The panaustral lichen *Pannaria sphinctrina* (Mont.) Tuck. and the related new species *P. lobulifera* from New Caledonia

A. ELVEBAKK

Dept. of Biology, University of Tromsø, N-9037 Tromsø, Norway; arve.elvebakk@ib.uit.no

Abstract – *Pannaria sphinctrina* (Mont.) Tuck. is redefined as an exclusively panaustral lichen species, characterized by thin thallus lobes, ellipsoid, verrucose perispores and with vicanicin as its major secondary metabolite. *Pannaria lobulifera* sp. nov. is described here as the only species known from the *P. sphinctrina* complex in New Caledonia. Instead of apothecia it produces vegetative propagules in the form of erect lobules. Its lobes are also thinner, rhizines are practically lacking and chlorobiont cells are much smaller than those of *P. sphinctrina*.

Pannaria / lichens / New Caledonia / endemic / Gondwanaland / austral

INTRODUCTION

The species *Parmelia sphinctrina* Mont. was described from the Chilean Juan Fernández Islands by Montagne (1835), based on the Bertero collections 1621, 1625, and 1630. It was later treated as *Parmelia rubiginosa* Ach. var. *sphinctrina* (Mont.) Hook. fil. (Hooker 1847, Babington 1855), and then as *Psoroma sphinctrinum* (Mont.) Nyl. by Nylander (1855). Later, Nylander (1859) reported it from austral areas such as Réunion, Mauritius, South Africa ("Promontorio Bonæ Spei"), antarctic America, Tasmania, and New Zealand, and also added its "var. *discretum* Nyl., in Chili", as a nomen nudum, until the taxon was formally described later, when the species was also reported from New Caledonia (Nylander 1863). Although treated within *Pannaria* in a very wide sense by Hue (1902), and also positioned in *Lecanora* by Nylander (1876), the species has mainly been known as *Psoroma sphinctrinum*, with a very wide austral as well as Paleotropical distribution, see a full list of references with geographical citation in Zahlbruckner (1925).

The species was more recently described in floras dealing with New Zealand (Galloway, 1985, who cited it as common and widespread, and cited several synonyms) and Australia (Jørgensen & Galloway, 1992), although Galloway (1985) cited it to possibly be a collective species, which might merit separation in further entities pending future studies. It was rather recently re-instated into *Pannaria*, as *P. sphinctrina* (Mont.) Hue (Jørgensen, 2000, 2001), who defined the *P. sphinctrina* complex as also including the phyllidiate *P. microphyllizans* (Nyl.) P. M. Jørg. and the sorediate *P. leproloma* (Nyl.) P. M. Jørg.

The present studies of the complex have confirmed that a syntype from the Juan Fernandez Islands agrees well with material of a widespread taxon in austral areas. However, Paleotropical material differs in several unrelated

characters and is planned accommodated within a new genus (Elvebakk & Jørgensen, unpubl.). Several of the synonyms listed from New Zealand by Galloway (1985) need further studies. Furthermore, the phyllidiate *P. microphyllizans* and the sorediate *P. leproloma* are not counterparts of *P. sphinctrina* according to own ongoing studies. Thus, there is a need to redefine *P. sphinctrina* in its strict sense, which is one aim of the present study. This study also treats the complex in New Caledonia, and the first of several austral species in the *P. sphinctrina* complex with vegetative propagules is described here.

MATERIALS AND METHODS

The collections in herbaria AK, BG, H, PC, S, TROM, UPS, UV, and WELT were examined, and selected material was borrowed for closer studies, including chemistry. All cited specimens were studied by thin-layer chromatography of acetone extracts using standardized procedures and solvents A and C (Culberson, 1972; Orange *et al.*, 2001). Iodine+ reactions were studied by adding IKI to mounts pretreated with KOH (Orange *et al.*, 2001). Perispore structures were studied in water mounts and restricted to spores liberated from their asci. Some TLC analyses were confirmed by HPLC analyses according to Feige *et al.* (1993) and Bjerke *et al.* (2002). Nomenclature of ascospore structures follows Nordin (1997).

