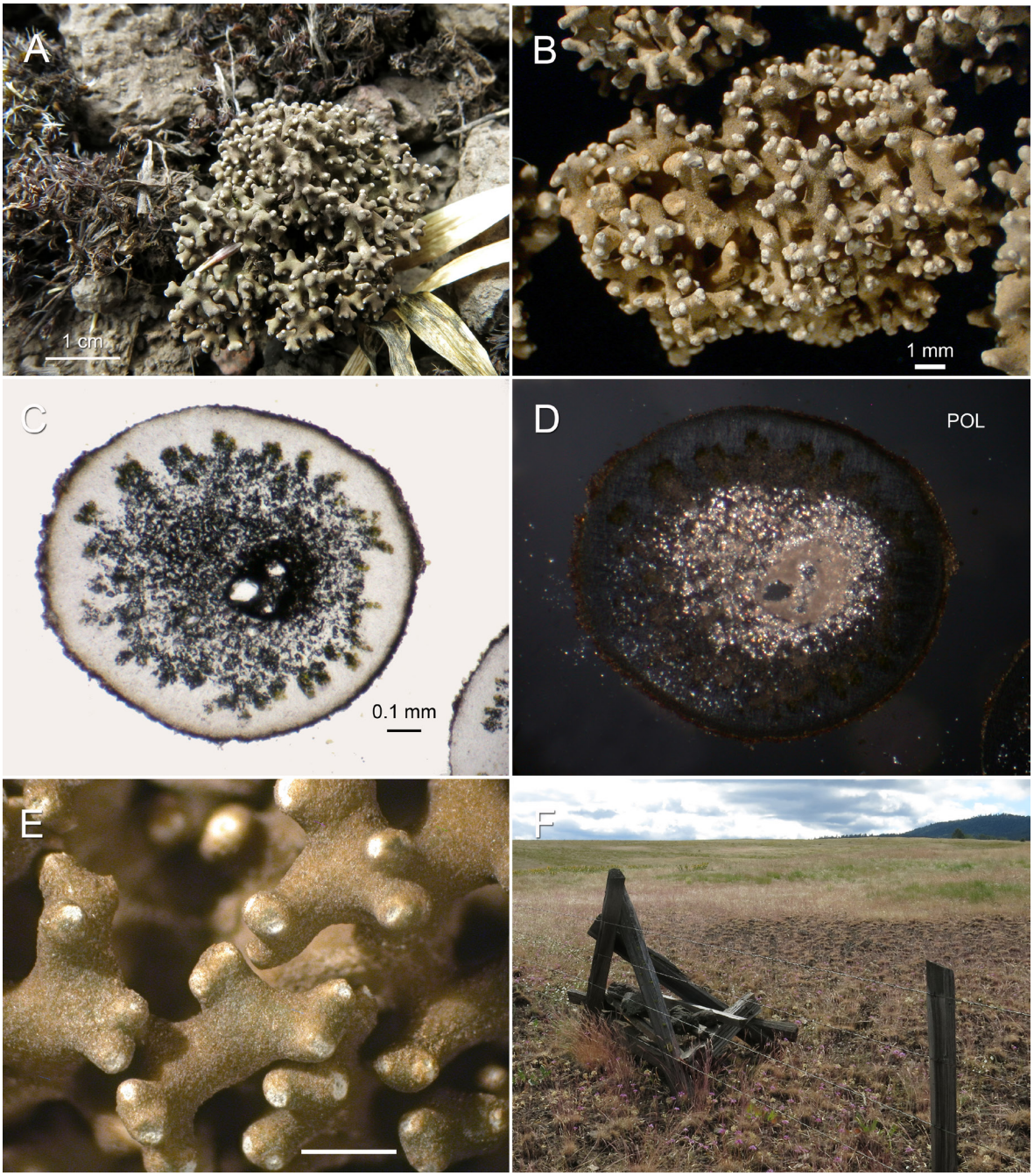

Figure 20. ***Aspicilia rogeri.*** — **A.** Habit, *McCune 34833*. — **B.** Habit, *Rosentreter 3516*. — **C.** Thallus section, *McCune 34833*. — **D.** Thallus section in polarized light, *McCune 34833*. — **E.** Branch tips, *McCune 34833*. — **F.** Habitat, *McCune 34833*.

***Chemistry*.** TLC: usually nil, sometimes with unknown fatty acid Rf A6–7 C6–7. Spot tests negative.

***Ecology and substrate*.** On calcareous soil, in grasslands, shrub steppe, and badlands at low elevations, rarely on rock.

***Distribution*.** In North America from eastern Oregon to Montana, south to Nevada, Utah, and Colorado.

Etymology. Named in honor of Roger Rosentreter, lichenologist and botanist from Idaho, U.S.A.

***Specimens examined*.** U.S.A. **Colorado**: Grand Co., E side of Highway 40 N of Kremmling, 40.17284°N 106.42339°W, 2314 m, with *Artemisia*, *Opuntia*, and native grasses, 11 August 2016, *Di Meglio 305*; Moffat Co., Massadona, E of Dinosaur National Monument, Divide Creek Wildlife Viewing Area, 1–2 miles S of Highway 40, UTM 12S E0706092 N4457590, rolling hilltop sparsely vegetated with *Artemisia tridentata*, 15 August 2011, *Scott Smith 0558*. **Idaho**: Caribou Co., near Border Summit, southeast of Montpelier, 1981 m, *Artemisia longiloba* habitat with calcareous siltstone soil, 7 August 1984, *Rosentreter 3516* (herb. McCune); Lemhi Co., Lemhi Valley, NE of Highway 28 on O'Brien Gulch Road, 44.2468°N 112.95703°W, 1996 m, with *Artemisia* and *Opuntia*, 16 August 2016, *Di Meglio 309*; SE of Salmon, south of the main highway, Kadletz Creek, 45.03738°N 113.69130°W, 1426 m, barren bentonite calcareous badlands, clay soil with some gravel, with Wyoming sagebrush and shadscale, 19 September 2012, *Rosentreter 17532* (SRP); Owyhee Co., flats on north side of canyon of North Fork Owyhee River near Juniper Mountain Road, 42.59599°N 116.99285°W, saxicolous on pebbles, 20 June 2019, *McCune 38174*. **Oregon**: Grant Co., W of town of Long Creek on Highway 402, 44.73695°N 112.21552°W, 1264 m, sparse bunchgrass with stony basalt soil, patterned ground, very gentle slope, June 2014, *McCune 34833*.

Comments. *Aspicilia rogeri* is the North American vicariad of the Eurasian *A. fruticulosa*, being morphologically similar but genetically distinct (Sohrabi et al. 2011b). Prior to 2011, North American material was included under *A. fruticulosa*. *Aspicilia rogeri* is a distinctive species that has been illustrated in various sources (McCune 2017, vol. 1, p. 179; McCune & Rosentreter 2007, p. 53; Brodo et al. 2001, p. 169, as *A. hispida*). In contrast to the compact, ropy prosoplectenchymatous POL– core of *A. californica* and *A. filiformis*, the central core of *A. rogeri* is of noncontiguous hyphae that are distinctly POL+.

Aspicilia rogeri has always been found on calcareous soil with one exception: coating small pebbles on a lithosol with poor drainage and sparse grasses (*McCune 38174*). In this case the thallus was not clearly fruticose, but more crustose with strongly swollen areoles that were tipped with pseudocyphellae. Some of these areoles were dividing dichotomously. Two of the four thalli were fertile. A population of normal *A. rogeri* was not seen at the site.

Although locally common in certain habitats, *Aspicilia rogeri* is rare enough to be a noteworthy find wherever it is encountered. It often co-occurs with *A. hispida*. However, the morphology of *A. rogeri* is singular, distinctive, and striking. It is surely one of the iconic lichens of the intermountain regions of western North America.

Aspicilia spicata McCune & J. Di Meglio *sp. nov*. **Fig. 21**

MycoBank: MB839766 Barcode: MZ536834

Diagnosis. Thallus beaded-lobate or stringy to reticulate-lobate or warty-areolate, producing short, dark spikes from lobe tips and warts, apothecia aspicilioid to lecanorine, ascospores 6–8 per ascus; spermatia 8–11 µm long; on noncalcareous soil and rock.

Type: U.S.A. **Washington**: Douglas Co., SSW of Grand Coulee, Steamboat Rock State Park, Northrup Canyon, 47.868581°N 119.05296°W, 600 m, undulating hilltop with *Artemisia tridentata* ssp*. wyomingensis, Pseudoroegneria spicata, Festuca idahoensis,* and *Bromus mollis*, on soil, overgrowing *Polytrichum piliferum*, 24 September 2013, *Hardman NC1–10* (holotype, osc).

Description. Thallus beaded-lobate, lobes branched to reticulate, sometimes with discrete areoles

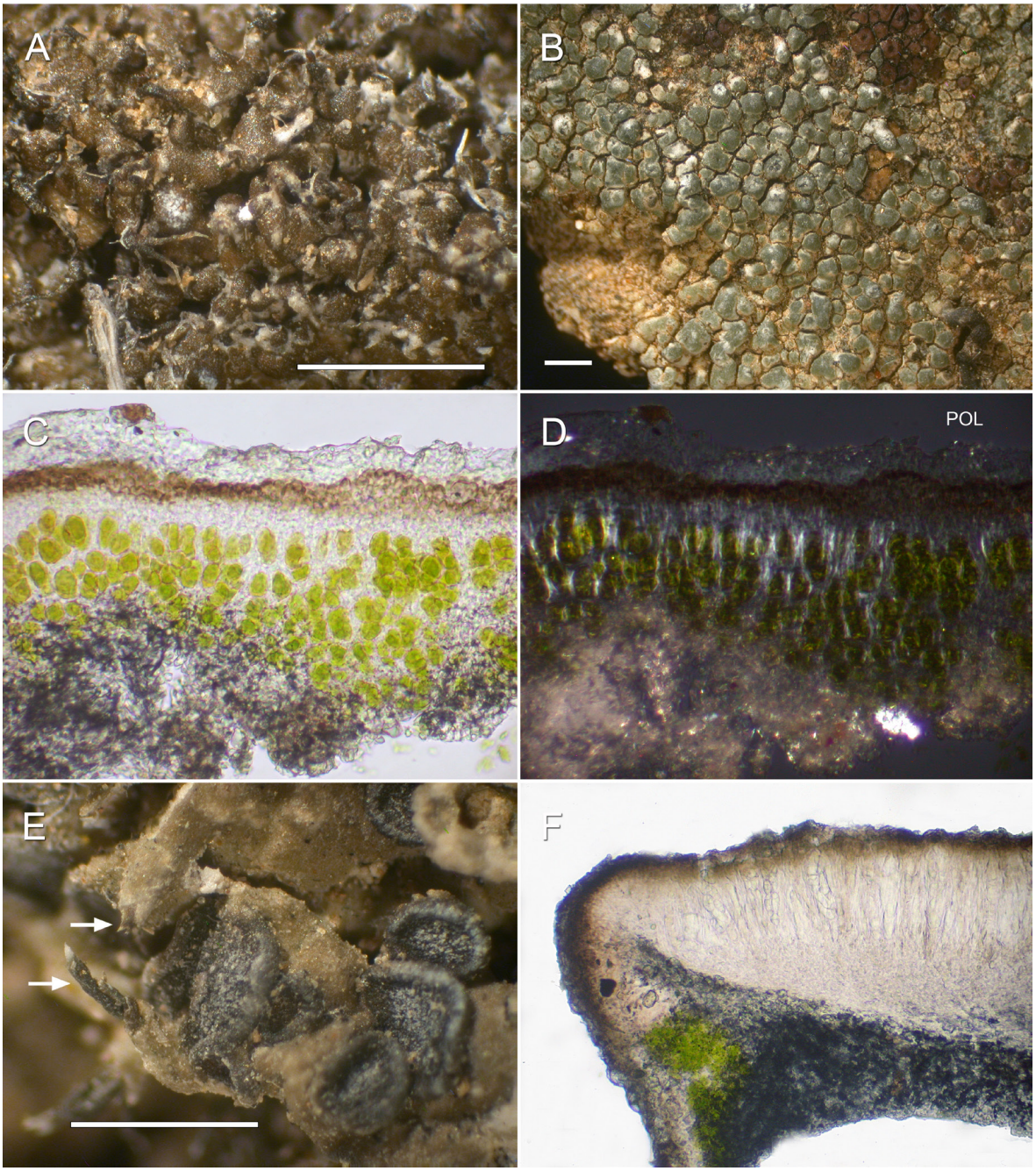

Figure 21. ***Aspicilia spicata***. — **A.** Habit with spicate lobe tips, *Hardman NC1–10* (holotype). — **B.** Habit of saxicolous specimen in *A. spicata* clade, *Di Meglio 255*. — **C.** Thallus section, *Hardman NC1–10*. — **D.** Thallus section in polarized light, *Hardman NC1–10*. — **E.** Spicate lobe tips and apothecia, *Root & Smith B1–15*. — **F.** Apothecial section, *Root & Smith B1–15*.

or warts on a white prothallus background, often with spicate tips on lobes or emerging from warts, the tips white, gray, black, or some gradient of these, often blackish with a white tip, simple or fasciculate, mostly 0.05–0.15 mm diameter; pruina variable, present in patches or diffuse or nearly lacking; epruinose parts of upper surface pale olive gray, brownish gray, olive brown, or brown, necrotic areas whitish; pseudocyphellae not apparent; epicortex (5)12–22(30) µm thick, usually weakly POL+, occasionally POL–, more intensely POL+ in pruinose areas; eucortex distinct, paraplectenchymatous, 22–37 µm thick, POL–, brown in the upper part, otherwise hyaline; algal layer type 1, even in thickness with scattered triangular or linear intrusions from the cortex; rhizomorphs pale, subtending thallus units and seeming to intergrade with the blackish spikes from lobe tips; medulla weakly POL+.

Apothecia infrequent, initially aspicilioid, becoming sessile and lecanorine, the rim concolorous with the thallus or somewhat darker or slightly white-pruinose in part; disk dark reddish brown to black, sometimes whitish pruinose, to 1.3 mm in diameter; parathecium distinct, much expanded at the surface, dark brown at the edge, grading to hyaline within, I– or yellowish, POL–, but medullary part of amphithecium I+ pale violet; algae present in base of amphithecium; hymenium 96–106 µm tall, POL–, I+ blue then greenish; epihymenium dark brown with olive tinge, POL–, K– (paling and slightly browner); paraphyses slender, 1–2 µm diameter at mid length (in water), some expanded at the tips to 5–8 µm, submoniliform; hypothecium hyaline, inspersed with POL– granules or oil drops, I+ blue; asci clavate, about 85–90 × 19–23 µm when mature; ascospores simple, broadly ellipsoid, 18–23 × 10–13 µm (median 20.3 × 10.7), 6–8 per ascus; pycnidia blackish, initially immersed but soon protruding as rough warts, in section compound, with a covering of dark brown cortical cells but otherwise the pycnidia hyaline; spermatia narrowly rod shaped or short-filiform, straight or slightly curved, 8.4–10.9 × 0.6–0.9 µm.

