Comparison of morphological, anatomical and chemical characters in *Pseudocyphellaria endochrysa* and *P. vaccina* (Lobariaceae, lichenised Ascomycota)

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A comparison of morphology, anatomy and chemistry of the two closely related lichens Pseudocyphellaria endochrysa and P. vaccina is presented. The presence of a scabrid-areolate upper surface in P. vaccina and a minutely pubescent, non-scabrid upper surface in P. endochrysa have been used as key characters for distinguishing the two species. However, the present study shows that in exposed habitats, such as in alpine habitats of southern South America and in low antarctic tundra on South Georgia, P. endochrysa also has a scabrid-areolate upper surface, almost without any hairs. In more protected sites, the upper surface of *P. endochrysa* is more pubescent and not scabrid. Previous reports of P. vaccina from the treeless zones in southernmost South America and the South Atlantic islands are referable to P. endochrysa. This conclusion is also supported by anatomical and chemical characters. Analyses by HPLC and TLC showed that pseudocyphellarins A and B, calycin, pulvinic dilactone and pulvinic acid are the principal lichen substances in P. endochrysa. In P. vaccina, pseudocyphellarin A is generally in minor amounts only, and pseudocyphellarin B was not detected. The three pulvinic acid derivatives are present in yellow-medullary thalli of P. vaccina. Distribution maps are presented. While P. endochrysa is very rare north of 50° southern latitude, P. vaccina is common north to 37°S.

Key words: HPLC, lichens, Pseudocyphellaria, taxonomy

Introduction

A few of the many southern South American species of *Pseudocyphellaria* are also known from the Falkland Islands and South Georgia in the South Atlantic. *Pseudocyphellaria endochrysa*, a broad-lobed and yellow-medullary species, has been reported several times

from these islands, e.g. from South Georgia by Huneck *et al.* (1973, 1984), Lindsay (1973, 1974) and Galloway (1986, 1992), and from the Falkland Islands by Delise (1825), Cotton (1915), Dodge (1965, as *P. latilobia*) and Galloway (1986, 1992). Other members of the genus that have been reported from South Georgia are *P. freycinetii* (Huneck *et al.* 1973, 1984, Lindsay 1973, 1974, Galloway 1986, 1992) and *P. vaccina* (Galloway 1986, 1992). Galloway (1992) reported a total of nine species of the genus from the Falkland Islands.

Pseudocyphellaria endochrysa and P. vaccina are closely related. They have a yellow medulla, although a white-medullary form of P. vaccina is common, a green photobiont, a pale tomentose lower surface, 1-septate spores and no isidia or soralia (Galloway 1986, 1992). The distinguishing features are the structure of the upper surface, which is scabrid-areolate and only rarely patchily pubescent in P. vaccina and smooth, delicately pubescent toward the lobe margins in P. endochrysa, the thickness of the lobe margins, and the shape of the ascospores, which are fusiform-acicular with both apices pointed in P. vaccina and acicular with one apex rounded in P. endochrysa (Galloway 1986, 1992, Galloway & James 1986). They are also chemically distinct (Galloway 1986). Huneck (1984) described the two fully substituted depsides pseudocyphellarins A and B from South Georgian material of P. endochrysa, and additional notes on these two substances in P. endochrysa were given by Elix and Lajide (1984) and Pulgarin et al. (1985).

In spite of these distinguishing characters, the separation of the two species is not unproblematic, as shown by the following statement by Galloway (1986): "In South Georgia *Pseudocyphellaria endochrysa* grows in association with *P. vaccina* and many of the identifications of the former species made for South Georgian material refer to *P. vaccina*. The two species are obviously closely related, as well as having similar habitat ecology and geographical distribution".

There has been some confusion regarding these two species also in southernmost South America, where a third species, *Pseudocyphellaria berberina*, also is involved. It has a yellow medulla and a green photobiont and lacks isidia and soralia. However, as discussed by Galloway and James (1977), *P. berberina* is more distinct from the two former species. It is distinguished by a smooth and glabrous upper surface, more elongated spores, and a different chemistry.

