

Three new species of lichenized fungi with cephalodia from the southern New Zealand shelf islands (Campbell Plateau)

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Abstract: The new species *Miriquidica effigurata*, *M. squamulosa* and *Pertusaria stellata* are described from the southern subpolar region from collections made by Henry Imshaug and co-workers in the early 1970s. All three species occur on Campbell Island, New Zealand, with *M. effigurata* and *P. stellata* also occurring on the Auckland Islands, New Zealand, and *P. stellata* also being reported from Isla Desolación in southern Chile. *Miriquidica effigurata* and *M. squamulosa* are similar to *M. complanata* but have apothecia with a dark (K+ purple-red) lower hypothecium and thalli containing confluent acid and norstictic acid respectively. *Pertusaria stellata* is similar to *P. macloviana*, but has shorter ascospores and a smoother, generally paler thallus lacking papillate isidia. Cephalodia are reported for the first time in both *Miriquidica* and *Pertusaria*.

Key words: biogeography, Chile, *Miriquidica*, oceanicity, *Pertusaria*, *P. macloviana*

Introduction

The ability to produce cephalodia (gall-like structures containing a secondary photobiont, usually a cyanobacterium) is usually a genus-specific character in lichens (Hertel & Rambold 1988); cephalodia being consistently produced in species of *Amygdalaria*, *Coccorema*, *Pilophorus*, *Placopsis* and *Solorina*, as well as all species of *Lobaria*, *Nephroma*, *Peltigera*, *Pseudocyphellaria* and *Sticta* with a green photobiont, and most species of *Psoroma* and *Stereocaulon*. However, in crustose genera, at least, some cephalodia-free specimens and populations are known (Brodo & Hertel 1987; Lamb 1947); in fact, *Placopsis lambii* Hertel & V. Wirth was originally described with the lack of cephalodia as its characteristic feature, but the circumscription of this species has since been revised to include collections with cephalodia (Moberg & Carlin 1996). In other genera, only a few species (e.g., *Micarea*), or a single species are known to produce

cephalodia (e.g., *Carbonea gallowayi* Hertel, *Rhizocarpon hensseniae* Brodo, and *Sphaerophorus stereocauloides* Nyl.). The three species described here are additions to this last group, being the only species in their respective genera known to produce cephalodia.

Campbell Island and the Auckland Islands are situated between New Zealand and Antarctica (Fig. 1). They are often referred to as subantarctic islands, although they lie in the cool-temperate zone between the antarctic and subtropical convergences, have a relatively mild, oceanic climate, which is wet (annual precipitation 1500–2000 mm) with little seasonal temperature fluctuation (mostly 5–10°C), and support a vegetation that includes trees and woody shrubs (Wardle 1991). Consequently, they are more correctly referred to the southern cool-temperate zone or, the less specific, southern subpolar region. Between 1965 and 1973, Dr Henry A. Imshaug and his graduate students collected lichens extensively in the austral regions of the Southern Hemisphere. These collections are now housed in the herbarium of Michigan State University (MSC) and are of the greatest importance because they represent one of

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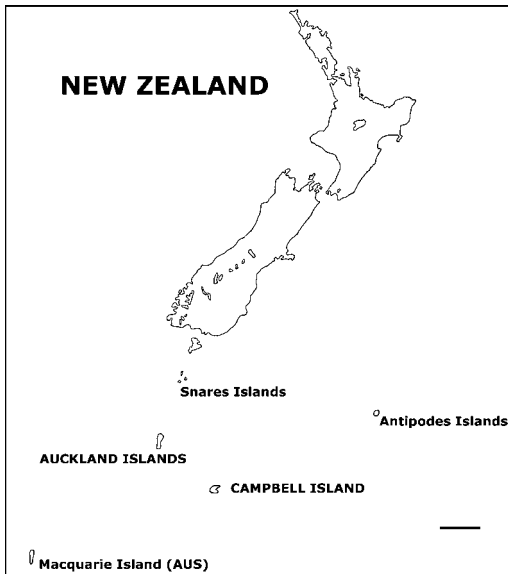


FIG. 1. Location of Campbell Island and the Auckland Islands. Scale=150 miles.

the few collections from these regions made by specialist lichenologists (Fryday & Prather 2001) and, consequently, saxicolous crustose taxa are fully represented. Recent awards by the US National Science Foundation (NSF) have made this collection readily accessible to researchers, both physically and electronically as the label data from the entire lichen collection is now available on-line (Johnson *et al.* 2005). Previous contributions (Coppins & Fryday 2006, 2007; Fryday 2000, 2001, 2003, 2004, 2007*a, b*) have described 15 species new to science and documented numerous lichen species new to New Zealand from these collections. Here, three new species, which sometimes occur together in the same collection, are described that are the only species in their genera known to produce cephalodia.

Materials and Methods

Apothecial characteristics were examined by light microscopy on hand-cut sections mounted in water, 10% KOH (K), 50% HNO₃ (N) or 0.15% aqueous IKI. Thallus sections were investigated in water and 10% KOH (K). The ascus structure was studied in 0.15% aqueous IKI, either without prior treatment or

after pretreatment with 10% KOH. Measurements of ascospores, paraphyses and conidia were made in 10% KOH. Thin-layer chromatography followed the methodology of Orange *et al.* (2001).

Additional comparative material examined (all in MSC). *Coccotrema cucubitiula* (Mont.) Müll. Arg. **Falkland Islands:** *West Falkland:* Port Howard, at base of Mt Maria, UTM 21F UC 2179, 1650 ft, above stone run, 1968, *Imshaug* (41400) & *Harris*.—**New Zealand:** *Campbell Island:* cliffs around Mt Lyall pyramid, 1300 ft, 1970, *Imshaug* 46522.

Miriquidica complanata (Körb.) Hertel & Rambold. **Great Britain:** *Scotland:* VC 105, West Ross, Kintail, Five Sisters, Coire a' Mhadaidh, GR: 18/978170 [57° 12' N 5° 21' W], 850 m, NE facing rock face just off ridge at head of coire, 2005, *Fryday* 9092.

