



## A trio of endemic New Zealand lichens: *Pannaria aotearoana* and *P. gallowayi*, new species with a new chemosyndrome, and their relationship with *P. xanthomelana*

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With 2 figures

**Abstract:** The endemic New Zealand lichen *Pannaria xanthomelana* has been restudied and found to be characterized by a secondary chemistry of pannarin and porphyritic acid in addition to terpenoids, and by always having abundant, conspicuously large, and mostly foliose cephalodia. Its verruciform pycnidia and bacilliform pycnoconidia/spermatia are described here for the first time. Two other related New Zealand endemics, *P. gallowayi* and *P. aotearoana*, are described as new. Both have small, relatively rare and inconspicuous cephalodia. They contain a new chemosyndrome, with pannarin, contortin and *O*-methyl-leprolomin together with major quantities of several unidentified terpenoids, previously reported from the related Australian species, *P. isidiata*. *O*-methyl-leprolomin is a novel compound, with similar TLC properties to leprolomin, but with different  $R_f$  values. Most collections of both species from the North and the South Islands of New Zealand contain additional porphyritic acid. However, this compound is absent from many collections of these species from the subantarctic Campbell and Auckland Islands. Aside from chemistry, *Pannaria gallowayi* is also distinguished by having broad, papery lobes. *Pannaria aotearoana* which appears to be the more common species, has a thick thallus and characteristic thick, convex, marginal phyllidia, larger spermatia and more conspicuous pycnidia than *P. gallowayi* and *P. xanthomelana*. The three species share two different major chlorobionts. *Trebouxia* dominates in the north, and is gradually replaced southwards by a type provisionally called cf. *Myrmecia*.

**Key words:** *Pannariaceae*, taxonomy, vegetative propagules, cyanobionts, *O*-methyl-leprolomin, contortin.

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## Introduction

Tripartite foliose *Pannaria* species are restricted to austral areas, where they are an important component in forests throughout New Zealand, the SE parts of Australia (Tasmania, Victoria, New South Wales, Lord Howe Island) and southern South America, with scattered occurrences in Queensland (Australia) and in New Caledonia (Elvebakk 2007, 2012a, Galloway 2007, McCarthy 2016). Elvebakk (2012a) concluded that 17 species had been accepted prior to his study, the majority of which were originally described within the genus *Psoroma*. Five additional species have been described subsequently (Elvebakk 2012a, b, 2013), giving a total of 22 recognized taxa.

In contrast to most bipartite *Pannaria* species, which only produce pannarin or lack lichen substances, the tripartite species produce a high diversity of secondary compounds. The most common compounds, pannarin and vicanicin, were characterized relatively early in chemical studies by Neelakantan et al. (1962) and reviewed by Culberson (1969), with further studies by Sargent et al. (1976) and Jackman et al. (1975). A lack of knowledge of these diagnostic compounds impeded early lichenological studies, but a number of additional metabolites were described during the 1970s and 80s, including norvicanicin (Sargent et al. 1976), leprolomin (Elix et al. 1978), scabrosin esters (Begg et al. 1978; Ernst-Russell et al. 1999), dechloropannarin, isovicanicin, allorhizin (Elix et al. 1982), contortin (Elix et al. 1984), and norpannarin (Elix et al. 1986).

When dealing with the New Zealand species, Galloway (2007) reported that most of the tripartite foliose species were characterized chemically by the presence of vicanicin alone or accompanied by  $\pm$  allorhizin, by vicanicin/isovicanicin with leprolomin, or by pannarin alone or with porphyrylic acid. Elvebakk et al. (2007) described *Pannaria farinosa* Elvebakk & J.Fritt-Rasm. with vicanicin, leprolomin and three constant terpenoids, and showed that *P. leproloma* (Nyl.) P.M.Jørg. had seven or eight compounds, including another terpenoid and one or two additional scabrosin esters. More recently, a new chemosyndrome was reported for the two Lord Howe Island endemics, *P. howeana* Elvebakk and *P. streimannii* Elvebakk, both containing a combination of porphyrylic acid, vicanicin and leprolomin (Elvebakk 2012a).

According to Elvebakk & Elix (2006), species containing pannarin occur with eight combinations of secondary compounds. This included the new and complex chemosyndrome present in *P. isidiosa* Elvebakk & Elix and three combinations reported by Passo et al. (2004). Subsequently, Passo & Calvelo (2006) revised the secondary chemistry of *P. contorta* (Müll.Arg.) Passo & Calvelo and described *Pannaria calophylla* (Müll. Arg.) Passo & Calvelo as containing pannarin and norpannarin.

Thus, there is increasing evidence that single tripartite *Pannaria* species or groups of closely related species, contain unique chemosyndromes, often with characteristic occurrences of as yet unidentified terpenoids. The aim of the present study was to describe two new pannarin-containing species with a very complex chemosyndrome which included terpenoids as major compounds. The new species are morphological similar to and have previously been included within *P. xanthomelaena* (Nyl.) Hue sens. lat. As a consequence, a detailed study of the latter was also required.

## Material and methods

This paper is based on material from the herbaria AK, CANB, H, MSC, OTA, S, TROM, UPS, WELT in addition to a holotype at BM. A total of 104 collections of these species were examined, all studied chemically. In microscope sections, iodine reactions were tested by adding IKI to mounts pretreated with KOH. Perispore structures were studied in water mounts and restricted to spores liberated from their asci. Ascospore morphology was studied in detail by drawing sketches of c. 160 single ascospores from 18 collections. Thin layer chromatography of acetone extracts followed standardized procedures and used solvents A and C (Orange et al. 2010, Elix 2014). A few samples were also studied by using HPLC, following the methods of Feige et al. (1993) and Bjerke et al. (2002). Nomenclature of ascospore structures follows Nordin (1997). The localities cited are indicated with the present political boundaries within New Zealand.

## Results

### The Species

*Pannaria xanthomelana* (Nyl.) Hue

Figs 1 A–C

Bull. Soc. Bot. France 48: LVI, 1902 ('1901')

BASIONYM: *Psoroma xanthomelanum* Nyl. *Syn. Meth. Lich.* 2: 26 (1863). Lectotype: New Zealand. Hawke's Bay, Ruahine Range. On *Nothofagus* bark. W.Colenso 4546, BM! Isolectotypes: H-NYL 30822!, WELT L1553!

*Lecanora xanthomelana* (Nyl.) Nyl. *Compt. Rend. Hebd. Séanc. Paris, Sér. D*, 83: 86 (1876).