The species

Pannaria sphinctrina (Mont.) Tuck., Gener. Lich. p. 43 (1872) (Fig. 1)

Basionym: Parmelia sphinctrina Mont., Annls. Sci. Nat. Bot. Ser. 2, 4: 90 (1835)

≡ Parmelia rubiginosa Ach. var. sphinctrina (Mont.) Hook. f. – Flora Antarct. II. Bot.: 533 (1847)

- ≡ *Lecanora sphinctrina* (Mont.) Nyl. Cmpt. Rend. Hebdom. Séanc. Acad. Paris 83: 89 (1876)
- ≡ Psoroma sphinctrinum (Mont.) Nyl. Annls. Sci. Nat. Bot. Sér. 4, 3: 181 (1855)
- = *Psoroma sphinctrinum* var. *discretum* Nyl., Syn. Lich. 2: 25 (1863), H-NYL 30763 (Type: New Zealand, Greymouth, R. Helms 1886, H-NYL 30804-lectotype!)
- = Pannaria discreta (Nyl.) Nyl., Lich, Novae Zeal. p. 52 (1888)
- = Pannaria sphinctrina var. discreta (Nyl.) Hue., Bull. Soc. Bot. France 48: LVI (1902 ("1901"))

Thallus foliose, corticolous, forming rosettes 3-15 cm in diam., closely attached to the substrate, unless growing over bryophytes or other uneven substrates. Lobes irregularly to subdichotomously branched, discrete in peripheral parts, imbricate to centrally coalescent, 0.7-1.5 mm wide and up to 10 mm long, flattened to weakly concave, margins entire, narrowly swollen, often with lobules in central parts, rarely weakly tomentose at apices, 120-160 μm thick. Upper surface pale greyish green when fresh and dry, salad green when fresh and moist, turning gradually chestnut brown after storage in herbaria, glabrous and glossy. Epicortex 30-50 μm thick, upper third developing brown pigmentation after storage and almost sclerenchymatic near the surface, below paraplectenchymatic with luminae globose to irregularly ellipsoid, 8-15 μm long, walls 1.5-3 μm thick. Photobiont layer 20-25 μm thick, of globose to subglobose cf. Myrmecia cells,



Fig. 1. Pannaria sphinctrina (AE 06:379) photographed in the field in the Juan Fernández Islands.

6-14 µm in diam. *Medulla* 50-80 µm thick, dark brown in lower part. *Lower cortex* lacking; *rhizines* common, brown and simple to sparingly branched; *hypothallus* felted, brown, and sometimes forming a blackish prothallus, particularly when growing on smooth bark.

Cephalodia common, laminal on the upper surface, globose to subglobose when young, later becoming irregularly pulvinate, and finally placodioid-nodulose and radially plicate and up to 1.5 mm in size, occasionally also developed on the hypothallus and the lower side; epicortex as in the chlorobiont; cyanobiont Nostoc, cells greyish blue, subglobose to ellipsoid, $3-4.5 \times 4.5-8$ µm large, not organized within distinct spherical glomeruli, and does not form visible chain structures.

Apothecia common, laminal, substipitate, 0.7-2.5 mm broad, discs rufous brown, flat, often becoming concave, and then sometimes with weak, concentric depressions and one or several small thalline granules or squamules centrally; thalline excipulum crenate-striate, with relatively small and regular lobe-like extensions; epithecium light brown, 15-25 μ m thick, hymenium colourless, but strongly IKI+ blue, c. 100 μ m thick; hypothecium light brown, c. 80 μ m thick, IKI negative; paraphyses simple to weakly branched, septate, with slightly swollen apices; asci clavate, 15 × 70-90 μ m in size, no internal IKI+ amyloid structures observed, with eight ascospores. Proper ascospores hyaline, non-septate, ellipsoid, 8-12 × 12-17 μ m in size; perispores ellipsoid, 9-13 × 15-20 μ m in size, distinctly verrucose when mature.

Chemistry. Vicanicin (major) and normally three unidentified terpenoids appearing through TLC analysis (traces), depending on concentrations. The preliminary results indicate that these terpenoids are different from those studied so far in other tripartite *Pannaria* species. Most specimens analyzed successfully for terpenoids have the same three terpenoids, but up to three additional ones are occasionally detected, although some of these can result from sample pollution.

Etymology. Montagne (1835) explained his choice of epithet ("sphinctrina" = "tied up" or "bound to"), by its resemblance to "Parmelia brunnea" (= Protopannaria pezizoides (Gyeln.) P.M. Jørg. & S. Ekman), particularly when comparing their apothecia.