Pertusaria macloviana Müll. Arg. **Argentina:** [*Tierra del Fuego:* Depto. Ushuaia] Isla de los Estados, Puerto Vancouver, summit of ridge E of Monte Tres Puntas, 54° 47' S 64° 06' W, 1971, *Imshaug* (62206) & *Ohlsson*.—**Chile:** *Prov. Magellanes:* Isla Desolación, *Hebe* scrub along S shore of Caleta San José, Bahía Tuesday, 1969, *Imshaug* (44746) & *Ohlsson*.—**Falkland Islands:** *East Falkland:* Stanley, Sapper Hill, UTM 21F VC 3871, 450 ft, outcrop, 1968, *Imshaug* (39740, 45174) & *Harris*.

Pertusaria sp. **New Zealand:** *South Island:* [West Coast], Buller Co., Nelson, Buller Gorge, 17.8 miles west of Inangahua Junction along Route 6 [c. 41° 50' S 171° 40' E], 200 ft, *Nothofagus* forest, 1972, *Imshaug* 55798.

The Species

Miriquidica effigurata Fryday & Coppins sp. nov.

Mycobank No.: MB 511693

A Miriquidicis ceteris cephalodiis praesentibus, praeter M. squamulosae, et acidum confluentium continens differt. Thallus areolatus; areolis ± subsquamulosis ad margines effiguratis.

Type: New Zealand, Campbell Island, summit of Mt Dumas [c. 52° 34' 30" S 169° 6' 20" E], 1650 ft [503 m], wet grassland and upland peat bogs, 2 January 1970, *R. C. Harris* 5023 (MSC—holotypus).

(Fig. 2)

Thallus effuse, pale grey to brownish, wide spreading, to 5 cm or more, 0.5–0.7 mm thick, deeply cracked-areolate, in places subsquamulose with effigurate margin and dark lower surface, areoles (0.5–)0.8(–1.1) mm, flat, sometimes slightly convex, often with numerous pale brown immersed pycnidia. *Upper cortex* 30–70 µm thick, composed of

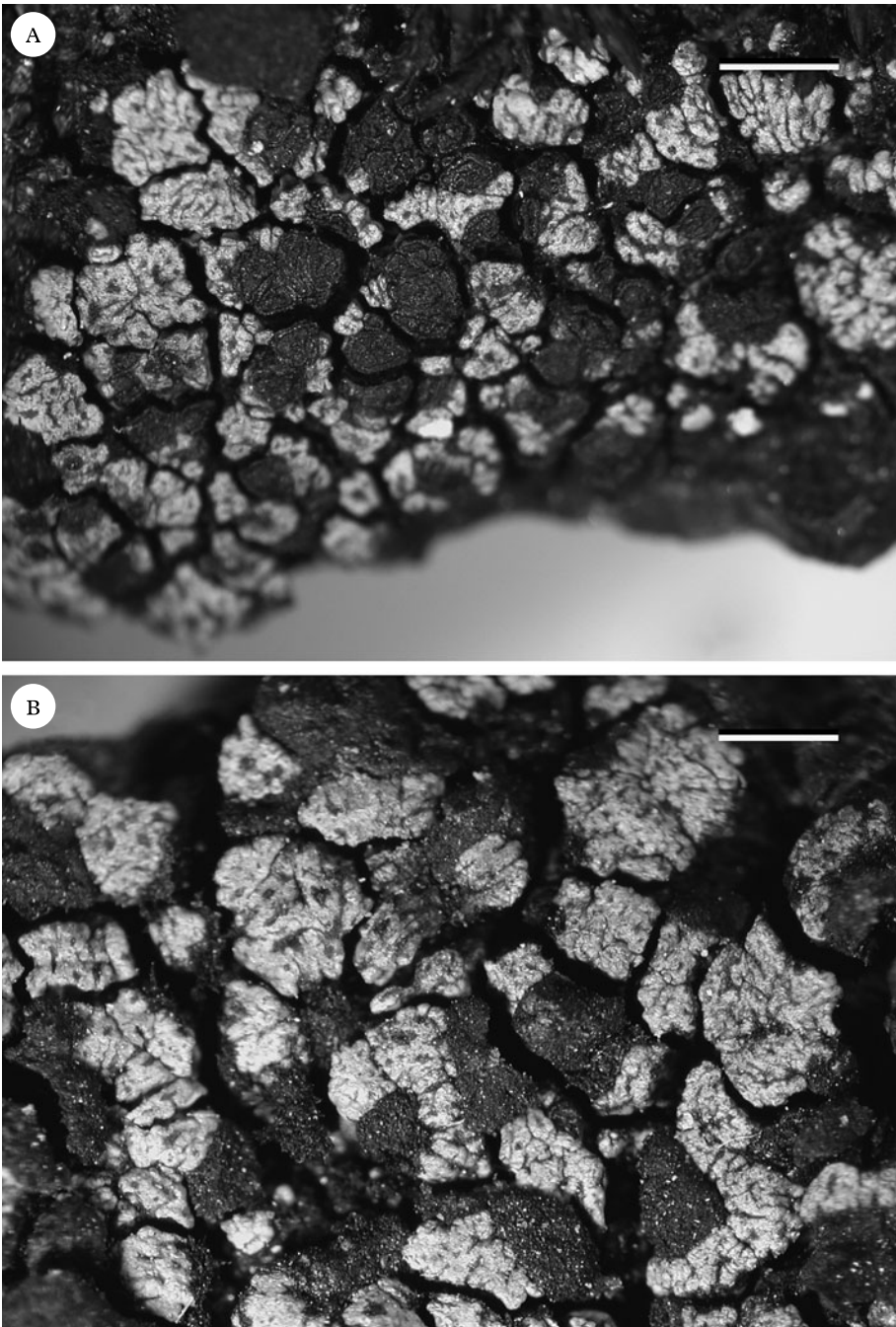


FIG. 2. *Miriquidica effigurata* (Harris 5023—holotype). A, thallus and apothecia; B, thallus and cephalodia. Scales: A & B=1.0 mm.

vertically arranged hyphae 3–4 µm thick, upper 5–10 µm pale- to mid-brown, cells brown pigmented, epinecral layer of hyaline cells 0–50 µm thick. *Basal layer* 60–70 µm thick dark red-brown (K+ red-purple). *Primary photobiont* chlorococcoid, cells 10–12 (–15) µm. *Secondary photobiont* cephalodia frequent, black, blue-black when wet, rounded to angular, flat to slightly convex, 0.5–0.8(–1.1) µm, between areoles, surface rough, occasionally becoming subfruticose, cyanobacterium ?*Scytonema*, in short, vertically aligned chains (3–)6–8 cells long, 30–60 × 10–18 µm; individual cells bright blue, ellipsoid 6–10 × 5–7 µm diam., dividing by binary fission, cells larger at the surface, 10–15 × 8–10 µm with a yellow-brown sheath that becomes dark yellow-brown at the surface.

