

Stereocaulon tomentosoides, a new combination for a western North American endemic species with cyanobiont and chemotype polymorphisms

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Abstract. Based on resampling the type locality and surrounding regions, along with phylogenetic analysis of molecular data, we elevate *Stereocaulon sasakii* var. *tomentosoides* to the species level, while we treat *S. sasakii* var. *simplex* as an environmental modification of *S. tomentosoides*. We found no phylogenetic evidence that any variety of *S. sasakii* occurs in North America, so we suggest that the species be removed from the North American list and its North American varieties transferred to *S. tomentosoides*. *Stereocaulon tomentosoides* is so far confirmed only from the Pacific Northwest of North America. Furthermore, it is largely allopatric with *S. tomentosum*, apart from a small region of overlap in northern Idaho and western Montana. While *S. tomentosum* always contains stictic acid and never lobaric acid as secondary metabolites, *S. tomentosoides* differs in having a predominant chemotype of lobaric acid as the major substance, with an infrequent chemotype containing both lobaric and stictic acids. While *S. tomentosoides* usually contains *Nostoc* in the cephalodia, occasional individuals, especially from old mossy lava flows, contain *Stigonema*; one specimen was found with both kinds of cephalodia on a single thallus. Phylogenetic analysis of these species and other close relatives revealed an additional species described here, *S. cyaneum*, so far known only from the Great Lakes region of the United States and Canada and separated from *S. tomentosum* by its bluish coloration, wet or dry.

Key words: lichens, lichenized fungi, North America, nuITS rDNA, nuLSU rDNA, *Stereocaulaceae*, *Stereocaulon cyaneum*, *Stereocaulon sasakii*, *Stereocaulon tomentosum*

Introduction

One of the few species of *Stereocaulon* Hoffm. that lichenologists in the northern Hemisphere confidently identify in the field, at least when fertile, is *S. tomentosum*. This large ground-dwelling species typically produces many small apothecia sprinkled over the thallus, instead of the larger, sparse, terminal apothecia produced by most *Stereocaulon* species (Lamb 1978).

A variant related to this species that is common in the Pacific Northwest of North America was apparently problematic for Lamb in his monumental worldwide studies on the genus (Lamb 1977, 1978). This variant is distinguished from *S. tomentosum* by lacking stictic

acid as a major secondary metabolite, instead containing lobaric acid, and thus having a P– medulla. Lamb’s early annotations of this material, for example in herbaria US and WIS, are as *S. tomentosum* “P– strain”. Later, but before publication of his monograph on *Stereocaulon* (Lamb 1977), he began to annotate them as *S. sasakii* var. *tomentosoides* Lamb, considering it as a morphological variant of that far east Asian species. Although Lamb (1977) did not justify this decision in detail, and did not report *S. sasakii* var. *sasakii* from North America, he implied that distributional differences of the P– variant from P+ *S. tomentosum* supported his conclusion. This conclusion is still accepted in the North American checklist (Esslinger 2019). Lamb (1977) also described *S. sasakii* var. *simplex* to accommodate upright, sparingly branched, hardly dorsiventral forms of *S. sasakii* in the Pacific Northwest. Both varieties were based on type material from southern Washington State (USA).

Lamb’s (1977) concepts of these taxa have been widely adopted (e.g., Esslinger 2019) although McCune & Geiser (2009) considered *S. sasakii* var. *tomentosoides* to be a P– chemotype of *S. tomentosum*, agreeing with

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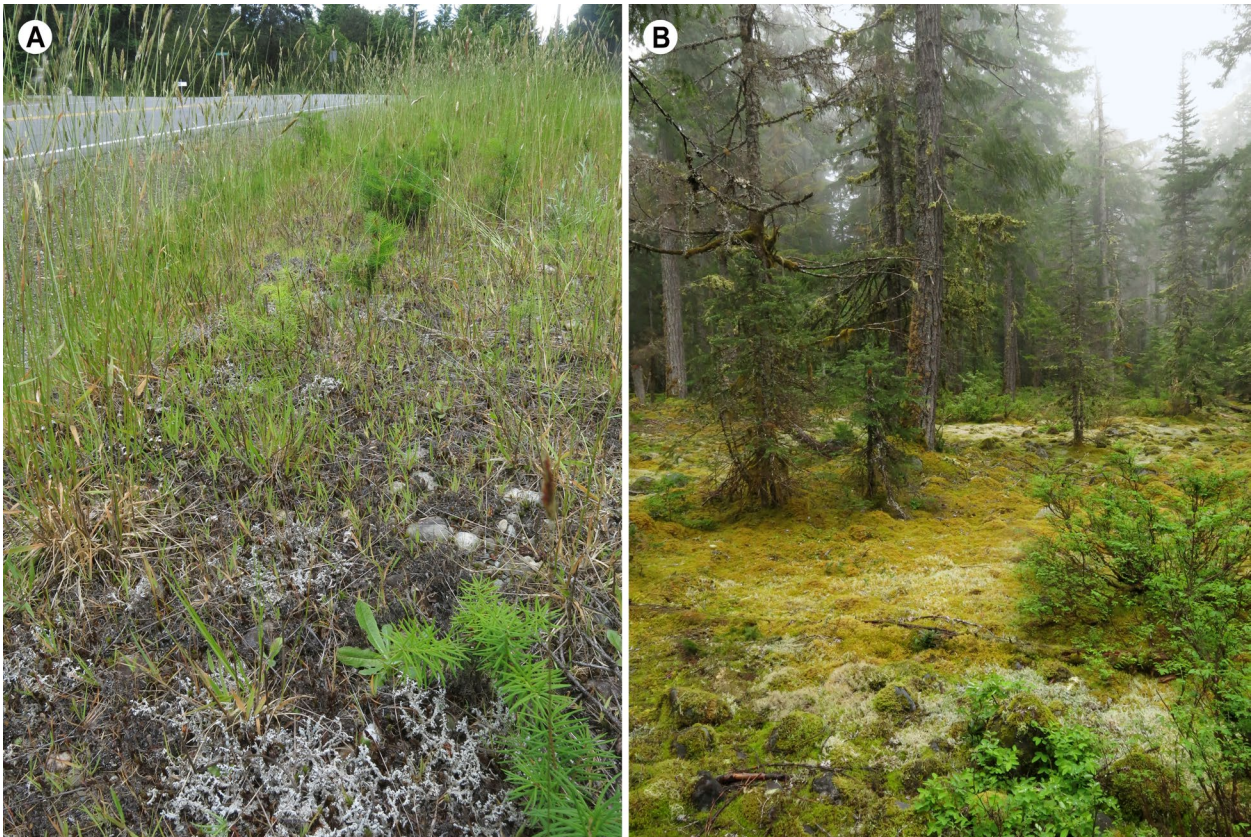


Figure 1. Habitat of recent collections near type localities of *S. sasakii* varieties from North America. A – *S. sasakii* var. *tomentosoides* from Webb Hill Road, base of Olympic Peninsula in Mason Co., Washington; B – *S. sasakii* var. *simplex* from near Nisqually River, Cascade Range near Longmire, Washington.

Lamb's earlier concept. Analysis of DNA sequences and an opportunity to recollect material from near the type localities of *S. sasakii* (Fig. 1) allowed us to re-examine the phylogenetic position of *S. sasakii* var. *tomentosoides* from western North America. Three mutually exclusive hypotheses can be addressed: (1) this material belongs to *S. tomentosum* and simply represents yet another case of a within-species polymorphism in major secondary metabolites, (2) the material belongs to *S. sasakii* as proposed by Lamb (1977), representing a disjunct occurrence between Asia and western North America, or (3) the material represents a distinct species. The purpose of this paper is to evaluate those three hypotheses and to propose appropriate taxonomic remedies. We recollected near the type localities, sequenced and determined the secondary metabolites in that material, and analyzed it in a global phylogenetic context for *Stereocaulon*.

Materials and methods

We collected new material to represent the North American range of the P- chemotype, along with multiple collections made near the type localities for *S. sasakii* var. *tomentosoides* and *S. sasakii* var. *simplex*. Neither location as given in the protologues was precise, but they were sufficiently well defined that our modern collections were probably within a few km of the original localities. The type of *S. sasakii* var. *tomentosoides* was part of a mass collection in Mason County, Washington, USA, by C. Westman in 1954, while the type of var. *simplex*

was apparently collected near Longmire, Washington, near what is now the southwest entrance to Mt. Rainier National Park. Collecting *S. sasakii* var. *simplex* was challenging, because extensive inspection of *Stereocaulon* colonies in the area showed a broad range of growth forms, from sprawling dorsiventral branches to nearly upright and sparingly branched forms. We sampled the latter as putative *S. sasakii* var. *simplex*. The problem was complicated by the abundance of other *Stereocaulon* species, in particular *S. alpinum*, but without apothecia.

We applied standard microscopy and chemical spot test methods. All newly sequenced specimens and many others were subjected to thin-layer chromatography (TLC), using the standard methods of Culberson (1972). Fragments of each specimen were extracted in acetone at room temperature, spotted on aluminum-backed silica gel plates (Merck 5554/7 Silica gel 60 F254), run in solvent systems A and C of Culberson (1972), lightly brushed with 10% H₂SO₄, and charred in an oven at 100°C.

