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Pannaria microphyllizans (Nyl.) P.M.Jørg. from New Zealand restudied and compared with P. athroophylla (Stirt.) Elvebakk & D.J.Galloway and the three new species Pannaria cassa, P. kantvilasii and P. wrightiorum

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Abstract

Pannaria microphyllizans, a previously misunderstood species, is shown here to have gibbose perispores with long-tailed apical extensions, and to lack TLC-detectable chemistry. It is related to *P. athroophylla*, a species with different phyllidia, a chemistry of isovicanicin and leprolomin, and spores of the same type but differing in several details. The latter has been too widely interpreted in New Zealand, because there are two more previously undescribed phyllidiate taxa. *Pannaria wrightiorum* contains vicanicin, leprolomin and scabrosin esters, has short phyllidia and characteristic spore details. *Pannaria kantvilasii* has the same chemistry, but distinctly different spores, revealing a position within the *P. leproloma* group. *Pannaria cassa*, a third new species described here, is primarily fertile and is related to *P. microphyllizans*, having the same chemistry and spore type. Apart from *P. kantvilasii*, the taxa dealt with here belong to the same group within *Pannaria* as the South American *P. patagonica*. The phyllidiate species in the group develop characteristic prothalli that recruit lichenized thallus fragments. The species dealt with here are probably widespread in New Zealand, although their distributions are insufficiently known. *Pannaria wrightiorum* is strikingly common on Campbell Island, and *P. kantvilasii* also occurs in Tasmania.

Introduction

Two decades ago, Jørgensen (2001) treated two former *Psoroma* species as *Pannaria leproloma* (Nyl.) P.M.Jørg. and *P. microphyllizans* (Nyl.) P.M.Jørg., then considered to be sorediate and phyllidiate members of the *P. sphinctrina* (Mont.) Tuck. ex Hue complex. That was the first modern recombination of tripartite, foliose *Psoroma* species into *Pannaria*. Many subsequent studies have contributed to an increased knowledge of the group (*see* Elvebakk & Elix 2017). Elvebakk & Elix reviewed its diverse secondary chemistry, described two new species, and concluded that the group then included 24 species.

The group is still very incompletely known. Recent Pannariaceae phylogenies, such as Passo *et al.* (2008), Ekman *et al.* (2014), Magain & Sérusiaux (2014) and Elvebakk *et al.* (2020), each included ten or fewer samples of the group, and no phylogenetic studies have yet addressed a more detailed phylogeny of *Pannaria.* Such a study is now planned with the aim of defining clades and, when a reasonable level of knowledge has been reached, to produce determination keys of species within those clades. That requires descriptions of new taxa, particularly from New Zealand, which is the centre of diversity of the foliose, tripartite species.

The present study defines *Pannaria microphyllizans* as a starting point. It was briefly suggested to be associated with *P. athroophylla* instead of being in the *P. sphinctrina* group by Elvebakk (2013), who left the topic for a future study. That requires a restudy of *P. athroophylla*, and the studies of those species have revealed two new phyllidiate species as well as an apparently new fertile counterpart of *P. microphyllizans*. The aim of the present study is, therefore, to describe those new species and revise the descriptions of *P. athroophylla* and *P. microphyllizans*.

Material and methods

This paper is based on material from AK, B, BM, CHR, H, HO, MSC, OTA and TROM. Ascospore structure was studied in water mounts and restricted to spores liberated from their asci. Detailed drawings were made of *c*. 400 spores from 56 specimens. Copies of the sketches were added to the specimen packets. Thin-layer chromatography of acetone extracts followed standardized procedures and used solvents A and C (Orange *et al.* 2010). Roughly one-third

of the specimens cited were studied by TLC. Nomenclature of ascospore structure follows Nordin (1997).

The species

Pannaria athroophylla (Stirt.) Elvebakk & D.J.Galloway, *Australas. Lichenol.* **53**, 5 (2003) Figs 1, 2 and 12A

Basionym: Psoroma athroophyllum Stirt., Rep. Trans. Glasgow Soc. Fld. Nat. 1, 21 (1873) ≡ Psoroma subpruinosum var. athroophyllum (Stirt.) C.Knight, Trans. New Zealand Inst. 7, 365 (1875)

Type: New Zealand: *sine loco*, Buchanan #245. Deposit from Otago Museum prepared by James Murray in 1961. Mixed collection including one specimen with *Pseudocyphellaria flavicans* (Hook.f. & Tayl.) Vain. (= probably *P. pickeringii* D.J.Galloway) and *Lopadium fuscoluteum*. (GLAM – lectotype (*n.v.*); BM – isolectotype!; WELT L2064 – isolectotype!)

Psoroma athroophyllum was lectotypified by Galloway (1985: 470) from a GLAM collection cited as Buchanan # 45 from "Tinakori Hills, Wellington". As shown in Fig. 1, Buchanan's collection number should be 245. As explained by Jørgensen (2003), the publication of *Phloepannaria athrophylla* by Zahlbruckner (1941: 276) was rendered invalid because the older name *Psoroma buchananii* was cited as a synonym.