Apothecia often absent, lecideine, immersed in the thallus, often compound, some becoming almost gyrose, occasionally singular and simple; black, disc red-brown when wet, flat with persistent, thin (0.05 mm thick) and barely raised, black margin. *Hymenium* 70–90 µm high, hyaline, upper 10–15 µm dilute brown, I+ blue, merging below with hyaline zone of hypothecium; *paraphyses* slender, sparingly branched and anastomosing, swollen at apex to 3–4 µm and brown pigmented but without distinct cap. *Hypothecium* upper 70–80 µm hyaline, lower 100–120 µm dark brown (K+ red purple). *Asci* ?*Lecanora*-type (I+ tholus, with a faint ocular chamber), broadly cylindrical to subclavate, 50–55 × (15–)20 µm; *ascospores* 8/ascus, simple, hyaline, broad ellipsoid (9–)10–12 × (5–)5.5–6.5(–7) µm. *Exciple* dark brown 20–30 µm wide.

Conidiomata: Pycnidia, frequent, often abundant; pale brown, immersed, rounded to linear, 0.05–0.1 × 0.03–0.05 µm. *Conidia* filiform, curved, *c.* 20 µm long.

Chemistry. K – , C – , Pd – , UV – ; confluent acid and accessories by TLC.

Remarks. Confluent acid is otherwise unknown in *Miriquidica*. However, the genus has a diverse chemistry; most species contain

the depside miriquidic acid whereas in others it is replaced or supplemented by the depsidones, lobaric acid, psoromic acid, protocetraric acid, stictic acid, or norstictic acids (Owe-Larsson & Rambold 2001), so the occurrence of the depside confluent acid is not unexpected.

Distribution and ecology. *Miriquidica effigurata* is known only from the Auckland Islands and Campbell Island, where it grows on siliceous rocks on the summits of mountains. Associated lichen species include *Micarea pannarica* Fryday, *Miriquidica squamulosa* Fryday, *Pertusaria stellata* Fryday, *Rimularia maculata* Fryday and *Tephromela* aff. *atra* (Huds.) Hafellner.

Additional specimens examined (all MSC). **New Zealand**: *Campbell Island*: near western summit of Mt Lyall, 1300 ft, rock outcrops and feldmark, 1969, *Harris* 4813-A; summit and summit ridge of Mt Honey, 1800–1867 ft, 1969, *Harris* 4902 (with *P. stellata*), 4908, 4913-B (with *P. stellata*), 4917; summit of Mt Honey 1867 ft, rock outcrops and feldmark, 1969, *Imshaug* 46380, 46381, 46387 (with *P. stellata*), 46419; around Mt Lyall pyramid, 1300 ft, cliffs, 1970, *Imshaug* 46486 (with *P. stellata*); summit of Mt Fizeau, 1655 ft, cliffs and shingle feldmark, 1970, *Imshaug* 46794 (with *M. squamulosa*). *Auckland Islands*: Adams Island, end of ridge from Magnetic Station leading to central ridge, 1600 ft, 1972, *Imshaug* 56928; Auckland Island, summit of Mt Raynal, 645 m, 1973, *Imshaug* 57303 (with *P. stellata*); *ibid.*, summit of Mt Eden, 1389 ft, 1973, *Imshaug* 57505.

***Miriquidica squamulosa* Fryday sp. nov.**

Mycobank No.: MB 511694

Miriquidica effiguratae similis sed bryicola, thallo squamuloso et acidum norsticticum continente, apothecii adnatis, epihymenio caeruleo differt.

Type: New Zealand, Campbell Island, rock outcrops at the summit of Mt Azimuth [c. 52°30'30" S 169°9'0"E], 1600 ft [488 m], 3 January 1970, *H. A. Imshaug* 46587 (MSC—holotypus).

(Fig. 3)

Thallus pinkish-brown to pale grey, effuse, but rarely extensive, to 2 cm, often of ± dispersed areoles, or on a black hypothallus when contiguous, areoles flat to strongly convex, (0.5–)0.8–1.5(–2.5) mm

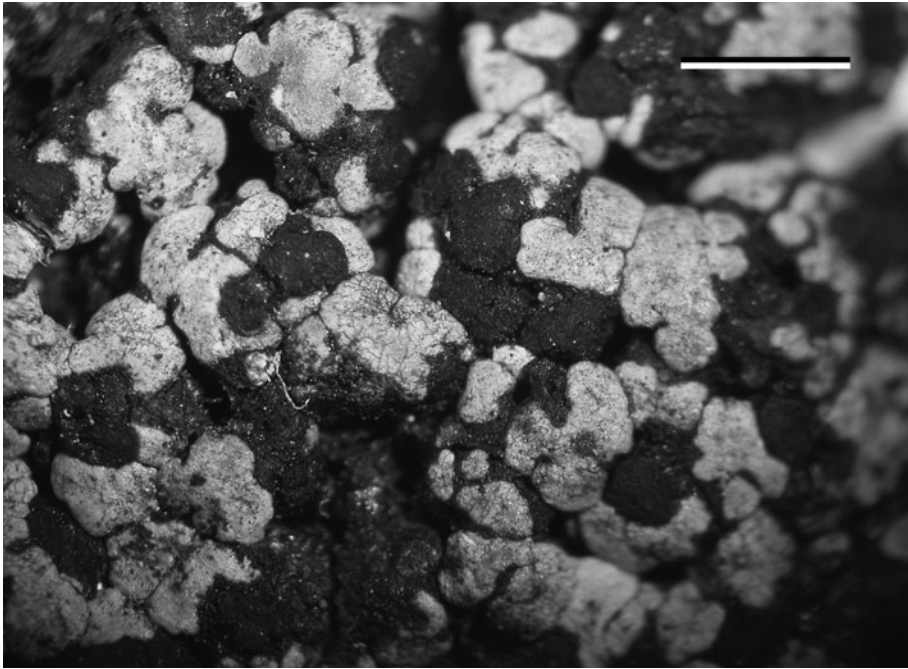


FIG. 3. *Miriquidica squamulosa*, thallus and apothecia (Harris 4920). Scale=1.0 mm.