***Chemistry*.** TLC: nil. Spot tests negative.

***Ecology and substrate*.** On noncalcareous soil and plant detritus. Associates include *Artemisia tridentata* ssp. *wyomingensis*, *Chrysothamnus nauseosus*, and perennial bunchgrasses, including *Stipa comata* and *Pseudoroegneria spicata*.

***Distribution*.** Known from four collections, two of them fertile, three on the Columbia Plateau in east-central Washington, one from south-central Oregon.

***Etymology*.** The epithet "*spicata*" refers to the nonlichenized spikes produced from lobe tips and thalline warts.

***Specimens examined*.** U.S.A. **Oregon**: Klamath Co., off of Gerber Reservoir Road about 1 mile from the reservoir, 42°12′3.0″N 121°8′39.3″W, 1507 m, old lava flow dominated by *Artemisia, Pinus ponderosa,* and *Juniperus occidentalis*, on rock in silty soil with fine gravel and detritus, 28 March 2015, *Di Meglio 255*. **Washington**: Douglas Co., ESE of Jameson Lake, along Burton Draw, 47.684503°N 119.603642°W, 662 m, with *Artemisia tridentata* ssp*. wyomingensis, Chrysothamnus nauseosus, Stipa comata,* and *Agropyron spicatum*, on silty loam of moderate depth, 23 September 2013, *H. Root & R. Smith B1–15* (fertile); N of Badger Mountain, BLM land, 47.7164°N 119.5922°W, ungrazed habitat in somewhat sheltered pass, with *Artemisia tridentata* ssp*. tridentata, Stipa comata,* and *Pseudoroegneria spicata*, on soil, *Hardman et al. EGL1* (fertile).

Comments. This species appears intermediate in form between the fruticose *A. filiformis* and the stringy-beaded *A. reptans*. The high frequency of spicate prothalline tips in *A. spicata* reflects its close relationship with *A. filiformis* and *A. californica* (**Fig. 7**), two species in which those tips are particularly conspicuous. The clearly fruticose growth form of those species readily distinguishes them from the crustose-areolate to beaded-lobate thallus of *A. spicata*.

In cases where the spicate lobe tips are sparse and tiny, this species would be difficult to separate morphologically in the field from *A. reptans*. We can, however, use the information that *A. reptans* is a calciphile, while *A. spicata* is known from noncalcareous sites. The simplest way of assessing free calcium carbonates is by noting the other species occurring where samples were collected. McCune & Rosentreter (2007) provided a simple species-based indicator to score this; for example, *Psora decipiens*, *To-*

ninia sedifolia, and *Collema tenax* are very common and widespread strict calciphiles.

The one saxicolous specimen (*Di Meglio 255*) differs strikingly in appearance from the terricolous specimens. On rock this specimen has a thickly areolate thallus, in a few places becoming slightly three dimensional as the areoles thicken and become compound. As the thallus wraps around a pebble, the thallus becomes appressed-lobate, with narrow, branched lobes. Near the tips of the lobes the lichenized part is discontinuous, showing beads of thallus developing on appressed rhizomorphs.

As a type specimen we chose *Hardman NC1–10* because of its size, the two other terricolous specimens being rather small, yet fertile, and morphologically more similar to each other than to *NC1–10*. The spicate tips are rather sparse on the type specimen, but nevertheless present. It is, however sterile; nor did we find pycnidia on it. The fourth specimen is saxicolous and morphologically anomalous as described above.

Aspicilia subcontinua McCune & J. Di Meglio *sp. nov*. **Fig. 22**

MycoBank: MB839767 Barcode: MZ536836

Diagnosis. Thallus brownish olive to dark greenish gray, darker than most other *Aspicilia* species, becoming bullate-areolate or papillate from a subcontinuous base; on noncalcareous soil.

Type: U.S.A. **Montana**: Lewis and Clark Co., 6 miles northwest of Helena, 46.67276°N 112.10087°W, 1455 m, on soil and moss (*Polytrichum piliferum*) among quartzite boulders, 22 March 2017, *Wheeler 7421* (MONTU).

Description. Thallus in small patches, most collections < 3(10) cm diameter; field color brownish olive to dark greenish gray, the absence of pruina giving a darker color than most species in this group; thallus partly molded to the substrate, partly becoming bullate-areolate or warty or beaded-lobate, monolayered or imbricate; vertical swellings mostly 0.2–1.0 mm broad, warty to compound warty; pruina lacking, the upper surface brownish olive to dark greenish gray; pseudocyphellae sparse to abundant, white, roundish to ± elongate; epicortex (2)5–25(37) µm thick, POL+ in upper part, otherwise POL–; eucortex distinct, paraplectenchymatous, 12–37 µm thick, POL–, brownish in the upper part, otherwise hyaline; algal layer type 1, interrupted by conical intrusions from the cortex, the intrusions sometimes sparse; rhizomorphs present, sometimes exposed by erosion of the substrate and forming obvious stipes below the thallus units.

Mature apothecia not seen; upper hymenium of incipient apothecia olive brown to olive green; pycnidia and spermatia not seen.

***Chemistry*.** TLC: nil. Spot tests negative.

***Ecology and substrate*.** On moss over rock, noncalcareous soil, and plant detritus. *Wheeler 7421* was overgrowing the moss *Polytrichum piliferum* among quartzite boulders.

***Distribution*.** Central Washington east of the Cascades, south to California, inland to central Montana and the Snake River Plain of southern Idaho. Although widespread it appears to be relatively rare.

***Etymology*.** The epithet "*subcontinua*" refers to the relatively continuous thallus of this species, as compared to others in the *A. reptans* group in western North America.

Specimens examined*.** U.S.A. **California**: San Benito Co., 36°29′9″N 121°10′0″W, 337 m, on SW exposed hillside with *Selaginella* and *Aesculus californica*, on mineral soil with gravel, 17 December 2014, *Di Meglio 253*. **Idaho**: Ada Co., Orchard Training Area, Red Tie area, 43.30017°N 116.11750°W, 967 m, shrub steppe with *Artemisia tridentata* ssp. *wyomingensis* and *Poa secunda*, 8 April 2014, *Rosentreter 18307*; Owyhee Co., south edge of canyon of North Fork Owyhee River near Juniper Mountain Road, 42.59337°N 116.99390°W, 1530 m, on moss over rhyolite outcrops, 20 June 2019, *McCune 38176.* **Washington:* Benton Co., Horse Heaven Hills, 0.5 km N of Chandler Butte, 46.25347°N 119.56451°W, 459 m,

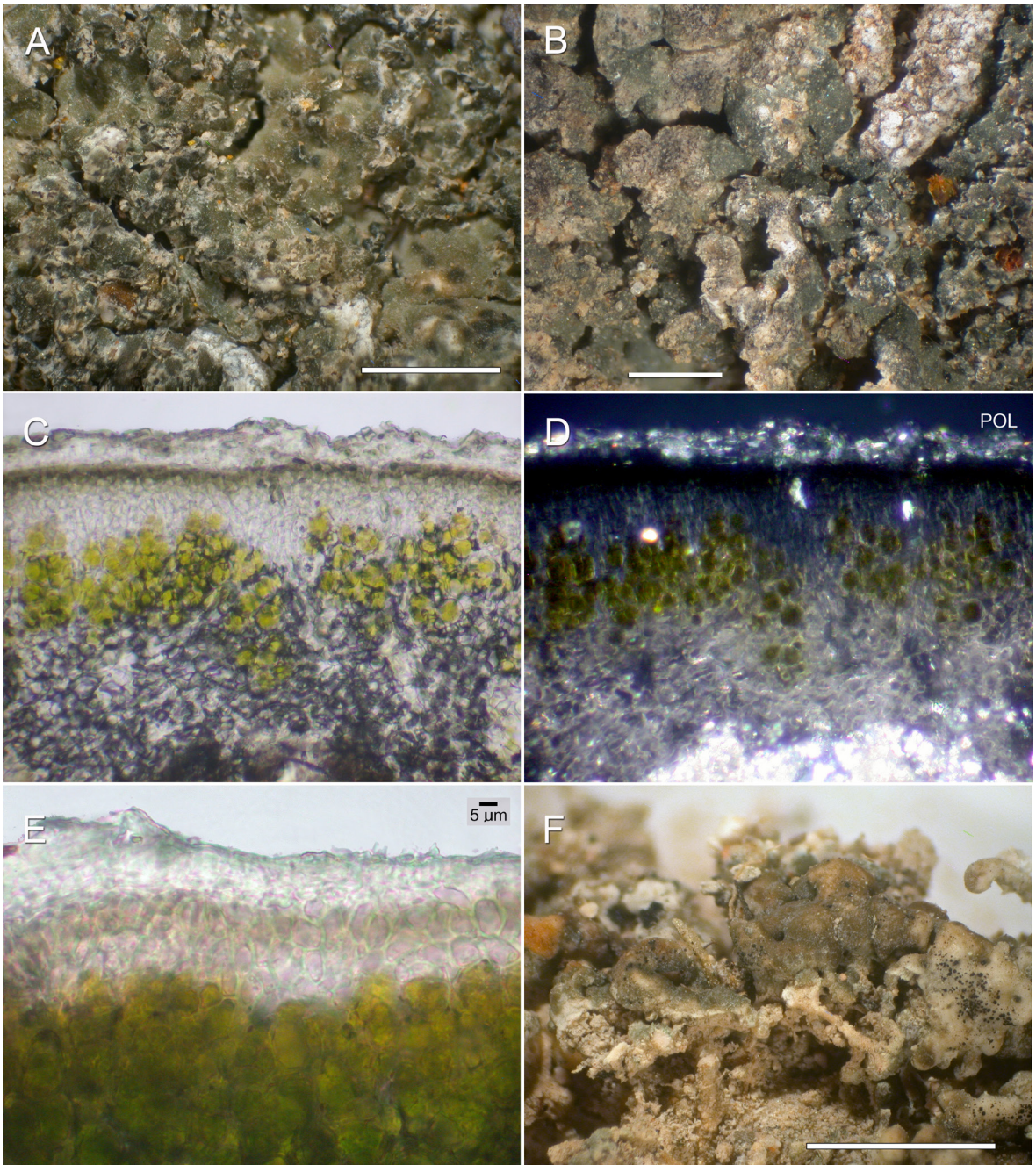

Figure 22. ***Aspicilia subcontinua***. — **A.** Habit, *Rosentreter 18307*. — **B.** Habit, *Di Meglio 259*. — **C.** Thallus section, *Di Meglio 259*. — **D.** Thallus section in polarized light, *Di Meglio 259*. — **E.** Thallus section, *Wheeler 7421*. — **F.** Rhizomorphs, *Di Meglio 253*.

grassland, on soil and plant detritus, 7 June 2019, *McCune 38115*; Grant Co., Saddle Mountain, ca 20 km W of Othello, 46.8077°N 119.4026°W, 225 m, 4 April 2015, *Di Meglio 259*.

Comments. The typical hand lens appearance of this species is a rough warty crust. It is perplexingly similar in basic morphological and anatomical characteristics to *Aspicilia albonota*, yet the sequence data show them not closely related (**Fig. 7**). Both are usually darker olive in coloration than the other *A. reptans*-like species. Both liberally produce white pseudocyphellae. *Aspicilia albonota* sometimes produces spicate clusters of hyphae, while *A. subcontinua* does not.

The species is more closely related to *Aspicilia papilliformis* and a clade containing the saxicolous species, *A. phaea*. These in turn fall in a larger supported clade with the *A. filiformis* group and *A. spicata* (**Fig. 7**).

Aspicilia subcontinua is less frequent than the other species in this group; we have only five collections of it and all but one (the type) are small. In the field the most obvious characters to recognize are the relatively dark olive coloration, as compared to other terricolous *Aspicilia* in western North America, and the thallus form as a lumpy subcontinuous network or sheet formed over soil, detritus, or moss over rock. Unfortunately, we have not found well developed apothecia or pycnidia, though incipient apothecia suggest that mature apothecia and pycnidia are likely to be found in the future.

The two supported subclades of *A. subcontinua* differ consistently in six positions of the ITS region. Too few specimens are known to evaluate whether or not these merit taxonomic recognition. Morphologically the two clades appear similar, based on the limited available material.

Aspicilia wyomingensis McCune & J. Di Meglio *sp. nov*. **Fig. 23**

MycoBank: MB839768 Barcode: MZ536769

Diagnosis. Thallus brownish olive to tan or completely white-pruinose, initially areolate but becoming knobby to branched, forming suberect to prostrate lobes; algal layer with narrow intrusions from the cortex; thallus containing aspicilin; on calcareous soil, pebbles, and plant detritus.

Type: U.S.A. **Wyoming**: Washakie Co., 5 km up Tenmile Creek Road from Highway 433, west of West River and north of Worland, 44.11661°N 108.01661°W, 1332 m, broad flat benches, shrub steppe with *Artemisia tridentata* ssp. *wyomingensis, Opuntia,* and *Bouteloua gracilis*, on soil and overgrowing pebbles, 18 September 2016, *McCune 37196* (holotype, OSC; isotypes, MONTU, SRP, UPS, WTU).

Description. Thallus mostly < 5 cm diameter, areolate or knobby-areolate, in part becoming branched, the branches suberect to prostrate; vertical swellings mostly 0.3–0.8 mm broad; pruina present or absent, varying from completely white-pruinose to lightly and patchily pruinose; upper surface of epruinose thallus matte, pale olive brown, pale brownish gray, tan, or whitish tan; pseudocyphellae present, whitish, slightly protruding, but clearly visible only in epruinose areas; epicortex 15–43 µm thick, brownish or grayish granular, POL+; eucortex distinct, paraplectenchymatous, 20–35(57) µm thick, POL–, brownish or olive in the uppermost layer of cells, otherwise hyaline; algal layer type 1, with narrow to broadly triangular to sometimes rounded intrusions of the cortex; prothallus sometimes apparent when contacting rock, otherwise with no apparent prothallus; rhizomorphs apparent where the lower surface exposed by erosion, cream to tan, simple or sparingly branched.

Apothecia not seen; pycnidia frequent, often developing under whitish scabrid warts, becoming large and compound; spermatia narrowly rod-shaped, 6–12 × 0.8–1.1 µm, median 8–9 × 0.9 µm.

***Chemistry*.** TLC: aspicilin. Spot tests negative.

***Ecology and substrate*.** Shrub steppe, on calcareous soil, pebbles, and plant detritus.

***Distribution*.** East of the Continental Divide in Montana and Wyoming, south and west to Lemhi Valley, Idaho, eastern Snake River Plain, and southeastern Oregon.