Thallus corticolous, foliose, closely attached, \pm free at the margins, forming rosettes 3–10 cm wide. Lobes 0.5–1.5 mm wide, c. 1.5 mm thick, weakly concave to flat, subdichotomously branched. Upper surface smooth, matt, green in the field when moist, pale greenish grey when dry; herbarium specimens becoming ochraceous. *Phyllidia* initially marginal, later also laminal, often forming a crust in the central part, always branched, 0.1-0.2 mm wide, up to 5 mm tall, 0.05–0.1 mm thick, erect, fragile and with a distinctly white lower side. \hat{U} pper cortex 25–30 µm thick, paraplectenchymatous, with lumina up to 10×15 µm, weakly ellipsoid, and arranged perpendicular to the surface with thin, c. 2 μ m thick walls, surface weakly sclerenchymatic. Chlorobiont layer 15–20 um thick, of Trebouxia cells, globose or subglobose, 7–17 µm in diam., the chloroplasts angular and papillose. Medulla 70–100 µm thick. Lower surface ecorticate, whitish to pale ochraceous along the margins, mostly hidden centrally by a cover of bluish black to black rhizinomorphs, c. 0.5 mm long, mostly pencilshaped and esquarrose, extending as a 2-6 mm wide prothallus, where the rhizinomorphs are partly orientated horizontally along the substratum, and partly vertically, in both cases with frequent lichenizations forming tiny thallus granules, squamules, occasionally lobe systems and often cephalodia. Cephalodia common, laminal on the upper surface, occasionally also on the lower surface or directly on the prothallus, c. 0.5-1.5 mm wide, distinctly pulvinate, subdivided and dissected when mature. Cyanobiont Nostoc, with cells greyish green, globose to irregularly subglobose, 4-8 µm in diam., arranged within indistinct 15-30 µm wide glomeruli and without visible chain structures. Apothecia uncommon, laminal, substipitate, 0.5-1.5 mm in diam.; disc chestnut-brown, plane to weakly concave or convex; *thalline* margin crenate-striate, 0.2–0.4 mm wide, sometimes with phyllidia; epithecium brown, 10–15 µm tall; hymenium colourless, intensely IKI+ blue, c. 70–80 µm thick; hypothecium pale brown, 60-80 µm, IKI negative; chlorobiont layer present below; asci clavate, 8-spored, c. $80 \times 15-20$ µm, without internal IKI+ apical structures; paraphyses simple, septate, 2–3 µm wide, with adglutinate and indistinctly swollen apices. Ascospores hyaline, non-septate, regularly ellipsoid, $13-18 \times 7-10$ µm; *perispores* $23-38 \times 9-13$ µm, gibbose laterally, single gibbae rather small, $2-3 \mu m$ wide, $1-1.5 \mu m$ tall, mostly regular like large vertucae, apical extensions 7–10 µm long, forming a filiform apex, gradually narrowing from a 3–5 µm wide, moderately swollen base. Pvcnidia not seen.

Chemistry: (by TLC) isovicanicin and leprolomin (mostly major), and one or two unidentified terpenoids.

Remarks

The species is easily recognized by its long, narrow, branched and fragile phyllidia, often forming a dense, thick crust in central parts of the thalli. All other phyllidiate species have much shorter, less branched and more robust phyllidia. The lobes of *P. athroophylla* are also thin and quite closely appressed to the substratum. All specimens have a black, peripheral prothallus, with partly erect hyphae, and the prothallus always recruits numerous small chlorobiont thallus fragments, some developing into rather large lobe systems. The prothallus frequently also recruits cephalodia separate from chlorobont thallus fragments. Passo *et al.* (2020) argued against the interpretation of such a prothallus structure in their concept of *P. athroophylla* from Argentina. The species also has distinct ascospores that are conspicuously regularly ellipsoid, whereas in other phyllidiate taxa they are weakly ovoid to lenticular. The apical perispore extensions are modelately long and swollen at the base, and the lateral gibbae are also moderately tall, $1.5-2 \mu m$.

Thallus chemistry is characterized by the presence of isovicanicin and leprolomin; in contrast specimens with vicanicin, leprolomin and scabrosin esters characterize two different, newly described species (see below). Isovicanicin is most easily told apart from vicanicin immediately after analysis when the spot is greenish *versus* bluish for vicanicin, before they become concolorous. Then they differ again after a longer period of storage, when isovicanicin spots from solvent A turn orange-brown, in contrast with vicanicin spots that become dirty violet.

Pannaria athroophylla was briefly dealt with by Elvebakk & Galloway (2003), who transferred it from *Psoroma* and cited two chemotypes, one with isovicanicin and leprolomin, the other with vicanicin and leprolomin. It was cited from New Zealand only by Galloway (2007). It was published as common in southern Argentina by Passo *et al.* (2020). However, material from southern South America is not dealt with here.

Pannaria athroophylla from New Zealand is now presented with 12 specimens and is less common than anticipated. It is known from between 730 and 1405 m in the Taranaki and Tongariro national parks on the North Island, and in the latter area it was collected in the uppermost, subalpine *Fuscospora cliffortioides* forests. It is known from scattered localities in forests of the South Island. I collected four samples along the Oakune Road in Tongariro in 2019, and because few herbarium specimens have yet been studied thoroughly in contrast to other phyllidiate species, its frequency in Tongariro indicates that it might be more widespread elsewhere as well. *Pannaria athroophylla* as interpreted here has not been found among the numerous unpublished collections from the Auckland and Campbell Islands determined as *Psoroma athroophyllum* by H.A. Imshaug and R.C. Harris. They collected extensively there during 1969 and 1970, with collections primarily deposited at MSC, but with numerous duplicates held by other herbaria around the world.

ADDITIONAL SPECIMENS EXAMINED

New Zealand. Taranaki: • Taranaki/Egmont National Park, North Egmont, Nature Walk just S of the Visitor Centre, 39°15'15"S, 174°05'45"E, alt. 960 m, on Podocarpus, A. Elvebakk 16:161, 26.ii.2016 (TROM L-42873); Manawatū-Whanganui: • Tongariro National Park, 5 km NE of Oakune, along Oakune Mountain Road, start of Blyth Track, 39°21'36.2" S. 175°28'07"E, alt. 980 m, A. Elvebakk 19:125, 30.iii.2019 (TROM L-44426); • c. 2 km above Rimu Walk, near the road, 39°22'42" S, 175°26'30"E, alt. 730 m, on trunk of Pseudopanax gilliesii near the roadside in a Lophosoria (Nothofagus) menziesii forest admixed with rimu, A. Elvebakk 19:165, 1.iv.2019 (TROM, L-44486); • upper part of Oakune Mountain Road, c. 1.5 km below Turoa Ski Centre, in the uppermost subalpine Fuscospora cliffortioides forest situated in a steep, N-facing slope near the road, 39°18'52.5" S, 175°30'35"E, alt. 1405 m, A. Elvebakk 19:133, 31.iii.2019 (TROM, L-44460); • loc. id., A. Elvebakk 19:135 (TROM L-44462); Tasman: • track from Flora Saddle to Mount Arthur Hut, 41°12'S, 172°44'E, alt. 1080 m, on bark of Nothofagus solandri var. cliffortioides, B.W. Hayward & A.E. Wright 11243, 13.i.1991 (AK 204439); • Cobb Valley, 41°0-S, 172°3-'E, J.K. Bartlett, 1975–1985 (AK 203368); Otago: • c. 7 km S of Haast Pass, along Makarora River near Cameron's Creek, 44°09.34'S, 169°18.13'E, alt. 360 m, on old trunk of Nothofagus menziesii in a forest

