Five new crustose *Stereocaulon* species in western North America

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**ABSTRACT.** Crustose *Stereocaulon* species have only recently been reported from North America, and targeting them specifically in recent fieldwork revealed an unexpected diversity of species. We sampled crustose *Stereocaulon* species in western North America from Alaska to Oregon and analyzed them by morphology, DNA sequencing, and thin-layer chromatography. Five new species were found, along with one species known from northern Europe and North America (*S. leucophaeopsis*), a second one previously known only from northern Europe and eastern North America (*S. plicatile*), and one previously known western North American endemic (*S. nivale*). Each of these species is supported by DNA sequences, as well as morphological and chemical characters, such that they can be distinguished by simple spot tests and morphology. One exception is that *S. leucophaeopsis* and *S. areolatum* may be difficult to distinguish when sterile without a DNA sequence. The number of crustose *Stereocaulon* species known from North America is increased from 3 to 8. Seven of those eight species occur in the national parks of southwestern Alaska (Katmai, Lake Clark, and Kenai Fjords). Two of the eight are known from Oregon and Washington.

**KEYWORDS.** Lichenized fungi, *Stereocaulon areolatum*, *Stereocaulon cephalocrustatum*, *Stereocaulon secundum*, *Stereocaulon hypothallinum*, *Stereocaulon nivale*, *Stereocaulon oregonense*, *Stereocaulon plicatile*, Stereocaulaceae.

Although *Stereocaulon* is usually an easily and reliably identified genus in the field, crustose *Stereocaulon* species are much less well known. In the field the whitish areolate thalli of crustose species of *Stereocaulon* are readily mistaken for those of *Porpidia* or Lecidea. In the lab, however, the septate spores of fertile crustose *Stereocaulon* readily differentiate it from those genera. The similarity in appearance of crustose *Stereocaulon* to those other common genera has probably resulted in undercollecting and consequently under-representation in regional floristic treatments. Furthermore, crustose *Stereocaulon* species are apparently infrequent in North America and rather selective as to microhabitat (Fryday 2006, 2010 and pers. obs.)

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Crustose *Stereocaulon* species were not included in the classic worldwide treatment of the genus by Lamb (1977). Recognition of crustose forms of *Stereocaulon* in North America began when Fryday & Glew (2003) concluded that *Bacidia nivalis* Follman from the Pacific Northwest (Follmann 1979) was actually a *Stereocaulon*. This species was unusual for *Stereocaulon*, not only because it was crustose, but also because it lacked cephalodia and contained only atranorin as a major lichen substance. Fryday (2006, 2010) then reported *S. plicatile* from eastern North America and another sorediate European species, *S. leucophaeopsis*, from Mt. Washington in New Hampshire. In the Pacific Northwest, McCune (2017) reported two species, *S. nivale* and *S. leucophaeopsis*. McCune et al. (2018) then reported *S. plicatile* and two additional undescribed crustose *Stereocaulon* species (*S. areolatum* and *S. hypothallinum*) from coastal southwest Alaska, both of those formally described here.
Meanwhile, Myllys et al. (2005), Högnabba (2006), and Högnabba et al. (2014) had been exploring the genus Stereocaulon with molecular tools. Högnabba et al. (2014) proposed the phylogenetic hypothesis that after divergence of two squamulose species (S. cumulatum and S. urceolatum), the crustose species formed a distinct group (Clade 3) that is sister to the remaining macrolichen Stereocaulon species. Alternative hypotheses for the basal structure of Stereocaulon were, however, nearly as well supported. One missing piece of the puzzle is the unusual squamulose to short-stalked, fertile species, S. azulense Yoshimura & W.A.Weber, described from the Galapagos Islands (Lichenes Exsiccati No. 645, Weber 1986) and apparently a local endemic. No sequences or recent specimens are available for this species and it was not mentioned in Högnabba et al. (2014).

Crustose Stereocaulon species are similar in most respects to their fruticose relatives, apart from gross morphology. One notable difference, however, is that the crustose species do not have well-organized cephalodia. These crustose species are, however, often associated with clumps of apparently free-living filamentous cyanobacteria, Stigonema. This appears to be another example of the case where tripartite cephalodiate macrolichens often have smaller relatives that lack an obligate cyanobacterial partner (Schneider et al. 2016). Schneider et al. hypothesized that evolutionary acquisition of cephalodia allowed the nutritional support of larger, faster growing thalli, providing an advantage in oligotrophic environments. This contrast can be found within the genera Pilophorus, Stereocaulon, as well as in the relationship between genera, for example increase in size and diversity from Trapelia to Placopsis (Schneider et al. 2016).

Searching for crustose Stereocaulon species in the Pacific Northwest and Alaska revealed that they were more common than previously recognized. Furthermore, many individuals appeared to have loose associations with the cyanobacterium Stigonema, in some cases in aggregations that appeared close to cephalodia.

Our purpose here is to re-appraise the crustose species of the genus Stereocaulon in western North America, specifically answering the following questions:

- Can the North American specimens of crustose Stereocaulon be accommodated in the similar-appearing taxa in Europe (S. leucophaeopsis, S. tornense)?
- Do additional species exist in North America, and if so, can they be defined by morphology, molecular tools, and lichen substances?
- Do cephalodial or other cyanobacterial associations with Stigonema occur in crustose Stereocaulon species?

Relationships among major clades across the genus of Stereocaulon require further work and currently cannot be reconstructed based on named specimens cited in nucleotide sequence databases due to inconsistent usage of names and misidentified or unidentified specimens. Furthermore, while a large number of new ITS sequences are available since Högnabba et al. (2014), coverage of other loci in Stereocaulon has not expanded much since their work. Therefore, we defer to Högnabba et al. (2014) as providing the best current backbone within the genus.

**Materials and Methods**

We applied standard microscopy and chemical spot test methods. Specimens 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.

Apothecial anatomy and measurements were studied with bright-field microscopy on freehand sections in water with no staining apart from 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 areoles were studied under the compound microscope in water, with bright field and polarized light (POL), KOH, and IKI. In all crustose Stereocaulon species the areoles are extremely brittle and difficult to section intact, so in most cases the structure of the areoles had to be pieced together from thin sections of fragments. Associated cyanobacterial colonies were hand sectioned and studied...
under the compound microscope to identify the cyanobiont genus and degree of lichenization.

**DNA extraction and PCR amplification.** We tried to obtain DNA sequences for all recent specimens available to us. 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 Stereocaulon (Högnabba 2006; Högnabba et al. 2014; Park et al. 2018; Vančurová et al. 2018).