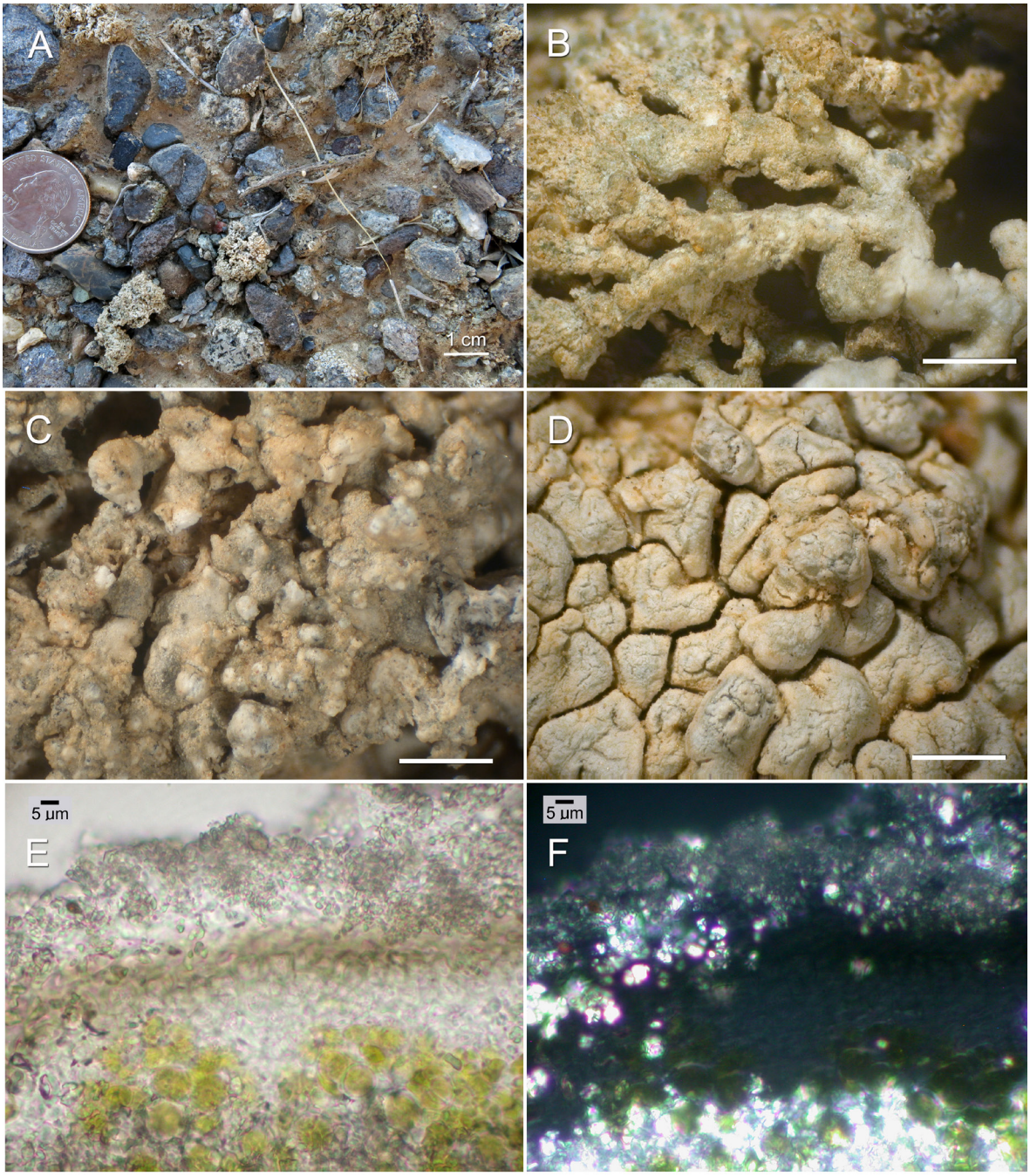

Figure 23. ***Aspicilia wyomingensis***. — **A.** Habit in situ, *McCune 37196* (type), U. S. quarter for scale (24 mm diameter). — **B.** Upper surface detail, *McCune 37196*. — **C.** Upper surface detail, *Perry 619*. — **D.** Pruinose areoles, *McCune 37199*. — **E.** Thallus section, *Perry 595*. — **F.** Thallus section in polarized light, *Perry 595*.

***Etymology*.** The epithet refers to the initial collections in the state of Wyoming by Tyrell Perry and the apparent concentration of this species farther east than many other species treated here.

***Specimens examined*.** U.S.A. **Idaho**: Ada Co., Kuna Butte study site, 43°31′N 116°29′W, 680 m, *Artemisia* grassland, 19 July 1995, *Rosentreter 9368* (SRP; not sequenced); Jefferson Co., Idaho National Engineering Laboratory, NE side, 43°52′N 112°37′W, *Artemisia tridentata* ssp. *wyomingensis* and *Eurotia lanata* habitat, disturbed site, 23 May 1995, *Rosentreter 9257* (SRP; not sequenced); Lemhi Co., Lemhi Valley, adjacent to Birch Creek, 44.23445°N 112.95708°W, 1996 m, on fine silty calcareous soil with small pebbles, 16 August 2016, *Di Meglio 300*. **Montana**: Chouteau Co., Above Coal Banks Landing, Missouri Breaks, along Missouri River, 48.03986°N 110.2335°W, 765 m, badlands with sparse steppe vegetation and calcareous sandstone outcrops, October 2007, *McCune 29308*; Musselshell Co., Milton Ranch, top of Big Wall, 46.59880°N 108.35680°W, 1072 m, sparse vegetation on thin soil over rimrock, common on soil and detritus, 15 September 2016, *McCune 37169*; on pebbles, *McCune 37170*. **Oregon**: Harney Co., east of Adel, large unit of Hawksie-Walksie RNA, 42.949°N 119.945°W, 1890 m, high desert with *Artemisia* and bunchgrass and large dry lake with fine soils, on soil in the dry lake bed, 25 June 2013, *Stone 9241* (not sequenced, TLC: aspicilin); Lake Co., NNE of Lakeview E of Route 395, Juniper Mountain RNA, low hillside with several *Artemisia* species and bunchgrasses on gravelly soil, *Hamill 13-209.14* (not sequenced; TLC: aspicilin and unknown fatty acid). **Wyoming**: Fremont Co., W of Boysen Reservoir, just S of quarry, stony calcareous hilltop with sparse grasses and *Opuntia*, 19 September 2016, *McCune 37199*; Washakie Co., 11.5 km NW of Worland, Worland Ant BLM exclosure, 44°7′11.3″N 108°0′40.9″W, 1331 m, with perennial grasses and *Artemisia tridentata*, 16 May 2013, *T. Perry 595*; 16.5 km NE of Worland, Tolman Ridge BLM exclosure, 44°8′35.1″N 107°50′26.5″W, 1348 m, with *Lepidium perfoliatum, Atriplex gardneri*, and *Artemisia tridentata*, 16 May 2013, *T. Perry 619*.

Comments. In the field this species appears as a pale olive brown to pale brownish gray or completely white crust, under the hand lens knobby-areolate to irregularly branched. In many sites, including the type locality, it grows as a profusion of small patches, the thallus freely spreading over soil, plant detritus, and pebbles.

The variation in pruinosity is remarkable, with some individuals completely white-pruinose (e.g., *McCune 37199*) and others not at all pruinose, and with all intermediates. The pruinosity is evident in thallus sections as a thickly granular, crumbly epicortex that is grayish in section. The variation is similar to that observed in some associates, for example, *Psora cerebriformis*, which ranges from completely white-pruinose forms to brown, epruinose forms. In both species we presume this variation relates to solar exposure and calcium carbonate availability in the substrate, the most heavily pruinose specimens in full sun on strongly calcareous soil.

One specimen represented in GenBank by an ITS sequence and identified as *Circinaria gyrosa* (*Barreno & Crespo 2041*, JX306734; Sohrabi et al. 2012) fell within the *A. wyomingensis* clade. The naming of this specimen in the GenBank record as *C. gyrosa* is puzzling, because in our trees it fell rather distant from the clade that includes the type of *A. gyrosa* and all other specimens of that species from Sohrabi et al. (2012). *Aspicilia gyrosa* is a vagrant species, while *A. wyomingensis* is not. We have not seen the specimen in question. It remains to be confirmed whether or not *A. wyomingensis* occurs in Spain, but *Barreno & Crespo 2041* is a candidate for that.

Unassigned Terricolous *Aspicilia* Species

The following terricolous specimens are isolated in the tree but lacked sufficient information and replication to describe as new.

1. U.S.A. **Oregon**: Umatilla Co., Ward Butte, 15 km SW of Hermiston, 45.73169°N 119.38637°W, 248 m, open xeric steppe with *Poa secunda*, savanna, on soil, 8 October 2015, *Kofranek 6884* (OSC). Thallus brown to grayish brown, with white mottles, warty-areolate to slightly lobate; areoles partly confluent, partly protruding and warty; pseudocyphellae present, developing from the white spots; epicortex weakly POL+ or POL–, 12–20 µm thick; eucortex 34–60 µm thick, algal layer type 1, penetrated by occasional intrusions from the cortex; rhizomorphs present, pale; medulla POL+ cloudy; sterile; no pycnidia found. TLC: nil. Forming a large brown patch on noncalcareous soil; occurring with *Arthonia glebosa*, *Endocarpon loscosii*, and the bryophytes *Aloina bifrons, Didymodon australasiae, D. vinealis, Pseudocrossidium obtusulum*, and *Syntrichia ruralis*. ITS and nuLSU sequences showed a close relationship to *A. reptans* s.str., but it did not fall in that clade.
2. U.S.A. **Idaho**: Ada Co., Orchard Training Area, S of Bigfoot Butte, 43.19037°N 116.22116°W, 975 m, winterfat shrub steppe (*Krascheninnikovia lanata*), 17 April 2014, *Rosentreter 18342* (SRP). Close to *Aspicilia aspera.*
3. U.S.A. **Wyoming**: Big Horn Co., 24 km E of Lovell, Kane Deer BLM exclosure, 44°53′21.6″N 108°5′50″W, 1432 m, west-facing slope, *Juniperus communis*, perennial grasses, and *Artemisia tridentata*, 15 May 2013, *T. Perry 501* (OSC). Close to *Aspicilia aspera.*

Key to Terricolous *Aspicilia* in Western North America

This key includes all of the known, routinely terricolous, *Aspicilia* species in western North America, except for *A. glaucopsina* and *A. praecrenata*. These species described from southern California were omitted pending further information.

Introductory Key

1a Thallus clearly fruticose, prostrate to more often suberect or erect with free, separate lobe tips
Group 1

1b Thallus crustose to prostrate subfruticose, often with beaded or stringy lobes

2a Thallus areolate-crustose (note: juvenile specimens of most species can be completely areolate; if in doubt key both ways)
Group 2

2b Thallus knobby-areolate to beaded-stringy
Group 3

Group 1

Fruticose, repeatedly branched, prostrate to suberect or erect

1a Thallus of minute ± appressed, prostrate or decumbent mats of narrow, elongate, ± flattened lobes; lobes ± flattened, often with distinctly forked tips like snake tongues; on noncalcareous soil and plant detritus

2a Thallus K-, norstictic acid lacking; widespread and common on noncalcareous soil east of the Cascade Range and in the Rocky Mountains
Aspicilia filiformis

2b Thallus K+ red (sometimes slowly), norstictic acid present

3a Main branches large, often 0.6–1.0(1.2) mm in diameter; thalli often > 2 cm in diameter; internodes usually 4-10 mm long; rare, endemic to south-central Oregon, rocky vernal pools on basalt flats
Aspicilia californica* var. *gigantea

3b Main branches narrow, seldom > 0.5(0.7) mm in diameter; thalli usually < 1.5(2) cm in diameter; internodes mostly < 5 mm long; endemic to California
Aspicilia californica* var. *californica

1b Thallus of erect hemispherical to spherical cushions or knobby balls; branches terete or nearly so; on calcareous soil

4a Branching dichotomous, thalli very compact; branches short, thick, blunt; pseudocyphellae mainly terminal on the branches; infrequent in dry steppe
Aspicilia rogeri

4b Branching irregular to dichotomous, thalli ± compact; branches short to elongate, tapered, often delicate, the tips spiky; pseudocyphellae lateral; widespread and frequent in dry steppe
Aspicilia hispida

Group 2

Crustose-areolate

1a Eucortex very thin, often only 1–3 cells and usually < 20 µm thick, and poorly delimited from the algal layer; substrate calcareous; pseudocyphellae lacking; algal layer even (type 0) but the border with the cortex somewhat ragged; thalli areolate to bullate-areolate, not becoming subfruticose; Snake River Plain in Idaho, eastern Oregon, Washington

Aspicilia diploschistiformis

1b Eucortex relatively thick, usually >3 cells and 20-40 µm thick, and well defined; substrate calcareous or not; pseudocyphellae present or not; algal layer type 1 or 2; well-developed specimens becoming subfruticose, developing a low, tangled mat of lobes; British Columbia, Idaho, Montana, Oregon, Wyoming

2a Algal layer usually markedly lobate (type 2); substrate various; thallus lacking aspicilin by TLC; spermatia 12–17 µm long

Aspicilia aspera (in part)

2b Algal layer even but with narrow intrusions from the cortex (type 1); substrate calcareous; thallus containing aspicilin by TLC; spermatia 6–12 µm long

Aspicilia wyomingensis (in part)

Group 3

Thallus knobby-areolate to beaded and/or stringy

1a Substrate calcareous soil and pebbles; thallus containing aspicilin; spermatia mostly < 10 µm long

2a Epicortex thin, usually < 10 µm, POL– or weakly POL+ in a superficial layer; thallus often epruinose, sometimes with pruinose patches or dull grayish necrotic areas; widespread, British Columbia to Saskatchewan, south to New Mexico

***Aspicilia reptans* s.str.**

2b Epicortex thicker, usually > 10 µm, often much thicker, POL+ throughout or in upper part; thallus commonly moderately to heavily white-pruinose, rarely epruinose; mostly east of the Continental Divide, Wyoming, Montana, Idaho, and Oregon

Aspicilia wyomingensis (in part)

1b Substrate noncalcareous or weakly calcareous; thallus lacking aspicilin; spermatia various

3a Apothecia present, lecideine, lacking a thalline margin

Aspicilia papilliformis (in part)

3b Apothecia lacking or if present, with algae in the margin

4a Spicate prothalline lobe tips common, the spikes blackish, often white tipped, also produced from thallus areoles and warts

Aspicilia spicata

4b Spicate prothalline lobe tips infrequent or absent

5a Algal layer lobate and discontinuous (type 2); upper surface weakly to distinctly pruinose; thallus various in color; pseudocyphellae lacking

6a Pruina in prominent discrete white patches or continuous over the whole thallus; apothecia lacking a thalline margin; thallus of high convex to papilla-like areoles,

becoming vertically elongate; Oregon, Idaho, Washington and California, most frequent in the Columbia Basin of central Oregon and Washington
Aspicilia papilliformis (in part)

6b Pruina absent to patchy and thin, diffuse; apothecia with thalline margin; thallus continuous to warty areolate (of confluent knobby areoles) to decumbent subfruticose, sometimes becoming terete-lobate; Idaho, Montana, Wyoming, Russia
Aspicilia aspera (in part)

5b Algal layer even (type 0) or with narrow intrusions from the cortex (type 1); upper surface epruinose or nearly so; pseudocyphellae present

7a Algal layer type 1, with triangular to slender intrusions from the cortex; thallus knobby, the knobs often becoming confluent or subcontinuous over areas 1–2 mm broad; pseudocyphellae sparse to abundant, white, roundish to ± elongate; on soil, moss over rock, or plant detritus; California to Washington, Idaho, and Montana
Aspicilia subcontinua

7b Algal layer type 0, but sometimes approaching type 1, with sparse, narrow intrusions from the cortex; thallus areolate to compound warty or short-lobate; pseudocyphellae usually conspicuous as whitish spots and lines, which are flat, slightly raised, or in the crevices at the edges of areoles; on soil or rock; Columbia Basin (Idaho, Oregon, Washington)
Aspicilia albonota

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Appendix 1

Table A1-1.Previously published sequences of Megasporaceae included in phylogenetic trees. Entries are in alphabetical order of collectors within epithets. GenBank accession numbers are given for ITS and nuLSU regions. New GenBank accessions are tabulated in **Table 1**. Proposed generic assignments by other authors are summarized in **Figure 7**.