edge bordering a meadow, A. Elvebakk 02:466, 6.xii.2002 (TROM L-44544); • Tuapeca West, Knight Bush, 45°54'32" S, 169°29'49" E, alt. 227 m, bark in regenerating Kunzea ericoides/broadleaf forest, on steep sunny NW face, A. Knight, 20.iii.2011 (OTA 61753; TROM L-42422); • Dunedin, Leith Saddle Track, 45°47'51" S, 170°30' 34" E, alt. 390 m, bark of *Pseudowintera colorata*, mixed mist forest, A. Knight, 9.x.2020 (OTA 61747; TROM L-42423); • c. 190 km N of Lake Wanaka, 1 km NW of Makarora, along Makarora Bush Nature Walk, at Pipson Creek, 44°13.72'S, 169°14.45'E, alt. 380 m, on Nothofagus menziesii in the forest, A. Elvebakk 02:46, 6.xii.20022 (TROM L-44548).

Pannaria cassa Elvebakk, sp. nov. Mycobank No.: MB 844587 Figs 3, 4 and 13A

Similar to *Pannaria patagonica* (Malme) Elvebakk & D.J.Galloway, but with narrower lobes, the perispore apical extensions longer and the thallus lacking secondary compounds detectable by TLC.

Type: New Zealand. South Island, Southland, Fiordland National Park, Lake Gunn, 44°53'S, 168°05'E, alt. 1800 ft, on trunk of mountain beech (*Nothofagus solandri* var. *cliffortioides*), *C.J. West*, 1.iii.1990 (WELT L4014–holotype!).

Thallus corticolous, foliose, closely attached, \pm free at the margins, forming rosettes 5–12 cm wide. Lobes 1–3 mm wide, 0.2–0.3 mm thick, concave to flat, subdichotomously branched. elongating peripherally. Upper surface smooth, weakly glossy, green in the field when moist, pale greenish grey when dry, herbarium specimens becoming ochraceous. Upper cortex 40-60 µm thick, paraplectenchymatous with the lowermost lumina weakly elongate, c. 13×15 μm, walls 2-3 μm, and arranged perpendicular to the surface. Chlorobiont layer 30-40 μm thick, of *Trebouxia* cells, globose to irregularly short-ellipsoid, 7–13 µm, the chloroplasts angular. Medulla 100-150 µm thick. Lower surface ecorticate, ochraceous, with scattered pale, esquarrose rhizinomorphs; prothallus not seen. Cephalodia common, laminal both on the upper and lower surfaces, mostly small, c. 0.5 mm wide, pulvinate or divided into pulvinate parts. Cyanobiont Nostoc, with cells greyish green, globose to irregularly subglobose, 3-8 µm in diam., arranged within indistinct glomeruli and without visible chain structures. Apothecia common, laminal, substipitate, 1-2 mm in diam.; disc chestnut-brown, plane to weakly concave; thalline margin crenulate-striate, 0.1–0.2 mm wide; epithecium pale brown, c. 20 µm tall; hymenium colourless, intensely IKI+ blue, c. 60–80 um thick; hypothecium pale brown, $60-80 \mu m$, IKI negative; *chlorobiont laver* present below; *asci* clavate, 8-spored, $80-100 \times$ 15–20 μm, without internal IKI+ apical structures; *paraphyses* simple, septate, 2–4 μm wide, partly with slightly swollen apices. Ascospores hyaline, non-septate, ellipsoid, often weekly asymmetrical or lenticular, $11-15 \times 7.5-11.5 \ \mu\text{m}$; perispores $20-35 \times 11-15 \ \mu\text{m}$, gibbose laterally, single gibbae 2–5 µm wide, 2–3 µm tall, irregularly arranged, apical extensions 7–12 μ m long, forming a filiform apex, sometimes absent, abruptly narrowing from a 5–10 μ m wide, swollen base. Pvcnidia not seen. Chemistry: nil by TLC.

Etymology: The epithet "*cassus*" (L., empty or devoid of) refers to the absence of secondary compounds.

Remarks

This species might be considered as the fertile counterpart of *P. microphyllizans*. However, its ascospores are shorter, and prothalli have not been observed. A total of 30 spore sketches were made from five samples. The perispores are of the same type as *P. microphyllizans* with strongly swollen and often irregular lateral gibbae and large and wide basal parts of the apical extensions. The combination of a negative thallus chemistry and characteristic perispores is unique among primarily fertile tripartite *Pannaria* species, even from some yet undescribed taxa. While several specimens have previously been determined as *P. patagonicum* Malme,





that is a South American species containing vicanicin. A closer study of the spores of *P. pata-gonica* is in preparation.

The endemic *P. cassa* is reported here with eight specimens from New Zealand. Two are from the North Island, from 930 and 1000 m in Taranaki / Mt Egmont National Park, and the remainder are from the South Island regions of Canterbury, West Coast and Southland.

