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***Psoroma spinuliferum* (Pannariaceae), a new corticolous lichen species
from Alaska with two different types of cephalodia**

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ABSTRACT. The species *Psoroma spinuliferum* is described as new to science here. It is only known from the holotype on a *Picea sitchensis* trunk near a sea-shore in southern, coastal Alaska. The species is distinct in having short, brittle, spinule-like hairs on both apothecium margins, thalline squamules and on pulvinate to coarsely coralloid cephalodia with emerald-coloured *Nostoc* photobionts. These spinules are unique within Pannariaceae as they are developed on both the chlorobiont and on one of two cyanobionts, but it is uncertain whether they can act as vegetative propagules. The presence of two types of cephalodia is also unique within Pannariaceae. The second type consists of glabrous, small-foliose, geotropically arranged cephalodia, containing a *Nostoc* strain with cells of an intense ultramarine color, when observed after long storage. The species also has shorter ascospores than *Psoroma paleaceum*, another hairy species. The hair types of *Psoroma hypnorum* and *P. paleaceum* are here by contrast referred to as tomentum and scales, respectively.

KEY WORDS. Taxonomy, biodiversity, North America, *Nostoc*, photobionts, vegetative propagules.

The genus *Psoroma*, as defined by its type species *P. hypnorum* (Vahl) S. F. Gray (Jørgensen 1978), is a *Pannariaceae* genus, mostly tripartite, consisting of chlorobiont squamules

29 and cephalodia, interconnected by an inconspicuous hypothallus. The genus has traditionally been
30 interpreted to comprise practically all tripartite species within *Pannariaceae*. However, all foliose
31 species and several squamulose species have now been transferred to other genera, see e.g. Elvebakk
32 et al. (2016). On the other hand, Ekman et al. (2014) transferred six bipartite species of *Pannaria* and
33 *Santessoniella* to *Psoroma*. The genus has apothecia with well-developed thalline excipuli, and asci
34 with IKI+ amyloid, tube-like internal structures. Its color is dominated by dark brown to greyish
35 melanins. TLC-detectable substances are absent, except for pannaric acid and substances related to
36 porphyrilic acid in the *Psoroma tenue* group (Henssen & Renner 1981) and in *P. asperellum* Nyl. and
37 *P. multifidum* P. M. Jørg. (Jørgensen 2004a). Another exception is pannarin in *P. aphthosum* Vain., a
38 surprising occurrence. In *Pannariaceae* this substance is restricted to the genus *Pannaria* and to
39 other even more distantly related genera (Ekman et al. 2014).

40 Like most genera within *Pannariaceae*, *Psoroma* has its center of biodiversity in the
41 Southern Hemisphere. Øvstedal & Smith (2001) included six species from Antarctica, a number
42 which has now increased to 10, in addition to another four species occurring in subantarctic areas
43 (Park et al. 2018). All these species, except the saxicolous *P. saccharatum* (Scutari & Calvelo 1995;
44 Olech 2004), share the terricolous to muscicolous habit of *P. hypnorum*. However, some corticolous
45 species occur in austral forests, such as *P. aphthosum* in South America (Vainio 1899), and *P.*
46 *asperellum* Nyl., *P. coralloideum* Nyl., *P. geminatum* P. M. Jørg. and *P. multifidum* P. M. Jørg. in
47 New Zealand (Galloway 2007), partly also in Australia. The species *P. filicicola* P. M. Jørg. &
48 Sipman described from Papua New Guinea by Jørgensen & Sipman (2006) is also corticolous, and
49 confined to stems of tree ferns. In addition, there are some austral, corticolous and squamulose
50 species presently positioned within *Psoroma*, but with deviating chemistry, indicating the need for
51 further studies and revised generic affiliations.

