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## Abstract

*Psoroma sphinctrinum* var. *crispellum* has been considered a synonym of *Pannaria implexa*, but it is a distinct species, recombined here as *P. crispella*. It forms a thin, filmy thallus on tree trunks, and consists of rounded, confluent squamules surrounded by a distinct black prothallus. The apothecia are initially simple with a well-defined central thalline plug. However, the plug soon expands into a labyrinth-like structure with undulate margins, unlike those of any other Pannariaceae. The ascospores are long-tailed, as in *P. implexa*, but otherwise smooth, and the species contains argopsin, very rarely reported from the family except for the parmelielloid clade. *Pannaria campbelliana*, previously also considered to be a synonym of *P. implexa*, is shown here to represent a second well-founded species, characterized by thick, geotropically arranged squamules, a distinct fibrous prothallus, apothecia with a prominent simple thalline plug and short-ellipsoid spores lacking apiculate extensions.

## Introduction

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During field work in Egmont National Park, Taranaki, in 2016, a conspicuous, corticolous, squamulose Pannariaceae species was collected. It was common and formed large patches, occasionally more than 50 cm across, although possibly formed by several confluent thalli. The thalli were thin and firmly attached, and their apothecia were abundant and densely packed.

During later herbarium studies, this distinctive lichen was identified as *Psoroma sphinc-trinum* var. *crispellum* Nyl., described by Nylander in 1863 and based on a Colenso collection from New Zealand (*Colenso 4705*, BM). At the time, Nylander treated *Psoroma* as part of *Lecanora*, and in a later paper on the lichens of New Zealand's subantarctic Campbell Island (Nylander 1876), he stated that the lichen was a 'quasi' *Lecanora sphinctrina*, because its thallus was microphylline and the margins of its apothecia were crispate-contorted. Hence, he recombined it as *Lecanora pholidotoides* f. *crispella* (Nyl.) Nyl., citing only the *Colenso 4705* specimen. Later, he recognized it among Filhol's collections from Campbell Island, and included it in his list from that island as 'sur les écorces' ('on bark') (Nylander 1888). He stated its basionym, and added to the *Colenso 4705* specimen a collection by Knight.

Hue (1906) maintained the *Colenso 4705* collection as the only reference for the name *Psoroma sphinctrinum* var. *crispellum*, and noted that it had long-apiculate perispores. However, the specimen from Campbell Island collected by Filhol in 1874 and determined as the same taxon by Nylander (1876), was instead described by Hue (1906) as *Pannaria campbelliana* Hue, characterized by spherical to short-ellipsoid spores.

Those two taxa have been interpreted as *Psoroma implexum* Stirt. by later review studies (Galloway 1985, 2007; Jørgensen 2006). The latter species was recombined as *Pannaria implexa* (Stirt.) Passo, Calvelo & Stenroos by Passo *et al.* (2008), who also provided phylogenetic support. Later Passo & Calvelo (2011) revised their interpretation, and the material from South America was transferred to a new species, *Pannaria byssoidea* Passo & Calvelo. *Pannaria implexa* was redefined as a New Zealand endemic, with *Psoroma sphinctrinum* var. *crispellum, Pannaria campbelliana* and *Psoroma spectabile* Zahlbr. listed as synonyms.

The aim of the present study is to investigate whether *Psoroma sphinctrinum* var. *crispellum* represents a separate taxon which deserves recognition at species level. The newly recognized species will be compared with taxa previously regarded as synonyms, *Pannaria campbelliana* in particular.

### Material and methods

This paper is based on material from the herbaria AK, BM, CHR, H, MAF, PC, TROM, TUR-V and WELT; *Pannaria crispella* was searched for in other herbaria, but unsuccessfully.

Ascospore structures were studied in water mounts and restricted to spores liberated from their asci. Detailed drawings of 23 ascospores from four samples of *P. crispella* and seven from the sample of *P. campbelliana* were made, and copies of the sketches were included with the specimens. Thin-layer chromatography of acetone extracts followed standardized procedures, and used solvents A and C (Orange *et al.* 2010). Nomenclature of ascospore structures follows Nordin (1997).