ADDITIONAL SPECIMENS EXAMINED

New Zealand. *Taranaki*: • Mount Egmont National Park, at North Egmont Chalet, 39°16'S, 174°06'E, alt. 930 m, in mixed podocarp-hardwood rainforest, on bark of *Senecio elaeagnifolius, L. Tibell 14971*, 25.xi.1983 (UPS L-97531); • Pouakai Range, 0.8 km NNW of Display Centre at Dawson Falls, at junction of Ridge Walk and Waingongoro Track, 39°19'S, 174°06'E, alt. 1000 m, in high montane *Weinmannia racemosa-Podocarpus hallii* forest, *L. Tibell 18886*, 5.i.1990 (UPS L-18163); *Canterbury*: • Peel Forest, 43°53'S, 171°14'E, alt. 1300 ft, occasional on bark of forest trees, *A.E. Wright 8992*, 10.viii. 1989 (AK 192986); • Clarence Ecological Region, Manakau Ecological District, Fyffe-Palmer Scenic Reserve, Podocarp Loop track, 42°20'S, 173°38'E, alt. 450 m, on bark of mature miro in tall podocarp forest, *A.E. Wright 12282*, 29.x.1993 (AK 215393); • *c*. 10 km N of Lake Wanaka, 500 m N of Makarora, 44°13.73'S, 169°14.45'E, alt. 380 m, on trunks of *Nothofagus fusca, A. Elvebakk 02:431*, 6.xii.2002 (TROM L-43876); *West Coast:* • along Haast River, 300 m SE of Roaring Billy Falls, 43°56.35'S, 169°17.13'E, alt. 20 m, on bark of *Nothofagus menziesii* in gallery forest along the gravelly river banks, *A. Elvebakk 02:561*, 8.xii.2002 (TROM L-44526; UPS); • *loc. id., A. Elvebakk 02:567* (TROM L-44520; AK).

Pannaria kantvilasii Elvebakk, sp. nov.	Figs 5, 6 and 13
MycoBank No.: MB 844588	

Similar to *Pannaria leproloma*, but with distinct, dorsiventral phyllidia instead of coarse isidia, and narrower, more glossy, less tomentose and less laciniate lobes, and perispores more clearly verruculose with distinct pulvinate apical extensions.

Type: Australia. *Tasmania*: Flinders Island, Walkers Lookout, 40°03'S, 148°05'E, alt. 400 m, on *Pomaderris apetala* in wet, low, scrubby woodland, *G. Kantvilas 31/07*, 3.iv.2007 (HO 544047–holotype).

Thallus corticolous, foliose, closely attached, \pm free at the margins, forming rosettes 5–12 cm wide. Lobes 1–2 mm wide, 0.15–0.25 mm thick, concave, irregularly to subdichotomously branched, coalescing except in a narrow peripheral zone. Upper surface smooth, matt to weakly glossy, indistincly tomentose only in youngest parts, green in the field when moist, pale greenish grey when dry, herbarium specimens becoming ochraceous. Phyllidia marginal, 0.4–0.8 mm wide, 0.1–0.15 mm thick, weakly ascending, initially isodiametric and constricted at the base, later moderately branched. Upper cortex $40-50 \mu m$ thick, paraplectenchymatous, with the lowermost lumina elongate and arranged perpendicular to the surface. Chlorobiont layer 20–30 µm thick, of large Trebouxia cells, globose to irregularly short-ellipsoid, 7–20(– 25) µm, the chloroplasts angular and papillose. Medulla 70–150 µm thick. Lower surface ecorticate, whitish to ochraceous, partly hidden by a dense and felty, black cover of strongly squarrose rhizinomorphs, forming a hypothallus that rarely projects beyond the thallus as a prothallus. Cephalodia scattered, laminal on the upper surface, occasionally also on the lower surface, mostly small, c. 0.5 mm wide and pulvinate, more rarely up to 2.5 mm and pulvinate with radiating fissures. Cvanobiont Nostoc, with cells bluish green, globose to subglobose, $3-7 \mu m$ in diam., arranged within indistinct glomeruli and without visible chain structures. Apothecia common, laminal, substipitate, 1-2.5 mm in diam.; disc pale rufous brown, plane to weakly concave, without thalline granules, sometimes with weak concentric depression structures; *thalline margin* crenulate-striate, 0.2–0.3 mm wide; *epithecium* pale brown, 10– 15 µm tall; hymenium colourless, intensely IKI+ blue, c. 100 µm thick; hypothecium pale brown, 60-80 µm, IKI negative; chlorobiont layer present below; asci clavate, 8-spored,

 $80-100 \times 15 \mu$ m, without internal IKI+ apical structures; *paraphyses* simple, septate, 1.5–2 µm wide, without swollen apices. *Ascospores* hyaline, non-septate, ellipsoid to ovate, more rarely citriform, $13-18 \times 7-11 \mu$ m; *perispores* of the same shape, $15-22 \times 8-12 \mu$ m, regularly vertuculose, vertuculae $1-1.5 \mu$ m wide, and with distinct pulvinate apical extensions, up to $2-2.5 \mu$ m wide and 2μ m tall. *Pycnidia* common, marginal, partly laminal, black, immersed, with a thin fissure-like ostiole; spermatia/conidia bacilliform, weakly thickened at the apices, $2.5-3 \times 0.5 \mu$ m.

Chemistry: (by TLC) vicanicin (major), leprolomin (major to minor), scabrosin acetate hexanoate (trace to major), another scabrosin ester (nil or minor), unidentified terpenoids (minor).

Etymology: Named after the eminent Tasmanian lichenologist Gintaras Kantvilas, who collected the first studied specimens, including the holotype.

Remarks

This species was first detected among Tasmanian specimens that are clearly phyllidiate, but more abundantly fertile than most species producing vegetative propagules. As indicated by the diagnosis, both lobes and perispores differ from those of *P. leproloma*, and *P. kantvilasii* should therefore be considered closely related to *P. leproloma*, but not as its phyllidiate counterpart. A total of four additional specimens have been determined from New Zealand. When fertile, *P. kantvilasii* is different from all the other species dealt with here. However, sterile specimens are difficult to tell apart from *P. wrightiorum* with its similar phyllidia and chemistry.