with \pm lobulate margin, 0.2–0.25 mm thick, with a dark (K+ purple-red) lower surface, forming squamules up to 5 mm across; pale brown immersed pycnidia usually present but rarely abundant. *Upper cortex* 30–50 μ m thick, composed of vertically arranged hyphae 3–4 μ m thick, upper 5–10 μ m pale to mid-brown, cells brown pigmented, epinecral layer absent. *Basal layer* 40–50 μ m thick, dark red-brown (K+ purple-red) forming a ‘root’ to 0.25 mm deep. *Primary photobiont* chlorococcoid, cells 10–12 (–15) μ m. *Secondary photobiont* cephalodia, frequent when present, black, rounded to angular, flat to slightly convex, 0.8–1.5 μ m, between areoles, surface rough; cyanobacterium ?*Chroococcus*, 3–4 enclosed together in a sheath 10–15 μ m across, rarely in short chains up to 30 μ m long; cells bright blue, dividing by binary fission, \pm globose, 8–10 μ m across, up to 15 μ m across at the surface, sheath becoming yellow pigmented in upper layers and dark yellow brown at the surface.

Apothecia usually frequent, lecideine, immersed in the thallus, often compound, some occasionally singular and simple; black, usually convex and immarginate, rarely flat with persistent, thin (0.05 mm thick) and barely raised, black margin. *Hymenium* 70–80 μ m high, hyaline, upper 10–15 μ m dark blue-green, I+ blue, merging below with dilute red-brown zone of hypothecium; *paraphyses* slender, sparingly branched and anastomosing, swollen at apex to 3–4 μ m and dark pigmented with distinct cap. *Hypothecium* upper 70–80 μ m dilute red-brown, lower 100–150 μ m dark brown (K+ red purple). Asci ?*Lecanora*-type (I+ tholus, with a faint ocular chamber), broadly cylindrical to subclavate, 50–55 \times (12–)15–18 μ m; *ascospores* 8/ascus, simple, hyaline, broadly ellipsoid (9–)10–12 \times (5–)5.5–6.5 (–7) μ m. *Exciple* dark brown, 20–30 μ m wide.

Conidiomata: pycnidia, usually present but abundant on only one collection (Imshaug 46802), pale brown, immersed, usually

round (rarely linear), 0.05–0.15 × 0.05–0.1 mm. *Conidia* filiform, curved, *c.* 20 µm long.

Chemistry. K+ yellow becoming red (acicular crystals in section), Pd+ orange, C–, UV–; norstictic acid and accessories by TLC.

Remarks. *Miriquidica squamulosa* is the only known species of the genus that is not primarily saxicolous, although *M. lulensis* (Hellb.) Hertel & Rambold, which also contains norstictic acid, has been reported as growing over bryophytes (Fryday 2006). However, that species has a white areolate thallus, black sessile apothecia, and a hyaline hypothecium. Other described species that also contain norstictic acid also have either a hyaline hypothecium (*M. leucophaeoides* (Nyl.) Andreev) or a granulose-verrucose thallus (*M. paanaënsis* (Räsänen & Laurila) Andreev) and are known only from siliceous rocks in the boreal-subarctic region.

Distribution and ecology. *Miriquidica squamulosa* is known only from Campbell Island, where it grows over bryophytes (e.g. *Andreaea* sp., *Gymnomitrium* sp.) on siliceous rocks on the summits of mountains. One collection (Imshaug 46802) is apparently growing directly on siliceous rock, but another collection from the same locality (Imshaug 46794) is clearly growing over bryophytes.

Associated lichen species include *Lithographa* cf. *olivacea* Fryday, *Micarea* cf. *magellanica* (Müll. Arg.) Fryday, *Miriquidica effigurata* Fryday & Coppins, *Pannaria* sp., *Pertusaria stellata* Fryday and *Placopsis venosa* Imshaug ex D. J. Galloway.

Additional specimens examined (all MSC). **New Zealand:** *Campbell Island:* summit and summit ridge of Mt Honey, 1800–1867 ft, 1969, Harris 4920; cliffs and shingle feldmark at summit of Mt Fizeau, 1655 ft (505 m), 1970, Imshaug 46794 (with *M. effigurata*), 46802.

***Pertusaria stellata* Fryday sp. nov.**

Mycobank No.: MB 511695

Pertusaria obvelata sensu Imshaug in sched., non Nyl.

Pertusariae macloviana similis sed cephalodiis sanguineis stellatis, ascomatibus gradioribus, ascosporis longioribus, thallo laevi isidia papillata destituito.

Typus: New Zealand, Auckland Island, summit of Mt Raynal [c. 50°43'30"S 166°3'15"E], 2114 ft [645 m], 2 January 1973, H. A. Imshaug 57311 (MSC—holotypus, CHR—isotypus).

(Figs 4 & 5)

Thallus effuse, wide-spreading, creamy-white to pale grey; 0.3–0.5 mm thick, cracked-areolate, areoles flat to uneven, 0.5–1.0 mm across; soredia and isidia absent. *Primary photobiont* green, in irregular colonies forming a discontinuous layer, cells globose, 8–10 µm diam. or oblong 15 × 10 µm; *secondary photobiont* frequent, often abundant, forming dark red-brown, linear to radiating-stellate groups, (0.2–)0.3–0.7 (–1.4) mm across, individual colonies linear, 0.2–0.4 × 0.05–0.1 mm, immersed in the thallus surface; ?*Gloeocapsa*, mostly singular but occasionally two cells enclosed in a sheath, cells red (K+ purple) at thallus surface, pale blue (K+ very pale blue-green) within thallus, irregularly globose, 12–15 (–20) µm diam.

Apothecia occasional, scattered, 1–3 (or more) immersed in scarcely raised thalline warts, (0.8–)1.0–1.2 (–1.4) mm diam., with pruinose surface; individual apothecia (0.25–)0.3 (–0.4) to 0.5 when singular. *Hymenium* 300–350 µm, I–; paraphyses slender (1–1.5 µm) mostly unbranched, but branched and anastomosing above and terminating in a conglutinate yellowish brown, granular epihymenium; *hypothecium* hyaline, composed of loosely arranged branched and anastomosing hyphae. *Asci* *Pertusaria*-type, 200–250 × 60–80 µm: *ascospores* 1/ascus, (127)157.5–193.5–230(247) × (36)49.0–70.0–91.0(105) µm.