For DNA isolation a 1 mm³ sample of thallus of each specimen was selected. To reduce the amount of secondary metabolites, the sample was washed in a 1.5 mL Eppendorf tube with one drop of 99.7% acetone for 30 min. The acetone was then removed via pipette and the remaining sample air dried for 10 min.

DNA was extracted without grinding using the REDExtract-N-Amp Plant PCR kit by Sigma-Aldrich. The procedure used was according to the manufacturer’s instructions except that 1/6th of the suggested amount was used for each sample: 15 µL extraction solution was added and incubated at 95°C for 10 minutes and finalized by adding 15 µL dilution solution.

When unsuccessful with the previous method, we used a larger sample FastDNA™ SPIN Kit (MP Biomedicals). Manufacturer’s instructions were followed with the Plant tissue CLS-VF and PPS cell lysis solutions. 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 (2×; Thermo Scientific Inc.), 3 µL nuclease free H₂O, 0.5 µL ITS1F (10 µL stock solution + 90 µL nuclease free H₂O) and 0.5 µL ITS4 (10 µL stock solution + 90 µL nuclease free H₂O). Each PCR reaction had 9 µL master mix and 1 µL DNA extract. PCR reaction conditions were initial denaturation at 94°C for 5 min, then 35 cycles of denaturation of 94°C for 30 sec, annealing at 52°C for 45 sec, and extension at 72°C for 1 min 45 sec, followed by an elongation cycle for 5 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.

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 manufacturer’s protocol 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, U.S.A.).

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 with those in GenBank to test for overlooked matches to existing taxa. Preliminary phylogenetic trees built with the addition of genus-wide sampling from GenBank showed support for our crustose specimens falling within Högnabba et al.’s (2014) crustose Clade 3. This is not shown because we do not have sufficient data to improve the genus-wide reconstruction over that provided by Högnabba et al. (2014). Note that two species that Högnabba et al. (2014) labeled “crustose” and fell outside of Clade 3 have, as Högnabba and colleagues pointed out, much larger thallus units (>4 mm diam) than the crustose species (<1 mm diam). Excluding those two species, which could be considered squamulose, leaves the monophyletic crustose “Clade 3” of Högnabba et al. (2014). Because our focus is on the separation of the crustose species, and the ITS region is quite variable among distant relatives within Stereocaulon, we...
could reduce ambiguities in the alignment by excluding many of the distantly related *Stereocaulon* species. We therefore realigned and analyzed a subset of the data focusing on the crustose species. This subset included new sequences from 20 crustose specimens along with the six pre-existing sequences from GenBank (Table 1). For the latter, we used ITS and nuLSU sequences for all closely related species, with special attention to crustose and squamulose species. This resulted in a total of 25 sequences for ITS and 17 for nuLSU. Sequences were aligned with MAFFT in Geneious using default settings (Auto algorithm selection, gap open penalty 1.53, offset 0.123). The ends of our new sequences were trimmed to match the annotated regions of those from GenBank, then concatenated into a single alignment (Supplementary Table S1). Phylogenetic trees were obtained by maximum likelihood analysis of the combined alignment using the GTR (general time-reversible) model with Geneious defaults, optimizing topology, length, and rate with an NNI search using the PhyML (Guindon et al. 2010) plugin to Geneious. Statistical support for branches was evaluated with 1000 bootstrap pseudoreplications.

**RESULTS & DISCUSSION**

**Phylogenetic reconstruction.** The ITS alignment had 563 bases with 31.4% (176) variable positions. After trimming the nuLSU alignment, 846 positions remained with 16.3% (138) of them variable. Although nuLSU in many groups is considered much less useful at the species level than the ITS, we found both the ITS and nuLSU to be informative in separating species.

### Table 1. Voucher information for the *Stereocaulon* species sampled and the associated GenBank accession numbers for ITS and nuLSU. All new sequences (in bold) are vouchered in osc unless otherwise specified in the text. Phinney’s specimens are also reported in Phinney (2016).

<table>
<thead>
<tr>
<th>Species</th>
<th>Specimen</th>
<th>Location</th>
<th>Dark centers</th>
<th>Chemo-syndrome</th>
<th>Fertile</th>
<th>Soredia</th>
<th>GenBank ITS</th>
<th>GenBank nuLSU</th>
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<td><em>S. areolatum</em></td>
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<td>lobaric</td>
<td>no</td>
<td>no</td>
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<td>yes</td>
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<td>yes</td>
<td>MK570474</td>
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<td>atranorin (tr.), unknown (tr.)</td>
<td>no</td>
<td>no</td>
<td>MK570475</td>
<td>MK570494</td>
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<td>no</td>
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<td>yes</td>
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<td>lobaric</td>
<td>no</td>
<td>yes</td>
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<td>Sweden</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<td><em>S. leucophaeopsis</em></td>
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<td>Norway</td>
<td>–</td>
<td>–</td>
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<td>–</td>
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<td>yes</td>
<td>yes</td>
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<td>U.K.: Scotland</td>
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<td>yes</td>
<td>yes</td>
<td>MK570481</td>
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<tr>
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<td>yes</td>
<td>atranorin only</td>
<td>yes</td>
<td>no</td>
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<td>MK570498</td>
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<td>no</td>
<td>atranorin only</td>
<td>yes</td>
<td>no</td>
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<td>atranorin only</td>
<td>yes</td>
<td>no</td>
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<td>MK570498</td>
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<td>sparse</td>
<td>lobaric</td>
<td>no</td>
<td>no</td>
<td>MK570483</td>
<td>MK570499</td>
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<td>yes</td>
<td>lobaric</td>
<td>no</td>
<td>no</td>
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<td>yes</td>
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<td>MK570501</td>
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<td>lobaric</td>
<td>yes</td>
<td>yes</td>
<td>MK570486</td>
<td>MK570502</td>
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<td>yes</td>
<td>yes</td>
<td>MK570487</td>
<td>–</td>
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<td>USA: Oregon</td>
<td>no</td>
<td>stictic</td>
<td>yes</td>
<td>yes</td>
<td>–</td>
<td>MK570503</td>
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<tr>
<td><em>S. tornense</em></td>
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<td>USA: Oregon</td>
<td>small</td>
<td>lobaric</td>
<td>yes</td>
<td>yes</td>
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<td>yes</td>
<td>MK570486</td>
<td>MK570502</td>
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</tbody>
</table>
Examination of separate reconstructions of the ITS and nuLSU regions showed no conflicts in branches with bootstrap support. Each region provided considerable species level resolution and together generally gave a slight increase in bootstrap support. We present the maximum-likelihood tree for the combined regions (Fig. 1), although in most cases the ITS region appears sufficient to distinguish species.