ADDITIONAL SPECIMENS EXAMINED

Australia. *Tasmania*: • Savage River, Pipeline Road, by 14.5 km peg, 41°16'S, 145°19'E, alt. 480 m, on *Cassinia aculeata* at edge of rainforest, *G. Kantvilas 262/93*, 8.xii.1993 (HO 312611); • near Goderick Plains, alt. 640 m, occasional on *Cassinia aculeata* (*Compositae*) at edge of rainforest, *G. Kantvilas 6/82*, 12.i.1982 (BM 000760159).

New Zealand. *Tasman*: • Nelson Lake District, Lakehead Track, map S33 630225, alt. 2000 ft, on beech, *B. Rietveld* 86-18, i.1986 (AK 290153); *Wellington*: • Wainuiomata Water Reserve, 41°15'30"S, 175°02'45"E, alt. 730 m, branch of fallen *Nothofagus menziesii* in temperate rainforest, *A. Knight*, 17.vii.2011 (TROM L-42425; OTA 61718); *Otago*: • Eglington [Eglinton] Valley, W. Otago, *W. Martin*, 27.ii.1972 (CHR 604736); *Stewart Island*: • Ocean Beach Forest, on trees, *W. Martin* 58, 11.ii.1947 (CHR 588113).

Pannaria microphyllizans (Nyl.) P.M.Jørg., *Biblioth. Lichenol.* **78**, 121 (2001) Figs 7, 8 and 12B

Basionym: *Psoroma sphinctrina* var. *microphyllizans* Nyl., *Syn. Meth. Lich.* **2**, 25 (1863) ≡ *Psoroma microphyllizans* (Nyl.) D.J.Galloway, *New Zealand J. Bot.* **21**, 196 (1983).

Type: Nova Zelandia, sine loco, *J.S.C. Dumont d'Urville* ex Herb. Buchinger (H-NYL 30782! – lectotype).

Thallus corticolous, foliose, closely attached, \pm free at the margins, forming rosettes 5–12 cm wide. *Lobes* 1–2 mm wide, 0.15–0.25 mm thick, weakly concave to flat, subdichotomously branched, elongating peripherally. *Upper surface* smooth, weakly glossy to glossy, green in the field when moist, pale greenish grey when dry; herbarium specimens becoming ochraceous. *Phyllidia* marginal, 0.2–0.7 mm wide, 0.1–0.15 mm thick, horizontally arranged or weakly sacending, weakly decumbent, initially isodiametric and constricted at the base, later weakly branched. *Upper cortex* 40–50 µm thick, paraplectenchymatous, with the lowermost lumina elongate and arranged perpendicular to the surface. *Chlorobiont layer* 20–30 µm thick, of *Trebouxia* cells, globose to irregularly short-ellipsoid, 5–15 µm; chloroplasts angular. *Medulla* 70–150 µm thick. *Lower surface* ecorticate, whitish to ochraceous, partly covered with rhizinomorphs, pale centrally, black near margins, either poorly developed or forming a dense



surface or directly on the prothallus, mostly small, c. 0.5 mm wide and irregularly pulvinate, more rarely up to 2 mm and placodioid to coarsely corallioid. *Cvanobiont Nostoc*, with cells greyish blue, globose to irregularly subglobose, 3–6 µm in diam., arranged within indistinct glomeruli and without visible chain structures. Apothecia common, laminal, substipitate, 1–3 mm in diam.; disc rufous brown, plane to weakly concave or convex; thalline margin crenulatestriate, 0.1–0.3 mm wide; epithecium pale brown, 10–20 µm tall; hymenium colourless, intensely IKI+ blue, c. 60–80 µm thick; hypothecium pale brown, 60–80 µm, IKI negative, chlorobiont layer present below; asci clavate, 8-spored, $80-100 \times 15-20$ µm, without internal IKI+ apical structures; *paraphyses* simple, septate, 1.5–2.5 µm wide, without swollen apices. Ascospores hyaline, non-septate, regularly ellipsoid, $13-20 \times 8-12 \mu m$; perispores $23-42 \times 10^{-10}$ $12-17 \mu m$, gibbose laterally, single gibbae $2-5 \mu m$ wide, $2-3 \mu m$ tall, irregularly arranged, apical extensions 7–15 μ m long, forming a filiform apex, abruptly narrowing from a 5–10 μ m wide, swollen base. Pvcnidia not seen. Chemistry: (by TLC) two unidentified terpenoids found near vicanicin and leprolomin positions in both solvents A and C, the upper one violet, the lower brownish. Remarks Pannaria microphyllizans was, for a long time, considered to be a phyllidiate species in the

hypothallus that sometimes extends into a 1–4 mm wide prothallus, where the rhizinomorphs are partly orientated horizontally along the substratum, partly vertically, in both cases with

frequent lichenizations forming tiny thallus granules, squamules and occasionally lobe

systems. Cephalodia common, laminal on the upper surface, occasionally also on the lower

P. sphinctrina complex. Specimens determined as *P. microphyllizans* in most recent taxonomic treatments and phylogenies represent *P. pulverulacea* Elvebakk or *P. minutiphylla* Elvebakk before those species were described (Elvebakk 2013), and in Australia possibly also *Pannaria phyllidiata* Elvebakk (Lumbsch *et al.* 2011). It could be added that P.W. James synonymized *P. microphyllizans* with *P. athroophylla* in an unpublished annotation tag added to the lectotype in 1965. The latter is indeed a more closely related species, although the interpretation is not evident because the lectotype of *Psoroma sphinctrinum* var. *microphyllizans* is sterile. Its chemistry is therefore critical to understanding this species, and when additional specimens with that chemosyndrome were detected and studied, it was shown that the perispores of *P. athroophyllizans* were similar, having long-tailed apical extensions. Laterally, the perispores are gibbose and not vertucose or vertuculose. However, the perispore structures are not identical in those two species. Instead, the spores of *P. anicrophyllizans*, based on 150 drawings from 21 samples, are very similar to those of *P. cassa*.