## The species

Pannaria crispella (Nyl.) Elvebakk, comb. nov.Figs 1–5, 7MycoBank No.: MB 842299Figs 1–5, 7

Type: New Zealand, (North Island, Manawatu-Wanganui Region) "on Podocarpus Cunningham. Forests, Ruahine", Oct. 27 [year not stated], *W. Colenso 4705*, (BM–lectotype!; WELT L1120–isolectotype!; H–isolectotype!). Basionym: *Psoroma sphinctrinum* var. *crispellum* Nyl., *Syn. Meth. Lich.* **2**, 25 (1863).  $\equiv$  *Lecanora pholidotoides* f. *crispella* (Nyl.) Nyl., *Compt. Rend. Hebd. Séanc. Acad. Paris*, Sér. D, **83**, 89 (1876).

Thallus squamulose, tripartite, corticolous, forming patches 10-60 cm wide; hypothallus/ prothallus distinct, prothallus forming a peripheral border 2 mm wide, black, fine-textured. Chlorobiont squamules initially as 0.1 mm wide, scattered granules on the prothallus, soon expanding to 1 mm wide squamules with weakly incised, obtuse lobes, then coalescing centrally into an areolate and continuous crust, some lobes overlapping, strongly attached, 0.05–0.1 mm thick. Upper surface matt, pale greyish green when fresh and dry, salad-green when fresh and moist, young herbarium specimens immediately turning reddish brown after application of water, older herbarium specimens gradually becoming dark brown after long storage, glabrous except for a minute tomentum along margins, seen as pruinose when moist. Cortex c. 30 µm thick, upper part thin and sclerenchymatic, lower part pale and paraplectenchymatic, lumina mostly isodiametric, 5-10 µm, or weakly elongated, arranged perpendicularly to the upper surface, walls 2–3 µm thick, *Chlorobiont layer c.* 30 m thick, below the cortex, of Trebouxia cells, globose, 5–10 µm diam., chloroplasts papillose. Medulla 20–30 µm thick, white; lower cortex absent. Cyanobiont Nostoc, in dark grey, placodioid cephalodia growing on the chlorobiont, 0.5–1 mm wide, forming densely adpressed, radiating lobules, c. 0.2 mm wide, common. *Nostoc* cells greyish green, irregularly subglobose to ellipsoid,  $4-6 \times 2-3 \mu m$ , organized within small glomeruli and without visible chain structures. Apothecia common, substipitate when juvenile and less than 0.5 mm wide, with smooth brown discs, but soon developing thalline structures consisting of a concave, central squamule, seen as a plug-like structure, mostly also accompanied on the disc by small secondary thalline granules. This develops further into an intricate, labyrinth-like, strongly convex apothecial structure 2–3 mm wide. Thalline excipulum 0.1–0.2 mm broad, crenulate, of small inrolled lobules, 0.1 mm wide, in older apothecia developing a strongly undulating, crispate pattern. *Epithecium* pale brown, c. 15 µm thick; hymenium pale, 100–120 µm, IKI+ blue; hypothecium brownish, 60-80 µm; algal layer discontinuous below the hypothecium, but forming extensions penetrating through the hymenium and forming thalline plugs. *Paraphyses* simple, septate,  $1.5-2 \mu m$  wide, weakly swollen and fused apically in the epithecium. Asci clavate, c.  $80 \times 15$  $\mu$ m, with 8 spores. Ascospores regularly ellipsoid to weakly citriform or ovoid,  $14-22 \times 9-12$  $\mu$ m, perispores thin and even except for long-apiculate, apical extensions,  $22-50 \times 10-14 \mu$ m. Pvcnidia not seen.

*Chemistry*: Argopsin detected by TLC.

*Etymology*: The species is named for its strongly crispate and undulate apothecial margins.