We hand sectioned apothecia and studied them under the compound microscope in bright field and polarized light (POL). We observed apothecial anatomy and spores in water with no staining. We measured ascospores and spermatia in sets of seven and expressed size as the median and range, excluding any obvious runts. Spores were photographed, cut and pasted onto a single canvas, then measured with the line tool in PhotoShop with *View | Info* displayed. These raw values were converted to micrometers using a conversion factor calibrated from a stage micrometer. On all newly sequenced specimens,

we hand sectioned cephalodia and identified the cyanobacteria to genus under the compound microscope.

Photomicrographs were made with a Nikon Coolpix 995 through an Olympus BX40 microscope, coupled with an Optem 25-70-14-03s to the UVT-1X C-mount on the trinocular head, using magnifications up to 400×. Photos under the dissecting microscope were made with the same camera and coupler to the SZ-CTV mount on the trinocular head of an Olympus SZ40, using magnifications up to 40× and photo stacking with Helicon Focus 6 (Helicon-Soft, Ukraine). Additional habit photos were made with either an Olympus OM-D E-M10 Mark III with M. Zuiko digital ED 60 mm f2.8 macro lens and focus bracketing followed by stacking.

Taxon sampling for phylogenetic analysis. We assembled a global data set of published and unpublished sequences for over 700 *Stereocaulon* specimens, but for this study, we included only a small selection of those shown to be closely related to *S. tomentosum* by preliminary phylogenetic analysis of the bigger data set. The subset (*S. tomentosum* group) included *S. nanodes*, *S. dactylophyllum*, and an undescribed species-level lineage. We included all available sequences of *S. tomentosum*, including locations in North America, northern Europe, and South America. We selected six specimens of “*S. alpinum* clade D” as an outgroup, based on its presence in the study area, the structure of preliminary phylogenetic trees, and the genus-wide phylogenetic reconstruction of Högnabba (2006). Because of the confusion between *S. tomentosum*, *S. myriocarpum*, and *S. sasakii*, we wished to supplement the existing data for those species, but were not successful in obtaining fresh material of the latter two species from the countries of their type localities (Mexico and Japan, respectively). This limited us to the few existing sequences of those species in GenBank. Regardless, both Högnabba (2006) and our preliminary analyses placed *S. myriocarpum* and *S. sasakii* outside of the *S. tomentosum* group.

DNA extraction and PCR amplification. We extracted DNA sequences from recently collected specimens (Supplementary Material Table S1). We chose to analyze nuclear internal transcribed spacer (ITS) and large subunit (nuLSU) rDNA regions due to their general utility for species- and genus-level problems in *Lecanorales* and their previous use in *Stereocaulon* (Högnabba 2006; Högnabba et al. 2014; Park et al. 2018; Vančurová et al. 2018; McCune et al. 2019).

For DNA isolation, a 1 mm³ sample of thallus of each specimen was selected. Samples were first eluted in a 1.5 mL Eppendorf tube with one drop of 99.7% acetone for 10 to 20 min. The acetone was then removed by pipette and the remaining sample air dried for 10 min.

DNA was extracted with various methods, but primarily the RED Extract-N-Amp Plant PCR kit by Sigma-Aldrich, substituting DreamTaq Green (2x, Thermo Scientific Inc.) for REDtaq. The procedure used was according to the manufacturer’s instructions: 15 µL extraction solution was added and incubated at 95°C for 10 minutes and finalized by adding 15 µL dilution

solution. We amplified ITS with primers ITS1F and ITS4 (White et al. 1990).

PCR reaction conditions for ITS were initial denaturation at 94°C for 5 min, then 35 cycles of denaturation at 94°C for 1 min, annealing at 54°C, and extension at 72°C for 45 sec, followed by an elongation cycle for 5 min at 72°C. We viewed PCR products with gel electrophoresis and successful samples were then cleaned using ExoSAP-IT™ Affymetrix 78200 following the manufacturer’s protocol. These were processed using thermocycler incubation of 37°C for 15 min followed by 80°C for 15 min. Cleaned PCR products were prepared for sequencing by combining 2.4 µL forward primer (as above), 7.7 µL nuclease free H₂O, and 1.9 µL ExoSAP-IT product, then sequenced with forward and reverse reads (Eurofins MWG Operon Inc., Kentucky, USA).

Our nuLSU amplifications used the same extracts as described above and most used the primer pair AL2R (Mangold et al. 2008) and LR5 (Vilgalys & Hester 1990) with alternate primers LROR and LR6 (Vilgalys & Hester 1990) used as the second choice. The PCR master mix was the same as above, but with different primers. PCR reaction conditions were initial denaturation at 94°C for 3 min, then 36 cycles of denaturation of 94°C for 25 sec, annealing at 54°C for 45 sec, and extension at 72°C for 1 min 45 sec, followed by an elongation cycle for 7 min at 72°C. An alternate method used had an initial denaturation of 95°C for 5 min, then 35 cycles of denaturation at 95°C for 1 min, annealing at 56°C for 1 min and extension at 72°C for 1 min 45 sec, followed by an elongation cycle for 7 min at 72°C.

Geneious version 10.0.9 (<http://www.geneious.com>, Kearse et al. 2012) was used to check quality of the raw sequences, align the two reads per sample, and generate a consensus sequence for phylogenetic analyses.

Phylogenetic analyses. We compared our sequences (Supplementary Material Table S1) with our database of all available sequences for *Stereocaulon* to test for overlooked matches to existing taxa. We then constructed phylogenetic trees for the *S. tomentosum* group, including all available sequences. In preliminary genus-wide trees, part of a broader work in progress, *S. myriocarpum* and *S. sasakii* were so far removed from the *S. tomentosum* group that we omitted them from our final, more focused phylogeny. This resulted in a total of 59 sequences for ITS and 44 for nuLSU. Sequences were aligned with MAFFT in Geneious using default settings (auto algorithm selection, gap open penalty 1.53, offset 0.123). We trimmed the ends of our new alignments to match the annotated regions of those from GenBank. The ITS alignment had 560 bases with 29.2% (164) variable positions. After trimming, the remaining nuLSU alignment had 765 bases with only 2.4% (18) variable positions. Both loci had low enough variability that the alignments were not problematic and required only minimal manual adjustments. ITS and nuLSU were analyzed both separately and concatenated, since we found no conflicts. Given the low variability in nuLSU, we excluded four specimens for which we had nuLSU, but not ITS, leaving 59 sequences in a concatenated alignment.

Phylogenetic trees were obtained by maximum likelihood analysis of the ITS and nuLSU alignments separately and concatenated. We found no conflicts, so we presented the combined data. Our analysis used the GTR (general time-reversible) model with PhyML defaults, optimizing topology, length, and rate with an NNI search using the online version of PhyML 3.0 (Guindon et al. 2010). These maximum likelihood GTR+I+G models follow recommendations of Abadi et al. (2019). 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. 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.

Results and discussion

Phylogenetic analyses. Based on a combined analysis of ITS+nuLSU, all specimens of *S. sasakii* var. *tomentosoides* formed a supported monophyletic group within the *Stereocaulon* core (section *Stereocaulon* of Lamb 1977 and group 8b of Högnabba et al. 2006), based on sampling from throughout its range and from near the type locality (Fig. 2). Because this group is not sister to either *S. sasakii* (not shown; outside the *tomentosum* group) or the broadly distributed clade A of *S. tomentosum*, and is morphologically and chemically differentiated from the most closely related taxa, this group of specimens deserves recognition at the species level. Accordingly, we elevate *S. sasakii* var. *tomentosoides* to the species level.

Our sequenced recollection of *S. sasakii* var. *tomentosoides* near its type locality (McCune 38972) confirmed its position in the *S. tomentosoides* clade. In the area of the type locality, the species was common in 2021 on sandy and gravelly roadcuts, growing with the moss *Racomitrium elongatum*, *Cladonia verruculosa*, and other *Cladonia* species.

Stereocaulon tomentosoides had a mutually supported sister relationship with *S. tomentosum* clade B from the Rocky Mountains (Fig. 2). Together, these form a supported clade with poorly resolved relationships to three other clades: *S. dactylophyllum* and *S. cyaneum*, *S. tomentosum* clade A, and *S. nanodes*.

We found no phylogenetic evidence that *S. sasakii* var. *simplex*, including samples from near the type locality for that variety, deserve taxonomic recognition. These less branched, more erect specimens did not segregate from the other specimens of *S. tomentosoides* or *S. alpinum* clade D, labeled as “simplex morph” in Fig. 2.

Phylogenetic analysis of ITS + nuLSU sequences revealed another clade of specimens similar to *S. tomentosum* and sister to *S. dactylophyllum*. Those specimens had subtle morphological differences from *S. tomentosum* and *S. dactylophyllum* and were restricted to the western Great Lakes region, thus we describe this as a new species, *S. cyaneum*.

Clade A of *S. tomentosum* is broadly distributed, including North America, South America, Fennoscandia, and Europe. Clade B of *S. tomentosum* is so far known only from the Rocky Mountains from Colorado to Montana. This clade appears sister to the remainder of the *S. tomentosum* group and is not monophyletic with *S. tomentosum* clade A.

Stereocaulon tomentosoides (I.M. Lamb) McCune, comb. nov., Brodo et al. 2001, p. 668 (Figs 3–4)
MycoBank MB 849815

Basionym: *Stereocaulon sasakii* var. *tomentosoides* I.M. Lamb, J. Hattori Bot. Lab 43: 230. 1977.

Type: USA. Washington, Mason Co., Webb Hill Road near Cranberry Lake, on the ground, 1954, C. Westman 7783 (FH – holotype).

= *Stereocaulon sasakii* var. *simplex* (Riddle) I.M. Lamb, J. Hattori Bot. Lab 43: 230. 1977. Basionym: *S. tomentosum* var. *simplex* Riddle, Bot. Gaz. 50: 298. 1910.