Pannaria microphyllizans is known from eight collections from the Auckland Islands, two from volcanic areas of the North Island, and eight from the South Island, five of those from the West Coast. The morphology of phyllidia is distinctive in *P. microphyllizans*. Thus they are laminal, rather small, often horizontal or partly ascending, and decumbent. Furthermore, the ascospores are homogeneous in all of the specimens cited. Two terpenoids have been detected as minor compounds in four specimens from the Auckland Islands, although not in the lectotype.

The specimens cited share all those characters, but specimens from the Auckland Islands differ from those further north. Most Auckland Island specimens have rather narrow lobes and develop a distinct prothallus that recruits lichenized granules. Northern specimens are less glossy and lack such prothallus formation, and some are more broad-lobed. Their habitats are quite different. However, there is a possibility that the smooth bark of small trees of *Metrosideros umbellata* initiate prothallus formation and lobe ramification in southern specimens, thus appearing as a habitat modification as compared with more northern populations.

During his last expedition in 1837–1840, D'Urville collected on the Auckland Islands as well as on the peninsulas east of Dunedin and Christchurch and in the northern Bay of Islands (Galloway 1985). From what is known of the distribution of *Pannaria* species today, the Auckland Islands appear to be the most likely collection site of the lectotype.

ADDITIONAL SPECIMENS EXAMINED

New Zealand. Taranaki: • Egmont National Park, North Egmont, along Veronica Walk, 39°175'S, 174°05'E, alt. 1000 m, in subalpine Weinmannia racemosa-Podocarpus hallii forest on tree trunk, L. Tibell 18753, 21.xii.1989 (UPS L-17835); Manawatū-Wanganui: • Central Volcanic Plateau NE, Tree Trunk Gorge, c. 10 km S of Rangipo, 39°10.24'S, 175°48.15'E, alt. c. 700 m, over Hymenophyllum stems on trunk, near the path in a shaded Nothofagus forest, A. Elvebakk 02:367, 30.xi.2002 (TROM, L-43888); Tasman: • NW Nelson Ecological Region, old track from Flora Saddle to Mount Arthur Hut, 41°12'S, 172°44'E, alt. 1050 m, on bark of Nothofagus solandri var. cliffortioides in 8 metre tall beech forest; with a prominent black hypothallus, B.W. Hayward & A.E. Wright 11211, 13.iv.1991 (AK 204407); Canterbury: • Banks Peninsula, 1 km SW of Mt Bossi, in remnant podocarp forest, on Podocarpus totara, alt. 640 m, J.A. Elix 18978 & J. Johnston, 3.iii 1985 (B 60 6119592 CANB not seen); West *Coast*: • 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, 188°31.64'E, alt. 25 m, on Nothofagus menziesii, at the edge of grazed meadows, A. Elvebakk 02:506, 7.xii.2002 (TROM, L-43889); • loc. id., A. Elvebakk 02:504 (TROM); • loc. id., A. Elvebakk 02:507 (TROM); West Coast: • North Westland. Mount Glasgow, lower slopes in dense bush, 41°28'S, 172°03'E, J.K. Bartlett 24516, undated (AK 203557); Southland: • Lake Hauroko, overlying vegetation on beech trees, W. Martin, 24.iii.1967 (CHR 578156); Auckland Islands: • Auckland Island, Sealers Creek Cove, mouth of Laurie Harbour, littoral zone and adjacent scrub, H.A. Imshaug 57667, 9.i.1973 (MSC 156177); • N Auckland Island, Cove of German Expedition (1874), on Coprosma on large peat tussocks, H.A. Imshaug 56744, 23.xii.1972 (MSC 146171); • loc. id., H.A. Imshaug 57674 (MSC 146178); • head of Tandy Inlet, H.A. Imshaug 57599, 8.i.1973 (MSC 146151) • Auckland Island, WNW of Chambres Inlet, mature Metrosideros forest with tree ferns on north-facing slope, on Metrosideros, H.A. Imshaug 56262A, 12.xii.1972 (MSC 146167); • Auckland Island N, Lookout Point, NW of Ranui Cove, on Metrosideros, H.A. Imshaug 56791. 24.xii.1972 (MSC 146172); • S side of Granger Inlet, *Metrosideros* forest with tree ferns, H.A. Imshaug 57634, 8.i.1973 (MSC 146156): • Terror Cove, along shore on Dracophyllum, H.A. Imshaug 56723, 23 xii 1972 (MSC 146170); • Ewing Island, southeast part of island, on Coprosma in Metrosideros forest, H.A. Imshaug 56444A, 13.xii.1972 (MSC 146169).

Pannaria wrightiorum Elvebakk, sp. nov. Mycobank No.: MB 844590 Figs 9, 10 and 11B

Similar to *Pannaria microphyllizans*, but with a chemistry of vicanicin, leprolomin and scabrosin acetate hexanoate; ascospores longer and weakly lenticular in outline; and perispores with much lower and more regular lateral gibbae and apical extensions with less swollen bases.

Type: New Zealand. *Marlborough*: Sounds-Wellington Ecological Region, Sounds Ecological District, Queen Charlotte Sound, west up ridge from saddle between Resolution Bay and Ship Cove, 41°06'S, 174°13'E, alt. 550 m, on bark of *Weinmannia racemosa*, *A.E. Wright 11791*, 2.i.1992 (AK 204976–holotype).