#### SPECIMENS EXAMINED

**New Zealand**. • C. Knight (TUR VAIN-12002b) (with no further information); Taranaki Region: • Taranaki/Egmont National Park, North Egmont, nature walk just S of the Visitor Centre, 39°16'15"S, 174°05'45", 960 m alt., on a trunk of *Podocarpus*, forming a 60-cm-long patch, A. Elvebakk 16:151, 28.ii.2016 (TROM); Hawke's Bay Region: • Hawke's Bay, near Napier, on rimu, W. Colenso, iv.1885 (WELT L1765); Wellington: • Wellington Land District, Tauwharenikau, V.D. Zotov, viii.194x (CHR 545611); Marlborough Region: • Queen Charlotte Sound, saddle 1 km S of Mount Furneaux, 41°06'S, 174°13'E, 580 m alt., on bark of Podocarpus totara, A.E. Wright 1184, 2.i.1992 (AK 205028); • loc. id.: B.W. Hayward (AK205390); *Canterbury Region*: • 700 m N of Arthur's Pass Village near bridge over McGrath Creek, 42°55'45"S, 171°33'29"E, 780 m alt., on light-exposed Nothofagus solandri trees near the road, A. Elvebakk 16:236, 1.iii.2016 (TROM); • 500 m S of Arthur's Pass, start of Bealey Valley Track, 42°54'53"S, 171°33'28"E, 870 m alt., forming a 20-30 cm wide patch on Nothofagus solandri in forest, A. Elvebakk 16:190, 28.ii.2016 (TROM); • Taranaki Region, Taranaki/Egmont National Park, nature walk just S of the Visitor Centre, 39°16'15"S, 174°05'45" E, 960 m alt., on a trunk of *Podocarpus*, forming a large patch, 26.ii.2016, • *loc*. id. A. Elvebakk 16:149 (TROM); A. Elvebakk 16.153 (TROM); • loc. id. A. Elvebakk 16:154 (TROM); • loc. id. also over moss and filmy ferns, A. Elvebakk 16:157a (TROM); • North Egmont, c. 1 km along Veronica Loop Track, S of the Park Centre, 39°16'39"S, 174°05'14"E, 1150 m alt., A. Elvebakk 16:120, 24.ii. 2016 (TROM).

Pannaria campbelliana Hue, Nouv. Arch. Mus. Nat. Hist. Sér. 4, 8, 271 (1906) Figs 6–7

Type: Expedition astronomique a l'Île Campbell, 1874, *M. Filhol* (H-NYL 30769–lectotype; *fide* Galloway 1985: 476); PC-HUE! – isolectotype, *fide* Galloway (2007: 1466);  $\equiv$  *Psoroma* campbellianum (Hue) Zahlbr., *Cat. Lich. Univ.* **3**, 267 (1925). For a description, see Hue (1906).

The isolectotype carries Nylander's handwriting, and Hue's personal species number "1136" has been written on the envelope; in contrast, he used "1133" for what is here recognized as *P. crispella*. The material (Figs 6A and B) consists of separate pieces of a squamulose thallus, possibly having measured 2–5 cm across. Squamules are entire to weakly divided, forming obtuse lobules, 0.2 mm thick, clearly scalariform, resting on a coarse black hypothallus continuing as a 2–3 mm wide, fibrose prothallus. No cephalodia were seen. Apothecia are common, 0.5–1.5 mm diam.; discs concave centrally with thalline plugs; excipulum 0.3 mm wide, crenate, of inrolled, obtuse lobes, 0.2 mm broad, on the isolectotype, mostly absent due to grazing by invertebrates. All apothecia have black necrotic spots centrally, and mature spores seen were very few. However, the ascospores are ellipsoid to ovoid and weakly citriform, 14–17 × 9–11  $\mu$ m; perispores indistinctly vertucese when immature, otherwise with low vertuce and without apical extensions, 15–18 × 10–12  $\mu$ m (Fig. 7). The lectotype contains pannarin by TLC (J.A. Elix pers. comm.).

# **Discussion and conclusions**

While Pannariaceae cyanolichens are well understood in New Zealand, tripartite species within the genera *Pannaria* and *Psoroma* are difficult to identify due to many undescribed or misunderstood taxa. Those challenges need to be solved species by species, which is time-consuming. The squamulose species of *Pannaria* are among the most difficult. Three South American taxa were recently transferred to the new genera *Hispidopannaria* and *Phormopsora* (Elvebakk *et al.* 2020), in addition to the two species documented by Passo *et al.* (2008) and Passo & Calvelo (2011).

Here, it is shown that the present interpretation of *P. implexa* is too broad. *Pannaria crispella* is instead a distinct species, with a very thin (< 0.1 mm), filmy thallus, strange labyrinth-like apothecia, deserving the description 'apotheciis crispato-contortis contiguis' by Nylander (1863). Cephalodia have radiating, placodioid lobules, and perispores are long-apiculate with otherwise smooth walls. Perispores resemble those of *P. implexa*, but differ in