Type: USA. Washington, Pierce Co., Mt. Rainier region, old bed of Nisqually River, Longmire Springs, on sand in old boulder-strewn river bed, 14 Aug 1904, T.C. Frye s.n. (FH-RIDD – holotype; MICH, WELC – isotypes not seen; photo of type in Riddle 1910).

Diagnosis: Large, ground-dwelling, tomentose, medulla P– (lobaric acid), infrequently P+ (stictic and lobaric acids), apothecia relatively small, numerous, lateral and terminal, common in the Pacific Northwest of North America; similar to *Stereocaulon tomentosum*, but containing lobaric acid.

Barcode: specimen from near type locality for *Stereocaulon sasakii* var. *tomentosoides* (Genbank OR475497).

Exsiccati: Kryptogamae exsiccatae a Mus. His. Vindobon. Cent. XLI (1957) No. 420 as *S. tomentosum*; Lichenes Canadense Exsiccati No. 65 (1970), Brodo 8244 (CANL, FH) as *S. myriocarpum*.

Description. Thallus fruticose, to 2–10(12) cm tall, decumbent to erect, stalks to about 12 cm, sometimes with ± planar branching; shoots usually dorsiventral, branching frequent; primary thallus not seen; phyllocladia granular, warty, or compound warty, becoming branched lobate and ± planar or flattened lobulate, often with crenate edges, or palmate, the upper surface white when warty, but commonly when flattened or palmate, then becoming bluish tinged centrally with whitish edges, the bluish tinge fading to pale olive or tan in the herbarium; cortical windows absent; tomentum moderate to thick, sometimes clumpy, beige, cream, or grayish; soredia unknown; cephalodia small and diffuse or forming large mounds, granular to warty, becoming compound, grayish, blue grayish, cream, or beige; tomentum on cephalodia present, whitish; cyanobiont usually *Nostoc*, occasionally *Stigonema* (variation discussed below).

Apothecia common, terminal and lateral, to 1(1.5) mm diam; *exciple* thick, radiate, hyaline to occluded with grayish or brownish crystals, POL+, tomentose on the outer surface; epihymenium POL+; hymenium (40)52–60(62) µm, POL– or POL+ streaky or POL+ in the upper part; hypothecium hyaline to pale grayish, POL– throughout or POL+ in the lower part; ascospores 1–3(5)-septate,

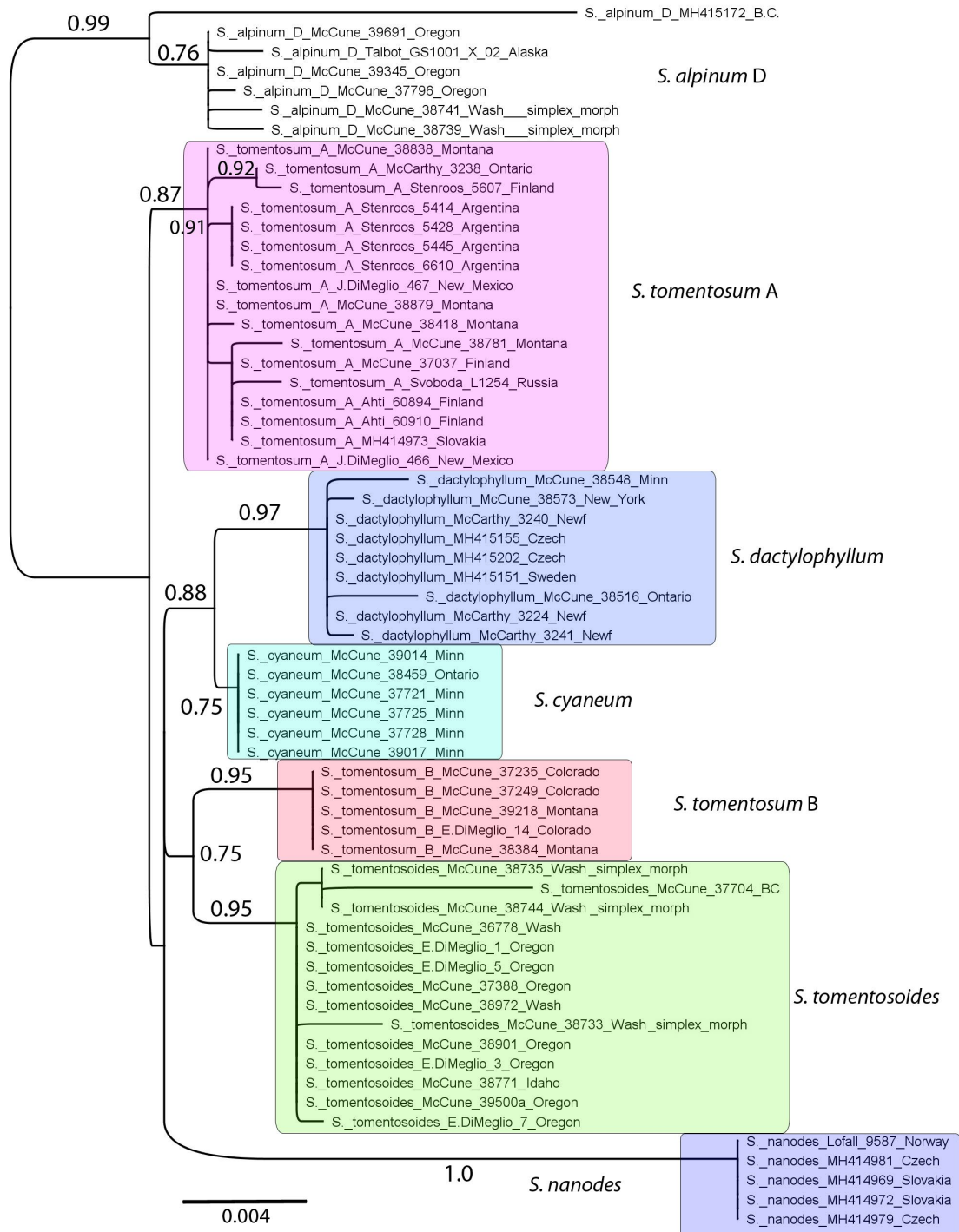


Figure 2. Maximum likelihood phylogenetic reconstruction from ITS+nuLSU data for *Stereocaulon tomentosum* and closely related species, with *S. alpinum* clade D chosen as an outgroup based on wider sampling. Support values (aLRT-SH) over 75% are shown. See Table S1 for sample sources.

24–39(48) × 2.2–3.3(3.7) μm, median 27–32(38) × 2.4–3.3 μm. Pycnidia and spermatia not seen.

Chemistry. Chemotype I – Thallus containing lobaric acid and associates and atranorin (cortex K+ yellow; medulla K–, KC+ orange-red, P–, UV+ whitish). Chemotype II – lobaric and stictic acid and associated compounds, including norstictic acid as minor substance (cortex K+ yellow; medulla K+ orange-red, KC+ orange-red, P+ orange, UV+ whitish). See discussion below.

Etymology. The epithet “*tomentosoides*” refers to the species’ morphological similarity with *S. tomentosum*.

Ecology and substrate. On soil or moss on the ground on those substrates over noncalcareous rock or gravel, mainly at low to mid elevations in the mountains.

Distribution and abundance. British Columbia to Oregon, inland to western Montana (Fig. 5). Common west of the Cascade crest, with more scattered locations on the east slope of the Cascades and inland to northern

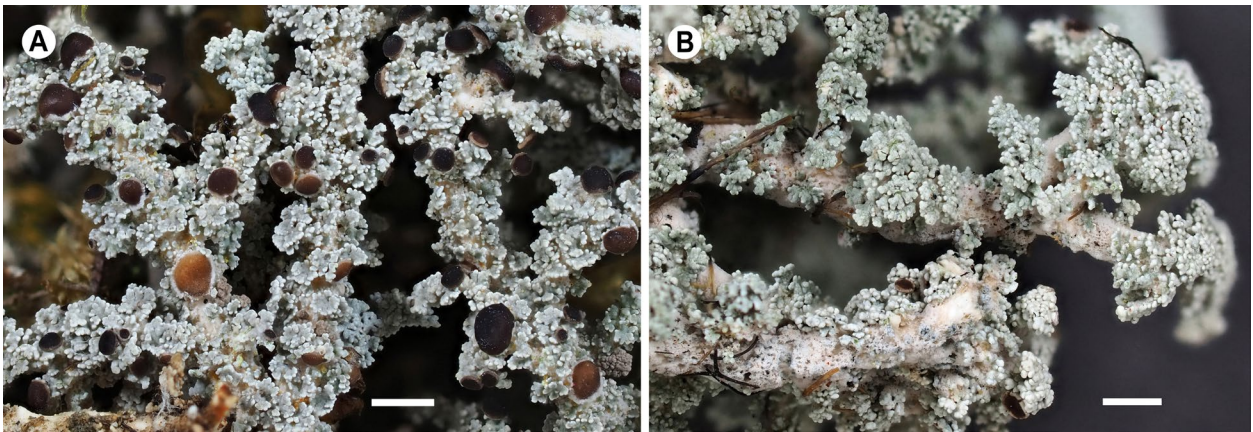


Figure 3. *Stereocaulon tomentosoides*. A – upper surface of branches, E. Di Meglio 07; B – lower surface of branch, E. Di Meglio 05. Scales = 1 mm.