The maximum likelihood tree from combined ITS and nuLSU showed numerous small well-supported groups of specimens, each group similar...
within itself in morphology and secondary metabolites. Relationships between these groups had low levels of support, except for two cases of supported sister relationships (areolatum – tornense; cephalocrustatum – leucophaeopsis). Within each of those sister relationships, one supported lineage was P– orange (stictic acid present) and one was P– (Fig. 1).

DNA sequences demonstrated that only a few North American specimens could be accommodated in the similar-appearing taxa in Europe (Stereocaulon leucophaeopsis, S. plicatile), while most of them belong to new species, which we describe below. In most cases the crustose species were recognizable by a combination of morphology and spot tests. These new North American species belong to the same phylogenetic group of crustose species as recognized by Högnabba et al. (2014, Clade 3). One Fennoscandian and British crustose species, S. tornense, was not found in our North American specimens.

Each species lineage was chemically uniform, having one of three patterns (Table 1, Fig. 1). Atranorin with stictic acid and satellite compounds occurred in Stereocaulon cephalocrustatum, S. hypothallinum, S. plicatile and S. tornense. Atranorin with lobaric acid and satellite compounds occurred in S. areolatum, S. secundum, S. leucophaeopsis and S. oregonense. Atranorin occurred by itself only in S. nivale.

**Morphological variation.** Crustose species with darker centered areoles (Stereocaulon areolatum, S. leucophaeopsis and S. oregonense, weakly in two other species) have an anatomy that is extremely similar to the phyllocladia of Stereocaulon vesuvianum and related species, despite no close relationship between S. vesuvianum and the crustose species with dark-centered areoles (Högnabba et al 2014). These dark spots are one or more per areole, tan to brown or grayish, punctiform to irregularly expanded or occupying most of the areole. In section, it is clear that these are transparent windows into the interior of the areole. Presence of these cortical windows is fairly consistent as a species-level character (Table 2).

Although we observed no cephalodia with a structure typical of Stereocaulon, we did observe distinct aggregations of fungal hyphae with cyanobacteria (Stigonema). We interpret these aggregations as primitive cephalodia, as discussed under S. cephalocrustatum.

**Taxonomy**

**Brief characterization of the genus.** Stereocaulon Hoffm. has a fruticose thallus in most species, and crustose in a few, to which the following description applies: thallus areolate, often well developed, white, cream, gray, or pale greenish gray; areoles slightly or not at all lobate; upper cortex present; hypothallus indistinct or apparent, cream, brownish, or grayish; cephalodia rudimentary or absent, when present consisting of dark brown-black cushions of Stigonema with bristly filaments emerging from a cyanobiont-fungus base, or apparently lacking but the thallus associated with freeliving Stigonema; soredia present or not, isidia lacking; apothecia adnate to sessile or between the areoles; disk dark brown to black, lecideine; proper exciple

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**Table 2. Summary of characters of crustose Stereocaulon species in North America.** Abbreviations: “AK” = Alaska, “Apo” = apothecia, “Eur” = Europe including Fennoscandia, PNW = Pacific Northwest of North America, “Stigo” = Stigonema. Stereocaulon tornense is included for comparison but is not yet known from North America. The chemosyndrome refers to the dominant secondary metabolite; “lobaric” = lobaric acid and satellites; “stictic” = stictic acid and satellites; atranorin was found in all samples.

<table>
<thead>
<tr>
<th>Species</th>
<th>Apo</th>
<th>Soredia</th>
<th>Associated cyanobacteria</th>
<th>Chemo-syndrome</th>
<th>Spore septa</th>
<th>Areoles with dark center</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>areolatum</td>
<td>occasional</td>
<td>+</td>
<td>freeliving Stigo</td>
<td>lobaric</td>
<td>3</td>
<td>yes</td>
<td>AK</td>
</tr>
<tr>
<td>cephalocrustatum</td>
<td>yes</td>
<td>+</td>
<td>+ Stigo mounds</td>
<td>stictic</td>
<td>3</td>
<td>weak</td>
<td>AK</td>
</tr>
<tr>
<td>secundum</td>
<td>usual</td>
<td>-</td>
<td>freeliving Stigo</td>
<td>lobaric</td>
<td>3</td>
<td>no/weak</td>
<td>AK</td>
</tr>
<tr>
<td>hypothallinum</td>
<td>yes</td>
<td>+</td>
<td>none</td>
<td>stictic</td>
<td>3(4)</td>
<td>no</td>
<td>AK</td>
</tr>
<tr>
<td>leucophaeopsis</td>
<td>rare</td>
<td>+</td>
<td>none or freeliving Stigo</td>
<td>lobaric</td>
<td>3(5)</td>
<td>yes</td>
<td>Eur+AK</td>
</tr>
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<td>nivale</td>
<td>usual</td>
<td>-</td>
<td>none</td>
<td>atranorin only</td>
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<td>no</td>
<td>PNW</td>
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<td>oregonense</td>
<td>rare</td>
<td>-</td>
<td>freeliving Stigo</td>
<td>lobaric</td>
<td>3-7</td>
<td>yes, small</td>
<td>PNW</td>
</tr>
<tr>
<td>plicatile</td>
<td>not yet in N Am</td>
<td>+</td>
<td>+ Stigo mounds</td>
<td>stictic</td>
<td>submuriform</td>
<td>no</td>
<td>Eur+AK</td>
</tr>
<tr>
<td>(tornense)</td>
<td>rare</td>
<td>+</td>
<td>freeliving Stigo or none</td>
<td>stictic</td>
<td>3</td>
<td>yes/no</td>
<td>Eur</td>
</tr>
</tbody>
</table>

Note: Data for North America was contributed by many collectors and labs. Fragments of PNW specimens belonging to the same species were included, even though they differed in morphological details. The table presents a summarized description of morphological variability among the species and distribution of the species in North and Central America.
distinct to turned under, in thin section often brown at the edge and within, often POL+; epithecium brownish to brown; hymenium hyaline; paraphyses mostly unbranched and with a brown cap; asci Porpidia like, with K/I+B dome and often with a central darker blue tube; ascospores hyaline, fusiform, 1– to many-septate, sometimes slightly constricted at the septa, 8/ascus; pycnidia immersed, with a darkened ostiole; ascospores filiform to cylindrical, straight or curved.

**The species.** The number of crustose Stereocaulon species known from North America is increased from 3 to 8. Seven of those eight species occur in the national parks of southwestern Alaska (Katmai, Lake Clark, and Kenai Fjords). Two of the eight are known from Oregon and Washington.

Each of the crustose species currently known from North America is described below. New species are given full descriptions, while existing taxa are summarized, based on our observations of North American material that has been supported by DNA sequences.