Notes on taxonomy

Pannaria sphinctrina has recently mostly been cited as P. sphinctrina (Mont.) Hue, but should be cited as P. sphinctrina (Mont.) Tuck. Tuckerman was cited as author of the species, placed in Pannaria already by Hue (1902), but it has been overlooked later, as it was done obscurely in a paper (Tuckerman 1872: 43) dealing with the lichen flora of North America where Pannaria sphinctrina s. l. is lacking.

Psoroma sphinctrinum was lectotypified by Jørgensen & Galloway (1992) based on a Bertero collection deposited at PC-MONTAGNE, and with an isolectotype at BM. It was not indicated, however, which one of the three Bertero collections (# 1621, 1625 and 1630) listed by Montagne (1835), was chosen. The lectotype was not available when searched for at PC in 2001, but one of the syntypes (Bertero # 1630) was deposited there and was studied, along with other collections from the Juan Fernandez Islands (Bertero # 1631, also at PC-MONTAGNE, three collections from MSC and several by the present author), and compared with numerous other collections from southern South America and New Zealand. These studies show that P. sphinctrina is a well-defined panaustral species.

Psoroma sphinctrinum var. discretum Nyl.

This taxon was cited at the species level as "Psoroma discretum Nyl." by Zahlbruckner (1925) and by several subsequent studies, including the recent list of Pannariaceae names by Jørgensen (2003), referring to a recombination made by Nylander (1888, p. 52). However, here Nylander briefly mentioned the epithet "discreta" in a comparison with Pannaria pholidota (Mont.) Nyl. The latter name was first published by Nylander (1863, p. 30), a combination correctly cited by Hue (1902), but omitted by later reviews. Strikingly enough, Pannaria discreta was the only case where Nylander treated a tripartite austral Psoroma s. l. taxon within Pannaria, as he possibly regarded what is now considered Psoroma pholidotum (Mont.) Müll. Arg. a bipartite species. The conclusion is that the valid citation of var. discretum at the species level should rather be Pannaria discreta (Nyl.) Nyl.

Nylander (1863) only described the taxon from Chile. Hue (1906) later cited eight collections as belonging to this taxon; two from mainland Chile, one from New Zealand, and five from the Juan Fernandez Islands; the Bertero collections 1620, 1627, 1630, 1631 and one s.n. The present study has considered both the lectotype from New Zealand designed by Galloway (1985) and the Bertero 1630 and 1631 collections, and found them to correspond with *P. sphinctrina*, a conclusion in agreement with previous studies.

The Bertero 1631 collection has numerous knobbled or phyllidia-like outgrowths, particularly from its abundant apothecia. This is, however, also the case with an accompanying specimen of a different *Pannaria* species, where such outgrowths are produced from distinctly eroded parts, and it is thought here that the outgrowths of the *P. sphinctrina* specimens also represent lobules arising for the same reason.

Notes on chemistry and distribution

Sargent *et al.* (1976) described two chemotypes of *P. sphinctrina*, one based on vicanicin and another on norvicanicin; materials of both chemotypes were collected at Clyde Mountain, New South Wales, Australia. Quilhot *et al.* (1989) reported vicanicin from the species, collected from the Juan Fernández Islands and from two sites in the IX Región of Chile. The present analyses have not detected norvicanicin, but Australian collections have not been studied. Some HPLC analyses yielded a weak "shoulder" structure on the vicanicin curve, but were not interpreted to represent norvicanicin (J.A. Elix, pers. comm.). The species is therefore best considered to consist of a vicanicin-dominated chemotype, with variation in accessory compounds mostly present in trace to minor amounts. The latter mostly include terpenoids, with an interesting pattern of variation which should be studied in more detail, including comparisons with other related species.

The species is very common in moist parts of Chile. Follmann (1965) listed if from all regions from "Provincia de Coquimbo" (= IV Región) and southwards, in addition to the Juan Fernández Islands. This is probably correct, but the occurrences at Parque Nacional Fray Jorge and the neighbouring Altos de Talinay in IV Región are certainly isolated northerly outposts, as is the whole forest ecosystem of these sites. Additional studies are needed to produce a distribution map of the species within Chile.

However, its distribution in the region of Magallanes shows a distinct pattern. No herbarium specimens correctly determined, have been seen from the deciduous *Nothofagus* forests, such as those much studied by the present author in the Torres del Paine National Park, and in several localities near Punta Arenas and at Puerto Natales. Two coastal collections from Magallanes are cited here. However, the species is decidedly much more common along the coast than reflected in the literature, as the Michigan State University Herbarium Databases list numerous collections by Imshaug and coworkers from coastal areas both in Chilean Magallanes and from Isla de los Estados in Argentina. Calvelo & Liberatore (2002) listed the species from all the southernmost provinces of Argentina, except the poorly studied province of Santa Cruz.