Redon (1973) reported Pseudocyphellaria

vaccina (as P. albidopallens) from East Patagonian steppes in southern Chile. In a later account Redon (1985) stated that P. endochrysa was a part of the Empetrum rubrum community occurring in the same area. Galloway (1986, 1992) considered both P. vaccina and P. endochrysa to be a part of the Magellanic tundra and steppe flora. In a subsequent review, Galloway (1998) considered P. endochrysa to be a part of the subalpine grassland scrub environment in association with P. freycinetii and several species of Cladina, Cladonia, Peltigera and Stereocaulon, and Pseudocyphellaria vaccina to be a part of the steppe grassland at lower levels in association with P. freycinetii, P. hillii, P. lechleri and Thamnolia vermicularis.

During field studies in southernmost Chile the present authors experienced problems distinguishing these two species when using published keys and descriptions. Therefore, a closer study of these two species was undertaken. Based on our preliminary results, Øvstedal and Smith (2001) did not cite *Pseudocyphellaria vaccina* from South Georgia. The details for this exclusion, a clarification of the limits between the two species, and their respective distribution ranges are given in the present paper.

Materials and methods

Material of Pseudocyphellaria endochrysa and P. vaccina collected by the authors in Chile, and herbarium specimens from their total distribution areas deposited in the herbaria AAS, H, HIP, S, UPS and UV were examined. Anatomical studies were undertaken following Malcolm and Galloway (1997). Thin-layer chromatography of acetone extracts was performed using standardised procedures (Culberson 1972, Wilkins & James 1979, White & James 1985). Selected specimens were also analysed by high performance liquid chromatography (HPLC) according to Bjerke et al. (2002). A slightly longer gradient run was used here. In brief, a mobile phase with two solvents was used. The proportion of methanol was increased from 30% to 72% during 4 min, and then to 90% during 26 min. The other solvent, 1% orthophosphoric acid in ultra-pure water, was decreased accordingly. Samples weighing ca. 0.010 g were extracted in 3.0 ml acetone for 1 h. The filtered extracts were injected twice at different volumes in order to detect as many substances as possible. Pure samples of pseudocyphellarins A and B were analysed using the same methods. Other substances detected by HPLC were identified by comparing with lichen samples of which the content is known, and by comparing with published data on retention times and UV absorbance (Feige *et al.* 1993, Yoshimura *et al.* 1994, Huneck & Yoshimura 1996).

The distribution patterns of the two species are compared with established bioclimatic divisions of southern South America and the South Atlantic islands (see e.g. Schmithüsen 1956, Bliss 1978, Tuhkanen 1992, Amigo & Ramírez 1998, Elvebakk & Moberg 2002). In particular, we focus on the east-western distribution in southernmost South America as mapped by Elvebakk and Moberg (2002). In this area, the bioclimatic regions are from west to east Magellanic moorland, antiboreal rainforest, antiboreal deciduous forest, Chiliotrichum-Empetrum heathland, and temperate steppe zones. Distribution maps are based on our own records and collections, examined herbarium specimens and published reports, excluding doubtful reports.

Results and discussion

Around 40 specimens collected by the present authors and 150 herbarium specimens were examined. Four herbarium specimens labelled *Pseudocyphellaria endochrysa* proved to be *P. berberina*. The remaining specimens are referable either to *P. endochrysa* or *P. vaccina*.

Specimens from the South Atlantic islands

Morphology and anatomy

The specimens from South Georgia and the Falkland Islands show some morphological variation. The most variable character is the structure of the upper surface. All specimens have some degree of scabrosity, but it varies from faint to prominent. In addition, some specimens have a shallowly areolate upper surface, and some even have cracks that penetrate the upper cortex and the photobiont layer. All specimens are more or less pubescent, especially towards the lobe apices. The lower surface varies from being almost entirely naked with a delicate tomentum only in patches, to more rarely being more or less entirely tomentose. In addition, some specimens have a prominently wrinkled lower surface, whereas in other specimens the wrinkles are not pronounced. Apothecia are common, having dark brown to black discs. All specimens have a yellow medulla. The mature spores are 1septate, acicular, pointed at one end and rounded at the other.