THALLUS foliose, corticolous, forming rosettes 3–12 cm diam., loosely attached to the substratum, particularly when growing over bryophytes on tree trunks, 150–350 µm thick. LOBES subdichotomously branched, 0.5–2 mm broad, discrete in peripheral parts, coalescing centrally, flat to weakly concave, sometimes with raised margins; secondary, small lobules developing commonly along margins, in the same level as the major lobes, but with 90° orientation, some developing further into lobes. UPPER SURFACE even, glossy, and glabrous, whitish grey when alive and dry, green with a bluish hue when alive and moist, changing to yellowish-brown after storage in herbaria. UPPER CORTEX 30–50 µm thick, upper half with brown pigmentation in old specimens, upper part sclerenchymatic, otherwise paraplectenchymatic with lumina subglobose to irregularly ellipsoid, 5–12 µm long, walls c. 2–4 µm thick. PHOTOBIONT layer 30–50 µm thick, of globose to subglobose TREBOUXIA or cf. MYRMECIA cells, 7–13 µm diam. MEDULLA 100–250 µm thick, lowermost 20–30 µm brown-pigmented. LOWER CORTEX lacking; RHIZINES common, from pale and pencil-shaped to squarrose, densely branched and black, sometimes forming a thick, felt-like hypothallus below the thallus, most often but not always extending up to 3 mm beyond the lobe margins as a thin or thick, black prothallus.

CEPHALODIA very common, laminal on the upper side, very rarely as tiny globules on the lower side, 2–8 mm wide, placodioid to foliose, greyish blue when alive and moist; LOBES CONVEX, erhizinate, becoming free from the substrate peripherally, 0.3–0.8 mm wide; UPPER CORTEX as in the chlorobiont; CYANOBIONT NOSTOC, cells greyish blue, subglobose to ellipsoid, 3–4.5 × 4.5–7 µm large, organized within spherical glomerules, 20–35 µm large, delimited by a mucilaginous sheath; no chain structures observed.



Fig. 1. *Pannaria xanthomelana*. A: The specimen Elvebakk 02:499 photographed in the field near Haast before being collected. B: Lectotype at BM. C: The specimen Elvebakk 16:188 photographed in the field near Arthur's Pass. Scale bar = 1 cm.

APOTHECIA common, laminal, substipitate, often contorted centrally, 1–4 (–5) mm broad; DISC concave, greyish rufous brown, often partially black and melanized, always with concentric, ring-like depressions; THALLINE EXCIPULUM crenulate-striate; EPITHECIUM pale brown, 20–35  $\mu\text{m}$  thick, IKI negative; HYMENIUM colourless, but strongly IKI+ blue, 100–150  $\mu\text{m}$  thick; HYPOTHECIUM light brown, IKI negative, 80–120  $\mu\text{m}$  thick; PARAPHYSES mostly simple, multiseptate, with slightly swollen apices; ASCI clavate, 13–18  $\times$  80–110  $\mu\text{m}$  large, no internal amyloid structures observed, containing eight ascospores. PROPER ASCOSPORES subglobose to short-ellipsoid, 10–14  $\times$  9–11  $\mu\text{m}$ ; PERISPORES subglobose to short-ellipsoid, distinctly verrucose, 12–16  $\times$  10–14  $\mu\text{m}$  large, single verrucae 1–2  $\mu\text{m}$  wide, 1  $\mu\text{m}$  tall.

PYCNIDIA scattered, marginal, as inconspicuous, low, pale brown-centered verrucae, 0.3 mm across, 0.2 mm high, conidiospores/spermatia abundant, 1.5–2.5  $\times$  0.5–1  $\mu\text{m}$ , bacilliform, rarely slightly curved.

CHEMISTRY: Pannarin (major) and porphyritic acid (major), '*Pannaria isidiosa* terpenoids 1, 2 and 3' and '*P. gallowayi terpenoid* 1' (indistinct/trace to major), occasionally with other unidentified terpenoids and dechloropannarin.



## ADDITIONAL SPECIMENS STUDIED:

A) Chemotype with pannarin, porphyritic acid and '*P. isidiosa* and *P. gallowayi terpenoids*' (37 specimens)