Pannaria sphinctrina appears to be genuinely rare in Australia, although an unpublished herbarium note by P.W. James indicates that it is frequent in Tasmania. Sargent et al. (1976) reported it from a mountain east of Canberra, whereas Jørgensen & Galloway (1992) only mapped it from two sites further to the north. Their record from Queensland may belong to the mainly Palaeotropical segregate referred to above. It was not included from Tasmania and south-eastern Australia by Kantvilas & Jarman (1999). The species is very common throughout the forests of New Zealand, and a large number of samples not cited here have been seen.

Selected additional specimens studied

CHILE: Región IV, Loma Fray Jorge, on *Drimys winteri*, 670 m, 20 Aug. 1917, *C. & I. Skottsberg* s.n. (S);

Arquipiélago Juan Fernández, April/May 1830, Bertero 1630; 1631(PC-MONT); Isla Robinson Crusoe, Valle Colonial, trail to Portezuelo de Villagra at head of valley, 450 m, 9 Dec. 1965, H. Imshaug 37679B; 37679C (MSC); El Pangal; slope on west side of gorge to Cordón Escarpado, 430 m, 12 Dec. 1965, H. Imshaug 37898B (MSC); Plazoleta del Yunque, on Drimys confertifolia, 250 m, 33°39'S, 78°50'W, 6 Dec. 2006, A. Elvebakk 06:379, 06:384 (TROM); Región X, Lago Riñihue, Riñihue, on Podocarpus nubigena in dense virgin rain forest, 2 Sept. 1940, R. Santesson 3558 (S); Enco, on tree trunks in the dense forest (Aextoxicum, Nothofagus dombeyi. etc.) above Enco, 28 Sept. 1940, R. Santesson 7618 (S); Enco, on Laurelia (probably sempervirens) in open Nothofagus dombeyi forest, 30 Sept. 1940, R. Santesson 3587 (S); Valdivia, Collico, on Podocarpus salignus in the outskirts of a rain-forest, 13 Sept. 1949, R. Santesson 8291 (S); Valdivia, Piedra Blanca, on Drimys winteri in a Drimys forest, 14 Sept. 1940, R. Santesson 3290 (S); Lago Llanquihue, 0.5 km N of Ensenada, on Eucryphia cordifolia, 19 Nov. 2000, A. Elvebakk 00:557 (TROM); Parque Nacional de Chiloé, Cucao, near Guardería, on Tepualia stipularis, 18 Nov. 2000, A. Elvebakk 00:508A (TROM); Región XI, Puerto Aysén, on fallen, decaying trunks in sparse forest (mixed rain forest), 10 Nov. 1940, R. Santesson 4343; 4349 (S); 15 km S of Lago las Torres, 44°56'S, 72°09'W, on Nothofagus dombeyii, 270 m, 10 Dec. 2006, A. Elvebakk 06:437 (TROM); Fiordo Queulat, 44°31'S, 72°08'W, on Fuchsia magellanica, 5 m, 11 Dec. 2006, A. Elvebakk 06:494 (TROM); Región XII: Tierra del Fuego, Fiordo Finlandia, Bahía Kairamoi, 3 Aug. 1929, H. Roivainen (H); Patagonian Channels, N side of Isla Grant, open hillside with outcrops, 25 Sept. 1969, H. Imshaug (43706) & K. Ohlsson (S).