Conidiomata not observed.

Chemistry. K–, C–, Pd+ orange-red; protocetraric acid (major), fumarprotocetraric acid (trace), confumarprotocetraric acid (trace) and virensic acid (trace) by HPLC.

Remarks. *Pertusaria stellata* is similar to *P. macloviana* Müll. Arg. in having a greyish

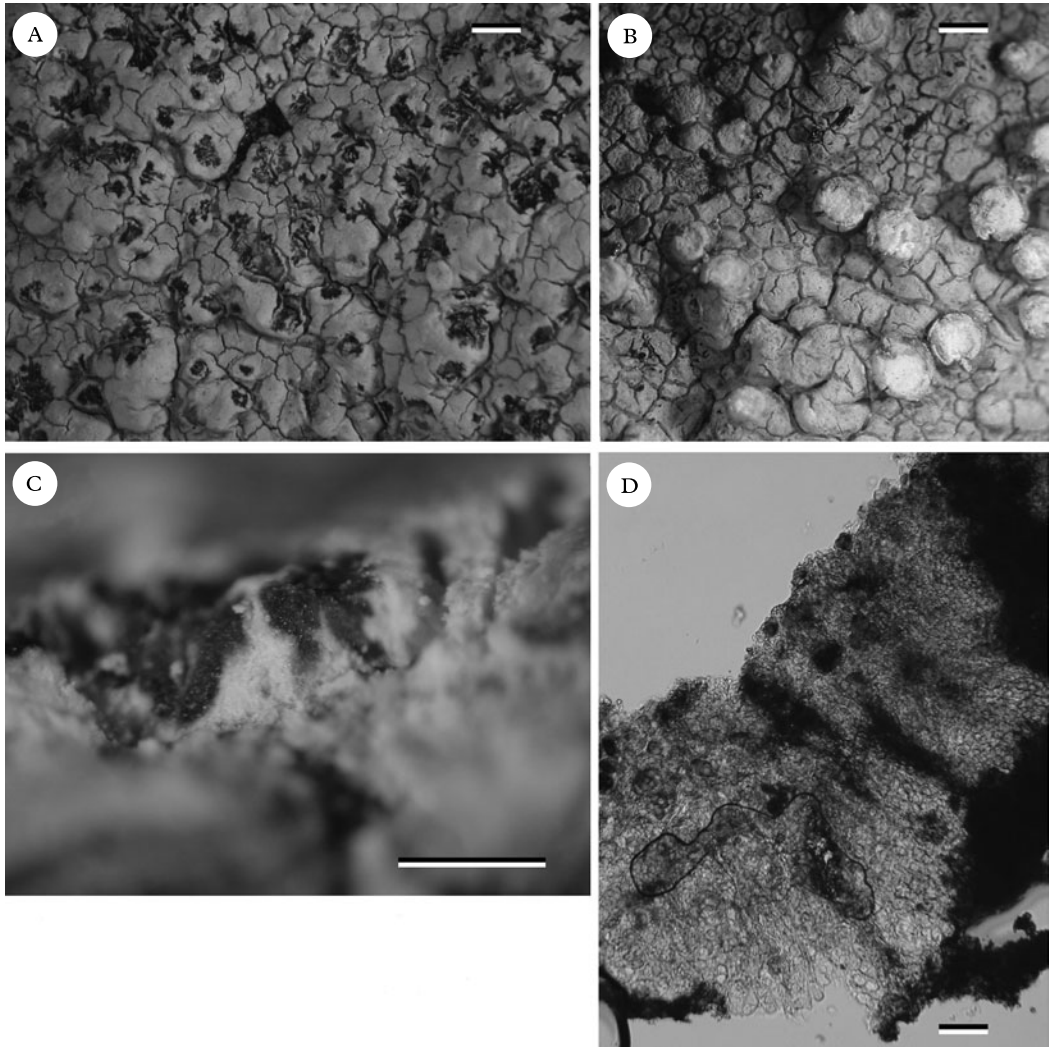


FIG. 4. *Pertusaria stellata*. A, thallus with cephalodia; B, thallus with apothecia; C & D, cross-section of thallus showing cephalodia (A, C & D, *Imshaug* 57329, B, *Imshaug* 57311—holotype). Scales: A & B=1.0 mm; C=0.5 mm; D=0.1 mm.

thallus containing protocetraric acid, disciform apothecia, and monosporous asci. Collections of *P. stellata* from the Auckland Islands and Isla Desolación were reported as that species by Messuti & Archer (1999) and Messuti & Vobis (2002) respectively. The report from the Auckland Islands was the first, and only, report of *P. macloviana* from New Zealand, which, consequently, has not been correctly reported from Australasia.

However, *Pertusaria macloviana* is correctly reported from Isla Desolación (*cf. Additional comparative material examined in Materials and Methods*).

Pertusaria stellata differs from *P. macloviana* most noticeably in having numerous dark-red, stellate colonies of a red (K+ purple), unicellular cyanobacterium (?*Gleocapsa*) immersed in its thallus, but also in having a smoother, generally paler thallus

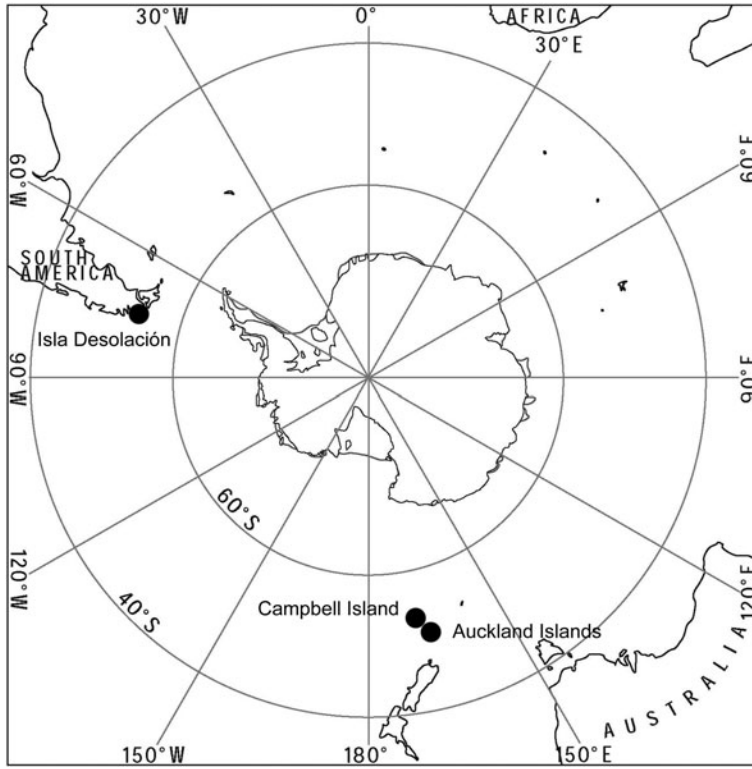


FIG. 5. Known distribution of *Pertusaria stellata*.