Epithet	Location	Voucher	ITS	nuLSU	Comments
affinis	China	Abbas 10081364	HQ389194	--	
affinis	Russia	Kulakov 1408	HQ171237	--	
affinis	Russia	Kulakov 1408B Russia	HQ389196	JQ797502	
alphoplaca	USA: California	AFTOL 4816	--	KJ766595	
alphoplaca	USA: Nevada	Leavitt 849	JX306739	KC667060	
alpicola	Kyrgystan	Litterski 4848	JQ797556	--	
alpicola	Kyrgystan	Ringel & Jashhof 5183	JQ797524	--	
alpicola	Kyrgystan	Ringel 5137	JQ797552	--	
alpicola	Kyrgystan	Ringel 5241	JQ797554	--	
alpina	China	Li XL0306	KX234706	--	
arida	USA: California	Knudsen 2046	HQ406801	--	
arida	USA: Arizona	Owe-Larsson 8759	HQ406800	--	
arida	USA: Arizona	Owe-Larsson 8770	EU057905	--	
aschabadensis	Turkmenistan	Borisva s.n.	GU289916	--	
aschabadensis	Turkmenistan	Borisva s.n.	JQ797519	--	
aspera	Russia	Owe-Larsson 9792	JQ797531		
berntii	Norway	Nordin 6392	EU502747	--	
bicensis	Canada: Quebec	Anderson 16123 (type)	KU341407	--	
bicensis	USA: Alaska	Muggia KTM-LM012	MH579756	--	See McCune et al. (2018)
bicensis	USA: Alaska	Muggia KTM-LM018	MH579757	--	
bicensis	USA: Alaska	Muggia KTM-LM023b	MH579758	--	
caesiocinerea	UK: Wales	Orange 17594	FJ532372	--	
caesiocinerea	Sweden	Tibell 22612	EU057897	HM060731	
calcarea	Sweden	Nordin 5888	EU057898	HM060743	
calcarea	Sweden	Nordin 5914	HQ406804	--	
calcarea	Sweden	Tibell 23702	HQ406805	--	
calcarea	Sweden	Wedin 6500	--	AY853358	
cerebroides	Kyrgyzstan	Ringel & Jashhof 5180	JQ797529	--	
cerebroides	Kyrgyzstan	Ringel 5138	JQ797534	--	
cerebroides	Kyrgyzstan	Ringel 5184	JQ797553	--	
cinerea	Sweden	Hafellner 37308	AF332111	--	
cinerea	Austria	Hafellner 40563	AF332110	--	
cinerea	Sweden	Hermansson 13275	EU057899	HM060733	
cinerea	France	Lumbsch 8113	AJ458278	--	
cinerea	USA: Alaska	McCune 35353	MN906262	--	dark thallus
cinerea	Sweden	Nordin 5542	HQ406799	HM060734	
cinerea	USA: Alaska	Tønsberg 42720	MN906290	--	
contorta	Sweden	Tibell 23702	HQ406805	--	
contorta	Austria	Hafellner 43516	AF332109	--	
contorta	Sweden	Nordin 5895	EU057900	--	
contorta	Finland	Pykälä 22463	--	JQ797501	
contorta	Finland	Pykälä 28872	--	JQ797500	
contorta	Finland	Pykälä 30701	--	JQ797499	
contorta	Austria	Wilfing s.n.	AF332108	--	
crespiana	Spain	Rico 1249/1	JX306733	JX306752	
cretacea	Armenia	Aptroot 73835	KX253974	--	
cretacea	Armenia	Gasparyan 600199170	KX253975	--	

Epithet	Location	Voucher	ITS	nuLSU	Comments
cuprea	USA: California	Owe-Larsson 9112	EU057902	HM060750	
cupreoglauca	Greece	Sipman 60010	MH248843	MH255584	
cupreoglauca	Greece	Sipman 62345	KY618844	KY576955	
cupreogrisea	Sweden	Nordin 6046	EU057903	--	
cyanescens	USA: California	Owe-Larsson 9151	EU057904	HM060745	
dendroplaca	Sweden	Nordin 5952	HQ259259	HM060744	
dendroplaca	Finland	Nordin 6366	HQ259260	HM060758	
digitata	Kyrgystan	Ringel 5185	HQ171230	--	
digitata	Kyrgystan	Ringel 5185-B	HQ171236	--	
dudinensis	USA: Alaska	McCune 36017	MN906265	--	TLC: stictic acid
dudinensis	Sweden	Nordin 5971	--	HM060757	
dudinensis	Sweden	Nordin 6036	--	EU057906	
dudinensis	Sweden	Nordin 6036	EU057906	HM060748	
elmorei	USA: Nevada	Rosentreter 3689	HQ389200	--	
elmorei s.l.	Russia	Owe-Larsson 9814	HQ406802	HM060727	
elmorei s.l.	Iran	Sohrabi 10128	JQ797542	--	
elmorei s.l.	Iran	Sohrabi 10205	HQ389203	--	
elmorei s.l.	Iran	Sohrabi 10405C	JQ797526	--	
elmorei s.l.	Ukraine	Vondrák 5671B	JQ797551	--	
emiliae	Kazakhstan	Kulakov 3702	JQ797512	HM060728	
emiliae	Kazakhstan	Kulakov 3702B	JQ797513	--	
emiliae	Kazakhstan	Kulakov 3798	--	HM060729	
epiglypta	Sweden	Nordin 6303	EU057907	HM060756	
epiglypta?	USA: Alaska	McCune 36432	MN906278	--	as *A.* aff. *intermutans* in McCune et al. (2020); ascospores 25–27 × 13–15 µm; norstictic acid
esculenta	Kazakhstan	Ivanova s.n. UFU L-1743	MK347507	--	
esculenta	Russia	Owe-Larsson 9796	JQ797510	JQ797493	
esculenta	Russia	Owe-Larsson 9796	JQ797511	--	
esculenta	Russia	Owe-Larsson 9824	HQ406803	--	
fruticulosa	China	Abbas 2008363-a	HQ171226	--	
fruticulosa	China	Abbas 940001	HQ171229	--	
fruticulosa	Turkey	John 9538	JQ797535	--	
fruticulosa	Russia	Kulakov s.n.	HQ171227	--	
fruticulosa	Kazakhstan	Lange 5186	HQ171228	--	
fruticulosa	unknown	Schmitt s.n.	--	KC020259	
fruticulosa	Iran	Sohrabi 10405A	HQ389195	--	
fruticulosa	Ukraine	Vondrák 5188	HQ389199	--	
fruticulosa	Ukraine	Vondrák 5670	JQ797555	--	
gibbosa	Sweden	Nordin 5878	EU057908	HM060740	
gyrosa	Turkey	John 11984A	JQ797532	--	
gyrosa	Spain	MAF-Lich 15363	JQ797557	--	
gyrosa	Spain	Printzen 8087	JQ797514	--	
gyrosa	Iran	Sohrabi 10085 (type)	JQ797540	JQ797504	
gyrosa	Iran	Sohrabi 10401A	JQ797528	--	
gyrosa	Iran	Sohrabi 9496	JQ797539	--	
haeyrenii	Sweden	Nordin 5997	--	HM060755	
hispida	USA: Washington	AFTOL 4922	--	KJ766544	
hispida	Turkey	Candan 11	HQ406806	HM060760	
hispida	Spain	Lumbsch, 2. June 2003	--	DQ780305	
hispida	USA: Wyoming	Muscha 121	HQ171234	--	
hispida	Russia	Ochirova s.n.	HQ171235	--	
hispida	USA: Idaho	Rosentreter 16233	HQ389198	--	
hispida	Iran	Sohrabi 10212b	HQ389197	JQ797503	
hispida	Iran	Sohrabi 15099	HQ171233	--	
hispida s.l.	Russia	Kulakov s.n.	HQ389201	--	

Epithet	Location	Voucher	ITS	nuLSU	Comments
hispida s.l.	Greece	Mayrhofer 15811A	JQ797522	--	
hispida s.l.	Greece	Mayrhofer 15811B	JQ797523	--	
hispida s.l.	Iran	Sohrabi 10405	JQ797509	--	
indissimilis	Sweden	Nordin 5943	EU057909	HM060746	
intermutans A1	Armenia	Zakeri 40475	MH210660	MH257184	
intermutans A1	Armenia	Zakeri 40763	MH210672	MH257193	
intermutans A3	Armenia	Zakeri 40494	KY596009	KY576945	
intermutans A3	Armenia	Zakeri 40529	MH210666	MH257189	
intermutans A4	Armenia	Zakeri 39727	KY596006	KY576941	
intermutans A4	Armenia	Zakeri 40719	KY596012	KY576948	
intermutans B	Azerbaijan	Zakeri 38734	MH210680	MH257197	
intermutans B	Iran	Zakeri 49960	MH210675	MH257195	
intermutans C	Czech Republic	Lenzova 25	MH248852	MH255581	
intermutans C	Slovakia	Palice 15987	MH248857	MH255575	
intermutans D	Greece	Sipman 61911	KY618848	KY576958	
intermutans D	Greece	Sipman 62105	MH210653	MH257204	
junipericola	USA: Utah	Leavitt 742	JX306744	JX306758	
junipericola	USA: Utah	Leavitt 767	JX306747	JX306761	
junipericola	USA: Utah	Leavitt 843	JX306748	JX306762	
junipericola	USA: Utah	Leavitt 844	JX306749	--	
junipericola	USA: Utah	Leavitt 845	JX306750	--	
junipericola	USA: Utah	Leavitt 850	JX306751	--	
junipericola	USA: Utah	Rosentreter 14521 (type)	NR_158997	--	
jussuffii	Algeria	Esnault 2033	JQ797518	JQ797495	
jussuffii	Morocco	Vezda 2381	JQ797521	--	
lacunosa	China	Abbas 940003	JQ797517	JQ797494	
lacunosa	Kazakhstan	Piregoudov s.n.	JQ797520	--	
laevata	Finland	Nordin 5846	--	HM060735	
laevata	Sweden	Tibell 23659	EU057910	HM060730	
laxilobata	China	Ismayil & Abbas 20111049	KP219720	--	
laxilobata	China	Ismayil & Abbas 20111099	KP219719	--	
leprosescens	Sweden	Nordin 5906	EU057911	HM060749	
leprosescens	Sweden	Nordin 6059	--	HM060752	
Lobothallia sp.	France	Roux 25856	KC667063	--	
mansourii	Iran	Sohrabi 10097	JX306736	--	
mansourii	Iran	Sohrabi 15077	JX306735	--	
mashiginensis	Sweden	Nordin 5790	EU057912	HM060732	
mastrucata	Sweden	Nordin 5481	EU057914	HM060737	
mastrucata	Norway	Nordin 5708	EU057913	HM060736	
mastrucata	Sweden	Nordin 5937	EU057916	--	
melanaspis	Sweden	Nordin 6622	--	HM060726	
myrinii	Sweden	Nordin 6025	--	HM060754	
nikrapensis	Sweden	Ebbestad SVL 2 1	--	HM060759	
olivaceobrunnea	USA: Arizona	AFTOL 1358	HQ650638	DQ986782	changed from *calcarea* to *olivaceobrunnea* fide T. Wheeler 2021
olivaceobrunnea	USA: Arizona	Pastore long20	KC990381	--	changed from *contorta* to *olivaceobrunnea* fide T. Wheeler 2021
olivaceobrunnea	USA: Arizona	Pastore long22	KC990382	--	changed from *contorta* to *olivaceobrunnea* fide T. Wheeler 2021
olivaceobrunnea	USA: Arizona	Pastore long23	KC990383	--	changed from *contorta* to *olivaceobrunnea* fide T. Wheeler 2021

Epithet	Location	Voucher	ITS	nuLSU	Comments
olivaceobrunnea	USA: Arizona	Pastore long24	KC990384	--	changed from *contorta* to *olivaceobrunnea* fide T. Wheeler 2021
permutata	Sweden	Nordin 5980	EU057930	--	
permutata	Sweden	Nordin 6027	EU057918	HM060747	
permutata	Sweden	Nordin 6029	EU057919	--	
permutata	Sweden	Nordin 6038	EU057920	--	
permutata	Sweden	Nordin 6039	EU057921	--	
portosantana	Portugal	Sipman 62854	KY618851	KY576961	
portosantana	Portugal	Sipman 63019 (type)	NR_153581	NG058600	
praeradiosa	China	Zhengli Huang s.n.	JX499229	--	
radiosa	Sweden	Nordin 5889	JF703124	--	
recedens	Sweden	Nordin 6035	HQ406807	--	
recedens	Sweden	Nordin 6582	--	HM060762	
rimisorediata	Iran	Valadbeigi 2250	JF825525	--	
rimisorediata	China	XJU 20111617	KT443788	--	
rimisorediata	China	XJU 91815043	KT443787	--	
rivulicola	Sweden	Nordin 5957	EU057922	HM060753	
rivulicola	Sweden	Nordin 5960	--	EU057923	
rogeri	USA: Oregon	Rosentreter 16333	HQ171232	--	
rogeri	USA: Wyoming	Rosentreter 16373	HQ171231	--	
rostamii	Iran	Sohrabi 10095	JQ797533	--	
rostamii	Iran	Sohrabi 10212 (type)	JQ797527	--	
rostamii	Iran	Sohrabi 10212 (type)	JQ797538	JQ797507	
rostamii	Iran	Sohrabi 9364	JQ797541	--	
saxicola	China	Ren 2722 (type)	KX234703	--	
saxicola	China	Ren 3352	KX234702	--	
simoensis	unknown	Hafellner 42361	AF332114	--	
simoensis	unknown	Hafellner 43014	AF332115	--	
simoensis	unknown	Hafellner 46532	AF332113	--	
simoensis	USA: Alaska	McCune 36482	MN906280	--	thallus dark gray; soralia small, discrete; no mature apothecia; TLC: stictic acid
simoensis	Sweden	Nordin 5940	EU057929	--	
simoensis	Norway	Owe-Larsson 8932	EU057925	--	
simoensis	Norway	Owe-Larsson 9000	EU057926	HM060739	
simoensis	Sweden	Owe-Larsson H-12a	EU057928	--	
simoensis	Sweden	Owe-Larsson H-310	EU057927	--	
simoensis	Sweden	Tibell 22575	EU057924	--	
sp.	USA: Alaska	McCune 36003	MN906264	--	as *A.* aff. *indissimilis* in McCune et al. (2020); on shaded boulder; epihymenium green; spores 8/ascus, about 19–20 × 11–13 µm; TLC: nil
sp.	USA: Alaska	McCune 36431	MN906277	--	as *A.* aff. *indissimilis* in McCune et al. (2020); on floodplain cobble; epihymenium olive green; spores 8/ascus, 22–24 × 12–13 µm; spermatia not found. TLC: nil
sp.	Iran	Søchting 11187	JQ797558	--	
sp.	China	Abbas 20130731a	KR872316	--	
sp.	China	Abbas 20130731b	KR872317	--	
sp.	China	D.B. Tong s.n.	KC509896	--	
sp.	China	H.Y.Wang s.n.	KC509898	--	