Chemistry

HPLC analyses revealed that four lichen substances are present in major amounts in the South Georgian material (Fig. 1a). These four substances are pseudocyphellarins A and B, calycin and pulvinic dilactone. Seven additional substances in trace or minor amounts were also detected in all specimens, and one of these is pulvinic acid. The other six substances remain unidentified. A substance with UV absorbance spectra very similar to pseudocyphellarins A and B were detected in some specimens at 13.2 min. This substance may be isopseudocyphellarin (see Huneck & Yoshimura 1996). The triterpenoids, which are so numerous in certain species of Pseudocyphellaria (Wilkins & James 1979), do not absorb in the UV range of the spectrum, and are therefore not detected by HPLC. By TLC analyses, eight to nine spots referable to triterpenoids were detected, and according to their positions on the plates, they appear to be the same in all specimens. The pseudocyphellarins were often difficult to detect on TLC plates, because their spots were partly or entirely masked by triterpenoids. None of the specimens from the Falkland Islands were analysed by HPLC, but their TLC patterns are similar to those of South Georgian specimens.

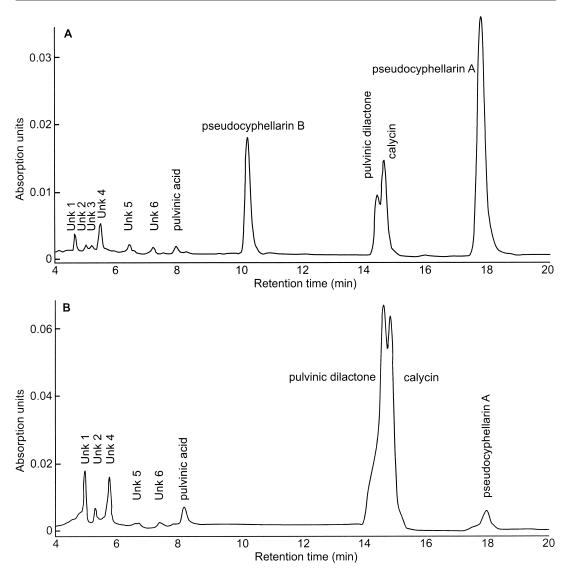


Fig. 1. Representative HPLC chromatograms. — A: *Pseudocyphellaria endochrysa* (South Georgia, *Greene 1507a*, AAS). — B: *Pseudocyphellaria vaccina* (S Chile, *Elvebakk 95:142*, TROM). — The unidentified substances are coded 'Unk 1–6'. Injection volumes are 8 µl for A and 50 µl for B. Sample sizes are ca. 0.010 g extracted in 3.0 ml acetone.

Specimens from open habitats in southern South America

Morphology and anatomy

This group of specimens is also variable in terms of morphology. Thalli collected from protected habitats have smooth, rather broad and papery lobes with more or less entirely pubescent, nonscabrid lobe apices. Apothecia are common. Thalli with these characters are found particularly in the coastal zone and from low altitudes at the southern side of Isla Grande. In more exposed habitats, for instance in East Patagonian heathlands and at higher altitudes close to and above the tree line in antiboreal deciduous forests, thalli have a more prominently scabrid upper surface with less pubescence, and the lobes are more narrow, and apothecia are rare. Samples collected along an altitudinal transect from 250 to 750 m alt in southern Patagonia indicate that this taxon becomes more scabrid, less pubescent, and slightly thicker with increasing altitude or exposure (*Domínguez 3, 10, 12, 13*; HIP). The buff-tomentose, plane to minutely wrinkled lower surface is, however, similar for all specimens in this group. In addition, areolae are absent, and all specimens have a yellow medulla. The apothecial discs are dark brown to black, and the spores are acicular with one end rounded and one pointed as in the South Georgian material.

Chemistry

Pseudocyphellarin A, calycin and pulvinic dilactone appear to always be present in major amounts. Pseudocyphellarin B is also present in all analysed specimens, but only in trace to minor amounts. The area of the HPLC peak of pseudocyphellarin B is never more than 5% of the area of the corresponding peak of pseudocyphellarin A, whereas for the South Georgian material, the ratio is always 40% or higher. Pulvinic acid is present in minor amounts, but for a few specimens the peaks are of the same size as for calycin and pulvinic dilactone. The same unidentified substances as in the South Georgian material were detected. 'Isopseudocyphellarin' was not detected. In general, eight triterpenoids were detected by TLC, but the number varied between six and nine. The triterpenoids are the same as in the South Georgian material.