52 All the four *Psoroma* species known to be bipolar are present in North America. *Psoroma*
53 *cinnamomeum* Malme could rather be referred to as an amphi-tropical species, as its only locality in
54 the Northern Hemisphere is on one of the Channel Islands in California (Jørgensen 2001). In addition
55 to the widespread *P. hypnorum*, *Psoroma tenue* var. *boreale* Henssen and *P. paleaceum* (Fr.) Timdal

56 & Tønberg may both have been overlooked in North America as very few localities have been
57 published so far (Jørgensen 2004b; 2005), whereas ongoing herbarium revisions by the first author
58 indicate that they are regionally common. During field work in Alaska, the second author collected a
59 strange *Psoroma* growing on a *Picea* trunk. On closer inspection, this collection turned out to be very
60 different from all known species in this genus. Except for *P. paleaceum*, it is the only known species
61 with erect hairs in *Psoroma* s. str. The species is also distinct in other characters. The aim of the
62 present paper is to describe this new species, still only known from its holotype collection.

63

64 MATERIALS AND METHODS

65 Herbarium material for this study is housed at BG. Material of the species has not been
66 found during the first author's extensive studies of the Pannariaceae collections in B, BM, C, CANB,
67 O, S, SGO, UPS, W, and WIS. Some reference samples of other species were also studied for
68 comparison. In microscope sections, iodine reactions were tested by adding IKI to mounts pretreated
69 with KOH (Orange et al. 2001). Perispore structures were studied in water mounts and restricted to
70 spores liberated from the asci. Ascospore morphology was studied in detail by drawing detailed
71 sketches of ascospores, and copies of all original drawings have been included with the sample. In an
72 attempt to reproduce true colors of the different parts of the lichen when moist, a painting was made
73 by the first author, after comparisons with colors of moistened fragments of the lichen, 17 years after
74 its collection. Thin-layer chromatography of acetone extracts followed standardized procedures and
75 used solvents A and C (Culberson 1972; Orange et al. 2001). Nomenclature of ascospore structures
76 follows Nordin (1997).

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79 RESULTS

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81 *Psoroma spinuliferum* Elvebakk & Tønberg, sp. nov.

82

83 **Figs. 1A-B, 2, 3B, 4.**

84

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86 *Differs from Psoroma paleaceum in having a cover of small, erect spinules on the sides of*
87 *the thalline excipuli and on many squamules and on one type of cephalodia, by spinules being*
88 *circular in cross-section and at bases concolorous with the adjacent parts of the thallus, by having*
89 *smaller apothecia with shorter ascospores with low verrucae and without apical extensions, and by*
90 *the occurrence of two different types of cephalodia.*

91

92 TYPE: USA. ALASKA: City and Borough of Yakutat, Yakutat Foreland, S of village Yakutat,
93 Cannon Beach, 59°29.6'N, 139°43.6'W, alt. 0–10 m, corticolous on trunk of *Picea sitchensis* at upper
94 edge of beach, 29 May 2001, T. Tønberg 29882 (BG-L-70447; holotype).

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96

97 **Description.** *Thallus* squamulose, corticolous, 4–5 cm wide, tripartite. *Chlorobiont*
98 *squamules* c. 200 µm thick, pulvinate, entire to very weakly lobate, 0.1–0.3 (–0.5) mm wide,
99 appressed to the substratum, and attached by pale rhizohyphae to the hypothallus. *Upper surface* pale
100 to ochraceous brown, weakly glossy, commonly, but not uniformly, with numerous erect and brittle,
101 30–60 µm tall spinules, at bases concolorous with the adjacent thallus, isodiametrical, tapering from
102 a 10–15 µm wide base, initially with long hyphae, later with paraplectenchymatic tissue extending
103 from the cortex, with inclusion of chlorobiont cells in the central lowermost parts of large spinules.
104 *Upper cortex* 15–25 µm thick, sclerenchymatic, hyaline and paraplectenchymatic; lumina elongate,
105 2–5 × 2–8 µm; walls 2–4 µm thick. *Chlorobiont layer* c. 60 µm thick, of cf. *Myrmecia* cells, globose
106 to irregularly globose, 8–17 µm diam. *Medulla* 70–100 µm thick; *lower cortex* absent.
107 *Prothallus/hypothallus* whitish, forming a weak, but distinct byssoid network.