Epithet	Location	Voucher	ITS	nuLSU	Comments
sp.	USA: North Carolina	Lutzoni 03.08.04-2, AFTOL 653	HQ650636	DQ986778	in GenBank as *A. caesio-cinerea*
sp. 1	Russia	Owe-Larsson 9821	HQ389202	--	
sp. 1	Iran	Sohrabi 10117b	JQ797544	--	
sp. 1	Iran	Sohrabi 4758	JQ797550	--	
sp. 2	Iran	Sohrabi 10092A	JQ797549	--	
sp. 2	Iran	Sohrabi 9380b	JQ797547	--	
sp. 2	Iran	Sohrabi 9380b	JQ797548	--	
sp. 3	Iran	Sohrabi 9347	JQ797546	--	
sp. 3	Iran	Sohrabi 9357	JQ797530	--	
sphaerothal-lina	Armenia	Mayrhofer 13-491	JQ797525	--	
sphaerothal-lina	Iran	Sohrabi 10117A	JQ797543	--	
sphaerothal-lina	Iran	Sohrabi 3679	JQ797537	--	
sphaerothal-lina	Iran	Sohrabi 5083	JQ797536	--	
sphaerothal-lina	Iran	Sohrabi 9369	JQ797545	JQ797508	
supertegens	Sweden	Nordin 6023	EU057938	HM060751	
supertegens	Norway	Owe-Larsson 9002	EU057936	HM060742	
supertegens	Norway	Owe-Larsson 9011	EU057937	--	
supertegens	Sweden	Owe-Larsson H-168a	EU057935	--	
supertegens	Sweden	Svensson 190	EU057934	--	
tibetica	China	Cheng 20116450	KX234705	--	
tibetica	China	Cheng 20116469	KX234704	--	
tibetica	Tibet	Obermayer 04386 (type)	NR_154475	--	
tibetica	China	Ren 2730	KX234707	--	
uxoris	Spain	Rico 3622	JX306743	JX306757	
uxoris	Spain	Rico 3622A	--	KC667057	
uxoris	Spain	Rico 3622B	--	KC667058	
uxoris	Spain	Rico 765	JX306745	JX306759	
uxoris	Spain	Rico 766	JX306746	JX306760	
uxoris	Iran	Sohrabi 9507B	--	JX306756	
uxoris?	Turkey	Halici s.n.	JX306742	--	
uxoris?	Iran	Sohrabi 9507B	JX306740	--	
verrucigera	Sweden	Tibell 22669	EU057939	--	
verrucosa	Austria	Hafellner 48544	AF332122	--	
verrucosa	Norway: Svalbard	Tao Zhang 2013046	KP314329	--	
verrucosa	Norway: Svalbard	Tao Zhang 2013052	KP314333	--	
verrucosa	Sweden	Nordin 6495	--	HM060725	
verrucosa	Austria	Trinkhaus s.n.	AF332121	--	
verrucosa	USA: Colorado	St. Clair 18429	KC667053	KC667062	
verruculosa	Sweden	Nordin 5942	EU057942	--	
verruculosa	Norway	Owe-Larsson 9003	EU057941	--	
verruculosa	Norway	Owe-Larsson 9007	EU057940	HM060741	
wyomingensis	Spain	Barreno & Crespo 2041	JX306734	--	original ID: *Circinaria gyrosa*
zerovii	Ukraine	Kondratyuk A12	KT456205	KT456208	
zerovii	Ukraine	Kondratyuk A15	KT456206	KT456209	
zonata	Sweden	Nordin 5461	EU057945	--	
zonata	Sweden	Nordin 5486	EU057944	--	
zonata	Sweden	Nordin 5932	EU057950	--	
zonata	Sweden	Nordin 5949	EU057953	--	
zonata	Sweden	Nordin 5998	EU057949	--	
zonata	Sweden	Nordin 6006	EU057952	--	

Epithet	Location	Voucher	ITS	nuLSU	Comments
zonata	Sweden	Nordin 6035	EU057951	--	
zonata	Sweden	Nordin 6219	EU057943	--	
zonata	Norway	Owe-Larsson 8942	EU057946	HM060738	
zonata	Sweden	Owe-Larsson H-254a	EU057947	--	

Appendix 2

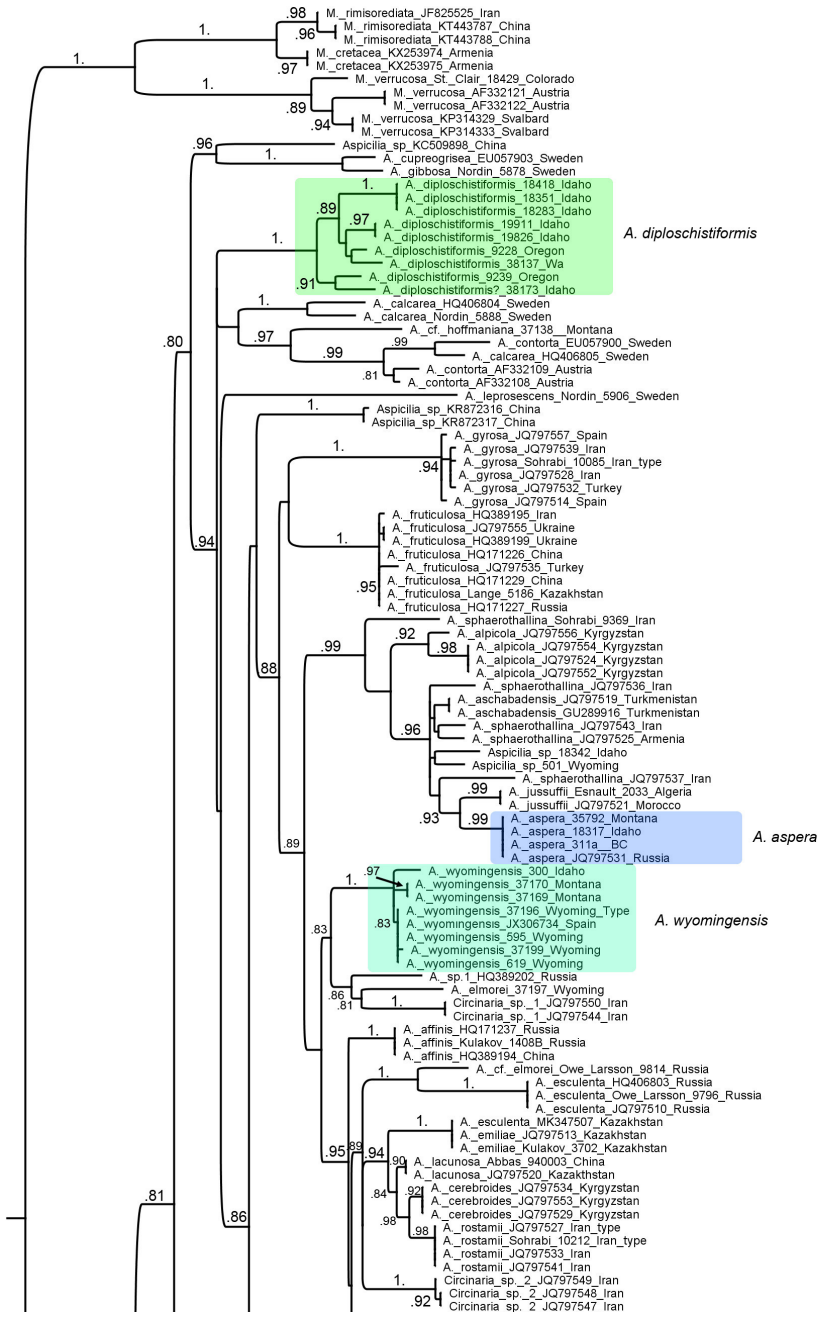

Figure A2-1 (4 pages). Maximum likelihood phylogenetic tree from PhyML based on ITS sequences. PhyML Approximate likelihood ratio test (aLRT-SH) support values at 0.80 and above are shown. New sequences are in **Table 1** and are labeled with a collection number. Pre-existing GenBank accessions are in **Appendix 1**. Colored rectangles indicate terricolous crustose species that occur in western North America and are similar in form to *A. reptans*. Gray rectangles indicate five non-terricolous species given detailed descriptions in **Appendix 3**.

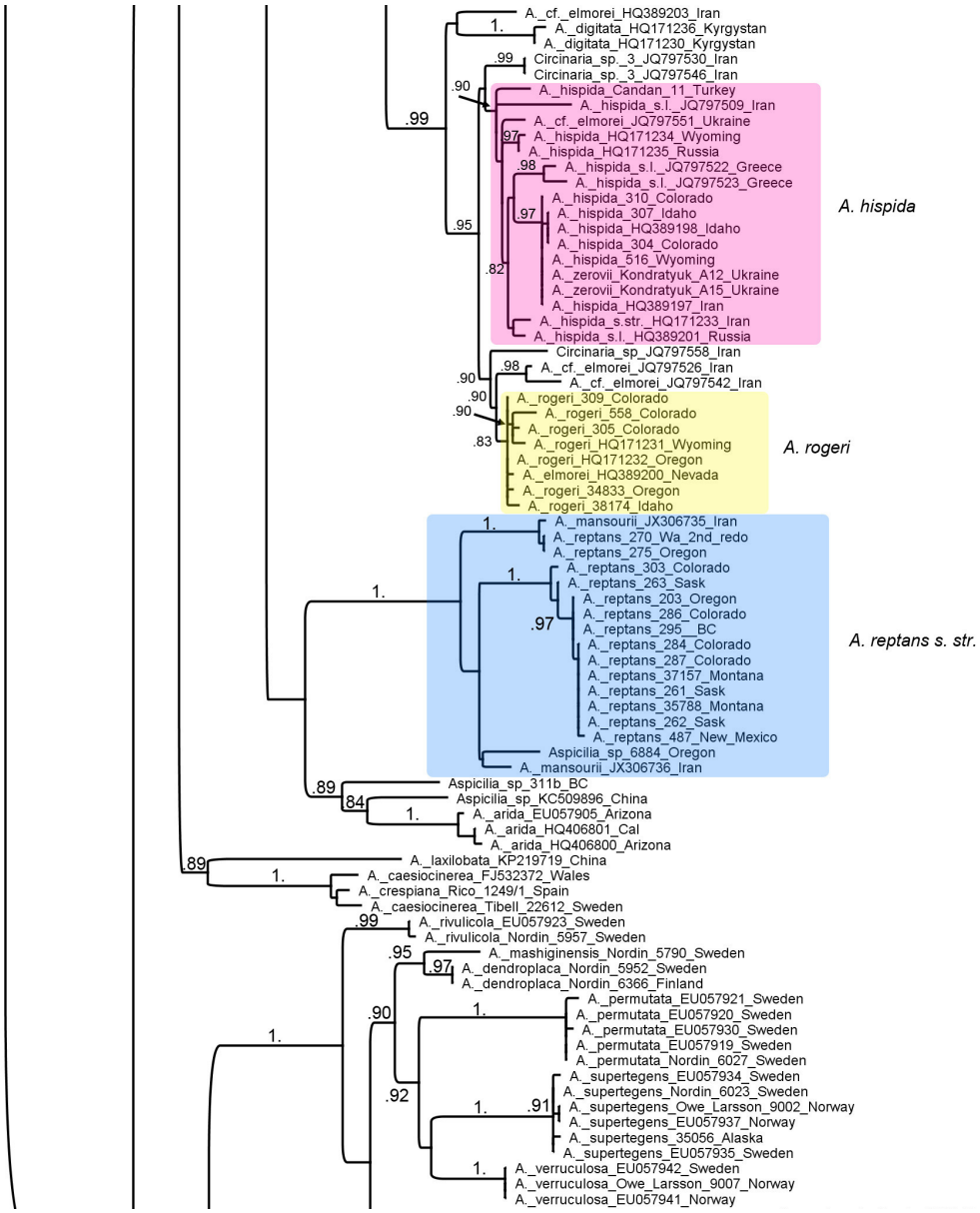

Figure A2-1, cont.

Figure A2-1, cont.

Figure A2-1, concluded.

Appendix 3

Supplemental species descriptions,
including *Aspicilia anglica*, *A. maritima*, *A. supralittorea*,
and the undescribed *Aspicilia* species X and species Y.

This appendix provides descriptions for five new or poorly known saxicolous species encountered in this study: *Aspicilia anglica*, *A. maritima*, *A. supralittorea*, and the perhaps undescribed species X and species Y. Our purpose in providing this information for these species, even though they are not terricolous, is to provide a basis for interpretation of GenBank records and to assist future work on the genus.

Aspicilia anglica Owe-Larsson & A. Nordin, Lichen Flora Gr. Son. Des. Region 3:66 (2007).

Fig. A3-1

Type: U.S.A. California: Los Angeles Co., San Gabriel Wilderness, below Crystal Lake, on siliceous rock, *Ryan 26434* (ASU).

The following description is based on sequenced material (**Table 1**) from Oregon and Washington. Our observations are sufficiently different from the original description that we felt it useful to expand the circumscription of the species.