NEW ZEALAND: North Island, Waitemata Co., Swanson, end of Tram Valley Road, 36°52'S, 174°34'E, growing on kauri bark, 17 Aug. 1985, A.E. Wright 7294 (AK); Central Volcanic Plateau, National Park, 39°11'SW, 175°23' E, 830 m, on *Hedycarya arborea*, 30. Nov. 2002, *A. Elvebakk* 02:327A (TROM); Tongariro Ecological Region and District, 39°N, 175°E, Mount Ruapehu, Whakapapanui Track, 1060 m, 19 April 2000, D.B. Rogan 430 (AK); Auckland Ecological Region, Hunua Ecological District, base of forest tree (rewarewa) on liverwort, 11 March 1976, A.J. Dakin s.n. (AK); Kawakawa Bay, Te Morehu Scenic Reserve, 36°58'S, 175°10'E, on bark of Pseudopanax arboreus shrubland on ridge, 21 Feb. 1976, A.J. Dakin s.n. (AK); Duder's Bush, hills between Clevedon and Maraetai, 36°55'S, 175°03'E, on Knightia on hill slope in kauri forest, A.J. Dakin s.n (AK); Volcanic Plateau, Tongoriro Forest, on bark of *Phyllocladus alpinus*, 860 m, 39°06'N, 175°30'E, 24 May 1988, A.E. Wright 8073 (AK); Coromandel Ecol. Region, Great Barrier Ecol. District, summit of Hirakimata (Mt. Hobson), 5-600 m, 36°11'S, 175°25'E, on trunks of kauri and towhai, 8 March 1978, A.J. Dakin 19 (AK); Otorohanga Co., South Kawhia, west of Awaroa Road, near lake Koraha, 200 m, 38°09'S, 174°55'E, on bark of 15 m *Prumnopitys* ferruginea in ridge-top forest, 28 Oct 1989, A.E. Wright 9119 (AK); Sounds-Wellington Ecol. Region, Sounds Ecol. District, Motuara Island, around Cook's Cairn, 41°06'S, 174°16'E, 120 m, on bark in mixed tea-tree forest, 4 Jan 1992, G.C. Hayward s.n (AK); South Island, Canterbury region, N of Lake Wanaka, 1 km N of Makarora, Pipson Creek, 44°13'S, 160°14'E, 380 m, 6 Dec. 2002, A. Elvebakk 02:451 (TROM); Otago region, Scenic Hills, 2.5 km S of Caberfeidh, 46°39'S, 169°30'E, 200 m, 10 Dec. 2002, *A. Elvebakk* (TROM); **Stewart Island**, Rakiura Ecol. Region, Mount Allen Ecol. District, Port Pegasus, Islet Cove, 47°12'S, 167°38'E, 2 m, on bark of Dacrydium intermedium, B.W. Hayward s.n. (AK).

Pannaria lobulifera Elvebakk, sp. nov. (Figs. 2 and 3) Etymol.: Latin, "carrying small lobes", referring to its vegetative propagules.

Pannariae sphinctrinae similis, sed absentia apotheciorum, lobis tenuioribus, rhizinis paene deficientibus, praesentia lobulorum ascendentium, et multo minoribus cellulis chlorobionticis differt.

Typus: New Caledonia, 10 km NE of Nouméa, W slope of Monts des Koghis, ca. 0.8 km E of Auberge and 200 m W of Belvedère, 22°10'S, 166°31'E, 740 m, on tree trunk, 4. Dec. 2005, A. Elvebakk 05:598 (PC-holotypus, IRD- isotypus).



Fig. 2. The 10 cm large type specimen of *Pannaria lobulifera* photographed in the field in New Caledonia, after moisturing and before it was sampled. The white spots are the lower sides of ascendent lobules.



Fig. 3. Details of the holotype of *Pannaria lobulifera*. The ascendent lobules with their white lower sides have been bent downwards after the samples have been pressed. Scale bar = 1 cm.

Thallus foliose, corticolous and on corticolous bryophytes, forming rosettes 5-10 cm diam., closely attached to the substrate. Lobes irregularly to subdichotomously branched, discrete in peripheral parts, imbricate to centrally coalescent, 0.7-1.5 mm wide and up to 10 mm long, flattened to weakly concave, margins entire, narrowly swollen and weakly recurved, often with secondary lobules in central parts, 90-120 μ m thick. Upper surface pale greyish green when fresh and dry, deep salad green when fresh and moist, herbarium specimens turning violet-brown when treated with water. Ascending lobules common, 0.2-0.4 \times 0.6-1.0 mm in size, often weakly constricted at base, white on the exposed lower side, regularly orientated perpendicularly to the thallus surface on vertical trunks (Fig. 3). Epicortex 25-50 μ m thick, almost sclerenchymatic near the surface, below paraplectenchymatic with luminae globose to irregularly ellipsoid, 8-15 μ m long, walls 2.0-3.5 μ m thick. Photobiont layer 15-25 μ m thick, of globose to subglobose, small cf. Myrmecia cells, 4.0-6.5 μ m in diam. Medulla 50-60 μ m thick, dark brown in lower part. Lower cortex lacking; rhizines rare; hypothallus not observed.