NEW ZEALAND, North Island, Manawatu-Wanganui: Tongariro National Park, Silica Springs Track 39°13'S, 175°32'E, 1260 m, on trunk of *Pseudopanax simplex*, 16.XI.1991, C.J.West (WELT L3893); South Island, Tasman: Golden Bay Co., Cobb, 41°S, 172°E, J.K.Bartlett 1975–1985 (AK 178965); (AK 178962); Lake Rototiti, NW corner of Kerr Bay, 41°49'S, 172°50'E, 625 m, on bark of *Halocarpus bidwillii* on lake shore, 14.IV.1991, B.W.Hayward & A.E.Wright 11284 (AK 204479); near Mt. Robert carpark, Lake Rototiti, Nelson Lakes, *Nothofagus* forest on *N. sp.*, 28.II.1980, J.A.Elix 7458 (CANB 9613697); Mount Arthur, 41°13'S, 172°41'E, J.K.Bartlett 1975–1985 (AK 197954); Track above Mount Arthur Hut, 41°12'S, 172°43'E, 1340 m, on branches of *Hebe topiaria* in subalpine scrub, 13.IV.1991, B.W.Hayward & A.E.Wright 11255 (AK 204450); Arthur Range, track from Graham valley to Mt. Arthur, 41°12'S 172°44'E. On *Nothofagus* in *Dracophyllum* bush. 1080 m, 29.I.1993, Wendy Nelson (WELT L 6256); Northwest Nelson Forest Park, Mt. Arthur 41°12'N, 172°44'E, 1080 m, branch of *Dracophyllum traversii*, 13.IV.1991, C.J.West (WELT L 3890); Marlborough: Queen Charlotte Sound, Mount Stokes, 41°05'S, 174°07'E, 1000 m, on windthrown twigs in *Nothofagus menziesii* forest, 5. I.1992, A.E.Wright 11908 (AK 205132); West Coast; c. 3 km E of Charleston, Nile River, end of Darkies Road. 41°55'S, 171°28'E. On *Nothofagus* bark in *Nothofagus menziesii* and *N. truncata* forest with *Dacrydium cupressinum* and tree ferns, 30 m, Barbara Polly, 2.XII.1997 (WELT L5687); Kahu Saddle, Klondyke Spur Track, 9 km from Springs Junction 42°18.50'S, 172°17'E, 685 m, on *Nothofagus* branch in a *N. menziesii*, *N. cliffortioides*, *N. fusca* forest. 30.X.2000, B.Polly (WELT L6433); Lewis Pass, State Highway 7 between Maruia Springs and Springs Junction, Jackson's Creek, growing on bank in beech forest on banks of river, 11. IX. 1985, A.E.Wright 7303 (AK 170786); 30–35 km SW of Haast, 9 km SW-wards along Cascade Road. 44°05.26'S, 168°38.67'E, 40 m, on bark of *Nothofagus menziesii*, 7. XII. 2002, A.Elvebakk 02:499 (TROM); 02:500A (TROM); 02:502B (TROM); c. 15 km S of Jackson Bay, Cascade Forest, along Cascade Road, 1 km before farm at the end of the road, 44°06.01'S, 168°31.64'E, 25 m, on *Nothofagus menziesii*, at the edge of grazed meadows, 7.XII.2002, A. Elvebakk 02:511 (TROM); 02:514 (TROM); Fantail Falls, Haast River, Haast Pass Highway, on *Nothofagus* sp. by river bed, 44°01'57"S, 169°21'54"E, 23. I. 2004, J.W.Bjerke 053/04 & E.Elverland (TROM L–51155); Bullock Creek, Farm Road, on fallen twig along road with *Cyathea medullaris*, etc., 26 m, 29.II.2000, (WELT L6419); Canterbury, Arthur's Pass National Park, Bealey River, track to Margaret's Tarn, 3000 ft, 42°55'S, 171°33'E, on bark of *Nothofagus solandri* var. *cliffortioides* in forest, 5.XI.1989, A.E.Wright 9397 (AK 187419); A.E.Wright 9331 (AK 187423); A.E.Wright 9338 (AK 187430); Arthur's Pass, Upper Bealey track to Margaret's Tarn, 810 m, lower reaches of track, 5 XI. 1989, W.A.Nelson (WELT L2593); 500 m S of Arthur's Pass, Bealey Valley Track, near Bealey River, 42°54'52.30"S – 171°33'26"E, 860 m, on *Nothofagus solandri*, 28 II.2016, A.Elvebakk 16:188 (TROM); 16:202 (TROM); 16:209 (TROM); 700 m N of Arthur's Pass Village near bridge over McGrath Creek, 42°55'45"S – 171°33'29"E, 780 m, forming large thalli on light-exposed *Nothofagus solandri* trees near the road, 29 II. 2016, A.Elvebakk 16:221 (TROM); Arthur Range, track from Graham Valley carpark to Mt. Arthur Hut, 41°12'S, 172°49'E, *Dracophyllum traversii* bush, on *Nothofagus*, 13.IV. 1991, W.A.Nelson (WELT L2976); Greyney's Flat, 6 km S of Arthur's Pass, Canterbury, on *Nothofagus solandri* var. *cliffortioides* in *Nothofagus* forest. 10.II.1980, J.A.Elix 7046 (CANB); 7071 (CANB); 7059 (CANB 9613679); Lewis Pass summit, start of St. James Walkway, 42°22'S, 172°25'E. 260 m. On bark of *Nothofagus* in area in red tussock shrubland with *N.S.clifford.*, 1.XI.2000, B.Polly (WELT L6468); McGrath's Creek area, Bealey Valley, Arthur's Pass, 800 m, on mountain beech trunk, 24.II.1976, Joy Singleton 76/37 (CANB); Southland: John O'Groats River, on *Nothofagus* branch in mixed W-coast rainforest, 44°30'23"S, 167°53'6"E, 213 m, 14.IV.2010, A.Knight (OTA61737; TROM L–42443); Fiord Bot. Distr., track from Lake Manapouri to Doubtful Sound, Halfway Hut, on *Nothofagus menziesii*, 1.III.1927, G.E. & G.Du Rietz 2046:1 (UPS); on *Olearia Macphersonii*, 1.III.1927, G.E. & E.Du Rietz 2045:1 (UPS); Fiordland, Borland Saddle, forest above road, 45°44'S, 167°23'E, 3400 ft, occasional on bark of very old *Nothofagus solandri* var. *cliffortioides* trees on ridge above saddle, 17.XI.1990, A.E.Wright 10658 (AK 205716).

B) Chemotype with pannarin, porphyrilic acid and three different, unknown terpenoids (2 specimens):

NEW ZEALAND, North Island, Manawatu-Wanganui: Tongariro, Silica Road, on twigs, 39°12.28'S, 175°31.92'E, 1164 m, 16.I.2004, J.W.Bjerke 024/04 & E.Elverland (TROM L-51143); Tasman: Queen Charlotte Sound, Mount Stokes, 41°05'S, 174°07'E, 1000 m, on bark of *Nothofagus menziesii*, 5.I.1992, A.E.Wright 11907 (AK 205131).

***Pannaria aotearoana*** Elvebakk & Elix, **sp. nov.**

Figs 2 B–D

Mycobank # MB818063

Similar to *P. gallowayi*, but differs in having thicker and narrower lobes and by the presence of thick, convex, marginal phyllidia.

TYPE: NEW ZEALAND: South Island, Canterbury, 500 m S of Arthur's Pass, Bealey Valley Track, near Bealey River, 42°54'52.30"S – 171°33'26"E, 860 m, on the base of a 3–4 cm thick and horizontal stem of mikimiki (*Coprosma linearifolia*) in a light-exposed *Coprosma* shrub stand near the river, 28.II.2016, A.Elvebakk 16:203 (AK – holotype; TROM – isotype).

THALLUS foliose, corticolous or saxicolous, forming rosettes 3–15 cm diam., loosely attached to the substratum, particularly when growing over bryophytes on tree trunks, mostly 200–400 µm thick, lobe apices occasionally thinner. LOBES subdichotomously to irregularly branched, 1–2 mm broad, discrete in peripheral parts, coalescing centrally, flat to weakly concave, sometimes with raised margins. PHYLLIDIA common, marginal, 2–3 mm broad, 2–4 mm long, 200–300 µm thick, convex with descending apices, occasionally forming coralloid masses. UPPER SURFACE even or weakly uneven, glossy, and glabrous, whitish grey when alive and dry, green with a bluish hue when alive and moist, changing to yellowish-brown after storage in herbaria. UPPER CORTEX 30–60 µm thick, upper half with brown pigmentation in old specimens, upper part sclerenchymatic, otherwise paraplectenchymatic with lumina subglobose to irregularly ellipsoid, 5–12 µm long, walls c. 2–4 µm thick. PHOTOBIONT layer 40–60 µm thick, of globose to subglobose TREBOUXIA, sometimes cf. MYRMECIA cells, 7–12 µm diam. MEDULLA 100–300 µm thick, lowermost 20–40 µm brown-pigmented. LOWER CORTEX lacking; RHIZINES common, from pale and brush-shaped to squarrose, densely branched and black, sometimes forming a thick, felt-like hypothallus below the thallus, rarely extending beyond the lobe margins as a thin or thick black prothallus.

CEPHALODIA scattered, laminal on both the upper and lower surfaces, 0.5–1.5 mm wide, globose, pulvinate or small-placodioid, greyish blue when alive and moist; UPPER CORTEX as in the chlorobiont; CYANOBIONT NOSTOC, cells bluish-grey, subglobose to irregularly ellipsoid, 3–4.5 × 4.5–7 µm large, organized within spherical glomerules, 10–20 µm large, delimited by a mucilaginous sheath; no chain structures observed.