Description. Thallus areolate-crustose to slightly lobate, light to dark gray, epruinose or with a pruina-like whitish superficial necrotic layer, rather thick (commonly 1 mm or more), to 5 cm or more in diameter, developing deep polygonal cracks about 1–5 mm apart; thallus margin often slightly zonate or slightly lobate or both, sometimes a thin white prothallus apparent, in other cases the extreme edge sometimes blackish, then whitish to light gray; pseudocyphellae lacking; upper surface soon becoming contorted with knobs, short ridges, and isidia; isidia irregular in shape, arising as hemispherical protrusions, about 0.05–0.1 mm diameter, becoming papilliform, knobby, or contorted, sometimes deteriorating into soredia, easily rubbed off, leaving an exposed white medulla; epicortex 0–15 µm thick, hyaline, POL– or POL+; eucortex distinct, paraplectenchymatous, 10–25 µm thick, POL– or more often POL+, brownish in the upper part, otherwise hyaline; algal layer type 0; medulla I–, POL+.

Apothecia infrequent (description based on *McCune 20369*), aspicilioid to lecanorine, with a rough to isidiate thalline rim, the outline circular or wavy; disk black, to 1.5 mm in diameter, concave to somewhat folded; thalline margin POL+ throughout; hymenium 130–140 µm tall, POL–, not inspersed; epihymenium blue green to olive, not granular; paraphyses submoniliform near tips; hypothecium hyaline, POL–; ascospores 18–21 × 10–12 µm, 8 per ascus. Pycnidia immersed; spermatia filiform, 12–14 µm long.

Chemistry: TLC: norstictic acid. Thallus K+ yellow to red, P+ orange, C–, KC–. Although the type of *A. anglica* reportedly contains substictic acid (Owe-Larsson et al. 2007) rather than norstictic acid, specimens tested from the Pacific Northwest and northern Rocky Mountains so far contain norstictic acid.

Ecology and substrate. On basalt in exposed sites, commonly overgrowing thinner crustose lichens such as *Lecidea atrobrunnea* group; less often on old, hard decorticate conifer wood; so far at low to middle elevations (530–1582 m).

Distribution. Eastern Oregon and eastern Washington.

Specimens examined (* = sequenced). U.S.A. **Oregon**: Crook Co., Lower Crooked River below Prineville Reservoir, rocky (basalt) gulch with old *Juniperus*, just upstream from Chimney Rock, 44°8′N 120°48′W, 945 m, May 1993, *McCune 20369*; Biak Training Center, just south of Highway 126, *Juniperus* woodland with bunchgrasses, 44.2542°N 120.0959°W, 940 m, on *Juniperus* wood, 26 March 2016, *McCune 36638*; Ochoco Mountains, just upstream from campground on Mill Creek, Mill Creek Wilderness, 44°22′N 120°34′W, 1135 m, on rock, May 1993, *McCune 20377*; Harney Co., east of Dry Mountain near

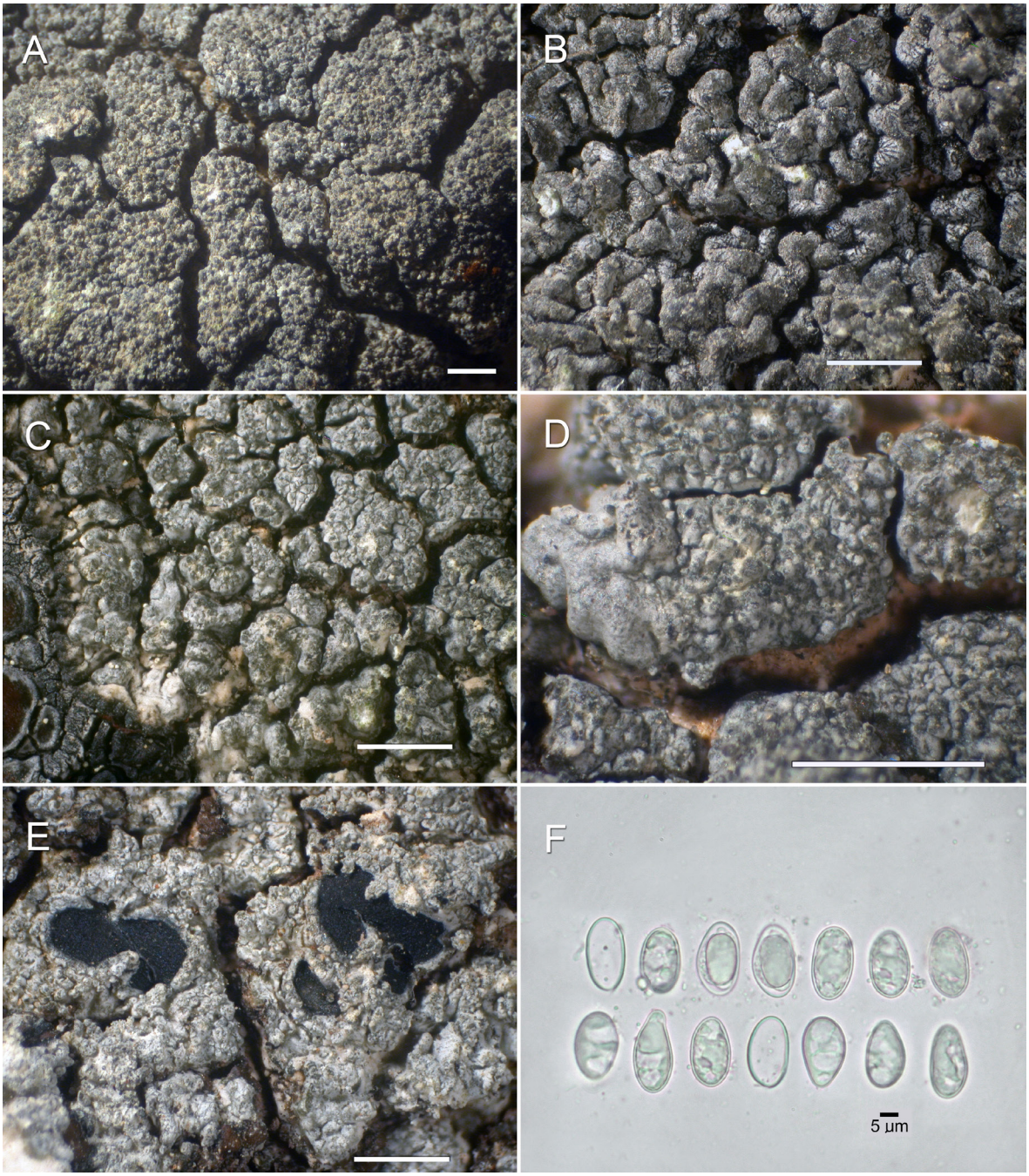

Figure A3-1. ***Aspicilia anglica***. **A.** Habit, *McCune 38230*. **B.** Habit, *McCune 38144*. **C.** Thallus margin, *McCune 38189*. **D.** Isidia, *McCune 38189*. **E.** Apothecia, *McCune 20369*. **F.** Ascospores, *McCune 20369*. Scale bars = 1 mm unless otherwise indicated.

Beaver Slide Road, 43.67845°N 119.52087°W, 1582 m, stony flats, shrub steppe with scattered *Juniperus* and *Pinus ponderosa*, 21 June 2019, *McCune 38189**; Jefferson Co., above Simtustus Reservoir on Deschutes River, *Juniperus – Artemisia* steppe, 44°41.2′N 121°13.9′W, 530 m, on wood, huge old rotting timbers from collapsed structure, May 2000, *McCune 25275*. **Washington**: Benton Co., Horse Heaven Hills, slope above Webber Canyon, 46.21415°N 119.43797°W, 313 m, 9 June 2019, *McCune 38144**; above West Yakitat Road and I-82, 46.24722°N 119.61510°W, 228 m, rocky gulch on lower slope, north facing; on basalt, 21 September 2019, *McCune 38230**.

Comments. Our material was assigned to *A. anglica* after incorporation of our sequences into trees by T. Wheeler (2021, unpublished). This showed that our sequenced specimens fall into a clade of *A. anglica* including material from both southern California and Montana.

We include a description here because our material differs in several respects from the original description in Owe-Larsson et al. (2004). At that time the species was known from a small number of locations in southern California. In particular, the original description does not mention isidia, while material from the Pacific Northwest often has isidia or isidioid structures. Furthermore, while the original material reportedly contained substictic acid, ours contains norstictic acid, but not all specimens have been analyzed by TLC. Last, we found two specimens on old, hard, decorticate wood (cited above), while the species has previously been reported only from rock.

Substictic acid is a little-known lichen substance, but it has been reported from several species of *Aspicilia*: *A. arctica*, *A. culicis*, *A. mashiginensis, A. mastoidea*, *A. narssaquensis*, and *A. sublapponica* (Øvstedal et al. 2009). Substictic acid is K+ yellow, P+ orange with rather low Rf values of A:13 B':4 C:10 (Elix 2014; Huneck & Yoshimura 1996, p. 350). Comparing this with norstictic acid at A:40 B':32 C:30 and stictic acid at A:32 B':9 C:18 and cryptostictic acid at A:14 B':10 C:10, it is clear that in the stictic acid group, it could easily be confused with cryptostictic acid in the commonly used solvents A and/or C. Thus, while we can confidently report norstictic acid from our specimens, the possible confusion between cryptostictic and substictic acids prevents a definitive conclusion on whether or not our specimens contain substictic acid.

Based on photos and comments by Wheeler (2017), *A. anglica* is highly variable in morphology. However, based on morphology, *Aspicilia anglica* might be confused with other isidioid norstictic acid-containing species on rock in the Pacific Northwest. One unidentified species has a relatively thin, dark olive thallus with small clusters of isidioid structures; another species has a thick thallus similar to *A. anglica* but a dark olive upper surface. A third species has a light gray to whitish gray thallus but produces masses of soredioid granules. These infrequently collected forms have not yet been sequenced, nor have we found them fertile for comparison to *A. anglica*.

Aspicilia maritima McCune & J. Di Meglio *sp. nov*. **Fig. A3-2**

MycoBank: MB839771 Barcode: MZ536801

Diagnosis. Thallus cracked-areolate to areolate, gray to olive gray, the areoles white-edged or mottled; upper cortex thin and only weakly delimited from the algal layer; apothecia aspicilioid, disk small, to 0.5 mm diameter; epihymenium dark olive; paraphyses hardly moniliform in water but moniliform near the tips in K; ascospores not seen; spermatia narrow, rod shaped, 6–7 µm long; thallus containing stictic acid; on noncalcareous rock.

Type: U.S.A. **Oregon**: Tillamook Co., roadcuts on east side of Highway 101 along west side of Neahkahnie Mountain, 45.7442°N 123.9598°W, 151 m, on exposed basalt cliffs, 30 November 2019, *McCune 38648* (holotype, OSC; isotypes, UPS, WTU).

Description. Thallus cracked-areolate to areolate, to 30 cm diameter or more, light to dark gray or dark olive gray, sometimes the areoles white-edged (in *McCune 37589*) or mottled white/gray, epruinose, very thin and flat (*McCune 38648*) to somewhat thickened and rugose (*McCune 37589*); pseudocyphellae lacking; prothallus not or only slightly apparent, though sometimes the thallus margin forming a thick-

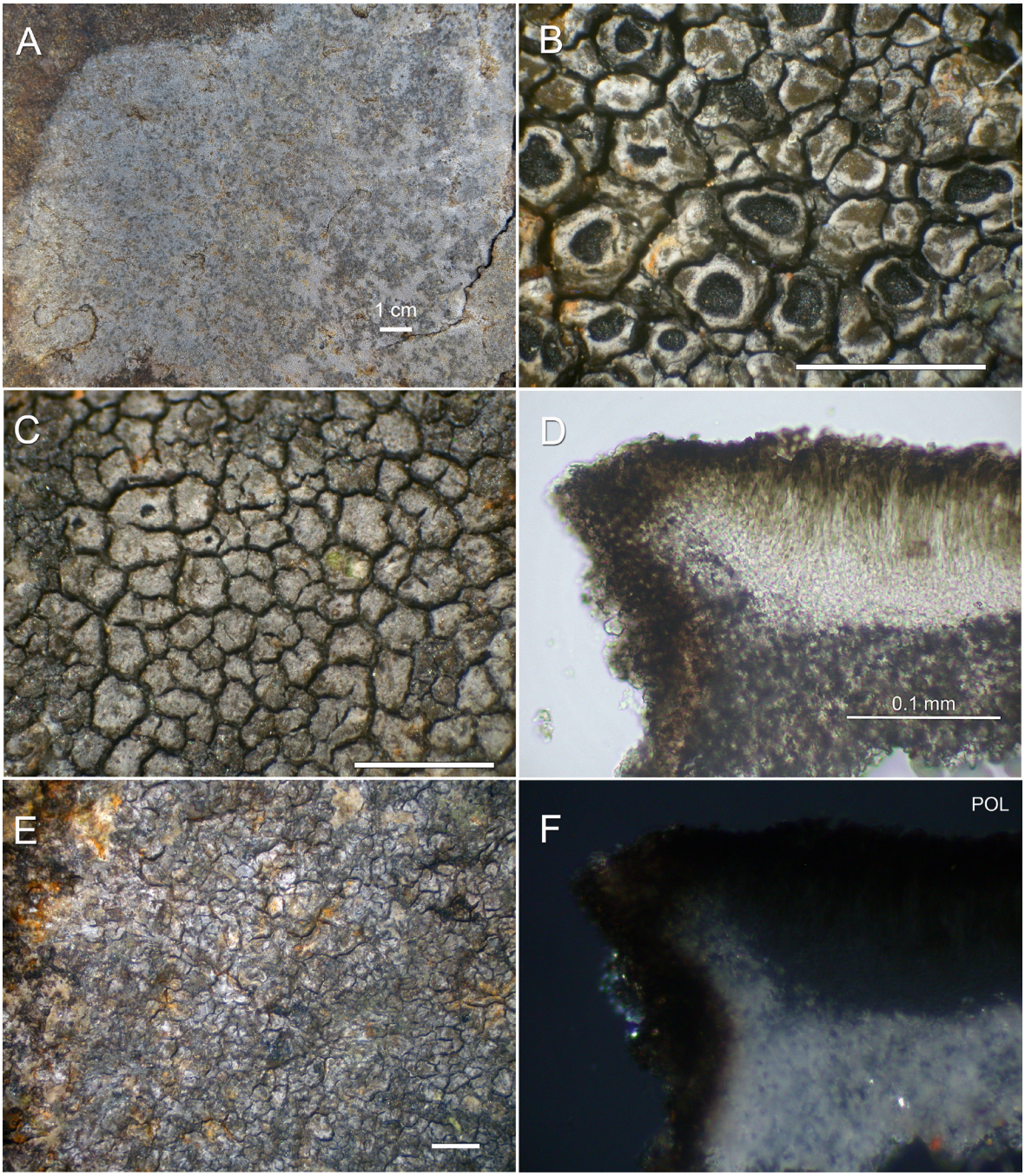

Figure A3-2. ***Aspicilia maritima***. **A.** Field habit of a very large individual, *McCune 34674*. **B.** Apothecia, *McCune 37589*. **C.** Thallus areoles, *McCune 38648*. **D.** Apothecial section, *McCune 37589*. **E.** Thallus margin, *McCune 38648*. **F.** Apothecial section in polarized light (POL), *McCune 37589*. Scale bars = 1 mm unless otherwise indicated.

ened, rough contact zone with other species; epicortex 0–5 µm thick, POL+ or POL–; eucortex distinct, paraplectenchymatous, 15–25 µm thick, POL–, brown throughout or just in the upper part, otherwise hyaline; algal layer type 0, weakly columnar in part; medulla I–, POL+.