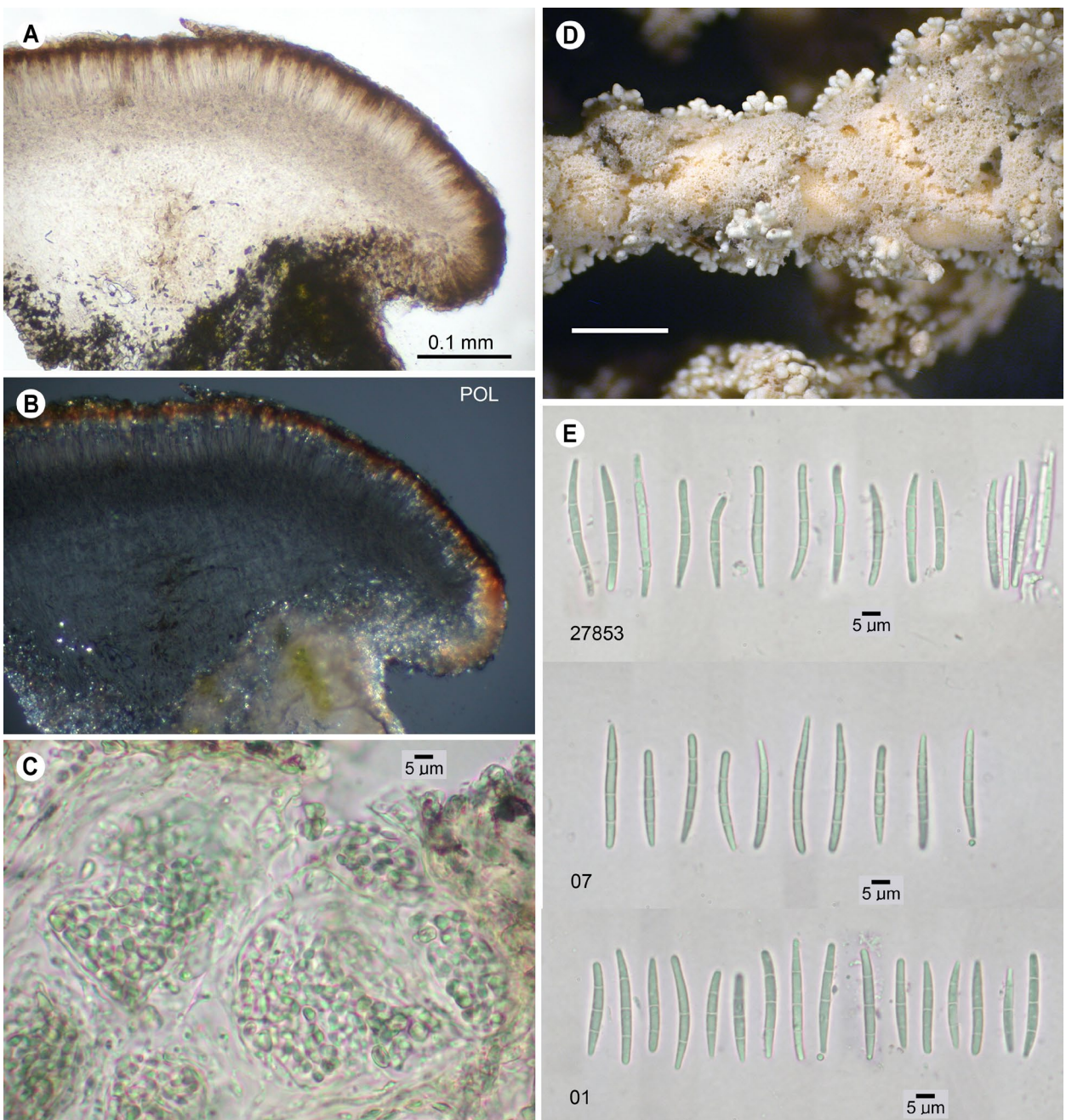


Figure 4. *Stereocaulon tomentosoides* morphological details. A – apothecial section, McCune 38972; B – apothecial section same as A, but under polarized light; C – section through cephalodium containing *Nostoc*, McCune 7761; D – closeup of tomentum on branches, McCune 19570; E – ascospores, McCune 27853, E. Di Meglio 07, E. Di Meglio 01.

Idaho and western Montana; north to Vancouver Island and coastal British Columbia.

The range of *S. sasakii* var. *tomentosoides* reported by Lamb (1977) is problematic, including many specimens from Asia that presumably belong to *S. sasakii* s.str. He also cited several states and provinces for *S. sasakii* var. *tomentosoides* from which we have not found examples (Colorado, New Mexico, Minnesota, Michigan, and Yukon Territory). Unfortunately, specific specimens were not cited and we have not yet found these in herbaria, nor are they likely to occur, given the clear affinity of *S. tomentosoides* to the oceanic Pacific Northwest (Fig. 5).

Discussion. *Stereocaulon sasakii* is similar to *S. tomentosum* in being tomentose, having numerous small apothecia, and containing *Nostoc*, but differs in the presence of lobaric acid rather than the stictic acid complex. *Stereocaulon sasakii* was most closely related to *S. alpinum*, *S. rivulorum*, and *S. groenlandicum*, relying on ITS and nuLSU sequences of Sasaki 13823 and 13825 (Japan: Honshu, both in H) by A. Thell and F. Högnabba. Based on these and other specimens from Japan and Far East Russia, morphological separation from *S. tomentosum* would be difficult, although the apothecia of *S. sasakii* can become strongly convex and marginless form early on and the tomentum of *S. sasakii* is often less developed than in *S. tomentosum*. From *S. alpinum*, *S. sasakii* is differentiated by its numerous small, terminal and lateral apothecia in contrast to the fewer, larger, terminal apothecia of *S. alpinum*. Out of hundreds of potential candidates, no sequenced North American specimens from the *Stereocaulon* core have grouped with *S. sasakii* from Japan.

Thus, we have no phylogenetic evidence for *S. sasakii* occurring in North America. Interestingly, Lamb (1977) foreshadowed this finding for *S. sasakii* var. *tomentosoides*: "...may eventually prove to be specifically distinct from *St. sasakii*; the different main distributional area would lend support to this view."

Lamb (1977) also applied the name *S. sasakii* var. *tomentosoides* to specimens from Asia, but he chose the type for that variety from North America. The name that should be used for Asian specimens that Lamb annotated as *S. sasakii* var. *tomentosoides* is uncertain. Specimens fitting his concept for the variety from Asia need to be sequenced to resolve this. They could potentially still be recognized as part of *S. sasakii*, but under a new varietal name, or as one or more undescribed species.

Fertile *Stereocaulon tomentosoides* is most likely to be confused with *S. tomentosum*, but when sterile it could easily be confused with several other species, especially *S. alpinum* clade D, a fairly frequent species roughly sympatric with *S. tomentosoides* and also endemic to the Pacific Northwest of North America, but extending farther north along the Pacific coast than *S. tomentosoides* (Fig. 6). This clade is not actually monophyletic with the remainder of *S. alpinum*, but it morphologically appears like a robust morph of *S. alpinum*. Work is ongoing to find morphological characters to separate this putative new species from the remainder of *S. alpinum*. We defer describing it until we can more clearly separate it by morphology and distribution from the other clades of "*S. alpinum*".

In contrast to the sympatry of *S. tomentosoides* and *S. alpinum* clade D, *S. tomentosoides* overlaps only slightly in range with *S. tomentosum*, for example in

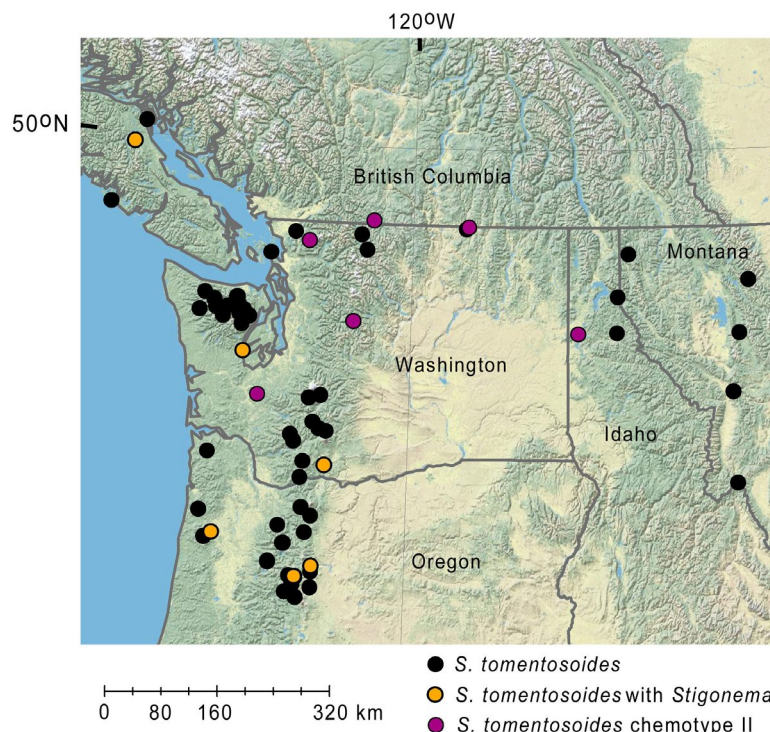


Figure 5. Distribution of *Stereocaulon tomentosoides* in the Pacific Northwest of North America. Black dots indicate the usual chemotype I (lobaric acid) with *Nostoc* as cyanobiont. Yellow dots indicate specimens with *Stigonema* as the cyanobiont. Red dots indicate chemotype II with both stictic and lobaric acids.