APOTHECIA common, laminal, substipitate, often contorted centrally, 1–4 mm broad, DISC concave, greyish rufous brown, always with concentric, ring-like depressions, and often with thalline grains or granules centrally; THALLINE EXCIPULUM crenulate-striate, c. 0.3 mm wide; EPITHECIUM pale brown, 20–35 µm thick, IKI negative; HYMENIUM colourless, but strongly IKI+ blue, 100–120 µm thick; HYPOTHECIUM light brown, IKI negative, 80–120 µm thick; PARAPHYSES mostly simple, multiseptate, with slightly swollen apices; ASCI clavate, 13–18 × 80–110 µm large, no internal amyloid structures observed, containing eight ascospores. PROPER ASCOSPORES subglobose to short-ellipsoid,



Fig. 2. *Pannaria gallowayi* and *P. aotearoana*. A: *Pannaria gallowayi* HOLOTYPE. Scale bar = 1 cm. B: *Pannaria aotearoana*. HOLOTYPE, photographed when moist in the field, before most of the specimen was collected. C: The fascinating label text of the oldest known specimen of *Pannaria aotearoana*, collected by W.Colenso on 9 Apr. 1850 at Te Houtotara near Wellington. D: Mixed collection of *P. gallowayi* (above) and (below) *P. aotearoana* (Du Rietz 2663 a:2). Scale bars = 1 cm.



13.5–18 × 9–13 µm; PERISPORES subglobose to short-ellipsoid, distinctly verrucose, 15–21 × 10.5–16 µm large, single verrucae 1–2 µm wide, 1 µm tall.

PYCNIDIA common, marginal or submarginal, on weak laminal ridges or on phyllidia, visible as 0.1 mm wide brown to black-centered verrucae, ostiole fissure-like, conidiospores/spermatia abundant, 2.5–3.5 × 0.5–1.5 µm, bacilliform, occasionally weakly curved, rarely reniform.

CHEMISTRY: Pannarin (major/minor), contortin, *O*-methyl-leprolomin, porphyritic acid, '*Pannaria isidiosa* terpenoids 1, 2 and 3' and '*P. gallowayi* terpenoid 1' (majors), '*P. gallowayi* terpenoid 2 and 3' (minor). Porphyritic acid is lacking from a chemotype mostly present in Auckland and Campbell Islands.

ETYMOLOGY: Named after 'Aotearoa', the Maori name for New Zealand.

ADDITIONAL SPECIMENS STUDIED:

Chemotype I with pannarin, contortin, *O*-methyl-leprolomin, porphyritic acid, and six '*P. isidiosa* and *P. gallowayi* terpenoids': (27 specimens)

NEW ZEALAND, North Island, Waikato: Kaimanawa Mountains, Waipahiki Valley, 39°10'S, 175°50'E, 1080 m, on *Phyllocladus alpinus*, SW aspect, 20 degree slope, 5.II.1975, A.J.Dakin 10 (AK 233248); Taranaki: Kapuni Track to Dawson Falls, Egmont NP, 910 m, on branches of rainforest trees, 6. V. 1980, J.A.Elix 7949 (CANB 9604328); Mt. Egmont, on trunks and branches of trees in forest at c. 900 m, Aug. 1925, H.H.Allan 102 (UPS); Taranaki/Egmont National Park, North Egmont, 3–400 m S of the Park Centre, near the Ambury Memorial, 39°16'19"S – 174°05'37"E, 980 m, on stem of tall *Hebe* along forest margin near a former meadow close to the path, 24.II.2016, A.Elvebakk 16:108 (TROM); Manawatu-Wanganui: Central Volcanic Plateau, c. 10 km S of National Park, slightly N of Makatota Scenic Reserve, 39°15.83'S, 175°23.43'E, c. 800 m, on *Coprosma* sp., 29.XI.2002, A.Elvebakk 02:302 (TROM); Tawhai Falls, c. 2 km N of Whakapapa Village, 39°10.52'S, 175°30.81'E, 960 m, on thin trunks of *Kunzea ericoides* and *Pittosporum tenuifolium* ssp. *colensoi*, not observed on the dominant *Nothofagus solandri* trees, 1.XII.2002, A.Elvebakk 02: 411 (TROM); 02:413 (TROM); Wellington: Te Houtotara, 9. IV. 1850, W.Colenso 3750 pro p. – "A lot of scraps; lichens, & c. from the interior." (WELT L001219); Near Te Hawera, W.Colenso 2722 (WELT L0980); Wainuiomata Water Reserve, 41°15'05"S, 175°02'55"E, 620 m, twig of fallen *Fuchsia excorticata*, damp gully by roadside, *Nothofagus menziesii* forest, 20 VII. 2011, A.Knight s.n. (TROM L-42433; OTA61713 – not seen). South Island, Tasman: Track from Flora Saddle to Mount Arthur Hut, 41°12'S, 172°44'E, 1080 m, on bark in low open *Dracophyllum traversii* and *Nothofagus solandri* var. *cliffortioides* forest, 13. IV. 1991, B.W.Hayward & A.E.Wright 11233 (AK 204429); Wangapeka Ecol. District, Kakapo Saddle, 41°23'S, 172°20'E, I. 1981, J.K.Bartlett (AK 241700); Marlborough: Mt. Starveall summit, edge of *Nothofagus solandri* forest, 1360 m, D.Glenny 3753 (WELT L 3757); Canterbury: Arthur's Pass, on *Casinia vauvilliersii* in scrub on the pass, 12.I.1927, G.E. & G.Du Rietz 1524:2 (II) (UPS); Arthur's Pass E, 1 km along Temple Basin Track, 42°54'38"S – 171°33'39"E, 1120 m, on stem of an *Olearia* shrub in the lower alpine belt, 1. III. 2016, A.Elvebakk 16:255 (TROM); 1 km N of Arthur's Pass, c. 1.5 km along Otira Valley Track, 42°53'50"S – 171°32'38–39"E, 1000 m, on stems of *Olearia* in the lower alpine zone, 28.II.2016, A.Elvebakk 16:216 (TROM); Dyer's Pass (SE of Christchurch), open rocks on the southern side of the ridge, 7. I. 1927, G.E. & G.Du Rietz 1450:32 (UPS); Arthur Range, track from Graham Valley carpark to Mt. Arthur Hut, 41°12'S, 172°49'E, *Dracophyllum traversii* bush, on *Nothofagus*, as a mixture with *P. xanthomelana*, 13. IV. 1991, W.A.Nelson (WELT L2976); West Coast: West Coast, Stockton Plateau, road towards Mt. Frederick, 41°41'S, 171°52'E, on *Coprosma foetidissima* in area of bog with small shrubs, 850 m, 9.III.1992, B.Polly (WELT L 3661); Bullock Creek, Farm Road, 42°06'S, 171°23'E, 26 m, on fallen twig along road with *Cyathea medallaris*, *Rhopalostylis sapida*, *Meliccytus*, *Aristotelia serrata*, 29.X.2000, B.Polly (WELT L6419); Otira Gorge, on *Olearia ilicifolia* at the road side in the *Dracophyllum traversii*-*Hoheria glabra*-*Olearia* belt, '*Pannaria-Collema*-ass.', 14. IV. 1927, G.E. & G.Du Rietz 2663 a:2 (II) (UPS); Northwestern side of Lake Kaniere, *Dacrydium cupressinum*