lacking papillate isidia or soralia, as well as statistically longer ascospores ($193.5 \times 70.0 \mu\text{m}$ compared with $164 \times 71 \mu\text{m}$ for *P. macloviana*: Table 1, Fig. 6). The thallus of *P. macloviana* is also generally darker grey than that of *P. stellata* and is often covered with numerous papillate isidia, and when these are lacking they are replaced with numerous raised soralia that, although usually sterile, appear to be apothecia initials. Although the apothecia of *Pertusaria stellata* are sorediate, they are scattered sparingly over the thallus and never form a conspicuous feature as in *P. macloviana*.

The recently described saxicolous species, *P. parathalassica* Kantvilas & Elix (2008) from Tasmania, is similar to *P. macloviana* and *P. stellata* in having monosporic asci and a thallus containing protocetraric acid. However, it differs from both *P. stellata* and *P. macloviana* in having larger, especially longer, ascospores [$(164\text{--}195\text{--}235\text{--}281 \times$

TABLE 1. *t*-test for ascospore length of *Pertusaria stellata* and *P. macloviana*

	<i>P.</i> <i>stellata</i>	<i>P.</i> <i>macloviana</i>
Mean	195.4	164.1
Variance	1342.8	601.9
Observations	30	31
Hypothesized Mean Difference		0
df		50
<i>t</i> Stat		3.91
<i>P</i> (<i>T</i> ≤ <i>t</i>) one-tail		0.14×10^{-3}
<i>t</i> Critical one-tail		1.676
<i>P</i> (<i>T</i> ≤ <i>t</i>) two-tail		0.28×10^{-3}
<i>t</i> Critical two-tail		2.009

$51\text{--}72\text{--}109 \mu\text{m}$] and non-pruinose apothecia. It further differs from *P. stellata* in occurring on maritime rocks and lacking cephalodia.

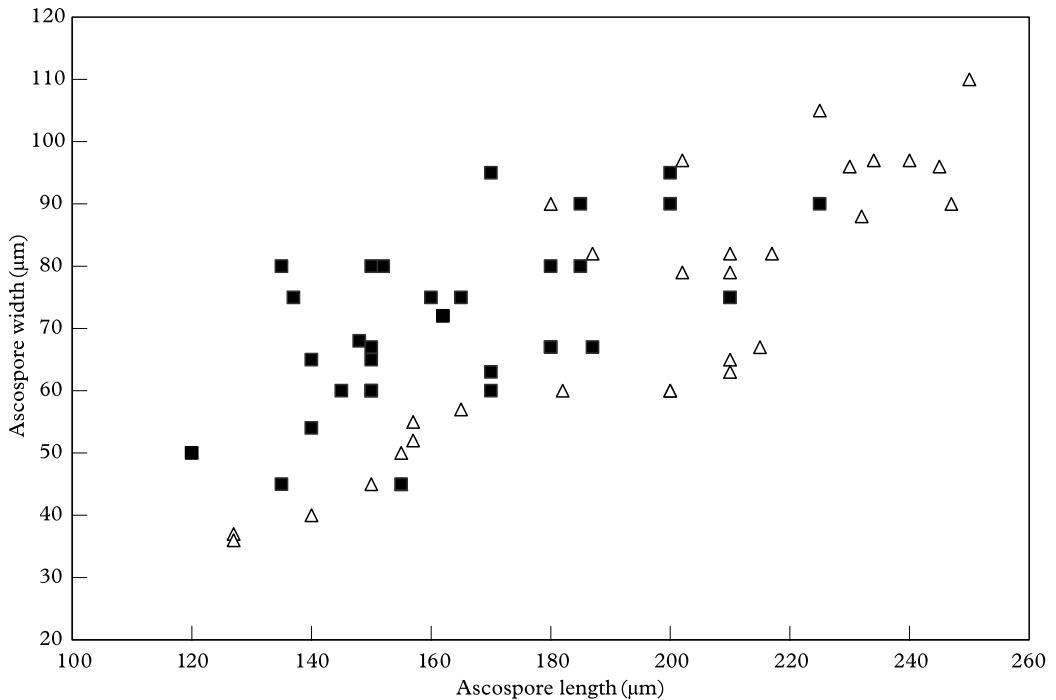


FIG. 6. Scatter diagram of ascospore dimensions of *P. stellata* (Δ) and *P. macloviana* (■).

Although *Pertusaria stellata* is unique among the described species of *Pertusaria* in that it has cephalodia, a single specimen of a further *Pertusaria* sp. from *Nothofagus* forest on South Island, New Zealand (see *Additional comparative material examined* in Methods and Materials) has colonies of *Scytonema* immersed in its thallus. This collection has a thallus containing barbatic acid and numerous urceolate, sorediate apothecia, but, unfortunately, the apothecia are poorly developed and no asci or ascospores were observed.

The genus *Coccotrema* has cephalodia and is similar to *Pertusaria* in that it has large ascospores. However, these are not as large as those of *P. stellata*, typically being 50–70 μm long and never exceeding 100 μm in length, and the ascomata of that genus are also perithecioid and immersed in thalline warts.

Imshaug referred the material here described as *P. stellata* to *P. obvelata* Nyl., and it is probable that duplicate material has

been distributed to other herbaria under that name. However, *P. obvelata* has since been lectotypified on a different entity that is a saxicolous form of *P. velata* (Turner) Nyl. (Fryday & Coppins 2006).