Apothecia aspicilioid, small, the disk to 0.5 mm diameter, mostly one per areole, sometimes partitioning into multiple disks; disk black, epruinose; algae sparse to none in the margin; parathecium distinct, hyaline, except dark greenish at the surface, POL–, I+ blue; hymenium 55–80 µm tall, POL– , I+ blue green; epihymenium dark olive, POL–; paraphyses with swollen tips, to 7 µm, not moniliform in water but ± moniliform near tips in K; hypothecium hyaline; mature asci and ascospores not seen. Pycnidia black, partially protruding; spermatia narrowly rod shaped, 6–7 µm long.

Chemistry: TLC: stictic acid (major, minor, or trace). Spot tests negative. Because of the variable concentration of stictic acid, the medulla is K– or weak yellowish, P– or slowly and weakly yellow orange.

Ecology and substrate. On hard mafic or ultramafic rock in exposed sites, immediate coast to Siskiyou Mountains.

Distribution. So far known from northwest coastal Oregon and the Siskiyou Mountains in northern California.

***Etymology*.** The epithet "*maritima*" refers to the maritime (oceanic) climate of the Coast Range in Oregon and northern California.

Specimens examined. U.S.A. **California**: Siskiyou Co., above Tree of Heaven Campground and above Klamath River, near Highway 96, 41.82915°N 121.6593°W, 671 m, on peridotite outcrops in steep *Arctostaphylos - Ceanothus* scrub, 24 March 2018, *McCune 37589*. **Oregon**: Tillamook Co., Neahkahnie Mountain, *McCune 34674, 34676* (both from type locality).

Comments. Despite its outlying position in the phylogenetic trees, not falling in any of the segregate genera from *Aspicilia*, this species is morphologically unremarkable, having a light to dark gray, cracked-areolate thallus. The chemistry is rather unusual, however, since the thallus contains stictic acid alone, though it can be in trace concentrations. Like *A. supralittorea*, but unlike most *Aspicilia* species, the cortex is thin and the boundary with the algal layer only weakly defined. Unfortunately, while apothecia have been found, all of the known collections have degenerate or underdeveloped hymenia, so a complete description is so far impossible. We must rely to some extent on the ITS sequence, thallus anatomy, habitat, and substrate for future identifications, until the morphology is better understood.

Aspicilia maritima was featured as "*Aspicilia* sp." in a coastal lichenometric project at its type locality, where it is one of the dominant species (McCune et al. 2019). There it grew with *Acarospora fuscata* (Schrader) Arnold, *Caloplaca luteominia* (Tuck.) Zahlbr., *Pertusaria chiodectonoides* Bagl. ex A. Massal., *Placopsis lambii* Hertel & V. Wirth, *Rhizocarpon haidense* Brodo & Fryday, and *Rinodina aspersa* (Borrer) Laundon. At the type locality it forms large circular thalli to about 30 cm in diameter. The estimated average diameter growth rate for *A. maritima* was 1.0 mm per year.

Aspicilia supralittorea also occurs on noncalcareous rock on the immediate coast, but that has norstictic acid as a minor or trace substance along with stictic acid, while *A. maritima* contains only stictic acid. Although sometimes similar in appearance to *A. maritima*, the ITS region demonstrates that they are not closely related.

Aspicilia supralittorea McCune & J. Di Meglio *sp. nov*. **Fig. A3-3**

MycoBank: MB839772 Barcode: MZ536775

Diagnosis. Thallus crustose, cracked-areolate to areolate, light to dark gray; algal layer with somewhat columnar structure and uneven boundary with cortex; apothecia aspicilioid, with black epruinose disk and blackish raised margin; ascospores 15–28 × 12–18 µm, 8 per ascus; spermatia 10–14 µm long; thallus containing stictic and norstictic acids; on noncalcareous seashore rock.

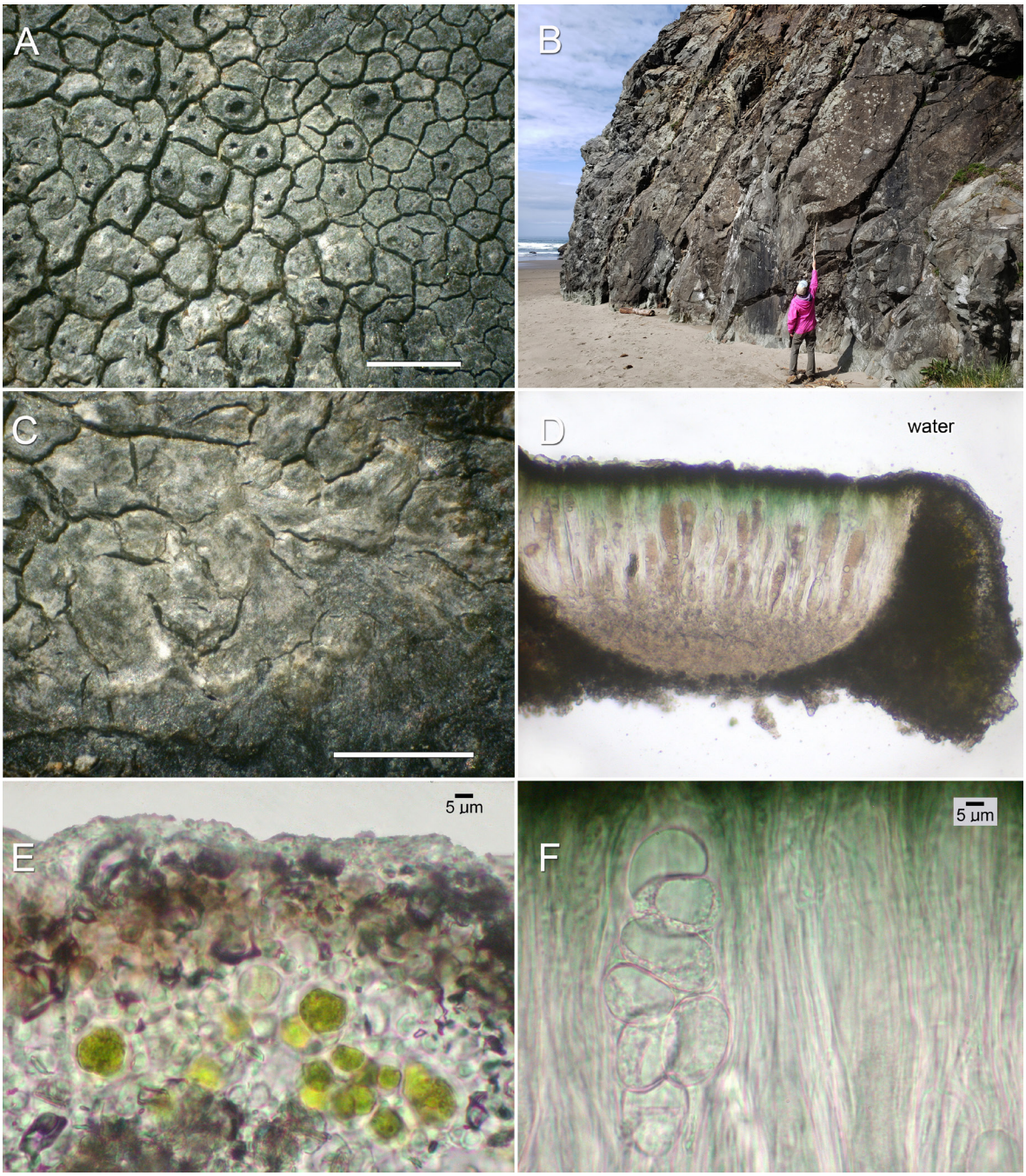

Figure A3-3. ***Aspicilia supralittorea***. **A.** Habit, *McCune 38048*. **B.** Habitat, *McCune 38929*. **C.** Prothallus, *McCune 38048*. **D.** Apothecial section, *McCune 38048*. **E.** Thallus section in K, *McCune 38929*. **F.** Ascus in hymenium in water, *McCune 38048*. Scale bars = 1 mm unless otherwise indicated.

Type: U.S.A. **Oregon**: Curry Co., South Jetty of Chetco River near its mouth, 42.0449°N 124.2700°W, 6 m, north-facing mafic rip rap, 23 March 2019, *McCune 38048* (holotype, OSC).

Description. Thallus crustose, cracked-areolate to areolate, to 5 cm diameter or more, light to dark gray, sometimes mottled white/gray, epruinose, very thin and flat to thick; prothallus sometimes apparent, with a thin, pale fimbriate zone with blackish edge or forming a thin, dark contact line with other lichens; epicortex (0)3–7 µm thick, POL– or weakly POL+ in part; eucortex distinct, paraplectenchymatous, (5)12–24(32) µm thick, POL–, brownish in the upper part in some areas, otherwise hyaline; algal layer type 0, in part weakly columnar, indistinctly delimited from the cortex, in part with wedges of POL+ hyphae extending up from the medulla into the lower part of the algal layer; medulla I–, strongly POL+.

Apothecia aspicilioid, sunken to emergent, with a raised margin; disk to 0.5 mm diameter, mostly 1–3 per areole; apothecial margin becoming slightly to distinctly raised, concolorous with the thallus to blackish; disk black, epruinose; parathecium distinct, hyaline, except dark green black at the surface, POL–, I–; hymenium 140–155 µm tall, POL– , I+ blue green fading to brownish green; epihymenium green black to blue-green black, POL–; paraphyses with swollen tips to 5 µm broad, submoniliform in water, moniliform in K; hypothecium hyaline to grayish, inspersed with oil drops, I+ weakly bluish; ascospores 15–28 × 12–18 µm, 8 per ascus. Pycnidia in pinholes, hard to find in the specimens seen; spermatia elongate, rod-shaped, 10–14 µm long.

Chemistry: TLC: stictic acid (constant), norstictic acid (trace or minor). Cortex K–, medulla K+ red or K– under dissecting scope, K+ yellow diffusion under compound scope, sometimes forming red crystals from norstictic acid.

Ecology and substrate. On noncalcareous supralittoral rock by the ocean, somewhat sheltered to exposed. Common associates are *Caloplaca luteominia* and *Buellia stellulata* (Taylor) Mudd.

Distribution. So far known only from coastal southern Oregon but likely widespread along the coast.

***Etymology*.** The epithet "*supralittorea*" refers to the supralittoral habitat on rocky ocean shores.

Specimens examined. U.S.A. **Oregon**: Coos Co., south of town of Bandon, 43.08965°N 124.43404°W, 4 m, east face of huge rock outcrop on beach, 21 March 2021, *McCune 38932*; just west of end of Strawberry Drive, south face of huge rock outcrop on ocean beach, 43.10330°N 124.43341°W, 5 m, 21 March 2021, *McCune 38929* (duplicates in UPS, WTU); Curry Co., South Jetty of Chetco River near its mouth, type locality, 23 March 2019, *McCune 38049*.

Comments. The ITS tree showed *A. supralittorea* to be sister to *A. cyanescens*, with which it shares numerous thallus characters, 8-spored asci, moniliform paraphyses, and a green to blue green epihymenium. These differ in *A. supralittorea* having shorter spermatia (10–14 µm vs. mostly 16–27 µm in *A. cyanescens*) and in the usual presence of norstictic acid in *A. supralittorea*, while it is absent in *A. cyanescens*.

The boundary between the cortex and algal layer is unusual among the specimens that we studied, having an uneven to indistinct transition, with some algal cells partly surrounded by cortical tissue. The only other species that we saw with a similar structure were *A. diploschistiformis* and *A. maritima.* We have not, however, studied the anatomy of most of the saxicolous species of *Aspicilia.*

The algal layer is also unusual for *Aspicilia* in having a weakly columnar structure, with individual algal cells sometimes forming loosely aligned stacks separated by one to several fungal hyphae. In some cases this structure is emphasized by wedges of medullary tissue penetrating between the columns from below. In some cases the columnar structure was visible as vertical banding in sectioned areoles under the dissecting scope.

Three of four collections were K+ red from norstictic acid; one collection was K– or reddish in spots in the medulla (*McCune 38929*). TLC demonstrated stictic acid as the primary substance, with small

amounts of norstictic acid. In one case crystals from norstictic acid formed in the margin of an apothecial section in K; in almost all cases K+ yellow diffusion was apparent from thallus sections and apothecia margins.

Aspicilia sp. X **Fig. A3-4**

The following description is based on three sequenced specimens (**Table 1**) from Montana and Oregon. Our material corresponds with an undescribed species under study by T. Wheeler and B. Owe-Larsson.