forest, on *Dacrydium cupressinum*, 17.I.1927, G.E. & G.Du Rietz 1561 c:2 (UPS); 30–35 km SW of Haast, 1.5 km SW-wards along Cascade Road, 44°03.21'S, 168°42.95'E, 20 m, on smooth bark of *Weinmannia racemosa*, associated with *P. xanthomelana*, 7.XII.2002, A.Elvebakk 02:489b (TROM); c. 10–15 km SW of Haast, 6 km from main road along Turnbull Road, 43°56.74'S, 168°56.24'E, 20 m, on *Prumnopitys taxifolia*, 7.XII.2002, A.Elvebakk 02:533 (TROM); c. 5 km S of Dillmanstown, Okuko Scenic Reserve, 42°41'S – 171°13'E, 160 m, on trunk of a tall shrub light-exposed near a parking site, 29. II. 2016, A.Elvebakk 16:231 (TROM); Auckland Islands: Adam Island, *Metrosideros* forest on slope of Manetic Station, SW of Camp Cove, Carnley Harbour, 5.I.1973, H.A.Imshaug 57434 (MSC); Campbell Island: rock outcrops on summit of Moubray Hill, 800 ft., 12.I.1970, H.A.Imshaug 46874 (MSC).

Chemotype II, as chemotype I, but lacking porphyrilic acid: (13 specimens)

NEW ZEALAND, Manawatu-Wanganui: Volcanic Plateau Bot. Distr., Ruapehu, timber line at the track above Whakapapa Huts, on a shrub of *Olearia nummularifolia* in the margin of *Nothofagus cliffortioides* forest, 24.V.1927, G.E. & G.Du Rietz 3182:3 (UPS); Auckland Islands: Rose Island, *Metrosideros* forest, Lucas Head Peninsula, on *Metrosideros*, 14.XII.1972, H.A.Imshaug 56362 (MSC); Auckland Island, Lookout Point, NW of Ranui Cove, 24.XII.1972, H.A.Imshaug 56816B (MSC); Mature *Metrosideros* forest with tree ferns on north facing slope, WNW of Chambres Inlet, 12.XII.1972, H.A.Imshaug 56262C (MSC); Mosaic of low scrub and tussock, above Ranui Cove, 11.XII.1972, H.A.Imshaug 56195A (MSC); Campbell Island: no further geographical information, 1874, M.Filhol (H-NYL 30821); summit of Moubray Hill, 52°33'S, 169°15'E, 246 m, rock outcrops, 12.I.1970, H.A.Imshaug 46874 (AK 233588; AK 233589; AK 241606; H); H.A.Imshaug 46886 (AK 233587); outcrops on summit of Beeman Hill, 649 ft., 14.I.1970, H.A.Imshaug 47029 (MSC); tussock grassland at base of cliffs on north side of Beeman Hill, 26.XII.1969, R.C.Harris 4620 (MSC); Rock outcrop in tussock grassland (with scattered *Dracophyllum*) on Filhol-Honey Saddle, 23.XII.1969, H.A.Imshaug 46024 (MSC).

***Pannaria gallowayi*** Elvebakk & Elix, **sp. nov.**

Fig. 2A, D

MycoBank # MB818064

Similar to *P. xanthomelana*, but differs in having a thinner thallus, broader lobes with an uneven and less glossy surface, denser branching and more raised margins, smaller, non-foliose cephalodia and in containing *O*-methyl-leprolomin and contortin.

TYPE: New Zealand, South Island, Nelson, North-west Nelson Forest Park, Mt. Arthur. 41°12'S, 172°44'E. On branch of *Dracophyllum traversii* on ridge. 1080 m., 13 April 1991, C.J.West (WELT L 3979 – holotypus).

THALLUS foliose, corticolous, forming rosettes 5–15 cm diam., loosely attached to the substratum, particularly when growing over bryophytes on tree trunks, 120–180 µm thick in distal parts, 150–250 µm in central parts. LOBES irregularly and densely branched, mostly 2–3 mm broad, discrete in peripheral parts, coalescing centrally, flat to weakly concave, with raised margins. UPPER SURFACE uneven, weakly glossy, and glabrous, whitish grey when alive and dry, green with a bluish hue when alive and moist, changing to yellowish-brown after storage in herbaria. UPPER CORTEX 30–40 µm thick, upper half with brown pigmentation in old specimens, upper part sclerenchymatic, otherwise paraplectenchymatic with lumina subglobose to irregularly ellipsoid, 5–12 µm long, walls c. 2–4 µm thick. PHOTOBIONT layer 20–30 µm thick, of globose to subglobose TREBOUXIA, sometimes cf. MYRMECIA cells, 7–12 µm diam. MEDULLA 70–170 µm thick, lowermost 20–30 µm brown-pigmented. LOWER CORTEX lacking; RHIZINES common, from pale and pencil-shaped to squarrose, densely branched and black, sometimes forming a thick, felt-like hypothallus below the thallus.

CEPHALODIA scattered, laminal on both the upper and the lower surface, 0.5–1.5 mm wide, globose to pulvinate, greyish blue when alive and moist; UPPER CORTEX as in the chlorobiont; CYANOBIONT NOSTOC, cells blue-green, subglobose to irregularly ellipsoid, 3–6 × 4.5–7 µm large, organized within spherical glomerules, 10–20 µm large, delimited by a mucilaginous sheath; no chain structures observed.

APOTHECIA common, laminal, substipitate, often contorted centrally, 1–4 mm broad; DISC flat, concave, when the apothecia are contorted, greyish rufous brown, always with concentric, ring-like depressions, often with thalline grains or squamules centrally; THALLINE EXCIPULUM finely crenulate-striate, even, 0.2–0.3 mm wide; EPITHECIUM pale brown, 20–35 µm thick, IKI negative; HYMENIUM colourless, but strongly IKI+ blue, 100–130 µm thick; HYPOTHECIUM light brown, IKI negative, 80–120 µm thick; PARAPHYSES mostly simple, multiseptate, with slightly swollen apices; ASCI clavate, 13–18 × 80–110 µm large, no internal amyloid structures observed, containing eight ascospores. PROPER ASCOSPORES subglobose to short-ellipsoid, 12–17 × 8.5–11 µm; PERISPORES subglobose to short-ellipsoid, distinctly verrucose, 13.5–17 × 10–13 µm large, single verrucae 1–2 µm wide, 1 µm tall.

PYCNIDIA scattered, marginal, appearing as low, brown-centered verrucae, 0.2 mm wide; CONIDIOSPORES/SPERMATIA abundant, 2.5–3 × 0.5–1 µm, bacilliform, rarely weakly curved.