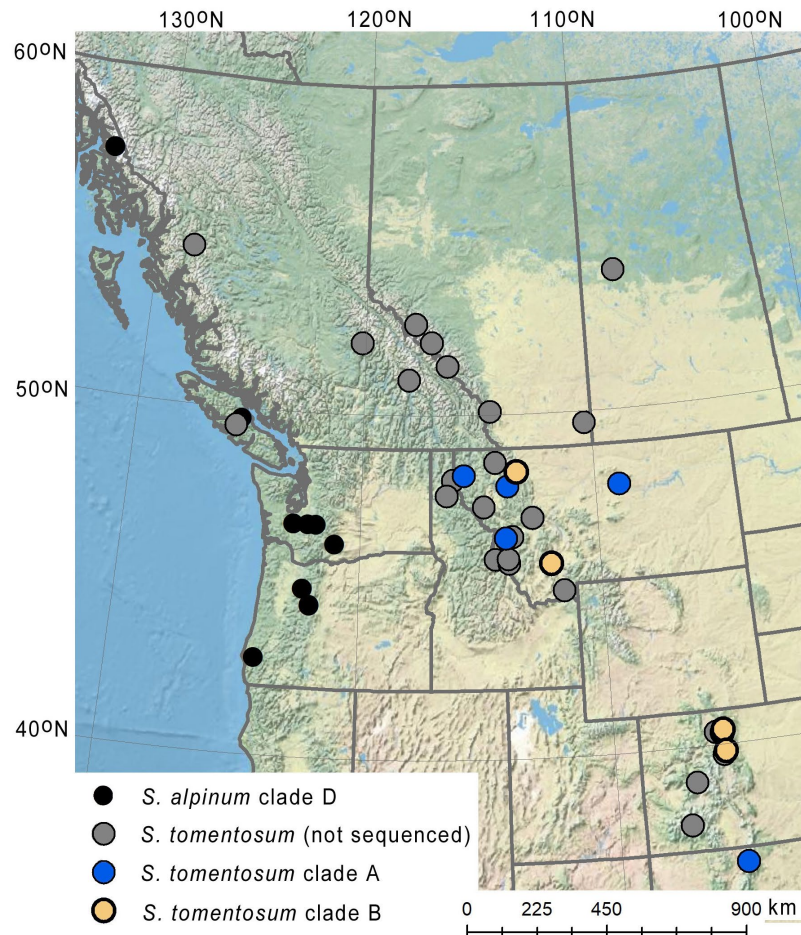


Figure 6. Distribution of *Stereocaulon tomentosum* and “*S. alpinum* clade D” in the Pacific Northwest of North America. Blue and yellow dots indicate the two major clades of *S. tomentosum*, gray dots indicate specimens seen, but not sequenced, and black dots indicate *S. alpinum* clade D. Specimens in that clade are similar in morphology and chemistry to *S. alpinum* and are known only from western North America, but fall well outside of other *S. alpinum* clades in phylogenetic trees.

northern Idaho (compare Fig. 5 with Fig. 6). As currently circumscribed, *S. tomentosum* is polyphyletic (Fig. 2), with clade A globally widespread and clade B so far restricted to the Rocky Mountains (Fig. 6).

Sterile material of *S. tomentosoides* can be difficult to separate from “*S. alpinum* clade D”. Both are fairly common, large species occurring in lowland to montane habitats in western Oregon and Washington. They commonly co-occur. *Stereocaulon tomentosoides* is more often fertile than *S. alpinum* clade D, but perhaps the best distinguishing character is that *S. alpinum* clade D has completely white phyllocladia when fresh, whereas in *S. tomentosoides*, the more broadly expanded crenate-lobulate phyllocladia often have a bluish tint when slightly shaded, contrasting with the knobby white margins (Fig. 3A and Brodo et al. 2001, p. 668). In the herbarium that bluish tint fades to olive or tan. Additionally, the species have subtle differences in the form of the phyllocladia (Fig. 7). In both species, the phyllocladia begin as warty, then become branched-lobate. In *S. tomentosoides*, however, they more often become flattened lobulate with a crenate edge, or sometimes palmate. Both species show a similar range of stance with erect forms and sprawling dorsiventral forms. The distinction between *S. alpinum* and *S. tomentosoides* is often difficult enough to remind us to look for apothecia when collecting these species.

Because of historical identification problems, maps produced for *S. sasakii* in North America by the Consortium for Lichen Herbaria (CLH) show a much broader range than that of verified *S. tomentosoides*. Similarly, hundreds of specimens of *S. tomentosum* are mapped in the oceanic Pacific Northwest, most of which should probably be reassigned to *S. tomentosoides* and *S. alpinum* clade D (see key below).

Stereocaulon tomentosum and *S. tomentosoides* are usually easily distinguished from each other by spot tests or TLC. The medulla of *S. tomentosum* is always P+ orange (often developing slowly; wait 3 minutes), K+ yellow to orangish, and KC-, always containing stictic acid, usually accompanied by minor or trace amounts of norstictic acid. In contrast, the medulla of *S. tomentosoides* is normally P- and KC+ orangish, containing lobaric acid. We have demonstrated by sequencing and TLC, however, an infrequent chemotype of *S. tomentosoides* that produces both lobaric and stictic acids. To our knowledge, this is the only species of *Stereocaulon* in which those two substances are found together.

Stereocaulon myriocarpum is another species producing small, dispersed apothecia similar to those of *S. tomentosum* (Lamb 1977, 1978). He reported this species from a very broad geographic range, including specimens similar in form and lichen substances to *S. tomentosum*,

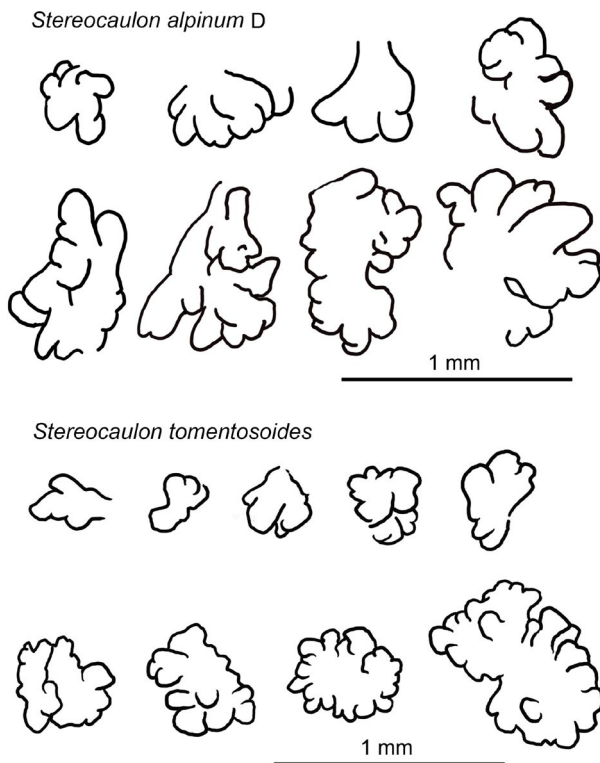


Figure 7. Comparison of typical phyllocladia of *Stereocaulon alpinum* clade D and *S. tomentosoides*.

but having less well-developed tomentum. Lamb (1977) applied the name *S. myriocarpum* Th. Fr. so broadly as to be almost certainly polyphyletic, with a wide range in western North America and a second area of occurrence in Asia, but absent in Europe. He included specimens that we would place in *S. tomentosum* or *S. alpestre* (Flot.) Dombr. Nevertheless, Lamb (1977) questioned the merit of the species: "...perhaps too closely related to *St. tomentosum* to qualify as a good, distinct species. Distinction from *St. tomentosum* var. *alpestre* Flot is often difficult, especially in North America. The distinguishing characters against *S. tomentosum* are the thinner and smoother tomentum and the more developed cephalodia (subglobose, botryose-divided, blueish-gray)."

We interpret *S. myriocarpum* more narrowly, applying it only to Central American specimens, where it appears morphologically and phylogenetically distinct from *S. tomentosum* and related species. The type locality is in Mexico (2700–3100 m, El Pelado, Sierra de Oaxaca); however, no specimens of *Stereocaulon* with DNA sequences have grouped with Central American *S. myriocarpum*, so perhaps it does not occur north of Mexico. So few sequenced specimens are available from South America that we can say nothing with certainty about the occurrence of *S. myriocarpum* on that continent.

Like *S. tomentosum*, *S. tomentosoides* usually has *Nostoc* in the cephalodia, but a handful of *S. tomentosoides* specimens (tabulated below) from the Cascade Range, Olympic Peninsula, and Vancouver Island had *Stigonema* rather than *Nostoc*, but resembled *S. tomentosoides* in other respects. The *Stigonema*-containing cephalodia were warty to compound warty, grayish, and tomentose. Most

records of *S. tomentosoides* with the *Stigonema* cyanobiont were from mossy lava flows.

One unusual specimen (Gasser 307, Oregon: Lane Co.) had both cyanobacterial partners, each in a different form of cephalodia. The cephalodia with *Stigonema* were on the upper surface, brownish, hardly tomentose, and compound warty. The cephalodia with *Nostoc* were on the lower surface, grayish, tomentose, and granular.

We sequenced three *Stigonema*-containing *S. tomentosoides* (McCune 36778, 38972, 39500) and they did not segregate from *Nostoc*-containing specimens within the *S. tomentosoides* clade. Given the plasticity of the cyanobacterial association and our finding no consistent difference in the sequences of fungal partners from the different cyanobacterial associations, we assign no taxonomic rank to the difference.