Thallus usually corticolous, occasionally saxicolous, foliose, closely attached, \pm free at the margins, forming rosettes 3–12 cm wide. *Lobes* 0.5–2 mm wide, 0.15–0.25 mm thick, weakly concave to flat, subdichotomously branched. *Upper surface* smooth, glossy, weakly tomentose along a narrow marginal zone, green in the field when moist, pale greenish grey when dry, herbarium specimens becoming ochraceous. *Phyllidia* marginal, ovoid/obovoid to spathulate, entire to weakly branched, 0.2–0.5 mm wide, 0.2–0.8 mm long, 0.05–0.15 mm thick, decumbent, arranged horizontally or weakly ascending. *Upper cortex* 40–60 µm thick, paraplectenchymatous with lumina up to 10 × 15 µm, irregularly ellipsoid, and arranged perpendicular to the surface with walls 3–5 µm thick, the surface weakly sclerenchymatic. *Chlorobiont layer* 20–40 µm thick, of *Trebouxia* cells, globose to irregularly short-ellipsoid, 6–12 µm, the chloroplasts angular and papillose. *Medulla* 70–150 µm thick. *Lower surface* ecorticate, ochraceous, white along the margins, with patches of bluish black to black

rhizinomorphs, c. 0.5 mm long, mostly pencil-shaped but rarely squarrose, pale centrally, on smooth substrata often extending as a 2-6 mm wide prothallus, where the rhizinomorphs are partly orientated horizontally along the substratum, and partly vertically, in both cases with frequent lichenizations forming tiny thallus granules, squamules and occasionally lobe systems. Cephalodia scattered, laminal on the upper surface, occasionally also on the lower surface or directly on the prothallus, c. 0.5-1.5 mm wide and irregularly pulyinate when young, later placodioid. Cyanobiont Nostoc, with cells greyish blue, globose to irregularly subglobose, $3-8 \mu m$ in diam., arranged within indistinct glomeruli and without visible chain structures. Apothecia common, laminal, substipitate, 0.5–2 mm in diam.; disc chestnut-brown, plane to weakly concave; thalline margin crenate-striate, 0.2-0.4 mm wide; epithecium brown, 10-20 µm tall; hymenium colourless, intensely IKI+ blue, c. 80-90 µm thick; hypothecium pale brown, 60–80 µm, IKI negative; chlorobiont layer present below; asci clavate, 8-spored, $80-100 \times 15-20 \mu m$, without internal IKI+ apical structures; *paraphyses* simple, septate, $2-3 \mu m$ wide, with swollen apices, c. 5 μm wide. Ascospores hyaline, non-septate, weakly lenticular to ovoid, $13-21 \times 8-11 \mu m$; perispores $21-40 \times 11-15 \mu m$, gibbose laterally, single gibbae rather small, 2–2.5 μ m wide, 1–2 μ m tall, rarely 4 × 3 μ m, sometimes confluent, mostly regular like large vertucae, apical extensions 5–16 µm long, forming a filiform apex, abruptly narrowing from a moderately swollen base to about 5 um wide. Pvcnidia not seen.

Chemistry: (by TLC) vicanicin, leprolomin, scabrosin acetate hexanoate, and unidentified terpenoids.

Etymology: During my first visit to AK in 2002, I noticed the numerous interesting Pannariaceae specimens from New Zealand collected by Anthony Wright, previously a curator there, and also how beautifully the specimens had been mounted. According to Ewen Cameron, the current curator, the mounting was done by Anthony's mother, Meryl M.G. Wright, who was a volunteer there. The holotype of the new species *Pannaria wrightiorum* was collected by Anthony and curated by Meryl (1931–2019). The species is named in honour of both (hence the epithet is plural).

Remarks

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This species has small phyllidia and is typically very different from *P. athroophylla*. Moreover, the ascospores are clearly different in being weakly but distinctly lenticular to ovoid, whereas those of *P. athroophylla* are very regularly ellipsoid. *Pannaria wrightiorum* is morphologically much closer to *P. microphyllizans*. The former is conspicuously more abundantly fertile than most of the species producing vegetative propagules. In the absence of information on secondary chemistry, *P. wrightiorum* can be recognized by its ascospore morphology. A total of 123 spore sketches were made from 20 collections, and the weakly lenticular outline of relatively large ascospores is characteristic. In addition, the relatively small and regular lateral gibbae are diagnostic, whereas the apical extensions extend from the moderately wide and swollen base. In *P. microphyllizans*, the lateral gibbae are much less regular, and single gibbae are larger and taller, whereas the basal part of the apical extensions is also more swollen.

Thallus chemistry is also distinctive. About 15 of the specimens cited have been studied by TLC. They all contain vicanicin, which is similar to the isovicanicin found in *P. athroophylla*. Both species also contain leprolomin. About 90% of the *P. wrightiorum* specimens contain the ester scabrosin acetate hexanoate.

Pannaria wrightiorum, a New Zealand endemic, is now known from three localities in the North Island. Two of them are Colenso collections. Spores from only one of them were studied. Eight collections are known from the South Island, the type specimen from the northernmost part and the other five from Otago. A single specimen is known from the Auckland Islands. However, 34 collections from Campbell Island were determined among the MSC collections made there in 1969 and 1970 by H.A. Imshaug and R.C. Harris. The species most commonly grew on *Dracophyllum (D. longifolium* and *D. scoparium* dominate on the island), but also on rock outcrops. It must be one of the most common *Pannaria* species on Campbell Island.