Ecology and distribution. *Pertusaria stellata* has been recorded only from the southern New Zealand shelf islands (the Auckland Islands and Campbell Island) and Isla Desolación in southern Chile (see below). It is a species of siliceous rocks on hills and mountain summits. Associated lichen species include *Fuscidea subasbolodes* Kantvilas, *Lithographa olivacea* Fryday, *Miriquidica effigurata* Fryday, *Placopsis* sp. and *Rimularia maculata* Fryday from New Zealand, and *Fuscidea subasbolodes*, *Lithographa graphidioides* (Nyl.) Coppins & Fryday, *Pertusaria* sp. and *Poeltidea perusta* (Nyl.) Hertel & Hafellner from Chile.

Specimens examined (all MSC). **Chile:** *Prov. Magallanes:* Isla Desolación, outcrops & moorland on hills at head of inner harbour, Bahía Tuesday, 1969,

Imshaug (44648, 44651, 44661, 44662, 44665) & *Ohlsson*; *ibid.*, moorland on hill, S side of Caleta San José, Bahia Tuesday, 1969, *Imshaug* (44698B, 44722) & *Ohlsson*; Pto Churruca, treeless ridge in cirque on W side of Fondeadero Nassau, 1969, *Imshaug* (44896) & *Ohlsson*; *ibid.*, moorland on hill at head of Brazo Lobo, 1969, *Imshaug* (44843) & *Ohlsson*.—**New Zealand:** *Campbell Island*: on Filhol-Honey saddle, rock outcrop in tussock grassland (with scattered *Dracophyllum*), 1969, *Imshaug* 46021; rock outcrops on W end of Lyall ridge, 1969, *Imshaug* 46158 A, 46184; rock outcrops and feldmark near western summit of Mt Lyall, 1969, *Harris* 4803, 4804, 4809, 4812 B; summit and summit ridge of Mt Honey, 1969, *Harris* 4902 (with *M. effigurata*), 4903, 4905; rock outcrops and feldmark at summit of Mt Honey, 1969, *Imshaug* 46397, 46407; around Mt Lyall pyramid, cliffs, 1970, *Imshaug* 46463, 46486 (with *M. effigurata*), 46509; at summit of Mt Azimuth, rock outcrops, 1970, *Imshaug* 46555; cliffs and shingle feldmark at summit of Mt Fizeau, 1970, *Imshaug* 46788; rock outcrops on summit of Moubray Hill, 1970, *Imshaug* 46885; rock outcrops and feldmark, on summit of Mt Dumas, 1970, *Imshaug* 46985, 46999; rock crags on summit of Mt Sorenson, 1970, *Imshaug* 47319; large boulders and rock outcrops on N side of W end of Lyall ridge, 1970, *Harris* 5629. *Auckland Islands*: *Auckland Island*, summit of ridge SE of Mt Easton, NW of Lake Hinemoa, 1972, *Imshaug* 56507, 56509, 56513 (with *M. effigurata*); cliffs and rock outcrops summit of peak just S of Mt Easton, 1972, *Imshaug* 56617; on summit of Hooker Hills, tussock and rock outcrops, 1972, *Imshaug* 56655, 56683, 56687; Adams Island, summit of S.W. Adams Trig. 520 m, 1972, *Imshaug* 57111; summit of Mt Raynal, 645 m, 1973, *Imshaug* 57303 (topotype; with *M. effigurata*); top of talus slope at base of outcrops on ridge, SE of Mt Raynal, on saddle at head of cirque, 1973, *Imshaug* 57329, 57341; summit of Mt D'Urville, 1973, *Imshaug* 57382; summit of Cloudy Peak, 1973, *Imshaug* 57553; summit of Mt Eden, 1973, *Imshaug* 57500, 57503, 57513, 57517, 57521, 57523, 57525.

Discussion

The two new species of *Miriquidica* are readily accommodated within the circumscription of that genus proposed by Andreev (2004). The apothecial anatomy, ascus structure (weakly developed *Lecanora*-type), and conidia are all consistent with that genus. In addition, the gross morphology of the thallus of both species bears a resemblance to that of *Miriquidica complanata* (Körb.) Hertel & Rambold (the type species of the genus), having a thick grey thallus that can become almost subsquamulose and effigurate at the margins. Although cephalodia are otherwise unknown in *Miriquidica*,

other species of the genus (e.g., *M. complanata*) are often associated with cyanobacteria, especially when growing in damp habitats (*cf. Additional comparative material examined in Materials and Methods*).

The colour of the thallus of *M. effigurata* and *M. squamulosa* appears to be related to the presence of an epinecral layer on the upper cortex. The thallus of *M. effigurata* is generally greyish and an epinecral layer is generally present on the upper cortex, whereas *M. squamulosa* generally has a pinkish-brown thallus and the upper cortex lacks an epinecral layer. However, where the epinecral layer is absent in *M. effigurata* (*Harris* 4197, 5023) the thallus has the pinkish-brown colouration typical of *M. squamulosa* and, conversely, where this is present in *M. squamulosa* (*Imshaug* 46802 A) the thallus is the pale grey colour typical of *M. effigurata*. In addition, in both *M. effigurata* and *M. squamulosa*, the production of cephalodia appears to be negatively associated with the presence of apothecia; that is, cephalodia are usually rare or absent in fertile specimens, and this character also appears to correlate with the presence/absence of the epinecral layer. Interestingly, the specimen of *M. squamulosa* with a grey thallus/epinecral layer is the only one that is growing directly on rock, so it would appear possible that the saxicolous habit of *M. effigurata* (as opposed to the bryophilous habit of *M. squamulosa*) results in that species experiencing a somewhat damper microenvironment that promotes the production of an epinecral layer on the upper cortex of the thallus and also promotes the production of cephalodia and suppresses the production of apothecia.

Distribution of cephalodiate species

Cephalodia-producing genera and species are predominately found in oceanic areas (e.g., *Coccotrema*, *Placopsis*) and all species that are unique in their genera in producing cephalodia occur in oceanic areas: *Carbonea gallowayii* is known only from south-west Chile, *Pertusaria stellata* from only Campbell Island/Auckland Islands and south-west

Chile, *Rhizocarpon hensseniae* from only the Queen Charlotte Islands and adjacent SE Alaska, and *Sphaerophorus stereocauloides* from only New Zealand.