Specimens with unbranched or sparingly branched stalks and with sparse phyllocladia have been called *S. sasakii* var. *simplex* (Riddle) Lamb (\equiv *S. tomentosum* var. *simplex* Riddle; photo in Riddle 2010). Like *S. tomentosoides* the tomentum is thick and woolly and apothecia are mainly lateral and <1 mm diam.

The type of *S. tomentosum* var. *simplex* was collected in Washington. According to Lamb (1977) the variety is distinguished by the simple to sparingly branched pseudopodetia and the scanty and scattered phyllocladia in a thick spongy tomentum. The type contains atranorin and lobaric acid, according to Lamb. We revisited the approximate location of the type locality, attempting to collect the *simplex* morphotype as close as possible to the type population. These specimens ranged from having decumbent branches with dense phyllocladia and often sterile to the 3-dimensional freely branched and often fertile typical form to non-dorsiventral, upright, sparingly branched forms. Sequences from all of these specimens were recovered in clades of *S. tomentosoides* and *S. alpinum* clade D, including sterile specimens that were ambiguous between *S. tomentosoides* and *S. alpinum*. We therefore interpret *S. sasakii* var. *simplex* in North America as one extreme of a gradation in forms taken by both *S. tomentosoides* and *S. alpinum* clade D. The *simplex* growth form has stronger vertical growth, presumably an environmental modification in response to a competitive environment with other tall lichens and tall mosses. Similar modification is likely in *S. sasakii* from Japan, and occurs in other larger terricolous *Stereocaulon*. Some of these have been given infraspecific names, such as *S. alpinum* var. *erectum* Frey. Because the type of *S. sasakii* var. *simplex* is fertile, showing numerous small apothecia, we are confident that it belongs to *S. tomentosoides*, but the name has certainly also been applied to erect morphs of *S. alpinum* clade D.

An infrequent chemotype (chemotype II) contains both lobaric and stictic acids, in addition to the usual atranorin. This is the only *Stereocaulon* species in which we have found both lobaric and stictic acids together in the same thallus. Because this is so rare at the genus level, in each case these anomalous results were verified by repeating the TLC runs. So far, we have found seven specimens of chemotype II (listed below). ITS and nuLSU sequences

were available for two of these specimens and they did not segregate as a supported clade.

Specimens examined of *S. tomentosoides* chemotype I, with *Nostoc cyanobiont*, Canada. BRITISH COLUMBIA, Vancouver Island: Victoria, 14 Apr 1887, Macoun 406a (CANL); Quadra Island: trail to Mount Seymour, 50.1738°N, 125.2867°W, 461 m, old logging road through *Thuja* – *Tsuga* forest, 23 Jun 2018, McCune 37704 (OSC); Lillooet Land Distr.: Pemberton, Garibaldi Mountains, 6 miles S of Pemberton, close to Green River, 50.2167°N, –122.867°W, 457 m, talus slope, 10 Jun 1966, Brodo 8244 (Lich. Canad. Exs. 65 as *S. myriocarpum*, CANL, etc.).

Specimens examined of *S. tomentosoides* chemotype I, with *Nostoc cyanobiont*, USA. IDAHO, Bonner Co: 10 km east of Clark Fork, 48.1000°N, 116.1000°W, 671 m, talus, Jul 1977, McCune 7761 (OSC); Shoshone Co: 0.5 km west of mouth of Coal Creek at Coeur d'Alene River, 13 km N of Kellogg, 47.6333°N, 116.1167°W, 690 m, north-facing talus slope, Aug 1987, McCune 16537 (OSC). MONTANA, Beaverhead Co: Chief Joseph Pass, 45.6833°N, 113.9317°W, 2100 m, *Pinus contorta* forest, 19 Jun 1981, McCune 10970a (OSC); Flathead Co: Near Paola Creek on US 2, T31N R16W S28, 48.3000°N, 113.6167°W, 1128 m, *Pinus contorta* forest, Jul 1977, McCune 7688 (OSC); Lake Co: Jim Creek Lookout Trail, T21N R17W S6, 47.6167°N, 113.8167°W, 1060 m, *Abies grandis* – *Thuja* forest, Aug 1977, McCune 8107 (OSC); Lincoln Co: Above Yaak River, near Yaak Falls, 48.6500°N, 115.8833°W, 750 m, 6 Sep 1977, McCune 8996a (OSC); Missoula Co: north slope of Mt. Sentinel near Missoula, 46.8583°N, 113.9667°W, 1021 m, May 1974, McCune 6049 (OSC). OREGON, Clackamas Co: 45.3200°N, 121.9000°W, 640 m, Summer 1945, Overlander 30228 (OSC), SW of Wapanitia Pass on Cascade Crest Trail, near Mt Hood on Highway 26, 45.2143°N, 121.7195°W, 1300 m, talus openings in montane *Abies-Tsuga* forest, 9 Jun 2017, McCune 37388 (OSC), above Lukens Creek, Cascade Range, 45.0750°N, 122.3000°W, 600 m, partly forested area of basalt outcrops, with *Pseudotsuga* – *Tsuga heterophylla* forest, Sep 1994, McCune 21962 (OSC); Clatsop Co: near summit of Saddle Mountain, Coast Range, 45.9667°N, 123.6667°W, 860 m, mossy outcrops on open rocky ridgetop, Oct 1993, McCune 21382 (OSC); Jefferson Co: near Trout Creek, east slope of Cascade Range, 44.3000°N, 121.6667°W, 1000 m, May 1990, McCune 18667 (OSC); Lane Co, Cascade Range, Middle Fork Willamette River drainage, Plot 2081146, 48.8620°N, 122.2520°W, 1097 m, talus slope of volcanic rock, open forest, 6 Aug 2001, Gasser 307 (OSC), HJ Andrews Experimental Forest, along road 1506 above Lookout Cr, 44.2289°N, 122.1236°W, 994 m, roadside, 3 Dec 2021, McCune 39353 (OSC), junction of Forest Roads 2676 and 710, ~2 km NNE of Clear Lake, Cascade Range, 44.3898°N, 121.9936°W, 976 m, roadside, through mature *Pseudotsuga* forest, 16 Oct 2020, McCune 38901 (OSC); Linn Co., Crabtree Lake, 44.6100°N, 122.4500°W, 22 May 1981, Denison 45852 (OSC), Fish Lake off of Highway 126, 44.4043°N, 122.0019°W, 1040 m, 7 May 2016, E. Di Meglio 05 (OSC), NW rim of Nash Crater, Cascade Range, 44.4167°N, 121.9500°W, 1425 m, *Pseudotsuga* – *Abies* – *Tsuga mertensiana* forest, 17 May 1992, McCune 19665 (OSC), Shaffer Creek RNA/ACEC, Cascade Range, 44.6000°N, 122.4500°W, 1065 m, talus above old-growth *Abies-Tsuga* forest, 10 Apr 1992, McCune 19632 (OSC), near McKenzie River near Sahalie Falls, 44.3500°N, 122.0000°W, 860 m, old forested lava flow near river, Aug 2000, McCune 25477 (OSC), 1/4 mile east of Hackleman old growth forest on Highway 20, 44.4407°N, 122.0588°W, 1040 m, 3 Jun 2015, E. Di Meglio 01 (OSC), near Fish Lake, on side of Highway 126, 44.4043°N, 122.0019°W, 1040 m, 3 Jun 2015,