108 *Cephalodia* common, and of two types. The most striking form develops from tiny granules
109 into 0.2–0.8 mm wide, mini-foliose, suberect and geotropically arranged, weakly scalariform,
110 glabrous cephalodia, divided into 0.1 mm broad lobules, and positioned directly on the hypothallus,

111 in some cases with visible contact with the chlorobiont squamules; lobes c. 100 μm thick, with both
112 upper and lower cortex layers 10–15 μm thick, paraplectenchymatic with lumina $2\text{--}3 \times 3\text{--}6 \mu\text{m}$,
113 walls 2–3 μm , uppermost part appearing sclerenchymatic. *Cyanobiont Nostoc*, small-celled, blue to
114 ultramarine blue, $3\text{--}4 \times 3\text{--}6 \mu\text{m}$. The other cephalodium type is pulvinate to coarsely coralloid, 0.1–
115 0.3 mm wide, directly attached to the hypothallus, or associated or embedded within the chlorobiont
116 squamules, with spinules like on the chlorobiont squamules, and with cyanobiont cells extending into
117 basal, central parts of the largest spinules; *Nostoc* cells deep sea-green or emerald green to turquoise,
118 $4\text{--}7 \times 5\text{--}8 \mu\text{m}$. Both *Nostoc* types are arranged in 10–30 μm large glomeruli or goniocysts without
119 chain structures, with glomeruli filling out most of the medullary layer.

120 *Apothecia* common, substipitate, 0.7–1.3 mm wide; *disc* orange-brown, flat, becoming
121 distinctly convex; *thalline excipulum* partly lacking, partly with scattered, very low and appressed
122 squamules, densely covered with spinules of the same type as on chlorobiont squamules. *Epithecium*
123 c. 15 μm thick, sclerenchymatic, pale brown. *Hymenium* c. 100 μm thick, colourless, but strongly
124 IKI+ blue. *Asci* clavate, $15 \times 70\text{--}80 \mu\text{m}$, with 8 ascospores and with cap to tube-like IKI + blue,
125 apical structures. *Proper ascospores* hyaline, non-septate, short-ellipsoid, $12.5\text{--}16 \times 8.5\text{--}10.5 \mu\text{m}$.
126 *Perispores* of the same shape, $13\text{--}17 \times 9\text{--}11.5 \mu\text{m}$, low-verrucose, no apical extensions seen.
127 *Parafyses* septate, simple to sparingly branched, c. 2.5 μm thick, apices slightly swollen.
128 *Hypothecium* light brown, 40–50 μm thick, IKI negative.

129 *Pycnidia* not seen.

130 *Chemistry*: brownish melanins present, but no TLC-detectable components found.

131 *Habitat ecology*: only known from relatively smooth bark of a *Picea sitchensis* trunk at
132 upper edge of a sandy sea-shore beach.

133 *Distribution*: U.S.A., Alaska; only known from the type collection.

134 *Etymology*: ‘Carrying spinules’, referring to the spinules on apothecia, squamules and
135 cephalodia.

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138 Two collections representing rare occurrences of *P. hypnorum* and *P. paleaceum* growing on
139 smooth bark were studied in detail for comparison and are cited below. The hair type of *P.*
140 *paleaceum* was studied on several collections in addition. These hairs were found to be white when
141 dry, 100–500 µm long, 20–80 µm wide at base, unistratose to thin and flattened, transparent when
142 moist, and composed of very long, septate hyphae, connected laterally (Fig. 3A). It is proposed here
143 that they should be referred to as long narrow scales, rather than hairs. Fig. 3C shows the hair types
144 of *P. hypnorum*, being composed of c. 3 µm wide hyphae, weak, and often branched and with
145 scattered septae, forming a c. 20 µm high tomentum.