CHEMISTRY: Pannarin (major/minor), contortin, *O*-methyl-leprolomin, porphyritic acid, '*Pannaria isidiosa* terpenoids 1, 2 and 3' and '*P. gallowayi* terpenoid 1' (majors), '*P. gallowayi* terpenoid 2 and 3' (minor). Porphyritic acid is lacking from the chemotype present in Auckland and Campbell Islands.

ETYMOLOGY: Named after the late D.J.Galloway, outstanding lichenologist from New Zealand and author of the New Zealand lichen flora.

ADDITIONAL SPECIMENS EXAMINED:

Chemotype I with pannarin, contortin, *O*-methyl-leprolomin, porphyritic acid, and six '*P. isidiosa* and *P. gallowayi* terpenoids': (11 specimens)

NEW ZEALAND, North Island, Manawatu-Wanganui Tongariro National Park, Punaruku Falls, 39°13'S, 175°32'E, on dead branch of *Griselinia littoralis*, 1260 m, 13.V. 992, C.J.West (WELT L 3883); Taranaki: Taranaki/Egmont National Park, North Egmont, at the start of the Summit Track near the junction with Ngatoro Loop Track, 39°16'25"S – 175°05'35"E, 970 m, among mosses and filmy ferns on a trunk of a small *Pseudopanax*, 25.II.2016, A.Elvebakk 16:123 (TROM); Among mosses and filmy ferns on a trunk of a small *Hebe*, 25. II. 2016, A.Elvebakk 16:123 (TROM); Wellington: Track from Rimutaka summit tearooms to Burnt Spur, SW boundary of Tararua State Forest Park, north of Wellington, c. 600 m, *Nothofagus menziesii*/*Weinmannia racemosa* forest on large branch of *Nothofagus solandri*, 3.III.1990, C.J.West & B.Polly (WELT L 2641); Ruahine Forest Park, No 1 Line, Pohangina, track to Matanganui Stream, c. 12 km NNE of Ashhurst, 40°11.3'S, 175°52.1'E, 360 m, on tawa branch, 9.XII.1995, B.Polly (WELT L6854); South Island, Tasman: Queen Charlotte Sound, Mount Stokes, subalpine tussockland, 41°05'S, 174°06'E, 1180 m, 5.I.1992, A.E.Wright 11921 (AK 205146); Kahurangi National Park, region montis Mt. Arthur, secus viam inter stationem 'Flora Carpark' et casam alpinam Mt. Arthur dictam, 1300 m, ad arbores, 21.IV.1997, W.Malcolm & A.Vězda, as '*A. Vězda*: Lichenes rariores exsiccate, 316. *Psoroma contortum* Müll.Arg.' (H); West Coast: Otira Gorge, on *Olearia ilicifolia* at the road side in the *Dracophyllum traverii*-*Hoheria glabra*-*Olearia* belt, '*Pannaria-Collema*-ass.', 14.IV.1927, G.E. & G.Du Rietz 2663 a:2 (I) (UPS); S slopes of Black Hill, Lake Rotoiti, 41°48'S, 175°51'E, dense *Leptospermum* thicket, on *L. scoparium*, 600 m, 28.II.1980, J.A.Elix 7497 (CANB 00809840); Bullock Creek, Farm Road, 42°06'S, 171°23'E, on fallen branch along stream with *Cyathea medallaris*, *Rhopalostylis sapida*, *Melicytus*, *Aristotelia serrata*, 26 m,

29.X.2000, B.Polly (WELT L6421B); Southland: Fjord Bot. Distr., lower Routeburn Valley, margin of the *Nothofagus menziesii* forest at the foot of Mount Sugarloaf just opposite Routeburn Hut, on a trunk of *Nothofagus menziesii*, 14.II.1927, G.E. & G.Du Rietz 1775 (UPS);

Chemotype II, like chemotype I, but without porphyritic acid: (11 specimens)

NEW ZEALAND, Auckland Islands, Enderby Island: at north west corner of Sandy Bay, 50°30'S, 166°17'E, *Metrosideros* forest, on *Metrosideros*, 13.XII.1972, H.A.Imshaug 56280 (AK 241417; MSC); Rose Island: *Metrosideros* forest, Lucas Head Peninsula, on *Metrosideros*, 14.XII.1972, H.A.Imshaug 56350 (MSC); Auckland Island: mature *Metrosideros* forest with rich bryophyte cover, Sealers' Creek Cove, mouth of Laurie Harbour, 9.I.1973, H.A.Imshaug 57681 (MSC); *Metrosideros* forest, head of North Harbour, on *Metrosideros*, 12.I.1973, H.A.Imshaug 57784 (MSC); along stream in *Metrosideros* forest at Ranui Cove, on *Coprosma*, 12.XII.1972, H.A.Imshaug 56233 (MSC); Mature *Metrosideros* forest on north side, near head, of Musgrave Inlet, near sea level, 19.XII.1972, H.A.Imshaug 56560 (MSC); Adams Island: *Metrosideros* forest on slope of Magnetic Station, SW of Camp Cove, Carnley Harbour, 5.I.1973, H.A.Imshaug 57450 (MSC); 57459 (MSC); Campbell Island: *Dracophyllum* scrub north of Beeman Station, on *D. scoparium*, 3.I.1970, R.C.Harris 5039 (MSC); Open *Dracophyllum* scrub on south base of Lyall ridge, across from Shoal Point, 24.XII.1969, H.A.Imshaug 46080C (MSC); Tall *Dracophyllum* scrub on south side of Perseverance Harbour opposite Moubray Hill, on *D. longifolium*, 16.I.1970, H.A.Imshaug 47178B (MSC).

## Discussion

### Species concepts, morphology and anatomy

The name *Psoroma xanthomelanum* was first introduced by Nylander (1859) with reference to the Colenso 4546 collection from New Zealand, but as a *nomen nudum* without a description. Later, Nylander (1863) made the formal description, and emphasized its thallus colour and hole-like depression in apothecial discs as being characteristic. Spores were described as subglobose and 11–16 µm. He cited it both from New Zealand, "(supra corticem?) ex hb. Hook. (coll. Colenso no. 4546)", and from South America, "Corticola ad Fret. Magellanicum (Lechler)". Nylander (1876) subsequently cited the species, as *Lecanora xanthomelaena* (Nyl.) Nyl., with a Filhol collection from Campbell Island ("sur les mousses et sur les branches du *Dracophyllum longifolium*"). However, in his New Zealand flora Nylander (1888) redetermined his South American collection of *P. xanthomelanum* as *Psoroma pallidum* Nyl. Hue (1902) transferred *Psoroma xanthomelanum* to *Pannaria* and, later (Hue 1912), recorded an expanded description. Galloway (1985) lectotypified the species based on the Colenso 4546 collection and included the information 'Wellington, Ruahine Range, on *Nothofagus bark*', in accordance with the label information "Lichen on *Fagus Ruahine*", annotated on the isoelectotype deposited at WELT.