E. Di Meglio 03a (OSC); Marion Co, Mt Hood National Forest, plot 2123166, 44.9951°N, 121.8195°W, 1219 m, shaded, 29 Aug 2001, Boyll 2123166-22 (OSC); between Ruth Mine Trail and Battle Ax Creek, 44.8499°N, 122.2025°W, 701 m, rocky cliffs, 21 May 2016, E. Di Meglio 07a (OSC); Ruth Mine, Opal Creek Scenic Recreation Area, Cascade Range, 44.8528°N, 122.1875°W, 774 m, edge of disturbed area from historical mining, 19 May 2018, McCune 28392, 37650 (OSC); Polk Co: Fanno Meadows, TNC meadow #2, Coast Range, 44.8752°N, 123.6315°W, 869 m, open *Sphagnum* wetland surrounded by *Abies procera* forest, with other conifers, 24 May 2006, McCune 28249 (OSC); Tillamook Co: rocky area on top of Mt Hebo, 45.2140°N, 123.7570°W, 960 m, 11 Jun 1991, Testa s.n. (OSC). WASHINGTON, Clallam Co: Deer Park Environmental Protection Agency, approx. 3.5 miles up Deer Creek, 47.9763°N, 123.3022°W, 1040 m, single story, fairly open 250 yr. old *Pseudotsuga* forest, 27 May 1999, Hutten 18 (OLYM), trail near Grand Lake, 47.8917°N, 123.3460°W, 1461 m, *Abies lasiocarpa* forest with herbaceous meadows and occasional rock outcrops, 31 Aug 2000, Hutten 4351 (OLYM), Appleton Pass ABAM Plot 1, 47.9354°N, 123.7376°W, 1292 m, 15 Aug 2000, Hutten 3785 (OLYM); Jefferson Co: Tunnel Creek Rd, Big Quilcene watershed, E side Olympic Peninsula, 47.7878°N, 123.9970°W, 450 m, S slope with *Pseudotsuga* – *Tsuga* forest, Mar 2011, McCune 31033 (OSC), Heather Creek ford, about 2 mi N of shelter remains, 47.8185°N, 123.1614°W, 987 m, *Pseudotsuga*-dominated forest, 21 Jul 2001, Hutten 5513 (OLYM), near bottom end of Hawk Creek, 47.7639°N, 123.2460°W, 810 m, conifer forest, dominated by *Pseudotsuga* and *Tsuga heterophylla*, 19 Jul 2000, Hutten 3456 (OLYM); Lewis Co, Skate Creek Road above Nisqually River, 46.7287°N, 121.8541°W, 786 m, rocky roadcut, 30 Jun 2020, McCune 38735 (OSC), Wonderland Trail above Muddy Fork Cowlitz River, Cascade Range, 46.7661°N, 121.6347°W, 932 m, outcrop opening in conifer forest, 9 Jun 2021, D. Smith 126 (OSC), near Blue Hole, Cispus River, Randle Ranger District, 396 m, young stand of *Pseudotsuga* on outwash gravel area along river, 8 Sep 1992, Riley 103 (OSC); Skagit Co, Cypress Island, near Mainline Road, SW part of island, 48°34'32.6"N, 122°42'31.8"W, *Pinus contorta* and *Pseudotsuga* forest, grassy area by road, 13 Sep 2022, Glew 220913-3 (WTU); Skamania Co, below Falls Creek Falls, 45.9100°N, 121.9140°W, 609 m, 20 May 1926, Ingram 2019 (OSC), Mt. St. Helens National Monument, Pumice Plains, near Crisafulli Plot PMP WEB, 46.2471°N, 122.1654°W, 1110 m, open volcanic flats and slopes, 14 Sep 2012, McCune 32304, 32305 (WTU), near Adams Fork Campground, ~25 km S of Packwood, 46.3393°N, 121.6480°W, 786 m, small, rocky roadcut surrounded by conifer forest, 30 Jun 2020, McCune 38732, 38733, 38736 (OSC), lahar on SE side of Mt St Helens, 46.1648°N, 122.1015°W, 926 m, nearly flat with scattered young conifers (*Pseudotsuga*, *Pinus*) and dense *Racomitrium* mats, 16 Sep 2012, McCune 32368 (WTU), Mt. St. Helens National Monument, 46.2462°N, 122.1691°W, 1136 m, open volcanic slopes, andesite boulders on N slope, 14 Sep 2012, McCune 32314 (WTU), below east end of Red Bluffs, north side of Columbia River Gorge, 45.7000°N, 121.9500°W, 365 m, along road through second growth *Pseudotsuga* forest, Apr 1993, McCune 20351 (OSC); Whatcom Co., Ross Lake, E side, near Dry Creek Campground, Ross Lake, 48.85587°N, 121.01898°W, 490 m, on mossy rock, 8 Jun 2021, K. Beck 2323 (herb. Beck); East Bank Trail, by Hwy 20, montane, open mixed conifer forest, 48.66729°N, 120.8718°W, 740 m, 16 Aug 2016, Beck 439; Yakima Co, Muddy Creek Lava Flow, N side Mt. Adams, N of Muddy Fork Cispus River, 46.3059°N, 121.5149°W, 1415 m, open lava flow with widely scattered conifers, Sep 2009, McCune 30229 (OSC).

Specimens examined of *S. tomentosoides* chemotype II, Canada. BRITISH COLUMBIA, Manning Prov Park: South Skagit River valley, 13.4 miles S of E gate, 850 m, ravine and talus slope, 31 May 1966, Brodo 7846 (CANL!, UBC).

Specimens examined of *S. tomentosoides* chemotype II, USA. IDAHO, Shoshone Co., between Prichard Creek and Thompson Pass Road, 1 km SE of Murray, 47.6219°N, 116.8472°W, 861 m, old placer mine tailings, 20 Jul 2020, McCune 38771 (OSC). WASHINGTON, King Co.: Stevens Pass area, subalpine meadow, 47.73762°N, 121.0970°W, 1390 m, 13 Aug 2013, Beck 725 (OSC); Lewis Co., above Nisqually River SW of Longmire, near park boundary, 46.7353°N, 122.8185°W, 790 m, forest floor, open old conifer forest on rocky high bench, 30 Jun 2020, McCune 38744 (OSC); Okanogan Co., Buckhorn Mt area, near W Fork Cedar Creek and Canada border, 48.99316°N, 118.9401°W, 1095 m, 29 Jul 2013, Beck 92, near Gold Cr, 48.96416°N, 118.9870°W, 1290 m, 17 Jun 2010, Beck 185 (OSC); Whatcom Co., Elbow Lake Rd, Middle Fork Nooksack River, 48.75635°N, 121.9780°W, 490 m, 25 Sep 2017, Beck 506 (OSC).

Specimens examined of *S. tomentosoides* with *Stigonema* cyanobiont, Canada. BRITISH COLUMBIA, Vancouver Island: shore of Upper Campbell Lake, outcrops above Strathcona Lodge on 49.8919°N, 125.4868°W, 320 m, rock outcrops surrounded by conifer forest, Aug 2005, McCune 27853a (OSC).

Specimens examined of *S. tomentosoides* with *Stigonema* cyanobiont, USA. OREGON, Jefferson Co: lava flow near Candle Creek, from E slope of Mt. Jefferson, E slope Cascade Range, 44.5750°N, 121.6667°W, 900 m, scattered conifers on old lava flow, May 1998, McCune 24120 (OSC); Linn Co., Highway 126 S of Clear Lake, 44.4305°N, 121.9616°W, 1134 m, semi-forested lava flow with scattered *Pseudotsuga menziesii* and shrubs, 20 Jun 2022, McCune 39500 (OSC). WASHINGTON, Klickitat Co: Just north of BZ Corner on Highway 141, 45.8714°N, 121.5157°W, 267 m, mossy lava flow surrounded by conifer forest, 21 May 2016, McCune 36778a (OSC); Mason Co., S of junction of E McReavy and E Webb Hill Road near Cranberry Lake, 47.2832°N, 123.1313°W, 100 m, gently sloping roadcut in gravelly soil, with *Racomitrium* and *Cladonia*, 8 Jun 2021, McCune 38972 (OSC); Whatcom Co: Sulfur Creek lava flow, Cascade Range, 44.9333°N, 123.5000°W, 550 m, sparse conifer forest on edge of lava flow, 28 Mar 1992, McCune 19565, 19570 (OSC).

***Stereocaulon cyaneum* McCune, sp. nov.** (Fig. 8)

Mycobank MB 849816

Diagnosis: Similar in most respects to *S. tomentosum*, but with bluish coloration, wet or dry (losing this color after years in the herbarium), and with consistently heavy and puffy tomentum.

Barcode: OR475499 (holotype).

Type: USA, Minnesota, Itasca Co., mine dumps S of Lower Prairie Lake, N of Grand Rapids and Highway 61, 47.2855°N, 93.5031°W, 407 m, iron-rich mine tailings, semi-forested, Aug 2021, McCune 39017 (OSC – holotype; MIN – isotype).

Description. Thallus fruticose, similar to *S. tomentosum*, to about 6 cm tall, forming decumbent to suberect mats; distinctly bluish in the field, wet or dry, but gradually losing this color in the herbarium; shoots dorsiventral, to 7 cm long or more, branching frequent; primary thallus not seen; phyllocladia granular or warty, becoming

± branched lobate (+/– planar), palmate, flattened lobulate; cortical windows absent; tomentum very thick, puffy, beige, cream, grayish, or tan, shedding in patches; soredia unknown; cephalodia compound granular or compound warty, often diffuse and small groups, bluish white, tomentose and commonly hidden by the thick tomentum; cyanobiont usually *Nostoc*, the cells usually 4.0–5.5 µm in diam, in one case *Stigonema*.

Apothecia common, usually numerous when present, terminal and lateral, relatively small, to 0.8(1.0) mm diam; ephihymenium POL+; hymenium 44–53 µm, POL– or POL+; hypothecium hyaline to pale tan, POL–; ascospores fusiform, straight to slightly curved, 1–3-septate, 22–34 × 2.0–2.9 µm, median 26–30 × 2.3–2.7 µm. Pycnidia not seen.

Chemistry. Thallus containing atranorin and stictic acid, ± norstictic acid and associates; cortex K+ yellow, P+ pale yellow, UV–; medulla K+ orange-red, P+ orange, UV–.

Etymology. The epithet “*cyaneum*” refers to the pale bluish coloration of the thallus.

Ecology and substrate. On soil, humus, or moss, or loosely attached in rock crevices or on humus over noncalcareous rock; well-lit forest floors, openings, rock outcrop areas, and roadcuts.

Distribution and abundance. So far known only from the western Great Lakes region of North America (Fig. 9), with locations in northern Minnesota and western Ontario, but likely to be more widespread.

Discussion. Although very similar to typical *S. tomentosum*, including growth form, phyllocladia, spores, habitat, and chemistry, *S. cyaneum* forms a clade that is sister to *S. dactylophyllum*. *Stereocaulon cyaneum* differs from *S. tomentosum* in coloration, but would otherwise be mistaken for that species. From *S. dactylophyllum* it differs in coloration, substrate (soil rather than rock), and the production of numerous small apothecia similar to those of *S. tomentosum*.

Specimens examined, Canada. ONTARIO, Dryberry Lake cabin, 49.5480°N, 93.7497°W, 348 m, granitic outcrops and boreal forest near lake, Sep 2019, McCune 38459 (OSC).