Specimens from forest habitats in southern South America

Morphology and anatomy

The specimens from forest habitats show a uniform morphology. The adpressed coriaceous lobes have a prominently scabrid upper surface, but areolae are absent or very shallow. Patches of delicate pubescence were observed in a few specimens. The lower surface is uniformly tomentose, pale brown to brown, and plane to minutely wrinkled. The Magellanic and Fuegian samples have a pale yellow to white medulla, often with intrathalline variations. The medulla of thalli collected at lower latitudes is mostly white. The thallus colour differs from that of the two other groups, being pale greyish in this group and bluish-green in the two other groups, and the colour difference is in particular apparent in herbarium specimens that are not older than ca. 20 years. Apothecial discs are pale brown to dark brown, never black, and the spores are 1-septate, but broader than the spores of the two other groups, being characterised as fusiform-acicular. Here, both ends are more or less pointed.

Chemistry

Traces to minor amounts of pseudocyphellarin A were detected in all analysed specimens from southernmost Chile (Fig. 1b). However, some specimens from regions IX-X in Chile do not contain any detectable amounts of pseudocyphellarin A. Calycin and pulvinic dilactone are present in major amounts in all specimens with a yellow medulla, and absent in all specimens with a white medulla. The amount of pulvinic acid is highly variable, varying from trace to major in all yellow-medulla specimens. Pseudocyphellarin B and 'isopseudocyphellarin' were not detected. The same unidentified substances as were found in the two other groups were also detected in this group of specimens, although one of these substances was not detected in all analysed specimens. Six triterpenoids were visible on TLC plates, which appear to be shared with the other groups.

Identity of the groups

Pseudocyphellaria vaccina (Mont.) Malme

Bih. K. Svenska Vet.-Akad. Handl. 25 Afd. 3, 5: 27. 1899. *Sticta vaccina* Mont., Ann. Sci. Nat. Bot. Sér. 3, 18: 307.
1852. — TYPE: Chile. *Sine loco*, *M. Gay s.n.* (cited lectotype PC-Montagne). — For additional synonyms, *see* Galloway (1986).

The specimens from forest habitats are distinguished from the two other groups both on morphological, anatomical and chemical char-

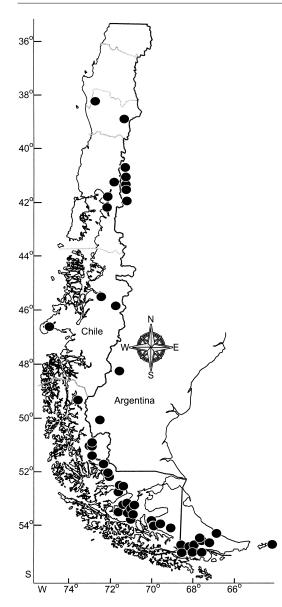


Fig. 2. Distribution of Pseudocyphellaria vaccina.

acters. The morphological and anatomical characters given above fit well with the descriptions given for this species by Malme (1899) and by Galloway (1986, 1992), although Malme (1899) stated that the spore apices are obtuse in shape. The reports on the chemistry of *Pseudocyphellaria vaccina* vary slightly. Huneck *et al.* (1973) reported calycin, pulvinic acid and zeorin from *P. vaccina* (as *P. albidopallens*). Galloway (1986) and Galloway *et al.* (1995) reported calycin, pulvinic dilactone, two principal stictane triterpenoids and traces of seven additional triterpenoids. Huneck and Yoshimura (1996) and Huneck (2001) listed *P. vaccina*, and not *P. endochrysa*, as reference species for pseudocyphellarins A and B, but Huneck (1984) is cited, and in that paper, material from South Georgia was used. Thus, the reports in Huneck and Yoshimura (1996) and Huneck (2001) are referable to *P. endochrysa*. We were not able to detect as many triterpenoids in *P. vaccina* as Galloway (1986) did.