*Stereocaulon areolatum* McCune, E.DiMeglio & Tønsberg, *sp. nov.*

**MYCOBANK** MB 829916

*Saxicolous areolate-crustose thallus, sorediate; areoles with dark centers and white margins, containing atranorin and lobaric acid; ascospores fusiform, mostly 3-septate but occasionally to 6-septate, (2)3-septate, (19)22–25(33) × (6)7–9(10) μm.

**TYPE:** U.S.A. ALASKA: Kenai Peninsula Borough, Lake Clark National Park, shoulder of mountain overlooking Tuxedni Bay, alpine tundra with noncalcareous outcrops and shrub thickets, 60.2381°N, 152.9567°W, 600 m, on stones in ephemeral snowmelt stream on north side of ridge, 17 July 2014, *McCune 35498* (holotype: OSC; isotype: ALA).

**Description.** Thallus crustose, areolate, often covering extensive areas but usually mixed with other lichens, bryophytes (*Andreaea*), and cyanobacteria; areoles flat to convex, mostly <0.5 mm diam but becoming compound to >1.5 mm diam, scattered or contiguous, roundish, polygonal, or irregular, often becoming slightly lobate; upper surface whitish, matte or glossy, neither scabrid nor pruinose, usually with one or more darker (tan to brown) central spots, the darker areas punctiform to irregularly expanded or occupying most of the areole, similar to the darker centers of *Stereocaulon vesuvianum* phyllocladia; thallus margin indefinite; thallus sections crumbly (difficult to make intact thin sections), I– throughout; upper cortex 10–100 μm thick, of compact, intricate hyphae with rectangular to roundish cells 2.5–6 μm diam, in some places with vertically oriented elongate hyphae; in water obscured by dense POL+ grayish granules, the granules dissolving in K; cortex penetrated by pellucid “windows” that penetrate deep into the algal layer, the windows POL+ but transparent, of vertically-oriented gelatinized hyphae; algal layer uneven in thickness; hypothallus not apparent; soredia sparse to abundant, whitish to light brown, round to irregular, laminal or marginal, sometimes confluent between areoles; isidia lacking; organized cephalodia lacking but with blackish colonies of *Stigonema* interspersed with the areoles.

Apothecia occasional, to 1.4 mm diam or more, roundish, sessile; disk black, flat to convex; apothecial margin initially distinct and slightly raised, persistent, brown to dark brown or black; exciple dark brown within, brown near edge, radiate, lacking algae, POL+ throughout, K–; epithecium brown, with brownish POL+ granules, K–; hymenium hyaline, 100–110 μm thick, POL–, I– except for asci; hypothecium dark brown, POL–; but occasionally with clumps of POL+ crystals, K–; paraphyses I–, coherent at tips in water but free in K, slender (about 1 μm diam), the tips expanded to about 2.5–3.0 μm diam, brownish and with thin dark caps; asci thin walled, the wall I+ and K/I+ blue; ascospores hyaline, fusiform, the ends blunt or subacute, (2)3-septate, (19)22–25(33) × (6)7–9(10) μm, median 24 × 8 μm, 8/ascus; pycnidia not seen.

**Chemistry.** Cortex K+ yellow; medulla K–, C–, KC+ reddish, P–, UV ± whitish; basal layer K+ reddish brown (unknown substance). TLC: atranorin, lobaric acid and associated compounds, with accessory unknown UV+ orange RF A7–8 C8.

**Etymology.** The epithet “areolatum” refers to the areolate crustose growth form of the species, in contrast to most fruticose *Stereocaulon*.

**Ecology and substrate.** *Stereocaulon areolatum* occurs on noncalcareous rock, particularly in alpine
areas with late-lying snow or in ephemeral snowmelt streams.

**Distribution.** So far known only from Lake Clark and Kenai Fjords National Parks in coastal south-central Alaska.

**Additional specimen examined.** U.S.A. **Alaska:** Kenai Peninsula Borough, Lake Clark National Park, shoulder of mountain overlooking Tuxedni Bay, 60.2381°N, 152.9567°W, 600 m, on metal-rich rock, 17 July 2014, **McCune 35486** (OSC); on pebbles, 17 July 2014, **Tønsberg 44269a,b, 44271** (BG); Kenai Pen.
Fjords National Park, near Harding Icefield Trail, ridge above Exit Glacier, 60.1828°N, 149.6713°W, 770 m, on stones in flat area with late snow, 11 July 2015, McCune 36370 (osc).

**Discussion.** *Stereocaulon areolatum* is distinguished by strong development of *vesuvianum*-type areoles, having cortical windows consisting of darker centers surrounded by a white cortex. This species and *S. leucophaeopsis* are the only crustose species of *Stereocaulon* that have both this structure and contain lobaric acid (P−, K−, UV+). Furthermore, in at least some specimens this species has a basal layer that is K+ reddish brown (unknown substance).

*Stereocaulon urceolatum* (P.M.Jørg.) Högnabba is also sorediate and produces lobaric acid, but it and *S. cumulatum* both produce relatively large squamules, commonly >4 mm in diameter, while *S. areolatum* and the other strictly crustose species have smaller thallus units, mostly <1 mm in diameter.

**Stereocaulon cephalocrustatum** McCune, E.DiMiglio & Tønsberg, sp. nov.

MYCOBANK MB 829917

*Saxicola* areolate-crustose thallus, sorediate, associated with lichenized mounds of *Stigonema*, the areoles with dark centers and white margins, containing atranorin and stictic acid, ascospores fusiform, 3-septate, (17.5)20–25 × 4.2–6.2(7.0) μm.

**Type:** U.S.A. ALASKA: Kenai Peninsula Borough, Kenai Fjords National Park, east side of Harris Bay, steep chasm, granitic cliffs and boulders at base of rocky chute, 59.7289°N, 149.8340°W, 6 m, 8 July 2015, McCune 36244 (holotype: OSC; isotype: ALA).

**Description.** Thallus crustose, areolate, to 8 cm or more in diameter; areoles soon convex or bullate, to 1.0 mm diam but becoming compound to >1.5 mm diam, roundish or irregular, often slightly lobate; upper surface whitish, matte, epruinose, usually with one or more darker (pale greenish to dark olive) spots that are punctiform to elongate or irregularly expanded; thallus margin not noticeably differentiated; thallus sections crumbly (best sectioned wet), hydrophobic, I− throughout; upper cortex 25–50 μm thick, with intricate hyphae and roundish cells, in water obscured by dense POL+ granules but interrupted by pellucid cortical “windows” corresponding to the darker spots in surface view, in section the windows hyaline, POL+ (K-insoluble granules) extending into the algal layer; cortical granules dissolving instantly in K with faint yellow diffusion; algal layer discontinuous, disrupted by the cortical windows and occasionally penetrated by narrow bundles of hyphae that begin in the cortex and extend through the algal layer; hypothallus not apparent; soredia sometimes present, laminal or marginal, whitish or brownish; primitive cephalodia present, mostly 0.3–1.0 mm diameter, blackish lichenized mounds of *Stigonema* with protruding tips of the cyanobacterial filaments.