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147 **Additional specimens examined:** *Psoroma hypnorum* (Vahl) S.F. Gray: USA. ALASKA: Klondike,
148 U.S.A., Alaska, NNW of Skagway, Klondike Gold Rush National Historical Park, along Chilkoot
149 Trail, N59 39.930 W135 15.912 (NAD27 Alaska), corticolous at base of *Tsuga* snag, 27 July 2008, *T.*
150 *Tønberg 38976* (BG). *Psoroma paleaceum* (Nyl.) Timdal & Tønberg: AUSTRALIA. TASMANIA:
151 Cradle Mountain-Lake St. Clair National Park, S end of Lake St. Clair, 2 km SW of Cynthia Bay
152 along path to Mt. Rufus. 42°7.078'S, 146°8.534'E, 975 m, on basis of an *Eucalyptus* with smooth
153 bark. 22 April 2008, *A. Elvebakk 08:196* (TROM).

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156 DISCUSSION

157 The new species represents a striking discovery, as it is the first accepted Northern
158 Hemisphere species of a genus otherwise strongly concentrated to austral areas. It also grows on
159 relatively smooth bark, an uncommon habitat among *Psoroma* lichens. In the absence of molecular
160 data, the question therefore arises, does the holotype instead merely represent a habitat modification
161 of a widespread species such as *P. hypnorum* or *P. paleaceum*?

162 Most collections of both these species look very different from *P. spinuliferum*. However, in
163 two rare cases, where *P. hypnorum* (*Tønberg 38976*) and *P. paleaceum* (*Elvebakk 08:196*) had been
164 collected from smooth bark, the specimens have an overall similarity to the new species. The

165 squamules are smaller and paler than in collections from terricolous/muscicolous habitats, apothecia
166 are also more orange-brown and smaller, although significantly larger than those of *P. spinuliferum*,
167 and are flat to weakly convex. These modifications may be a response to a habitat exposed to
168 relatively low light intensities. A closer examination of the collection of the corticolous *P. hypnorum*
169 specimen, which has been published by Spribille et al. (2010), immediately reveals its distinctive
170 squamulose thallus margins, different from both *P. paleaceum* and *P. spinulosum*. The two smooth-
171 bark reference collections of *P. hypnorum* and *P. paleaceum* have significantly larger apothecia than
172 *P. spinuliferum*, and also larger ascospores. In *P. spinuliferum* the proper spores are in the range 11–
173 16 µm, in both *P. hypnorum* and *P. paleaceum* they are 16–20 µm. In addition, the two latter have
174 very distinct nodulose apical extensions of the perispores, lacking in *spinuliferum*. Thus the total
175 perispore lengths are 12–17 µm (*P. spinuliferum*), 18–21 µm (*P. hypnorum*) and 19–23 µm (*P.*
176 *paleaceum*). The spore widths are quite similar in these specimens, although the two latter have
177 higher verrucae.

178 The hair types of *P. hypnorum* var. *hypnorum* and *P. paleaceum* (as *P. hypnorum* var.
179 *paleaceum*) were illustrated by Jørgensen (1978). The former was shown to have ‘short, irregular
180 hairs’, the latter ‘long, straight hairs’ which are ‘100–300 µm long’, ‘situated at the uppermost parts’,
181 ‘on the outer part of the apothecia’, ‘with somewhat variable density’ (Jørgensen 1978). Jørgensen &
182 Kristinsson (2003) stated that two hairy taxa were present in Europe, *P. hypnorum* var. *paleaceum*
183 with glabrous thalline squamules, and *P. hirsutulium* Nyl. ex Crombie differing e.g. by hairy thalli.
184 However, these two taxa were united by Timdal & Tønsberg (2006) as *P. paleaceum*, and our studies
185 confirm that the same type of hairs are frequently also found also on the thalline squamules and on
186 cephalodia, similar to the situation in *P. spinuliferum*. The hair types are very different in these three
187 species and they are referred to here as *scales* in *P. paleaceum*, *spinules* in *P. spinuliferum*, and
188 *tomentum* in *P. hypnorum* (Fig. 3). The tomentum of *P. hypnorum* is very distinct, forming a low mat
189 of branched hyphae, bent towards all directions when seen in the microscope, more erected upwards
190 when dry. *P. paleaceum* scales are long and flat and consistently white when dry. Large spinules of

191 *P. spinuliferum*, on the other hand, have a circular cross-section and take on the color of the
192 mycobiont in lower parts, where the photobiont is present.