Cephalodia common, laminal on the upper surface, subglobose to pulvinate when young, later becoming irregularly pulvinate and finally radially nodulose, up to 1.5 mm large; *epicortex* as in the chlorobiont thallus; *cyanobiont Nostoc*, cells bluegreen, globose to ellipsoid 3.0-5.5 × 4.5-6.5 µm in size, sometimes seen forming 15-20 µm large glomeruli, but not seen forming chain structures.

Apothecia not observed.

Chemistry. Vicanicin (major) and one unidentified terpenoid (trace to minor).

The most characteristic aspect of *P. lobulifera* is the presence of conspicuous, erect lobules, easily visible because of the white contrast colour of their exposed lower sides. Their regular development, positions and frequent constricted bases indicate that they are vegetative propagules. This is also witnessed by frequent scars of broken-off lobules, and the fact that the samples are well-developed lichens, all observed specimens were about 10 cm in size and totally lacked apothecia. Such large specimens of *P. sphinctrina* would always have apothecia in abundance.

Visually, the ascendent lobules resemble basal squamules of primary thalli of certain *Cladonia* species. However, the lobules of *P. lobulifera* are adapted to vegetative propagation by having a morphology and orientation differing from normal lobes. It is striking that two more species collected in New Caledonian forests have almost identical lobules. These can easily be confused in the field with *P. lobulifera*, and have not been studied yet, but appear to belong to the genera *Phyllopsora* and *Psoroma* s.l. Specialized vegetative propagules of this kind are not familiar to the present author, and are considerably larger than common soredia, isidia and phyllidia. These structures may mostly act as diaspores working on a local scale, but animal activity in tree crowns or strong winds can certainly carry the diaspores even further.

The species was only collected three times in the same area at altitudes between 690 and 740 m, but is probably much more common than presently known. No extensive New Caledonian lichen collections have been studied by the present author, except own collections from the year 2005. However, *P. lobulifera* has neither been found in large New Zealand collections, nor in moderately large Australian collections studied by the present author, and no such species have been described in the literature. Therefore it will most probably remain an endemic species in the future.

Additional samples studied

NEW CALEDONIA, 10 km NE of Nouméa, W slope of Monts des Koghis, ca. 0.8 km E of Auberge, 300 m W of Belvedère, 22°10'S, 166°31'E, 700 m, on tree trunk, 4. Dec. 2005, *A. Elvebakk* 05:594 (TROM); along path to Les Sommets, 300 m after its bifurcation with path to Belvedère, 22°10' S, 166°31 E', 690 m, on tree trunk, 8 Dec. 2005, *A. Elvebakk* 05:704 (TROM).

DISCUSSION

Pannaria sphinctrina is best recognized in the field by its narrow and thin lobes, closely attached to the substrate, and by its pale greyish green colour, becoming deep salad green when moistened. Herbarium specimens slightly older than one month turn immediately violet-brown after application of water. The colour is present in both the epicortex and the medulla, but strongest near the green algal layer. It is absent from the cephalodia, and the colour obviously arises from the decomposition of green algae. The colour is not produced in herbarium specimens younger than one to two months, probably corresponding to the living state of the green algae. The various dark colours of old herbarium specimens of tripartite Pannaria species probably represent a slow release of these substances. The chemistry of this process does not seem to have been studied, although own preliminary studies indicate that a variety of chemical compounds are involved, even within the Pannariaceae.

Frequently, mature apothecia have developed a central depression associated with granules of thalline substrate as clearly seen in the illustration by Malcolm & Galloway (1997, p. 108). Chemically, its content of vicanicin as the only major compound is so far among the tripartite *Pannaria* species only known from *P. patagonica* (Malme) Elvebakk & D.J. Galloway, in addition to the two species dealt with here. *Pannaria patagonica* is a much more robust species with thicker and broader lobes, which are not closely attached to the substrate. Reports of chemotypes with vicanicin as the only major compound in the species *P. microphyllizans* (Quilhot *et al.* 1989) and *P. allorhiza* (Nyl.) Elvebakk & D.J. Galloway (Elix *et al.* 1982) do not seem to be correct according to own ongoing studies.

Pannaria sphinctrina was reported from New Caledonia by both Nylander (1863), Smith (1922), and Elix & McCarthy (1998). None of the specimens cited by these authors have been studied here, but results from the field work in 2005 indicates that it has probably been confused with material belonging to the undescribed Palaeotropical genus referred to above, some specimens being superficially similar to P. sphinctrina.