The description by Hue (1906) is very detailed in both morphological and anatomical aspects, and was based on the small specimen of Colenso 4546 then deposited at Paris. However, this specimen was not found in PC by the present first author, but is probably identical with the isoelectotype H-NYL 30822. As it was so small, Hue (1906) also included a separate description of the Filhol specimen collected on Campbell Island. However, the latter, now deposited as H-NYL 30821, has been re-examined and found to represent *P. aotearoana*. Hue (1906) added the character 'subsorediate' for lobes of the Campbell Island specimen, whereas apothecium anatomy (spores were

described as either spherical and 10–12 µm in diameter, or ellipsoid and 13 × 16 µm, and externally papillose to exasperate) was identical in the two collections except for details of the paraphyses.

Material previously included in *Pannaria xanthomelana* is shown here to represent three species. These species can be readily distinguished morphologically. *Pannaria xanthomelana* is the most characteristic in always having large, branched and often foliose cephalodia, several mm across, whereas the cephalodia are inconspicuous and small in the two other species. In the two latter they are generally less than 1 mm wide, usually globose to pulvinate, and are nearly as common on the lower surface as on the upper side. In several specimens, cephalodia were not observed, although they are easily overlooked on the lower surface or can be hidden by the substrate.

Thallus morphology of the chloromorph can most often, but not always differentiate the three species. In *P. xanthomelana* the lobes are lacinate, ± 1 mm broad, with rather open branching, and with a smooth, glossy surface. Some specimens, but far from all, have a characteristic black prothallus surrounding the thallus of the chloromorph. Such a prothallus is absent in the other two species. *Pannaria aotearoana* has more densely branched lobes, but lobes can vary a lot and be quite narrow, and can in some specimens appear similar to those of *P. xanthomelana*. However, *P. aotearoana* develop marginal phyllidia, which are small, thick and convex with decumbent apices, and look very different from lateral lobules commonly present in *P. xanthomelana*. The latter are not particularly thick, are not convex, and they develop in the same plane as the major lobes. Some lateral lobules can be seen developing into larger lobes. *Pannaria aotearoana* has the thickest thalli among these species, although there may be an overlap when comparing individual lobes.

*Pannaria gallowayi* is a particularly beautiful species. The lobes are broader, generally 2–3 mm wide, are densely branched, papery and usually with strongly raised margins. The lobes are moderately glossy and distinctly uneven. Phyllidia are absent, and the short lobules on older thalline parts are not as common as in *P. xanthomelana*.

The three species often have apothecial discs with several concentric rings, and frequently with thallus grains or squamules deposited centrally. *Pannaria gallowayi* has flat discs, with narrowly and regularly crenulate thalline excipuli, but the apothecia become concave when contorted in the central parts of the thallus. In *P. aotearoana* the apothecia are nearly always densely packed and extremely concave, whereas *P. xanthomelana* maintains an intermediate position in this respect. However, scattered apothecia of the latter are smaller, more concave and have less finely crenulate thalline exciple than *P. gallowayi*.

The ascospores are quite similar in all three species. They are short-ellipsoid, always have a very well-developed, verrucose perispore, and lack apical extensions. The verrucae measure 1–2 µm across and are c. 1 µm tall. When mounted in water, these verrucae often look balloon-like, and are much more robust than those observed in species of the *P. sphinctrina* complex. *Pannaria xanthomelana* has shorter spores than the other two species. The perispores are generally 12–15 µm long, a few reach 16 µm. Those of *P. aotearoana* scarcely overlap and are 15–21 µm long. The ascospores



of *P. gallowayi* are intermediate in size, with a few specimens having ascospores reaching *P. aotearoana* size, that is 17–20 µm long. The ascospore width differs little in the three species, meaning that *P. xanthomelana* has more shortly ellipsoid spores than the others, particularly *P. aotearoana*. Under the microscope, apparently globose ascospores are often observed. However, in most cases this is an artifact, and due to ascospores which are vertically or partly vertically orientated.

Pycnidia have not previously been described for *P. xanthomelana*. They are identical in all three species, and appear as low-verrucose structures developing along margins, being more conspicuous in *P. aotearoana* than in the other two species. The spermatia (conidiospores) are basically bacilliform, although a few are weakly curved. In *P. aotearoana* they are larger than in the two other species, mostly  $3 \times 1 \mu\text{m}$  vs.  $2\text{--}2.5 \times 0.5 \mu\text{m}$ .

Chlorobionts have generally been described as '*Myrmecia*' or '*cf. Myrmecia*' in *Pannariaceae*. This pattern is now being challenged by Park et al. (2016), who reported *Trebouxia* from *Psoroma*. The present material has two clearly different chlorobionts, with different distributions. The dominant one in northern parts of New Zealand corresponds well with other samples of *Trebouxia*, whereas most samples from southern parts have irregularly shaped, non-papillose and often sharply angled chloroplasts. These are referred to here as *cf. Myrmecia*, pending molecular studies.

*Pannaria gallowayi* and *P. aotearoana* differ mainly in their vegetative propagules. Small, robust and weakly convex phyllidia develop along the margins of the latter, whereas *P. gallowayi* may have some lobules in central parts of the thallus, but no true phyllidia. After the surface of the thalli become grazed (probably by snails), regrowth takes place in the form of granules which may eventually become coralloid, but these differ from true phyllidia. The collection Du Rietz 2663 a:2 is a mixture of the two species growing together (Fig. 2 D). Here one can see the regular development of true marginal phyllidia on *P. aotearoana*, but these are lacking from *P. gallowayi*. In addition, *P. aotearoana* has narrower and thicker lobes, which are slightly more yellowish and their surface smoother by comparison with the uneven surfaces of *P. gallowayi*. The chemistry of the two species is identical.

### **Distribution and habitat ecology**

In Galloway (1985), *P. xanthomelana* was reported from southern parts of the North Island and throughout the South Island of New Zealand. Galloway (2007) subsequently added Stewart Island, Auckland Islands and Campbell Island further south. In the material studied here, *P. xanthomelana* has not been found south of the South Island. However, a total of 25 collections of *P. gallowayi* and *P. aotearoana* from Auckland Islands and Campbell Island cited here, indicate that both are apparently very common in these islands, particularly in the *Metrosideros umbellata* Cav. forests of the former and the *Dracophyllum longifolium* (J.R.Forst. & G.Forst.) R.Br. ex Roem. & Schult. scrubs of the latter.