Pseudocyphellaria vaccina is a southern temperate-antiboreal species confined to forest habitats in southern South America (Fig. 2). It is primarily an epiphyte of Nothofagus pumilio, N. betuloides and N. antarctica. In the northern part of its distribution area, P. vaccina is an epiphyte of several other forest trees, such as Araucaria araucana, Drimys winteri and Nothofagus dombeyi. It prefers the trunks of old-growth forest trees, in areas where the field layer plant growth is below 1 m tall. Here, it also invades soil and even moss-covered rocks adjacent to the base of the trees and their spreading roots. It is not present in antiboreal heathlands and steppes east of the forest zones in south-eastern Patagonia and the northern part of Isla Grande.

SELECTED SPECIMENS EXAMINED: Chile. IX Region. Malleco, Lago Lleu-Lleu, 1973 Quilhot 0045 (UV). X Region. Valdivia, Lago Riñihue, Enco, 1940 Santesson 3569, 3665 (S); Lago Panguipulli, 1940 Santesson 3927 (S). XI Region. Aisén, Pto. Aisén, 1940 Santesson 4287, 6957 (S); Coihaique, Coihaique, 1940 Santesson 4434 (S). XII Region. Última Esperanza, Torres del Paine, 1995 Elvebakk 95: 142 (TROM); Magallanes, Punta Arenas, Punta Carrera, 1938 Kalela 301e (H); Fuerte Bulnes, 1992 Elvebakk 92: 016, 92:017, 92:028 (TROM); Tierra del Fuego, Río Bueno 1929 Roivainen 3, 19 (H); Puerto Yartou. Antártica Chilena, Isla Navarino, Puerto Navarino, 1940 Santesson 7394 (S). Argentina. Neuquen. Lago Espejo, 1937 Kalela 18h (H). Río Negro. Lago Nahuel Huapí, 1936 Donat 67 (H); Lago Mascardi 1937 Kalela 123b (H). Tierra del Fuego. Laguna Escondida, 1971 Imshaug 54663 & Ohlsson (H); Cerro Chenen, 1989 Stenroos 3719a (H).

Pseudocyphellaria endochrysa (Delise) Vainio

Res. Voy. S. Y. Belgica Bot. Lich.: 28. 1903. — Sticta endochrysa Delise, Mèm. Soc. Linn. Calvados 2: 43. 1825. — TYPE: [Falkland Islands] Isles Malouines. M. Gaudichaud s.n. (holotype PC-Lenormand; isotype PC-Hue). — For additional synonyms, see Galloway (1986).

The specimens from the South Atlantic islands and from treeless habitats in southern South America share many important characters. They have for instance the same type of apothecia and ascospores. They also have a bright vellow medulla, and the same thallus colour. The structure of the upper surface is variable within both groups, viz. from a non-scabrid, pubescent upper surface to a scabrid upper surface with few or no tomental hairs. When only looking at presence-absence of lichen substances, the two groups have an identical chemistry, except that the South Atlantic specimens occasionally contain 'isopseudocyphellarin'. However, the difference in the amount of pseudocyphellarin B is noteworthy, because it may indicate some genetic variation, and that the increased production of pseudocyphellarin B on the South Atlantic islands is a response to the harsher climate there. These two groups both correspond to Pseudocyphellaria endochrysa. The main reason why some of the specimens of P. endochrysa previously were identified as P. vaccina is certainly the presence of a scabrid upper surface and the lack of pubescence. However, as shown here, in exposed habitats also P. endochrysa gets a scabrid upper surface completely or partly without hairs, and therefore we do not consider these characters as good distinguishing features for separating the two species. Instead, we consider the thallus colour, the structure of the lobe margins (coriaceous in P. vaccina, more or less papery in P. endochrysa), the colour of the discs, the shape of ascospores, and the presence or absence of pseudocyphellarin B as the most important distinguishing features. The number of triterpenoids and the concentration of pseudocyphellarin A may prove useful as secondary distinguishing characters.