the lengths of the apiculi and the structure of the walls. *Pannaria crispella* contains argopsin, which is common in parmelielloid genera, such as *Erioderma*, e.g. Jørgensen (2001b), but rarely reported from other major clades within Pannariaceae. Pannaria crenulata P.M.Jørg. was reported to contain vicanicin and argopsin by Jørgensen (2001a:115: 2004: 239), and Ekman et al. (2014: 648) indicated in their key that Fuscopannaria and Protopannaria rarely contain argopsin. *Pannaria crispella* will probably turn out to be a widespread forest species in much of New Zealand. During my field work, it appeared to be common both in Taranaki and near Arthur's Pass. It is also very conspicuous, easily identified in the field, and is a New Zealand endemic. Pannaria campbelliana has been the subject of a limited study here, which, however, confirms Hue's claim (1906) that it is a distinct species. The thallus differs from that of *P. crispella*, and more closely resembles *P. implexa*. However, the squamules are clearly geotropically arranged, and the ascospores differ from both of those species in lacking apiculate extensions. The spores more closely resemble the South American P. byssoidea Passo & Calvelo, which also has a strongly developed, fibrose prothallus. However, the squamules of the latter are not geotropically arranged, its thallus has a thicker, almost pulvinate hypothallus/prothallus, and the species contains leprolomin (Passo & Calvelo 2011).

Many specimens collected on the Auckland and Campbell Islands by H. Imshaug and coworkers have been determined as *Psoroma campbellianum*. According to GBIF there are 43 specimens in MSC alone, and many have been distributed to other herbaria. Among those seen by me, only one (Auckland Island, mature *Metrosideros* forest on north side, near head of Musgrave Inlet, near sea level, *H.A. Imshaug* 56536, 28.ii.2016, (MAF L4559)) has been examined microscopically. Based on spore characters, it was determined as *P. implexa*. The status of *Pannaria campbelliana* in these islands remains unknown, except for the studied type material. Further herbarium specimens should be studied, as well as material from the southern part of South Island and Stewart Island, and fresh samples for a phylogeny would be particularly welcome. In any case, it remains clear that *P. campbelliana* should be recognized as a separate species rather than a synonym of *P. implexa*.

After the segregation of Hispidopannaria and Phormopsora from Pannaria, Pannaria byssoidea formed a well-supported sister group to the remaining foliose species of Pannaria represented in the phylogram by Elvebakk et al. (2020). The generic affiliations of an apparently heterogeneous assemblage of squamulose *Pannaria s.l.* species remain unresolved, and a future phylogenetic study is planned. However, type studies are also required to resolve species circumscriptions. *Psoroma pholidotoides* (Nyl.) Trevis. is a name that has mostly been erroneously used for specimens of *Xanthopsoroma contextum* (Stirt.) Elvebakk; see Elvebakk et al. (2010). However, the basionym of Psoroma pholidotoides is either conspecific with *Pannaria implexa*, in which case the former name would take priority, or it represents a neighbouring taxon. The latter interpretation is presently used also for Psoroma caliginosum Stirt., a topic under further study. The type of *Psoroma spectabile* Zahlbr. at W was on loan and not available during a visit there. However, the species was described by Zahlbruckner as having small squamules (< 1 mm wide), and apothecia that are large, lecanorine, rounded, undulate at maturity, and measuring up to 3.5 mm wide (Zahlbruckner 1941). He also stated that the spores had rounded apices and were evenly surrounded by perispores ("apicibus rotundatis, membrane mediocri et laevi cinctae"). That would exclude P. spectabile from being a synonym of *Pannaria implexa*, and related to *P. campbelliana* instead. If shown to be conspecific by future studies, the name *P. campbelliana* will take priority.

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Fig. 1. Psoroma sphinctrinum var. crispellum, lectotype.



Fig. 2. *Pannaria crispella* along a path in Egmont National Park. The specimen was sampled as *Elvebakk* 16:151.



Fig. 3. A moist specimen of *Pannaria crispella* in Egmont National Park, sampled as *Elvebakk* 16:157A. The associated species in the upper left corner is *Megalospora knightii* Sipman.



Fig. 4. *Pannaria crispella, Elvebakk 16:151*, photo: Julia Brekmo. Scale-bar = 1 cm.

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Fig. 5. Pannaria crispella, Elvebakk 16:151, photo: Julia Brekmo. Scale-bar = 0.5 cm.



Fig. 6A. Pannaria campbelliana, isolectotype. Scale bar = 1 cm.

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Fig. 6B. Pannaria campbelliana, isolectotype, photo: Mari Karlstad

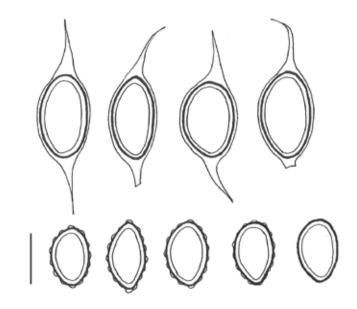


Fig. 7. Ascospores of Pannaria crispella (upper row) and P. campbelliana.