Pannaria lobulifera therefore remains the only known tripartite Pannaria species from New Caledonia. This represents the northernmost extension of the important panaustral group of tripartite Pannaria species within the subgenus Pannaria. This is an important knowledge, bearing in mind the concentration of ancient plant groups in New Caledonia, e.g. the numerous conifer species within Araucariaceae and the monotypic family Amborellaceae, containing the oldest extant angiosperm on earth. It is too premature to speculate whether this is an indication that this group of lichens has a younger evolutionary history than the

numerous Gondwanaland groups present on New Caledonia, or whether it points to an origin further to the south in Gondwanaland, and a disability to conquer true subtropical forests.

Pannaria lobulifera appears to be rather closely related to the widely distributed panaustral species P. sphinctrina, although apothecia would be needed to confirm this. Thin lobes are an important character, uniting species within the P. sphinctrina complex now being studied by the present author in other areas as well. The lobes of Pannaria lobulifera appear to be significantly thinner than even P. sphinctrina. It also grows more strongly attached to the substrate, mostly directly fastened by the lower side, as poorly developed rhizines were observed just a very few instances. No traces of hypothallus/prothallus were observed. The latter character is modified by the substrate, and a broad prothallus is very well developed in P. sphinctrina when growing on smooth bark or on evergreen coriaceous leaves, but in coarser habitats P. sphinctrina at least produces abundant rhizines.

In both species, the cyanobiont has been proven to be a *Nostoc*, and closely related to very similar tripartite species from Chile and New Zealand (Elvebakk *et al.* subm.). In contrast, the green algae are very different. They appear to belong within *Myrmecia* in both species, but all the three studied collections of *P. lobulifera* have cells with a mean size of about 5 μ m, in contrast to about 10 μ m in *P. sphinctrina*. A full understanding of these lichens would require knowledge about all the three components, in particular the chlorobiont, which has not been studied yet.

Acknowledgements. Corporación Nacional Forestal (CONAF) in Chile and Direction des Ressources Naturelles in New Caledonia are acknowledged for permission to collect lichens, and the guide Alain Fort for company in the field in New Caledonia. John A. Elix, Australian National University, kindly helped with interpreting HPLC chromatograms, Eli H. Robertsen, University of Tromsø, with TLC analyses, Ellen Kathrine Thomassen, University of Tromsø, with language proofreading, and Per P. Aspaas, University of Tromsø, with Latin translations. The author is also grateful to the curators of the herbaria AK, H, PC, and S for the possibility to borrow the specimens cited here.

REFERENCES

- BABINGTON C., 1855 *CIV Lichenes. In*: HOOKER J.D. 1855. The botany of the Antarctic Voyage of H.M. ships Erebus and Terror, in the years 1839-1843. II. Flora Novæ-Zelandiæ. Part II. Flowerless plants. Pp. 266-311. London:Reeve.
- BJERKE J.W., LERFALL K., & ELVEBAKK, A., 2002 Effects of ultraviolet radiation and PAR on the content of usnic and divaricatic acids in two acrtic-alpine lichens. *Photochemical and Photobiological Sciences* 1: 678-685.
- CALVELO S. & LIBERATORE S., 2002 Catálogo de los líquenes de la Argentina. *Kurtziana* 29(2) 1-174.
- CULBERSON C.F., 1972 Improved conditions and new data for the identifications of lichen products by a standardized thin layer chromatography method. *Journal of Chromatography* 72: 113-125.
- ELIX J.A., ENGKANINAN U., JONES A.J., RASTON C.L., SARGENT M.V. & WHITE A.H., 1978 Chemistry and crystal structure of leprolomin, a novel diphenyl ether from the lichen *Psoroma leprolomum*. *Australian Journal of Chemistry* 31: 2057-2068.
- ELIX J.A., LAJIDE L. & GALLOWAY D.J., 1982 Metabolites from the lichen genus *Psoroma*. *Australian Journal of Chemistry* 35: 3225-2333.