Specimens examined, USA. MINNESOTA, Itasca Co: mine dumps S of Lower Prairie Lake, N of Grand Rapids and Highway 61, 47.2855°N, 93.5031°W, 407 m, iron-rich mine tailings, semi-forested, Aug 2021, McCune 39014 (OSC), above lake (Arcturus Mine), west of Marble and north of Highway 169, Mesabi Range, 47.3230°N, 93.3148°W, 411 m, partly forested edge of rubble pile, 4 Aug 2018, McCune 37721 (OSC), mine tailings on State Park Road, ~1.5 km NE of Calumet, 47.3311°N, 93.2642°W, 450 m, N facing side of tailings, 4 Nov 2022, Liulevicius 2 (MIN); 47.3314°N, 93.2649°W, 444 m, N base of tailings mound, rocky slope, 4 Nov 2022, Liulevicius 1 (MIN); St. Louis Co: S of Crane Lake, E side of Crane Lake Road, 48.2536°N, 92.4890°W, 375 m, roadside outcrops, partly shaded, 10 Aug 2018, McCune 37725 (OSC); St. Louis Co: Gheen Hill, west of Highway 53, S of Orr, 47.9781°N, 92.8267°W, 451 m, open *Pinus resinosa* forest, 10 Aug 2018, McCune 37728 (OSC).

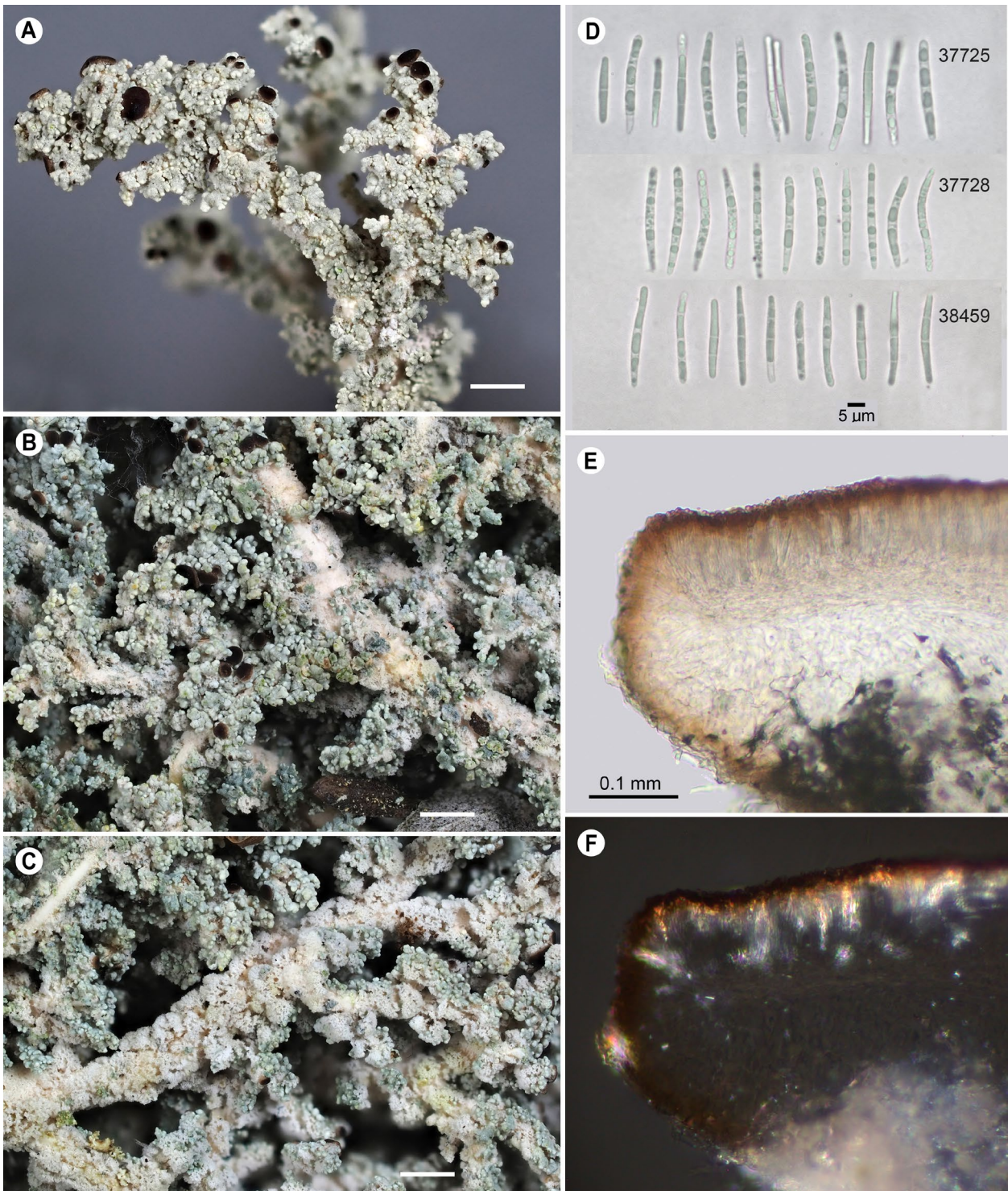


Figure 8. *Stereocaulon cyaneum*. A – habit, McCune 37728; B – phyllocladia in top view, McCune 38459; C – lower surface of branches showing tomentum, McCune 38459; D – ascospores, McCune 37725, 37728, 38459; E – apothecial section; F – same as E, but under polarized light. Scales = 1 mm unless otherwise stated.

Key to large, ground-dwelling species of *Stereocaulon* in the oceanic Pacific Northwest of North America

- 1 Medulla P+ orange (stictic acid present) 2
- Medulla P– (stictic acid lacking) 4
- 2(1) Phyllocladia becoming compound warty, flattened lobulate phyllocladia infrequent or absent, when present thick and convex rather than planar. Arctic Alaska rarely south to coastal Alaska; Fennoscandia *S. alpestre*

- Phyllocladia becoming flattened-lobulate; distribution circumboreal to montane 3
- 3(2) Thallus UV+ whitish, lobaric acid present in addition to stictic acid and satellite compounds; distribution Cascade Range inland to Montana
- infrequent chemotype, *S. tomentosoides*
- Thallus UV–, lobaric acid absent, containing only stictic acid and satellite compounds; distribution mainly east and north of Cascade Range *S. tomentosum*

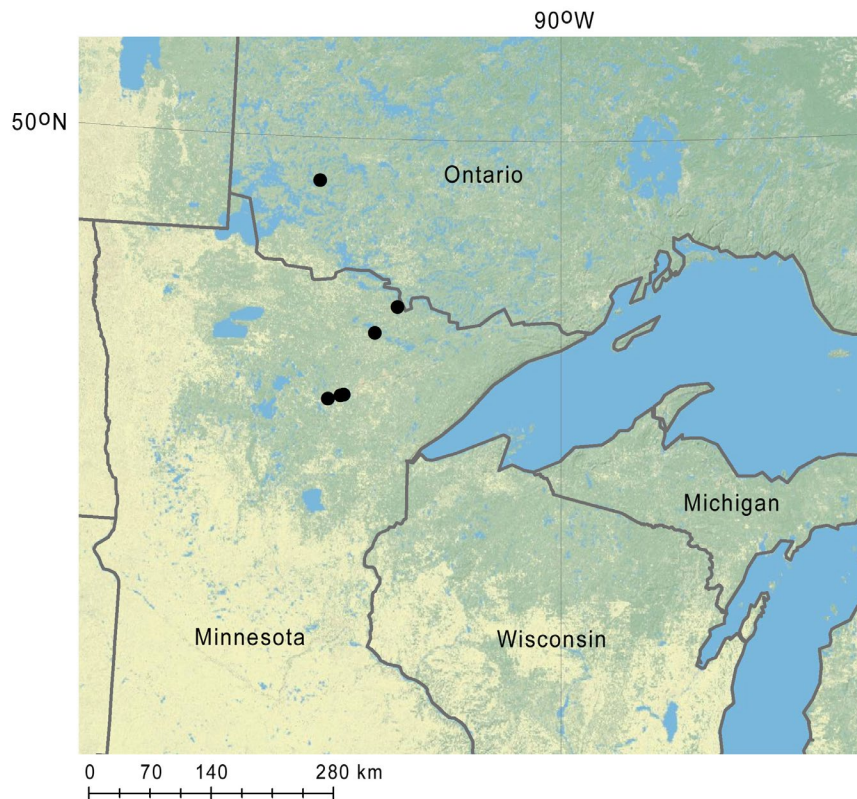


Figure 9. Distribution of *Stereocaulon cyaneum* in the Great Lakes region of North America.

- 4(1) Apothecia present. 5
 Apothecia lacking. 6
- 5(4) Apothecia numerous, small (mostly < 1 mm diam), lateral, terminal, or terminal on short side branches.
 *S. tomentosoides*
 Apothecia large (commonly > 1 mm diam), primarily terminal. "*S. alpinum* clade D"
- 6(4) Phyllocladia warty to branched lobate, flattened lobulate with crenate edge, or palmate; expanded or flattened phyllocladia of fresh dry specimens commonly bluish tinged with white edges, the bluish tinge fading to pale olive or tan in the herbarium *S. tomentosoides*
 Phyllocladia warty to branched-lobate and ± flattened; expanded or flattened phyllocladia of fresh dry specimens white "*S. alpinum* clade D"

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Supplementary electronic materials

Table S1. Sequences of DNA used for phylogenetic inference. Specimens with new sequences are indicated by bold face. [Download file](#)

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