All three species appear to be widespread in the western, moist part of South Island, and approximately a quarter of the collections of *P. gallowayi* and *P. aotearoana* originate from the North Island. All three species occur on branches of shrubs in the lower alpine

zone. *Pannaria xanthomelana* and *P. gallowayi* both have their altitudinal record from Mt. Arthur, at 1340 and 1300 m, respectively. *Pannaria aotearoana* has been collected on the summit of Mt. Starveall in Marlborough, at 1360 m. *Pannaria xanthomelana* appears to be restricted to very wet areas. It was the most common *Pannaria* species in the wet *Nothofagus colensoi* forests very close to Arthur's Pass in the South Island, whereas it was completely lacking from considerably drier forests only 10 km further to the east. *Pannaria aotearoana* appears to have the widest ecological amplitude. It has been collected in the Waikato province, in the north-central area of the North Island. *Pannaria aotearoana* has also been collected once from rocks at Dyer's Pass at 330 m on the eroded volcanic range on Banks Peninsula just SE of Christchurch. This is the only record of the complex from eastern parts of the South Island. In Campbell Island it has been collected several times from rock outcrops of exposed hills.

*Pannaria xanthomelana* was reported from Río Azopardo in Chilean Tierra del Fuego by Zahlbruckner (1917), and this report was maintained by Follmann (1965: 63), although there was an obvious misprint in his listing. The species was lacking from the Argentinian lichen catalogue of Grassi (1950) and also from the more recent catalogues for Argentina (Calvelo & Liberatore 2002) and Chile (Galloway & Quilhot 1998). The specimen reported by Zahlbruckner (1917), housed in W, has been examined by us and found to represent a species in the *Pannaria athroophylla* (Stirt.) Elvebakk & D.J.Galloway complex. A handful of specimens of the *Pannaria pallida* complex, including *P. contorta*, from southernmost South America, contain a contrasting chemistry including porphyritic acid. However, these samples have a morphology corresponding to the *P. pallida/contorta* complex, and also lack the large foliose cephalodia of *P. xanthomelana*. Filson (1996) considered *P. xanthomelana* to have been incorrectly reported from Australia, and its status as a New Zealand endemic (Galloway 2007) is maintained by the present study. Thus we treat all three species as endemic to New Zealand.

## Chemistry

*Pannaria xanthomelana* was reported by James & Henssen (1975) to have the same chemistry as *P. durietzii* (James & Henssen) Elvebakk & Galloway, that is pannarin,  $\pm$ zeorin and three unknowns. Passo et al. (2004) reported it to contain contortin and zeorin (majors) and small amounts of pannarin and its derivatives. This latter report was based on material from the Auckland and Campbell Islands, but Elvebakk & Elix (2006) reported that porphyritic acid was a major compound and pannarin present in trace to minor amounts based on an HPLC analysis of the lectotype. TLC analyses of the 40 specimens determined as *P. xanthomelana* here confirm this pattern, except that pannarin is the major compound in almost all cases. The terpenoids exhibit a marked variability in concentration, ranging from being almost indistinct to being present as major metabolites. However, the cohort of terpenoids present is identical to that observed in *P. isidiosa* and *P. gallowayi*. '*Pannaria isidiosa* terpenoids 2 and 3' and '*P. gallowayi* terpenoid 1' occur in most collections. '*P. isidiosa* terpenoid 1' occurred sporadically, once as a major component, and dechloropannarin was found in two samples. It is notable that porphyritic acid was always present, and that the selection of terpenoids indicates a close evolutionary relationship between the species.

However, two collections contained quite dissimilar terpenoids. They contain three unique terpenoids, two of them in major amounts, but otherwise have typical *P. xanthomelana* chemistry. Bjerke 024/04 & Elverland is a small specimen, but *Wright 11907* is a large and robust one, somewhat resembling *P. gallowayi*. Both share the large foliose cephalodia of *P. xanthomelana*.

The compound contortin was described from *Pannaria contorta* (Müll.Arg.) Passo & Calvelo by Elix et al. (1984) based on material collected from near Lake Rotoiti, Tasman, New Zealand as Elix 7497. *Pannaria contorta* used to be accepted for New Zealand (Galloway 1985), but is now excluded (Galloway 2007), and the most recent study on this species defined it containing pannarin as the only secondary compound (Passo & Calvelo 2006). The material used to isolate contortin by Elix et al. (1984) refers to *P. gallowayi*. The five MSC samples published by Passo et al. (2004) from New Zealand (Campbell Island, Auckland Islands) as *P. xanthomelana*, most certainly represent *P. gallowayi* and/or *P. aotearoana*. More than 20 samples from this complex collected in these subantarctic islands by Imshaug and coworkers have now been studied, and none correspond to *P. xanthomelana*. One duplicate among the specimens cited by Passo et al. (2004) (Imshaug 46886) proved to be *P. aotearoana*.

*Pannaria gallowayi* exhibits two major chemotypes, differing only by the absence or presence of porphyrilic acid. The remaining metabolites (comprising 9 or 10 compounds) are remarkably constant. Pannarin is usually one of the major compounds present (reduced to minor quantities in a few cases), whereas contortin and the new compound *O*-methyl-leprolomin are always present in major quantities. The TLC spot characteristics of *O*-methyl-leprolomin are identical to those of leprolomin, except that the  $R_f$  values are 65 vs. 63 and 58 vs 50 in solvents A and C, respectively. Four of the six terpenoids present occur in major quantities. Three of these are in common with those reported by Elvebakk & Elix (2006) and illustrated in a chromatogram by Elvebakk et al. (2010). Three of the terpenoids have not been observed previously and are provisionally named '*P. gallowayi* terpenoids 1–3'.

*Pannaria aotearoana* also exhibits two major chemotypes, with porphyrilic acid present in collections from the North and South Islands of New Zealand, but absent in collections from the subantarctic Campbell and Auckland Islands. Three of the 40 samples deviate from this pattern. One collection from Wellington lacks porphyrilic acid (several pieces sampled separately), and two collections from the subantarctic islands do contain minor amounts of porphyrilic acid.

## Conclusions

*Pannaria gallowayi* and *P. aotearoana* are two morphologically distinct new species sharing a new chemosyndrome. They have previously been confused with *P. xanthomelana*, from which they differ significantly, in both morphology and chemistry. With these two new species added, the number of accepted pannarin-containing, tripartite and foliose *Pannaria* species has increased to 9, and at least two more species remain to be described. This group is modestly represented in

*Pannariaceae* phylograms, with at most four sequences analyzed (Passo et al. 2008). A larger phylogenetic study is planned, based on the hypothesis that these large, beautiful and austral species represent a well-supported clade. Characters related to pycnidia, spermatia, perispore structures and compounds other than pannarin should also be explored as possible synapomorphies.

### Acknowledgements

We are indebted to the directors and curators of the cited herbaria for allowing us to study *Pannaria* material held in their care and for sending material on loan. The New Zealand Department of Conservation kindly granted a collection permit, P.J.de Lange, The New Zealand Department of Conservation supplied valuable comments included in the manuscript and M.Karlstad and E.M.Beck, both Tromsø University Museum, helped with some of the illustrations.

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Manuscript received May 12, 2016; accepted September 13, 2016