- ELIX J.A. & McCARTHY P.M, 1998 Catalogue of the lichens of the smaller Pacific islands. Bibliotheca Lichenologica 70: 1-361.
- FEIGE G.B., LUMBSCH H.T., HUNECK S. & ELIX J.A., 1993 Identification of lichen substances by a standardized high-performance liquid chromatographic method. Journal of Chromatography 646: 417-427.
- FOLLMANN G., 1965 Catálogo de los líquenes de Chile. III. Thelotrematales y Cyanophiliales. Revista Universitaria (Universidad Católica de Chile) 49: 17-65.
- HOOKER J.D., 1847 LVIII Lichenes. In: HOOKER, J.D. The botany of the Antarctic Voyage of H.M. Discovery ships Erebus and Terror, in the years 1839 - 1843. I. *Flora Antarctica. Part II*. Botany of Fuegia, the Falklands, Kerguelen's Land etc. Pp. 519-542, London: Reeve.
- HUE A., 1902 ("1901") Causerie sur les Pannaria. Bulletin de la Societé Botanique de France 48: XXXI-LXV.
- HUE A., 1906 Lichenes morphologice et anatomice disposuit. Nouvelles Archives du Muséum d'Histoire Naturelle de Paris 8: 237-272.
- GALLOWAY D.J., 1985 Flora of New Zealand lichens. Hasselberg, Wellington, New Zealand, 662 pp.
- JØRGENSEN P.M., 2000 Survey of the lichen family *Pannariaceae* on the American continent, north of Mexico. The Bryologist 103: 670-704.
- JØRGENSEN P.M., 2001 New species and records of the lichen family Pannariaceae from Australia. In: McCarthy, G. Kantvilas & S.H.J.J. Louwhoff (eds.). Lichenological contributions in honour of Jack Elix. Bibliotheca Lichenologica 78: 109-139.
- JØRGENSEN P.M., 2003 Conspectus familiae Pannariaceae (Ascomycetes lichenosae). Ilicifolia 4: 1-78.
- JØRGENSEN P.M. & GALLOWAY D.J., 1992 Pannariaceae. Flora of Australia, 54: 246-293. KANTVILAS G. & JARMAN S.J., 1999 Lichens of rainforest in Tasmania and south-eastern Australia. Flora of Australia Supplementary Series 9: 1-212.
- MALCOLM W.M. & GALLOWAY D.J., 1997 New Zealand lichens. Checklist, key and glossary. Museum of New Zealand Te Papa Tongarewa, Wellington, 192 pp.
- Michigan State University Herbarium Databases http://herbarium.msu.edu/Database/index.html
- MONTAGNE C., 1835 Prodromus florae fernandezianae. Pars prima, sistens enumerationem plantarum cellularium quas in Insulá Juan Fernandez à Cl. Bertero collectas describi edique curavit. Annales des Sciences Naturelles, Botanique 4: 86-90.
- NORDIN A., 1997 Ascospore structures in Physciaceae: an ultrastructural study. Symbolae Botanicae Upsalienses 32; 1: 195-208.
- NYLANDER W., 1855 Additamentum in floram cryptogamicam chilensem, quo lichenes præcipue saxicolas exponit. Annales des Sciences Naturelles, Botanique Séries 4; 3: 145-187.
- NYLANDER W., 1859 Dispositio Psoromatum et Pannariarum. Annales des Sciences Naturelles, Botanique, Séries 12, 4: 293-295.
- NYLANDER W., 1863 Synopsis methodica lichenum omnium hucusque cognitorum praemissa introductione lingua gallica tractata. Fasc. II. Parisiis.
- NYLANDER W. 1876 Lichens rapportés de l'île Campbell, par M. Filhol, déterminés par. M. W. Nylander. Comptes Rendus Hebdomadaires des Séances de l'Académie de Paris 83: 87-90.
- NYLANDER W., 1888 Lichenes Novae Zelandiae. Paul Schmidt, Parisiis.
- ORANGE A., JAMES P.W. & WHITE F.J., 2001 Microchemical methods for the identification of lichens. London: British Lichen Society.
- QUILHOT W., PIOVANO M., ARANCIBIA H., GARBARINO J.A. & GAMBARO V., 1989 Studies on Chilean lichens, XII. Chemotaxonomy of the genus Psoroma. Journal of Natural Products, 52: 191-192.
- SARGENT M.V., VOGEL P., ELIX J.A., & FERGUSON B.A, 1976 Depsidone synthesis. VII Vicanicin and norvicanicin. Australian Journal of Chemistry, 29: 2263-2269.
- SMITH A.L., 1922 Lichens. In: A systematic account of the plants collected in New Caledonia and the isle of Pines by Compton in 1914. Journal of the Linnean Society of London, Botany 46:
- TUCKERMAN E., 1872 Genera lichenum: an arrangement of the North American lichens. Amherst. ZAHLBRUCKNER A., 1925 — Catalogus lichenum universalis. Band III. Verlag Gebr. Borntraeger, Leipzig