Apothecia to 1.5 mm diam or more, roundish, sessile, dark brown to black, the margin initially distinct and raised, dark brown, soon blackening and turned under with age; exciple dark brown within, somewhat paler near the edge, radiate, lacking algae, POL+; epithecium orangish brown, with brownish POL+ granules; hymenium hyaline, 90–100 μm thick, POL−; hypothecium dark brown, POL+, with K+ yellow diffusion, K/I− but bluish above; paraphyses slender, coherent at tips in water, about 1 μm diam, the tips expanded to about 3 μm diam; filled asci about 55 × 20 μm, thin walled, the wall I− blue, K/I+ deep blue; ascospores hyaline, fusiform, (1)3-septate, (17.5)20–25 × 4.2–6.2(7.0) μm, median 22.8 × 5.7 μm, 8/ascus, K/I−; pycnidia not seen.

**Chemistry.** Cortex K+ yellow; medulla K+ yellow, C−, KC−, P+ orange, UV ± whitish; TLC: atranorin, stictic acid and associated compounds.

**Etymology.** The epithet “cephalocrustatum” refers to the presence of primitive cephalodia on a crustose thallus.

**Ecology and substrate.** *Stereocaulon cephalocrustatum* occurs on noncalcereous rock near sea level on steep rocky areas along somewhat sheltered ocean bays. The seaside locations suggest that it may be salt tolerant.

**Distribution.** So far the species is known only from near sea level in Kenai Fjords National Park, southwest of Anchorage, Alaska.

**Additional specimens examined.** U.S.A. ALASKA: Kenai Peninsula Borough, Kenai Fjords National Park, Coleman Bay, shoreline granitic boulders and
Figure 3. Stereocaulon cephalocrustatum (McCune 36298), unlabeled scale bars 1 mm. A. Habit. Small, dark structures are clusters of the cyanobacterium Stigonema, hypothesized to be primitive cephalodia. B. Apothecia, fully developed. C. Apothecial section in water. D. Same as C but under polarized light. E. Transverse section through primitive cephalodium. F. Detail of cephalodium showing pockets of cyanobacteria (Stigonema) surrounded by fungal tissue. G. Ascospores.
outcrops, 59.8807°N, 149.6167°W, 5 m, 9 July 2015, McCune 36298 (OSC).

Discussion. This species is distinguished by its K+, P+ medulla (stictic acid) and abundant small mounds of Stigonema, which we interpret as loosely organized cephalodia. Unlike the other P+ crustose Stereocaulon in North America, its areoles resemble the phyllocladia of Stereocaulon vesuvianum, having punctiform to expanded olivaceous centers surrounded by white cortex.

The cyanobacterial structures are small blackish mounds associated with the areoles and apparently lichenized. In section (Fig. 3E–F) their structure approaches that of normal Stigonema-containing cephalodia in Stereocaulon. The central part is densely consolidated, with pockets of very short filaments of Stigonema surrounded by a thin matrix of fungal hyphae. The surface is often spiky with projecting tips of the Stigonema, similar to cephalodia in Stereocaulon paschale. Too few specimens are available to conclude whether these are always present in Stereocaulon cephalocrustatum, but in the specimens seen so far, they are numerous and rather conspicuous. In contrast, the freeliving Stigonema that is often found growing intermixed with lichens on damp rocks in cool climates are usually diffuse rather than in discrete mounds and usually partly overgrowing the associated lichens.

Stereocaulon fecundum McCune, E.DiMeglio & Tønsberg, sp. nov.

Figure 4. Stereocaulon fecundum (McCune 36117), unlabeled scale bars 1 mm. A & B. Habit. C. Apothecial section in water. D. Ascospores (upper row from 36117, lower row from 36726).

MYCOBank MB 829918
Saxicolous areolate-crustose thallus, lacking soredia; areoles white, sometimes with dark spots or creases but lacking cortical windows, containing atranor-
in and lobaric acid, ascospores fusiform, fusiform, mostly 3-septate but occasionally to 6-septate, 22.5–27.0(36.0) × (4.2)5.2–6.3(6.5) μm.

**Type**: U.S.A. ALASKA: Kenai Peninsula Borough, Kenai Fjords National Park: bay on east side and south end of McCarty Fjord, 59.4841°N, 150.3386°W, 4 m, on creeside rock, 6 July 2015, McCune 36117 (holotype: osc; isotype: ALA).

**Description.** Thallus crustose, areolate, often covering extensive areas to 10 cm or more in diameter; areoles flat to convex, to 1.0 mm diam but becoming compound to >1.5 mm diam, scattered or contiguous, roundish, polygonal, or irregular, often becoming slightly lobate; upper surface whitish, matte or glossy, sometimes becoming minutely rugose but neither scabrid nor pruinose, uniform in color or frequently with a darker spots or creases; thallus margin indefinite; areoles flat to convex or with a flat perimeter and central wart, to 0.7 mm diam and 0.3 mm thick, roundish but becoming compound to 2.5 mm diam; hypohenium dark orangish brown, POL+ reddish, P–, UV ± whitish; TLC: atranorin, lobaric acid and associated compounds.

**Etymology.** The epithet “fecundum” refers to the abundantly fertile, esorediate reproduction of the species, in contrast to soredia production and sparse fertility of most crustose Stereocaulon.

**Ecology and substrate.** Stereocaulon fecundum occurs on noncalcareous rock along streams and ocean bays.

**Distribution.** So far known only from Kenai Fjords National Park on the outer coast of the Kenai Peninsula in Alaska.

**Additional specimen examined.** U.S.A. ALASKA: Kenai Peninsula Borough, Kenai Fjords National Park, Verdant Cove, north side at shoreline, 59.7092°N, 149.7459°W, 4 m, granitic boulders with adjacent Picea forest, on rock, 9 July 2015, McCune 36276 (ALA, OSC).

**Discussion.** This crustose species appears to lack organized cephalodia but is associated with Stigonema colonies, has mostly 3-septate, but up to 6-septate spores, and does not show the vesuvianum-type areoles with darkened centers. It falls on the large branch including most crustose Stereocaulon species in North America, except for S. oregonense.