Pseudocyphellaria endochrysa has its main distribution area in the antiboreal zone (southern South America and the Falkland Islands) and the northern part of the antarctic zone (South Georgia) (Fig. 3). It is a terricolous species that is most common at higher altitudes in the open antiboreal deciduous forests where tree growth is slow, and at lower altitudes in *Chiliotrichum–Empetrum* heathlands. It thrives in open habitats with a rather low and discontinuous plant vegetation. It avoids the steppe zones

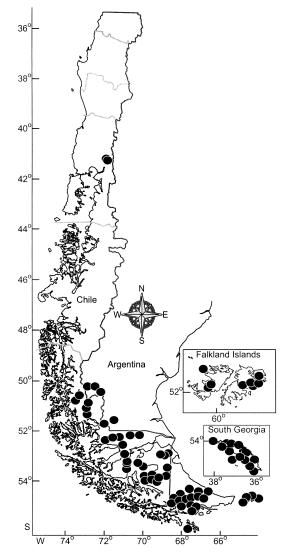


Fig. 3. Distribution of Pseudocyphellaria endochrysa.

east of *Chiliotrichum–Empetrum* heathlands, such as *Festuca gracillima–Stipa* steppes along the eastern part of the Strait of Magellan. From antiboreal rainforests, it was recorded from the forest margins close to the seashore, and only once from the forest floor. Galloway (1992) places its northern range at ca. 50°S. Its northern distribution range is here extended to 37° southern latitude. In Region X in Chile it grows at altitudes higher than 1000 m, in alpine habitats that appear climatically and compositionally similar to habitats at lower altitudes in southernmost South America. Thus, *P. endochrysa* is another

example of a lichen that is confined to high altitudes in southern Central Chile, and to low altitudes in southern Patagonia and Tierra del Fuego. Bjerke *et al.* (2003) listed other species with a similar distribution. On South Georgia, it is widespread and locally abundant, especially in the northern parts of the main island, and on Bird Island, and is found in a wide range of habitats (Lindsay 1974, Øvstedal & Smith 2001). Here, it often overgrows mosses, which remain closely attached to its lower surface. At several localities it is becoming rare due to the grazing and trampling by reindeer (Lindsay 1973).

SELECTED SPECIMENS EXAMINED: Chile. X Region. Llanquihue, Vicente Pérez Rosales, Portezuelo, 1975 Redon 0519 (UV, TROM), 0522 (UV). XII Region. Última Esperanza, Fiordo Peel, 1969 Imshaug 44404 & Ohlsson (H); Torres del Paine, 1998 Elvebakk 98:333 (TROM); Glaciar Serrano, Puerto Toro, 1998 Bjerke 231/98, 234b/98, 262/98 (TROM), 245/98 (UV); Magallanes: Cordillera Vidal, Cerro la Virgen, 1998 Domínguez 3, 10, 12, 13 (HIP); Cañadon Bombalot, 1998 Elvebakk 98:573 & Bjerke 212/98 (TROM); Punta Arenas Airport, Cordonier, 1974 Lanfranco 4, 5 (HIP); Tierra del Fuego, Porvenir, 1941 Santesson 5507 (S); Río Chico, 1986 Stenroos 2008 (H). Argentina. Tierra del Fuego. Ushuaia, 1902 Skottsberg s.n. [3 specimens] (S); Monte Martial, 1989 Ahti 47936 (H); Isla de los Estados, Cabo San Bartolome, 1971 Imshaug 53210 & Ohlsson (H, S); Isla Observatorio, 1971 Imshaug 50950 & Ohlsson (H); Isla Aferéz Goffre, 1971 Imshaug 51041 & Ohlsson (H). U.K. Falkland Islands. Port Stanley, Lechler 65a (S); Port Louis, 1902 Skottsberg s.n. (S); East Falkland, Carcass Bay, Darwin Harbour, 1968 Imshaug 40262 & Harris (H); East Falkland, Fish Creek, Goose Green, 1963 Corner 84 (AAS); West Falkland, Fox Bay, Kelp Pt., 1968 Imshaug 42270 & Harris (H). South Georgia. Cumberland Bay, Moraine Fiord, 1902 Skottsberg s.n. (S); Cumberland Bay, Brown Mountain, 1968 Greene 1507a (AAS); Rogged Bay, 1972 Lindsay 4432 (AAS); Prince Olaf Harbour Whaling Station, 1981, Smith 3104 (AAS); Holmestrand, Esmark Glacier, 1961 Greene 2712 (AAS); Gold Harbour, 1971 Lindsay 3583 (AAS); Bird Island, 2000 Smith 10734 (AAS).

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