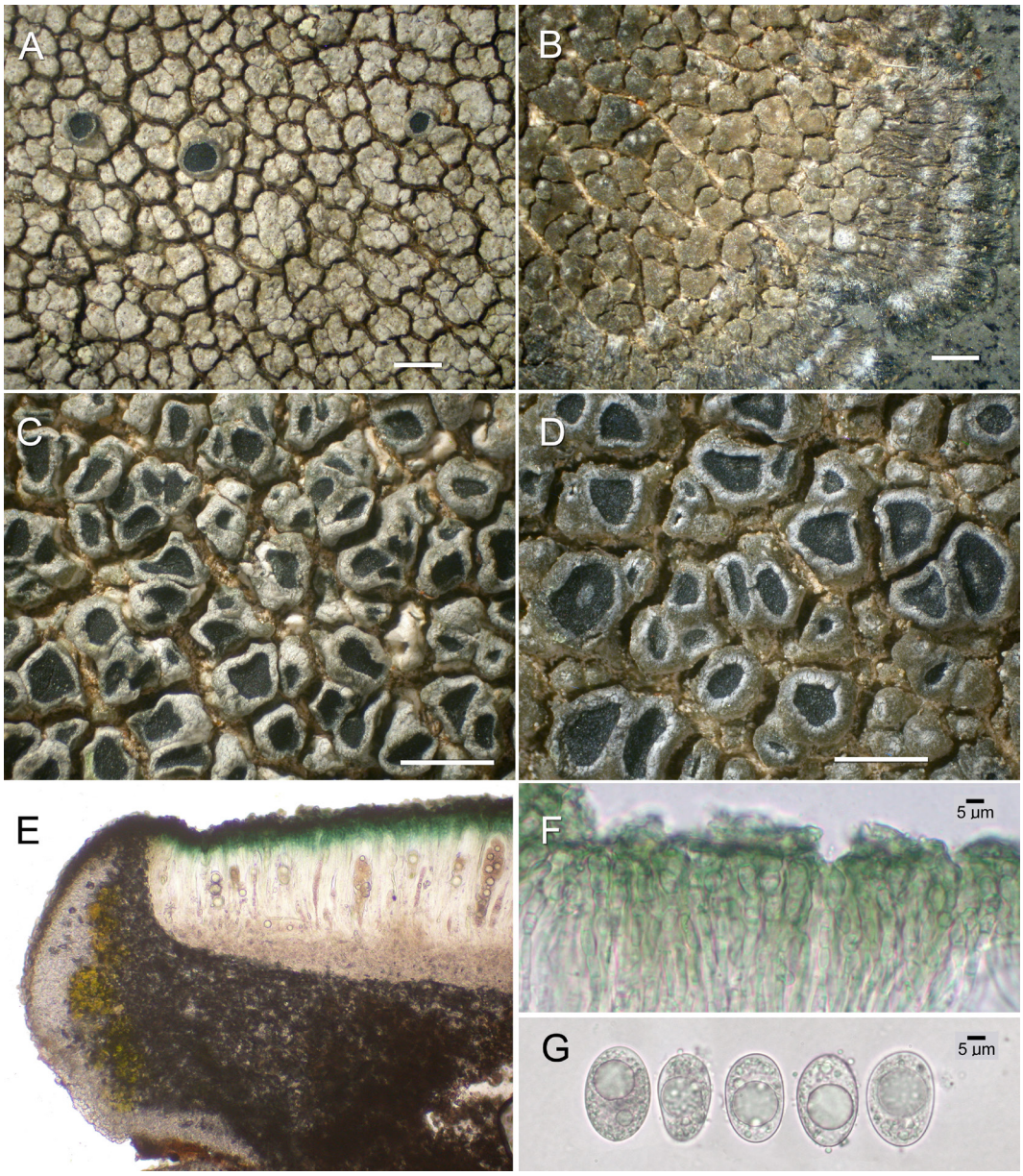

Figure A3-4. ***Aspicilia* sp. X. A.** Habit, *McCune 38790*. **B.** Thallus margin, *McCune 38858*. **C.** Apothecia, *McCune 38145*. **D.** Apothecia section, *McCune 38858*. **E.** Apothecial section in water, *McCune 38858*. **F.** Upper hymenium, *McCune 38790*. **G.** Ascospores in water, *McCune 38858*. Scale bars = 1 mm unless otherwise indicated.

Description. Thallus areolate-crustose, pale gray to medium gray or olive gray, flat or swollen, commonly to 1 mm or more in thickness, becoming thickly warty to substipitate so that the cortex wraps around the sides and even below the areole; upper surface dull, with a variable necrotic layer but mostly epruinose, sometimes developing fine secondary polygonal cracks in the surface; thallus margin sometimes zonate, the marginal differentiated zone to 2.5 mm wide, sometimes a thin prothallus apparent with light and dark bands or just a thin, dark edge; epicortex variable, often discontinuous, (0)5–21 µm thick, weakly POL+; eucortex distinct, paraplectenchymatous, (17)25–40(51) µm thick, fairly even, POL–; algal layer rather even, type 0 but with sparse narrow type 1 penetrations from the cortex; medulla thick, grayish, occluded, weakly POL+.

Apothecia aspicilioid, sunken to subsessile, often in swollen, substipitate areoles; disk dark gray to black, 1–2(4) per areole, to 1 mm diameter, round to angular or irregular, sometimes with sterile inclusions; apothecial margin concolorous with the thallus or slightly white-pruinose; hymenium 100–120 µm tall, POL–; epihymenium green, blue green, or bright blue green, POL–; paraphyses submoniliform to moniliform near tips; hypothecium hyaline to grayish, POL–, inspersed with oil drops; ascospores 18–30 × 13–19 µm, 4–8 per ascus. Pycnidia immersed; spermatia filiform, 15–23 µm long.

Chemistry: TLC: nil. Thallus K–, C–, KC–.

Ecology and substrate. On noncalcareous rock, including argillite and volcanic rock; elevation 2100-2400 m for the three sequenced specimens.

Distribution. Eastern Oregon and western Montana.

Specimens examined. U.S.A. **Montana**: Flathead Co., ridge near summit of Mount Aeneas, exposed subalpine ridge, 48.14848°N 113.92181°W, 2257 m, outcrops with argillite interbedded with weakly calcareous rock, 27 July 2020, *McCune 38858*; Lake Co., Mission Mountains, Cedar Lake Pass, 47.66534°N 113.94713°W, 2104 m, 23 July 2020, *McCune 38790*. **Oregon**: Harney Co., Trout Creek Mountains, volcanic hoodoo on top of ridge, 42.0256°N 118.2716°W, 2399 m, 18 June 2019, *McCune 38145*.

Comments. The ITS tree showed *Aspicilia* sp. X to be sister to sp. Y; together they are sister to a clade containing *A. knudsenii* and *A. albonota.* The sp. X and Y are similar in many respects, the most consistent and conspicuous difference being a thick cortex in sp. X, mostly 25–40 µm thick, versus a thin cortex in sp. Y, mostly < 17 µm thick. While both species develop a thick thallus to 1 mm or more, the older areoles become substipitate in sp. X, with a cortex on the sides and lower surface, while in sp Y. the areoles are divided by deep cracks but seldom become substipitate.

Aspicilia sp. X has many similarities to descriptions of *A. americana* and *A. confusa*. A comparison with those species (**Table A3-1**) suggests that *A*. sp. X differs in developing a cortex on the sides of the areoles, sometimes extending to the lower surface, while the other two species develop deep cracks but do not develop substipitate areoles. The habitats and ranges of all three species are poorly known, but *A.* sp. X appears to be more associated with cool montane to subalpine habitats in the northern United States.

Aspicilia sp. Y **Fig. A3-5**

The following description is based on two sequenced specimens (**Table 1**) from Oregon and Washington.

Description. Thallus thickly areolate-crustose with deep polygonal cracks, about 1 mm thick but more thickly mounded in spots, whitish gray; upper surface dull, slightly pruinose or not, developing very fine secondary polygonal cracks and an uneven to verruculose surface; thallus margin hardly differentiated, just thinner; epicortex highly variable, 0–32(50) µm thick but fragmenting and flaking off, POL– or weakly POL+ in part; eucortex distinct but thin, hyaline, paraplectenchymatous, 7–17 µm thick, POL–; algal layer thick and continuous, even or lumpy, type 0 but with widely scattered type 1 penetrations of narrow bundles of hyphae; medulla very thick, grayish, occluded, weakly POL+.

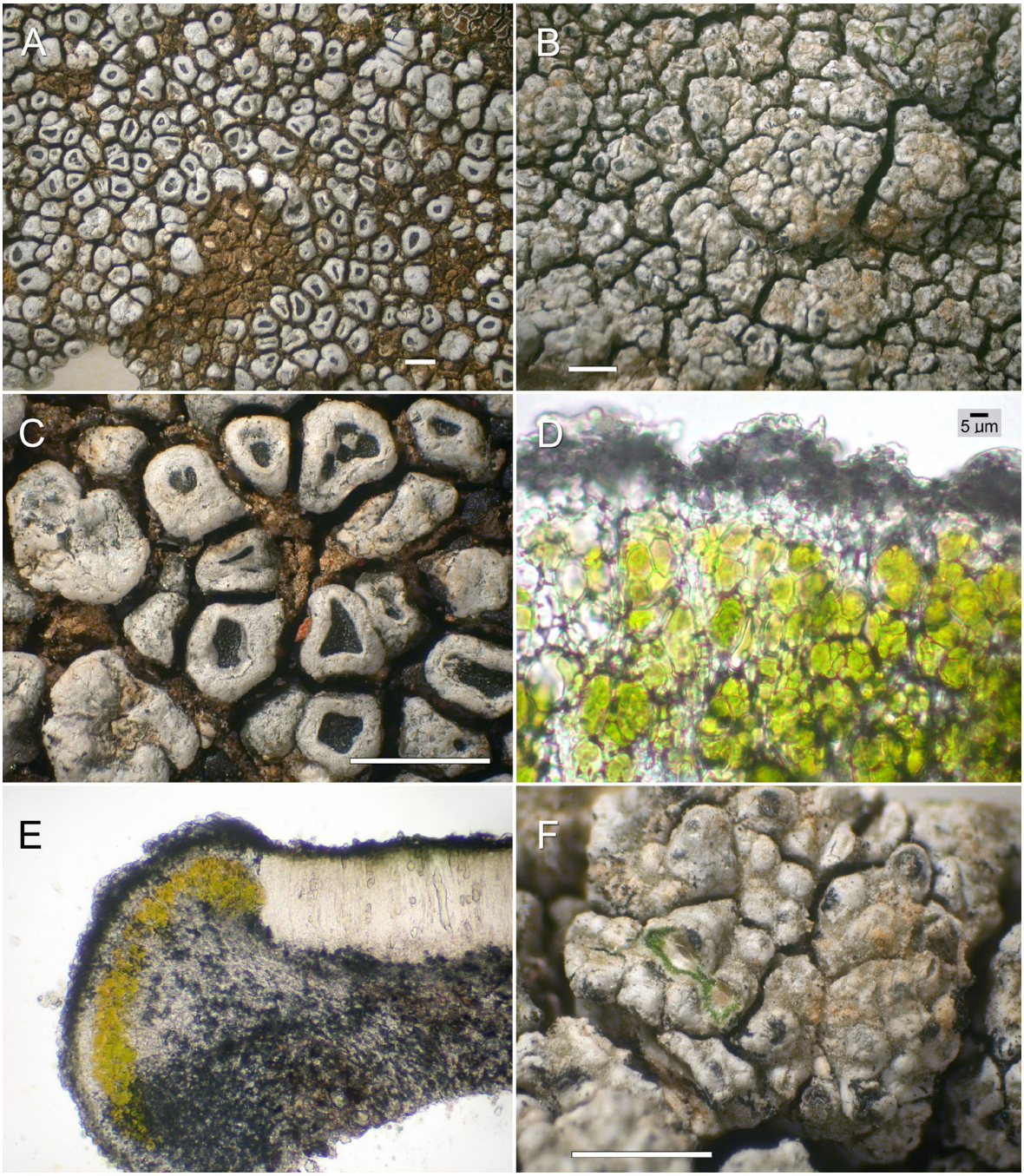

Figure A3-5. ***Aspicilia* sp. Y**. **A.** Habit, *McCune 38723*. **B.** Habit, *McCune 38238*. **C.** Apothecia, *McCune 38723*. **D.** Thallus section, *McCune 38238*. **E.** Apothecial section in water, *McCune 38723*. **F.** Pycnidia, *McCune 38238*.

Table A3-1. Comparison of *Aspicilia* species X and Y with *A. americana* and *A. confusa*. Because we have no sequenced material confidently identified as *A. americana* or *A. confusa*, characters for those species are based on the original descriptions in Owe-Larsson et al. (2007).

Character	***A. americana***	***A. confusa***	***A.* sp. X**	***A.* sp. Y**
upper surface	dull but shiny when brownish	dull to sometimes sightly shiny, sometimes with a thin white pruina	dull, with a variable necrotic layer, mostly epruinose, sometimes developing fine secondary polygonal cracks in the surface	dull, slightly pruinose or not, developing very fine secondary polygonal cracks and an uneven to verruculose surface
areoles	flat to convex, contiguous but separated by deep cracks	rounded to warty, dispersed or contiguous, separated by large cracks	warty with deep cracks, becoming substipitate with cortex on sides and below	with deep polygonal cracks
epicortex thickness, µm	(0)5-25(35)	(0)2-10(12)	(0)5-21	highly variable, 0-32(50)
eucortex thickness, µm	(10)20-45(60)	(12)20-35(40)	(17)25–40(51)	7-17
prothallus	absent or present as a narrow, dark band, sometimes fimbriate	often present, fimbriate, brown-black to black	sometimes apparent with light and dark bands or just a thin, dark edge	hardly apparent
apothecia	aspicilioid	aspicilioid becoming sessile	aspicilioid becoming sessile	aspicilioid
epihymenium	usually green, olive green or olive brown	green, olive, or olive brown	green, blue green, or bright blue green	green black
paraphyses	moniliform, rarely submoniliform	moniliform, sometimes submoniliform	submoniliform to moniliform near tips	moniliform near tips
spermatia length, µm	(8)10-18(28)	(11)16-25(27)	15–23	12–18
habitat	highly variable, interior SW N Am	chaparral to montane forest, California	montane to subalpine, Montana to Oregon	steppe and dry forest, eastern Washington and Oregon

Apothecia aspicilioid, sunken in swollen areoles; disks 1–2 per areole, dark gray to black, epruinose, to 0.8 mm diameter, depressed between the swollen margins, roundish or somewhat angular, the margins developing fine irregular cracks as in the sterile areoles; parathecium very thin, hyaline, POL-; hymenium about 100 µm tall, POL–; epihymenium green black, POL–; paraphyses moniliform near tips; hypothecium thin (about 25–30 µm), hyaline to grayish, POL–, inspersed with oil drops; asci abortive, mature ascospores not seen, but apparently 8 per ascus. Pycnidia immersed or in protruding bulges, the opening roundish to irregular; spermatia filiform, 12–18 µm long.

Chemistry: TLC: nil. Thallus K–, C–, KC–.

Ecology and substrate. On noncalcareous rock (basalt) at low elevations just east of the Cascade Range, in *Artemisia* steppe and *Pinus ponderosa* woodland.

Specimens examined. U.S.A. **Oregon**: Deschutes Co., Pole Creek area south of Sisters, volcanic sand flats, 44.21963°N 121.65711°W, 1374 m, 9 May 2019, *McCune 38723*. **Washington**: Benton Co., Horse Heaven Hills, above West Yakitat Road and I-82, 46.24722°N 119.61510°W, 228 m, rocky gulch on lower slope, north facing; on basalt, 21 September 2019, *McCune 38238* (duplicate in UPS).

Comments. The ITS tree showed *Aspicilia* sp. Y to be sister to sp. X; together they are sister to a clade containing *A. knudsenii* and *A. albonota.* Morphologically sp. Y is unremarkable, similar in many respects to descriptions of *A. confusa* and *A. americana*. See under sp. X for comparison to that species. Not having seen the type specimens of *A. confusa* and *A. americana*, comparisons to those are uncertain. It appears, however, that sp. Y is distinguishable from the other three species by its unusually thin cortex, typically < 17 µm (**Table A3-1**). None of these species show substances by TLC.

Index to Fungal Epithets

This index includes only fungal epithets applied within *Aspicilia* and related genera in the Megasporaceae. Main entries for featured species are shown in *italics*. Pages with illustrations of a species are shown in **bold**. Pages where a species appears in a phylogenetic tree are in red.