**Stereocaulon hypothallinum** McCune, E.DiMeglio & Tønsberg, sp. nov. Fig. 5

**MycoBank** MB 829919

Saxicolous areolate-crustose thallus, whitish sorediate, the areoles rather uniform in color and lacking cortical windows, containing atranorin and stictic acid, whitish hypothallus present, ascospores fusiform, 3-4(5)-septate, 22.5–27.0(36.0) × (4.2)5.2–6.3(6.5) μm, median 23.3 × 5.5 μm, 8/ascus; pycnidia not seen.

**Chemistry.** Cortex K+ yellow; medulla K–, C–, KC+ reddish, P–, UV ± whitish; TLC: atranorin, lobaric acid and associated compounds.

**Type**: U.S.A. ALASKA: Lake & Peninsula Borough, Katmai National Park, north end of ridge west of Contact Creek, cliffs and alpine fellfield, 58.26553°N, 155.8839°W, 1140 m, on rock, 30 July 2013, Tønsberg 42884 (holotype: BG).

**Description.** Thallus crustose, areolate; areoles flat to convex or with a flat perimeter and central wart, to 0.7 mm diam and 0.3 mm thick, roundish when isolated to more often contiguous and polygonal, separated by narrow cracks, not lobate;
upper surface of areoles whitish centrally with a tan to light brown edge, the white parts matte or glossy, epruinose, and brownish parts matte; thallus margin not differentiated except for a narrow extension of the hypothallus; thallus sections crumbly (difficult to make intact hand sections), I– throughout or with I+ violet spots; upper cortex 40–50 μm thick, paraplectenchymatous but partially obscured by

Figure 5. Stereocaulon hypothallinum (Tønsberg 42884), unlabeled scale bars 1 mm. A. Young apothecia. B. Old apothecium. C. Soredia and young apothecia. D. Paraphyses in K. E. Soralia. F. Ascospores.
dense POL+ granules, the granules partially dissolving in K; algal layer penetrated by narrow bundles of elongate hyphae; hypothallus apparent, cream to brownish; soredia present, powdery; soralia scattered, roundish, whitish, erupting from the centers of the areoles and soon occupying most of the areole; isidia lacking; cephalodia lacking.

Apothecia mostly 0.2–0.5(1.7) mm diam, roundish, black, sessile, initially flat with a well-defined raised margin, becoming hemispherical with margin turned under; exciple radiate, dark brown internally to orangish brown or nearly hyaline at the edge, POL+ within; epitheicum orangish brown, with POL+ streaks into the hymenium, brownish crystals dissolving in K, otherwise K–; hypothecium brown, K+ strong orangish yellow diffusion; hymenium 79–84 μm tall; paraphyses about 2 μm broad, with thin brownish caps, the tips to 5 μm diam; asci thin walled, cylindrical to clavate in water, swelling in K; ascospores hyaline, fusiform, 3–4(5)-septate, 21–27 × 5.6–7.5 μm, 6–8/asccus and lying nearly parallel to each other, often sticking to each other outside the ascus; pycnidia not seen.

Chemistry. Cortex K+ yellow; medulla K+ yellow to pale orange, C–, KC– reddish, P+ orange, UV–; TLC: atranorin, stictic acid and associated compounds.

Etymology. The epithet “hypothallinum” refers to the unusually well-developed hypothallus.

Ecology and substrate. Stereocaulon hypothallinum was found on granite on an exposed alpine ridgeline, on rock on the shaded floor under a freelifing cyanobacteria.

Stereocaulon leucophaeopsis (Nyl.) P.James & Purvis

Originally described as Lecidea leucophaeopsis Nyl. in 1873, based on a specimen from Scotland, and Bilimbia cambriaca Whelden in 1920, this species was first recognized as a Stereocaulon by Purvis and James (1985). Both types are in BM, and were studied by Purvis & James (1985), but not seen by us.

Description. Thallus crustose, areolate; soredia usually present, laminal or marginal or irregular; apothecia occasional; exciple edge dark brown, orangish brown to dark brown within, POL+; epitheicum brown, POL+; hypothecium brown, POL+; paraphyses coherent at the tips, free below in water under pressure, 1–1.5 μm diam; ascospores hyaline, fusiform, the ends rounded or one end pointed, some slightly curved (banana shaped), mostly 3–septate, sometimes 4– or 5–septate, 24–36 × 5.3–6.9 μm, cephalodia lacking but some individuals with associated colonies of cyanobacteria.

Discussion. The species is similar to Stereocaulon tornense and S. cephalocrustatum in being a sorediate species containing stictic acid; however, S. hypothallinum differs from both in having a white to light brown hypothallus. A hypothallus is rarely visible in crustose Stereocaulon species; so far we have seen it only in S. hypothallinum and S. plicatile. The areoles of S. hypothallinum are unlike any other crustose Stereocaulon, having a flat, light brown edge with a raised central white corticate wart that occupies just a small part to most of an areole. Unlike most of the crustose Stereocaulon in Alaska, we have seen no association with Stigonema or other freelifing cyanobacteria.
Stereocaulon leucophaeopsis appears to be one of the rarer crustose Stereocaulon in western North America.

**Stereocaulon nivale** (Follman) Fryday

**Brief characterization.** Thallus crustose, areolate, sometimes slightly lobate, white or grayish white; phyllocladia uniform in color; cephalodia lacking; soredia lacking; apothecia usually abundant, lecideine; ascospores hyaline, fusiform, 3–5 septate, 18–25 × 5.0–7.1 μm; thallus containing only atranorin; on noncalcareous rock, montane to alpine, usually in areas where the snow lies late; Oregon Cascades north to coastal southern Alaska (McCune 2017).

**Discussion.** First described as *Bacidia nivalis* by Follman (1979), the species was transferred to *Stereocaulon* by Fryday & Glew (2003). The species is readily overlooked in the field because of its similarity to common but often avoided species of *Lecidea*, *Lecidella* and *Porpidia* that have with a white thallus and black lecideine apothecia.

**Selected specimens examined.** U.S.A. **ALASKA:** alpine lake system on Harris Peninsula, 59.7492°N, 149.8021°W, 394 m, on rock, N-facing rocky tundra with seasonal seepage, 18 July 2016, McCune 37008 (OSC). **OREGON:** Linn Co., NE slope of Sentinel Ridge, near trail to Jefferson Park, west slope Cascade Range, 44.70814°N, 121.8478°W, 1653 m, large talus blocks near ridge top, light-colored volcanic rock, 29 July 2008, McCune 29712 (OSC). **WASHINGTON:** Mt Rainier National Park, south flank, Golden Gate Trail through Paradise Valley, drainage area above Myrtle Falls, 1800 m, on volcanic pebbles and...