SELECTED SPECIMENS EXAMINED

New Zealand. Manawatū-Wanganui: • NW of Taihape, Mataroa, Paengaroa Scenic Reserve. 39°38'S, 175°43'E, on Prumnopitys taxifolia bordering bush and grassy patch, B. Polly, 4.iii.1997 (WELT L5629); • banks of Makakahi River, dense forest, W. Colenso 2802 (WELT L1001); • Dannevirke, on bark of living trees, W. Colenso 1748, 22.v.1854 (WELT L1562); Marlborough: • D'Urville Island, SE ridge to Attempt Hill, 40°51'S, 173°52'E, alt. 400–500 m, on beech forest, B.W. Hayward, 6.i.1988 (AK 181652); • c. 10–15 km SW of Haast, 4 km from main road along Turnbull Road, 43°56.23'S, 168°55.32'E, alt. 10 m, on Prumnopitys taxifolia, A. Elvebakk 02:526, 7.xii.2002 (TROM, L-44552); Otago: • Otago Land District, Swampy Hill, Pipeline Track, Leith Saddle, Melicytus bark, D.J. Galloway, 25.v.1995 (CHR 627983); • Catlins, Table Hill. 46°30'S, 169°28', on Nothofagus menziesii in N. menziesii forest. 500 m, B. Polly, 23.xi.1998 (WELT L6104); • Central Otago, Remarkables, Wye Valley, 45°08'S, 168°46'E. On rock in black beech forest, SE aspect, alt. 2800 ft, C.J. West, 30.xii.1991 (WELT L4001). Campbell Island / Motu Ihupuku: • Dracophyllum scrub north of Beeman Station, on Dracophvllum scoparium, R.C. Harris 5039, 3.i.1970 (MSC 112793, sterile in admixture with *Pannaria gallowayi* Elvebakk & Elix); • S side Perseverance Harbour, 1 mile W of South Point, tall Dracophyllum scrub, R.C. Harris 5292, 13.i.1970 (MSC 104985); • S side of Perseverance Harbour, 1 mile W of South Point, tall *Dracophyllum* scrub, R.C. Harris 5305, 13.i.1970 (MSC 104986); • loc. id., R.C. Harris 5306 (MSC 104987); • loc. id., R.C. Harris 5452B (separated from MSC 110691).

Conclusions

A previous subdivision of the genus *Pannaria* into three subgenera as proposed by Jørgensen (1994) was abandoned by Ekman *et al.* (2014), who demonstrated good support for the *Pannaria lurida* group as a distinct subgeneric clade within *Pannaria*. Thus far, other potential groups have only moderate support due to the low number of sequences and a limited number of thorough studies of accompanying characters. Four of the species dealt with here have long-tailed and gibbose perispores, strongly deviating from other tripartite groups in *Pannaria*. The South American species *P. patagonica* can be added to the group which is dealt with here as the *P. athroophylla* group, from its first described taxon. The three phyllidiate species develop a distinct prothallus, as described from the squamulose species *P. byssoidea* (Passo & Calvelo 2011). However, a prothallus has not been observed for the two primarily fertile species *P. cassa* and *P. patagonica*. So far, the single sequence of *P. athroophylla* from Argentina first published by Passo *et al.* (2008) is the only one available for the group.

Within the group, the four species dealt with here are easy to identify, even without knowing their chemistry. *Pannaria microphyllizans* and *P. wrightiorum* have rather similar thalli and shapes of phyllidia. However, their spores are distinctive, and the specimens are usually fertile. The fourth phyllidiate species dealt with here, *P. kantvilasii*, with very different spores, belongs to the *P. leproloma* group. It is also usually fertile, which makes identification easy. However, sterile samples can be challenging, because the species is also chemically identical to *P. wrightiorum*.

Pycnidia have not been seen in the four species from the *P. athroophylla* group, although they are frequently heavily infected by what appears to be an unidentified pyrenomycetous fungus. *Pannaria kantvilasii*, on the other hand, is abundantly pycnidiate, with pycnidia of the same type as those in other members of the *P. leproloma* group.

In New Zealand there are now six known phyllidiate, tripartite *Pannaria* species, including also *P. aotearoana* Elvebakk & Elix and *P. minutiphylla* Elvebakk. The latter is the most widespread of them (Elvebakk 2013). It contains vicanicin but lacks leprolomin, and has indistinct perispores which are finely verruculose, with modest or absent apical extensions. *Pannaria aotearoana* and *P. kantvilasii* also have ellipsoid spores (short-ellipsoid in the former), and the latter has distinct apical perispore extensions. The former contains pannarin and a series of associated substances (Elvebakk & Elix 2017), and like most pannarin species it has a glaucous green colour when moist, as opposed to a salad-green colour in most other

species. In *P. aotearoana* the phyllidia are quite swollen and mostly decumbent, whereas in *P. minutiphylla* they are mostly small, but can overlap in size with those of *P. kantvilasii*, in which case they can be separated using spore morphology or chemistry.

At present, I refrain from writing an identification key, because one additional and distinct phyllidiate species still remains to be described.

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Fig. 1. Pannaria athroophylla (isolectotype at WELT); scale bar = 1 cm.



Fig. 2. *Pannaria athroophylla (Elvebakk 16:161)*. Specimen from Taranaki showing prothalli with thallus fragments; scale bar = 1 cm.



Fig. 3. *Pannaria cassa* (holotype); scale bar = 1 cm.

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Fig. 4. *Pannaria cassa (Tibell 18886* UPS); scale bar = 1 cm.



Fig. 5. *Pannaria kantvilasii* (holotype); scale bar = 1 cm.



Fig. 6. *Pannaria kantvilasii* (part of holotype); scale bar = 5 mm.



Fig. 7. *Pannaria microphyllizans* (lectotype); scale bar = 1 cm.

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Fig. 8. *Pannaria microphyllizans (Tibell 18753*, UPS); scale bar = 5 mm.



Fig. 9. *Pannaria wrightiorum* (holotype); scale bar = 1 cm.





Fig. 10. *P. wrightiorum (Polly*, WELT L5629); scale bar = 1 cm.



Fig. 11. Ascospores of *Pannaria athroophylla* (A) and *P. wrightiorum* (B); scale bar = $10 \mu m$.



Fig. 12. Ascospores of *Pannaria cassa* (A) and *P. microphyllizans* (B); scale bar = $10 \mu m$.



Fig. 13. Ascospores of *Pannaria kantvilasii*; scale bar = $10 \mu m$.

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