193 The spinules are numerous, stiff and brittle, and break off easily when old. Theoretically,
194 they can act as vegetative propagules also when alive, as well-developed spinules contain both the
195 mycobiont and one of the photobionts. This would then be the first Pannariaceae species which has
196 similar vegetative propagules on both the chlorobiont and on one among two cyanobionts. On the
197 former they are scattered, on the latter they dominate on every cephalodium of the pulvinate to
198 coralloid type, whereas they are totally absent from the small-foliose cephalodia with ultramarine
199 *Nostoc* cells.

200 The photobiont diversity in *Pannariaceae* is diverse. The family is basically cyanobacterial,
201 however, 30 % of the genera also include tripartite species or green-algal species or are entirely
202 composed of tripartites (Jørgensen & Zhurbenko 2002; Ekman et al. 2014; Elvebakk et al. 2016).
203 Among the latter, there is a high diversity in cephalodium morphology, in several cases with
204 adaptations to vegetative dispersal (James & Henssen 1976; Jørgensen & Wedin 1999; Jørgensen
205 2004a). There are also several cases where cyanobiont diversity results in morphological diversity. The
206 generitype of the tropical genus *Lepidocollema* deviates significantly from the other species of the
207 genus by being homoiomerous from having a distinctly chain-celled *Nostoc* strain (Ekman et al 2014).
208 Elvebakk (2016) indicated that the tropical species *Lepidocollema polyphyllum* (P. M. Jørg.) P. M.
209 Jørg. has two different cyanobionts, one forming the ‘normal’ thallus, the other forming cephalodium-
210 like lobe systems. Recently, the homoiomerous cyanobacterial genus *Kroswia* was shown to be included
211 in *Fuscopannaria*, a surprising result as the homoiomerous thalli of the former look very different from
212 the heteromerous thalli of the latter (Magain & Sérusiaux 2015). However, *P. spinuliferum* is the first
213 example of a Pannariaceae lichen, where two clearly anatomically different cyanobionts lead to the
214 formation of two morphologically different types of cephalodia. The two types are obviously attached
215 to a common hypothallus.

216 Figure 2 illustrates *Psoroma spinuliferum* as a very colourful lichen. The chlorobiont
217 squamules have been given a fresher green colour corresponding to those of other fresh *Psoroma*

218 species, the colour is less intense in the 17-year old specimen. The cephalodia are illustrated with
219 exact colours, the scalariform cephalodia are truly ultramarine blue, the other type intensely emerald
220 green, less intensive on the outside, although the colours have probably altered and become more
221 intensive after storage. Still, the first author has not observed such intensity in these colours of
222 cyanobionts in numerous herbarium specimens of tripartite Pannariaceae species studied from the
223 Southern Hemisphere. When studied by microscope, cyanobiont diversity appears to be very large in
224 Pannariaceae, a fact which has also been documented genetically, e.g. by Elvebakk et al. (2008) and
225 Magain, & Sérusiaux (2014). However, without striking cyanobiont colors, the two known *P.*
226 *spinuliferum* specimens known so far are inconspicuous and not easily discovered, and the species
227 may not be common. Only one of the large *Psoroma* collections in North America has so far been
228 studied by the first author, and *P. spinuliferum* was lacking from 218 examined WIS specimens
229 originally determined as *Psoroma hypnorum*, many of these collected in Alaska.

230 The species grew on a trunk on the leeward side of a narrow forest belt just above a sandy
231 sea-shore beach. Thus, the two holotype specimens were probably exposed to occasional sea-spray,
232 and were obviously in a shaded position and therefore less exposed to drought there than in
233 neighboring habitats.