James & Henssen (1976) reported that cyanobacterium-containing forms of *Sticta* species tended to occur in more shaded, humid environments than the chlorococcoid-containing forms of the same species. Cyanobacteria are well known for their ability to fix atmospheric nitrogen and it seems reasonable to assume that the high precipitation levels characteristic of the oceanic climate provide the ideal environment for them to remain metabolically active for long periods of time, thus maximizing their benefit to the lichen. Further the high precipitation level also causes leaching of nutrients from the lichen's substratum so that the presence of cyanobacterium-containing cephalodia confirm a distinct evolutionary advantage in such conditions.

Fogg *et al.* (1973) suggested that the ability to produce cephalodia may be related to the acidity of the substratum, reporting that "in *Stereocaulon*, *Nostoc*-containing cephalodia developed only in neutral or alkaline areas and were absent from *Stereocaulon* in acid habitats". However, with the exception of *S. stereocauloides*, which is generally corticolous, all the species that are unique in their genera in having cephalodia are saxicolous crusts occurring on siliceous rocks.

Biogeography

The distribution pattern of SW Chile–Campbell Plateau shown by *P. stellata* is also reported for other lichenized fungi (e.g. *Degelia symptychia* (Tuck.) P. M. Jørg. (Fryday 2007a), *Lithographa olivacea* Fryday (Fryday 2004), *L. serpentina* Coppins & Fryday–*L. skottsbergii* (Zahlbr.) Fryday & Coppins (Fryday & Coppins 2007)) and is possibly explained by the close proximity of these landmasses on the southern coast of Gondwana before the break up of that supercontinent in the late Jurassic. The Falkland Islands and Tasmania, in contrast, which are the centres of distribution of *P. macloviana* and *P. parathalassica* respect-

ively, occupied a more central, continental position and it is possible that *P. stellata* evolved from these species and developed cephalodia as a response to the damper, oceanic climate.

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REFERENCES

- Andreev, M. P. (2004) Notes on the lichen genus *Miriquidica* (Lecanorales, *Lecanoraceae*) in Russia. *Bibliotheca Lichenologica* **88**: 15–42.
- Brodo, I. M. & Hertel, H. (1987) The lichen genus *Amygdalaria* (*Porpidiaceae*) in North America. *Herzogia* **7**: 493–521.
- Coppins, B. J. & Fryday, A. M. (2006) New or previously misunderstood species of *Lithographa* and *Rimularia* (*Agyriaceae*) from the southern sub-polar region and western Canada. *Lichenologist* **38**: 93–107.
- Coppins, B. J. & Fryday, A. M. (2007) Three new species of *Bacidia* s. lat. (*Ramalinaceae*) from Campbell Island (New Zealand). *Bibliotheca Lichenologica* **95**: 155–164.
- Fogg, G. E., Stewart, W. D. P., Fay, P. & Walsby, A. E. (1973) *The Blue-Green Algae*. London and New York: Academic Press.
- Fryday, A. M. (2000) Additional lichen records from New Zealand 31. *Australasian Lichenology* **46**: 36–39.
- Fryday, A. M. (2001) Additional lichen records from New Zealand 33. *Australasian Lichenology* **48**: 38–39.
- Fryday, A. M. (2003) Additional lichen records from New Zealand 39. *Australasian Lichenology* **52**: 25–26.
- Fryday, A. M. (2004) New species and records of lichenized fungi from the Auckland Islands and Campbell Island, New Zealand. *Bibliotheca Lichenologica* **88**: 127–146.
- Fryday, A. M. (2006a) New North America records of lichenized and lichenicolous fungi from the alpine and sub-alpine zones of Mt. Katahdin, Maine. *Bryologist* **109**: 570–578.
- Fryday, A. M. (2006b) Additional lichen records from New Zealand 46: *Degelia symptychia* (Tuck.) P. M. Jørg. *Australasian Lichenology* **60**: 4–5.
- Fryday, A. M. (2007b) Additional lichen records from New Zealand 47: *Coccotrema corallinum* Messuti, *Coccotrema pocillarium* (C.E. Cumm.) Brodo. *Australasian Lichenology* **61**: 3–5.

- Fryday, A. M. & Coppins, B. J. (2006) Typification and identity of *Pertusaria obvelata* Nyl. *Australasian Lichenology* **59**: 34–35.
- Fryday, A. M. & Coppins, B. J. (2007) A second species of *Lithographa* with submuriform ascospores. *Lichenologist* **39**: 245–250.
- Fryday, A. M. & Prather, L. A. (2001) The lichen collection of Henry Imshaug at the Michigan State University Herbarium (MSC). *Bryologist* **104**: 464–467.
- Hertel, H. & Rambold, G. (1988) Cephalodiate Arten der Gattung *Lecidea* sensu lato (Ascomycetes lichenisati). *Plant Systematics and Evolution* **158**: 289–312.
- James, P. W. & Henssen, A. (1976) The morphological and taxonomic significance of cephalodia. In *Lichenology: Progress and Problems* (D. H. Brown, D. L. Hawksworth & R. H. Bailey, eds.): 27–77. London: Academic Press.
- Johnson, A. J., Fryday, A. M. & Prather, L. A. (2005) The Michigan State University Herbarium Lichen Database. n. pag. Michigan State University Herbarium: <http://www.herbarium.msu.edu/> Database.
- Kantvilas, G. & Elix, J. A. (2008) Additions to the lichen genus *Pertusaria* in Tasmania. *Sauteria* **15**: 249–263.
- Lamb, I. M. (1947) A monograph of the lichen genus *Placopsis* Nyl. *Lilloa* **13**: 151–288.
- Messuti, M. I. & Archer, A. W. (1999) The lichen genus *Pertusaria* in the Falkland Islands (Islas Malvinas). *Bryologist* **102**: 208–214.
- Messuti, M. I. & Vobis, G. (2002) *Flora Criptogámica de Tierra del Fuego. Vol. 13, Fasc. 13. Lichenes Pertusariales: Coccotremataceae, Megasporaceae, Pertusariaceae*. Buenos Aires: Consejo Nacional de Investigaciones Científicas y Técnicas.
- Moberg, R. & Carlin, G. (1996) The genus *Placopsis* (Trapeliaceae) in Norden. *Symbolae Botanicae Upsaliensis* **31**: 319–325.
- Owe-Larsson, B. & Rambold, G. (2001) The sorediate species of the lichen genus *Miriquidica* (Lecanorales, Lecanoraceae). *Bibliotheca Lichenologica* **78**: 335–364.
- Wardle, P. (1991) *Vegetation of New Zealand*. Cambridge: Cambridge University Press.

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