Stereocaulon oregonense McCune, E.DiMeglio & Tønsberg, *sp. nov.*

**MYCOBANK** MB 829920

*Saxicolous areolate-crustose thallus, lacking soredia, the areoles rather uniform in color and with mostly small cortical windows, containing atranorin and lobaric acid, ascospores fusiform, 3- to 7-septate, 20–34 × 6.3–8.0 μm.*


**Description.** Thallus crustose, areolate, often covering extensive areas to 10 cm or more in diameter; areoles flat to more often convex or bullate, to 0.8 mm diam but becoming compound to ≥1.5 mm diam, roundish, polygonal, or irregular, not or only slightly lobate; upper surface whitish, matte or glossy, sometimes becoming minutely scabrid or textured but epruinose, uniform in color or frequently with a darker (pale greenish to dark olive) central spot that is punctiform to elongate or irregularly expanded; thallus margin...
not differentiated but sometimes forming contact lines with other species; thallus sections crumbly, hydrophobic, I– throughout; upper cortex 27–50 \( \mu \text{m} \) thick, paraplectenchymatous but partially obscured by dense POL+ granules with a pattern of vertical strips of hyaline tissue and densely gray granule-infused tissue, the granules dissolving instantly in K with yellow diffusion; algal layer

Figure 8. *Stereocaulon oregonense* (McCune 37514, except as noted), unlabeled scale bars 1 mm. A. Young apothecia. B. Old apothecium. C. Areoles with little to no development of cortical windows (McCune 26642). D. Apothecial section in water. E. Ascospores. F. Same as D but under polarized light.
penetrated by narrow bundles of hyphae that begin at the upper surface of the cortex and extend completely through the algal layer, such that the algal layer appears divided into columns; hypothallus not apparent; soredia lacking; cephalodia lacking and thallus not particularly associated with *Stigonema*.

Apothecia to 1.7 mm diam or more, roundish, sessile, black, the margin initially distinct and raised, dark grayish brown but soon blackening and turned under with age; exciple dark brown, radiate, lacking algae, POL+ at upper edge, otherwise POL-, K+ yellow diffusion; epithecium light brown, with brownish POL+ granules, K+ yellow diffusion; hymenium hyaline, 115–180 μm thick, POL–; hypothecium brown, POL–, becoming very thick, with K+ yellow diffusion, K/I+ blue; paraphyses slender, coherent at tips in water, about 2 μm diam, the tips expanded to about 3 μm diam and with small dark caps; filled asci 57–69 × 22–25 μm, thin walled, the wall K/I+ deep blue; ascospores hyaline, fusiform, 3–7-septate, 20–34 × 6.3–8.0 μm, median 26.2 × 7.4 μm, 8/ascus, K/I–; pycnidia not seen.

**Chemistry.** Cortex K+ yellow; medulla K–, C–, KC+ reddish, P–, UV ± whitish; TLC: atranorin, lobaric acid and associated compounds.

**Etymology.** The epithet “oregonense” refers to our originally finding the species in the state of Oregon, U.S.A.

**Ecology and substrate.** *Stereocaulon oregonense* occurs on noncalcareous rock, exposed to somewhat sheltered, particularly in areas with deep snow.

**Discussion.** The species is readily identified by the combination of (1) presence of cortical windows (though often small and weakly developed), (2) absence of stictic acid (P–) and (3) the absence of soredia.

**Stereocaulon plicatile** (Leighton) Fryday & Coppins

**Brief characterization.** Thallus crustose, areolate, sorediate; areoles flat to more often convex, to 0.5(1) mm diam, becoming rather thick (0.1–1.0 mm) and crowded, roundish to polygonal, not or only slightly lobate, mostly contiguous but when crowded then separating by deep cracks; upper surface whitish, matte or glossy, becoming minutely wrinkled or verrucose, epruinose, cortex of the central part of the areole not darkened unless becoming sorediate; soralia initially laminal, discrete or becoming confluent; thallus margin not differentiated; upper cortex 30–50 μm thick or more, paraplectenchymatous but obscured by dense POL+ granules that dissolve in K with yellow diffusion; algal layer uneven in thickness but ± continuous; hypothallus sometimes apparent, cream to brownish; soredia present, granular to powdery, whitish to brownish or grayish white, in discrete laminal or marginal soralia that often become confluent, but sometimes persisting as roundish laminal soralia centered in each areole; primitive cephalodia present as loosely organized mounds of *Stigonema* containing some fungal hyphae.

Mature apothecia not seen in Alaskan material, but juvenile apothecia present, dark brown black, urceolate with a thick margin; exciple brown black, pale at the basal edge, POL+ at upper edge, otherwise POL–, with K+ yellow diffusion; epithecium dark orangish brown, with brownish POL+ granules and K+ yellow diffusion; mature hymenium not seen; hypothecium brown, POL–; ascospores not seen in Alaskan material but in British material hyaline, submuriform, 20–32 × 10–15 μm; pycnidia not seen.

**Chemistry.** Cortex K+ yellow; medulla K+ yellow, C–, KC– reddish, P+ orange, UV–; TLC: atranorin, stictic acid and associated compounds.

**Ecology and substrate.** *Stereocaulon plicatile* occurs on noncalcareous rock, exposed to somewhat sheltered, particularly in areas with deep snow.
Figure 9. *Stereocaulon plicatile* (A and B McCune 36987, others Tønsberg 42994), unlabeled scale bars 1 mm. A. Young apothecia. B. Confluent soralia. C. Discrete soralia. D. Section of cyanobacterial colonies showing nonlichenized projecting filaments of *Stigonema*. E. Cyanobacterial colonies approaching cephalodia. F. Same as D but with *Stigonema* embedded in fungal tissue that we interpret as a loosely organized cephalodium.
Fryday (2006) reported this from areas with late snow lie, which definitely applies to at least one of the Alaskan sites, where it occurred on granitic talus in a small subalpine ravine near a ridgetop.

**Distribution.** This species was first reported from North America (Maine) by Fryday (2006); also known from British Isles and Scandinavia, then by McCune et al. (2018) from coastal Alaska. Although Fryday (2006) characterized the distribution of this species as amphi-Atlantic, the Alaskan records suggest that the species is likely to be found in cold oceanic climates around the Northern Hemisphere.


**Discussion.** Originally placed in Lecidea by Leighton in 1869 on the basis of a specimen from Wales, Fryday and Coppins (1996) transferred it to Stereocaulon, reporting one additional site from Wales and numerous sites from Scotland. Its distribution was extended to one site in North America on Mt. Katahdin, Maine (Fryday 2006).