234 To conclude, *P. spinuliferum* is basically different from *P. paleaceum* and *P. hypnorum* in
235 its hair types and ascospores. It is also unique in its bicephalodiate cyanobiont structure. Pale and
236 convex apothecia and small, pale squamules are characters shared by rare smooth-bark occurrences
237 of *P. hypnorum* and *P. paleaceum*, and one would therefore predict future collections of *P.*
238 *spinuliferum* from open habitats to be more robust, without modifications from habitats with low
239 light intensities. Hopefully, the particular cyanobiont structure will be confirmed by studies of future
240 collections, however, a given lichen species might also occur as associated with other photobionts. It
241 should also be added that the genus *Psoroma* is still very insufficiently known world-wide, and a rich
242 material under study by the first author and co-workers will also reveal additional novelties for both
243 North and South America.

245

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250

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320 **FIGURES /FIGURE CAPTIONS**

321



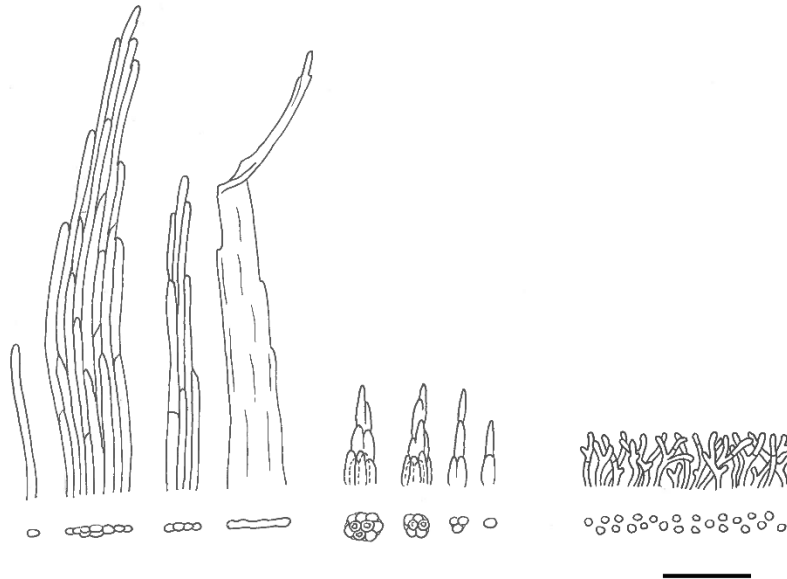
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323 Figure 1. The holotype of *Psoroma spinuliferum*; A) the entire collection, scale bar = 10
324 mm; B) close-up, scale bar = 5 mm.

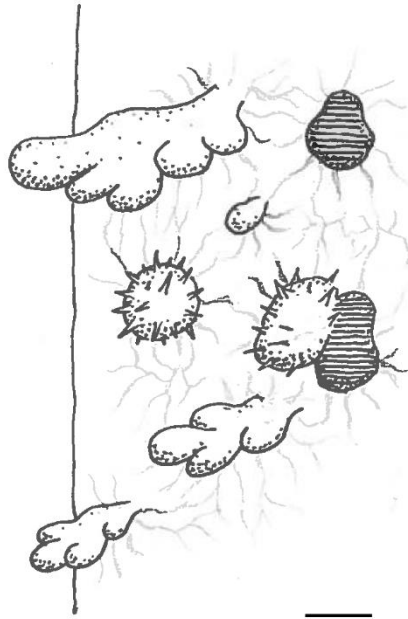


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 326 Figure 2. A painted presentation of *Psoroma spinuliferum* with colors matching moistened
 327 fragments of the holotype, scale bar = 1 mm.



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 329 Figure 3. Hair types in *Psoroma*. A) *P. paleaceum* scales (left), B) *P. spinuliferum* spinules
 330 (center) and C) *P. hypnorum* tomentum (right), scale bar = 30 μ m. The illustrations are based on
 331 microscoped samples, except one folded *P. paleaceum* scale, drawn from its dry state.

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334 Figure 4. Minifoliose cephalodia with ultramarine *Nostoc* cells, spinulose cephalodia with
335 emerald green *Nostoc*, and chlorobiont squamules (hatched) interconnected by hypothalline hyphae,
336 scale bar = 0.1 mm

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