Fryday (2006) pointed out that Stereocaulon plicatile can be separated from all other crustose Stereocaulon species by having submuriform ascospores. When sterile, however, it can be difficult to differentiate from *S. tornense*, and several sterile collections by Fryday from Maine (op. cit.) were not determined to species. Although apothecia were not found in our Alaskan material, DNA sequences matched those for *S. plicatile* rather than *S. tornense* (Fig. 1).

Although Stereocaulon plicatile has previously been described as lacking cephalodia, both Alaskan collections (from distant sites) were distinctly associated with mounds of Stigonema, which we interpret as primitive loosely organized cephalodia. Thin-sectioning these mounds revealed a mixture of fungal hyphae and cyanobacterial cells.

**Stereocaulon tornense** (H.Magn.) P.James & Purvis

**Brief characterization.** Areoles with dark centers or not, sorediate; thallus containing atranorin and stictic acid with satellite compounds; apothecia occasional; exciple edge dark brown, orangish brown to dark brown within, POL–; epithecium brown, POL–; hypothecium dark brown, POL–; ascospores hyaline, fusiform, some with one end pointed, some slightly curved (banana shaped), mostly (1)3-septate, rarely 4-septate, 17.8–24.5 × 5.0–7.1 μm. See more complete descriptions in Purvis & James (1985) and Gilbert et al. (2009).

**Selected specimens examined.** NORWAY: other collection data not recorded, Dahlkild s.n (h).

SCOTLAND. DUMFRIES: Wanlockhead: valley between Limen Rig and Wanlock Dod, 7 Dec 1991, Coppins 14771b (e); VC105 West Ross: Kintail, Ghlaschoire, acidic crags, 900 m, 26 Aug 1993, Fryday 4521 (e).

**Discussion.** In light of the unexpected biodiversity of crustose Stereocaulon in North America and the morphological diversity in specimens named *S. tornense*, more scrutiny and molecular data are needed for *S. tornense* in Fennoscandia and the British Isles. In particular, some specimens have dark-centered areoles but others do not. At present only one sequence of *S. tornense* is available in GenBank, that from iron-rich rock in Norway (Dahlkild s.n.). That specimen had dark-centered areoles, in contrast to examples from Scotland with weak or no development of dark centers. The thallus lacked apothecia and had quite variable soralia, often central and dark, becoming excavate or mounded.

**KEY TO NORTH AMERICAN CRUSTOSE STEREOCAULON SPECIES**

Key characters precede the long dash (—), while supplemental information follows the dash. Stereocaulon tornense is included although it has not yet been demonstrated from North America.

1a Medulla and/or soralia P+ orange and UV– (stictic acid present; lobaric acid lacking); soredia generally present .............................. 2

1b Medulla and soralia (if present) P–, UV– or UV– (stictic acid absent, lobaric acid present or not); soredia present or not ...... 6

2a Areoles with darker centers and whitish edges .................................. 3

2b Areoles more uniformly colored, except for developing soralia, or with paler centers; primitive cephalodia present or not .......................... 4

3a Primitive cephalodia present as blackish convex mounds with *Stigonema* filaments protruding from the surface; epithecium POL+; soredia present or not; SW Alaska........................................ ................................. Stereocaulon cephalocrustatum

3b Cephalodia lacking, though thallus sometimes associated with freeliving *Stigonema*; epithecium POL–; soredia usually present or not; U.K. and Fennoscandia................. (Stereocaulon tornense)

4a Hypothallus distinct, cream to brownish; areoles with pale raised centers and tan to brownish edges; cephalodia lacking. — Spores

4b Areoles more uniformly colored, except for developing soralia, or with paler centers; primitive cephalodia present or not .......................... 5

5a Medulla and/or soralia P–, UV– or UV– (stictic acid absent, lobaric acid present or not); soredia present or not ...... 6

5b Medulla and/or soralia P+ orange and UV– (stictic acid present; lobaric acid lacking); soredia generally present .............................. 2
mostly > 24 μm long, transversely 3–5-septate; SW Alaska; rare .............................................................. Stereocaulon hypothallinum

4b Hypothallus apparent or not; areoles rather uniform in color except for incipient soralia; cephalodia often present, loosely organized, developing into blackish convex mounds with Stigonema filaments protruding from the surface ....................... 5

5a Hypothallus sometimes apparent, whitish to cream; spores muriform; epithecium POL— SW Alaska, Maine, and northern Europe.............................................................. Stereocaulon plicatile

5b Hypothallus not seen; spores transversely 3–5-septate; epithecium POL— Scandinavia to British Isles.............................................................. (uniform-colored morph of Stereocaulon tornense)

6a Soredia lacking; lobaric acid lacking, containing atranorin only (UV−, KC−); apothecia usually abundant, lecideine; areoles uniform in color. — SE Alaska to Oregon Cascades..........................

6b Soredia present or absent; lobaric acid present (medulla P−, UV+ blue white, KC− or KC+ reddish) along with atranorin; apothecia sparse or lacking; areoles often with darker or translucent centers and whitish edges .............................................................. 7

7a Soredia lacking; apothecia present or not; areoles with or without darkened centers ................................................................................................. 8

7b Soredia usually present; apothecia occasional or absent; areoles with darkened centers, at least in part, similar to phyllocladia in S. vesuvianum ................................................................................. 9

8a Areoles nearly uniform in color not resembling phyllocladia of S. vesuvianum; apothecia usually present. — Alaska..........................

8b Areoles with darkened centers, at least in part, similar to phyllocladia in S. vesuvianum, though the darker centers often small or punctiform; apothecia fairly frequent, but also commonly sparse or absent. — Common in concave or sheltered topography in lava flows and talus slopes, in or near where snow accumulates; Oregon Cascades............................. Stereocaulon oregonense

9a Western North America; spores 3-septate, 24–33 × 8–10 μm. — Oregon and Alaska.............................................................. Stereocaulon areolatum

9b Europe and North America; spores 3–5-septate, (24)26–38(40) × 5.3–7 μm. — Fennoscandia, British Isles and North America ........................................ Stereocaulon leucophaeopsis

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Figure 10. Stereocaulon tornense, all specimens from Scotland; unlabeled scale bars 1 mm. A. Habit (Fryday 1299). B. Soralia (Fryday 1299). C. Asci (Fryday 4521). D. Ascospores (upper row from Fryday 1299, lower row from Fryday 4521).
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Literature Cited


Supplementary document online:

Supplementary Table S1. Final nucleotide alignment for the markers used for the phylogenetic reconstruction (concatenated ITS, then nuLSU).