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World survey of the genus *Lepraria* (*Stereocaulaceae*, lichenized Ascomycota)

Lauri SAAG, Andres SAAG and Tiina RANDLANE

Abstract: A comparative review of 57 *Lepraria* species and 2 varieties is provided together with species descriptions and a key. *Lecanora leuckertiana* is transferred to *Lepraria.* In addition some putative taxa by different authors are discussed.

Key words: taxonomy, new combination, sterile lichens, secondary substances, morphology

Introduction

The genus *Lepraria* Ach., with a worldwide distribution, comprises morphologically simple lichen-forming fungi that never develop fruiting bodies. Most species have a leprose thallus with the surface entirely composed of soredia (Laundon 1992; Tønsberg 1992), while a few taxa are squamulose or develop isidia-like structures (Tønsberg 2004; Wirth *et al.* 2004; Crespo *et al.* 2006). Their taxonomy is largely based on the chemistry of secondary metabolites as these lichens produce a wide variety of lichen substances, and other characters are often scarce.

The genus *Lepraria* was described by Acharius (1803) for various sterile sorediate lichens. It is a *nomen conservandum* after the proposal by Laundon (1963). The genus was placed in *Leprariaceae* in *Fungi Imperfecti* (Reichenbach 1841). Later it was regarded as belonging to *Ascomycota, incertae sedis* by several authors (e.g. Henssen & Jahns 1974; Kirk *et al.* 2001).

The modern treatment of this genus started when Laundon (1974, 1981) who transferred the bright-coloured species producing anthraquinones to *Caloplaca* Th. Fr. and *Leproplaca* (Nyl.) Nyl. ex Hue (a current synonym of *Caloplaca)* and species containing pulvinic acid derivatives to *Chrysothrix* Mont. The number of species in *Lepraria* was further reduced when taxa producing dibenzofuranes were placed in *Leproloma* Nyl. ex Cromb. (Laundon 1989; Leuckert & Kümmerling 1991). The concept of the genus was developed further by Laundon (1992) who also moved some species from *Crocynia* (Ach.) A. Massal. into *Lepraria*, and by Tønsberg (1992), Lohtander (1995) and Leuckert *et al.* (1995). *Lepraria lesdainii* was transferred to a new monotypic genus *Botryolepraria* Canals, Hern.-Mar., Gomez-Bolea & Llimona (Canals *et al.* 1997), while leprose, usnic acid-producing taxa were generally treated under *Lecanora* Ach. at that time. Later, *Leproloma* was synonymized with *Lepraria* by Kukwa (2002).

Ekman & Tønsberg (2002) first showed the monophyly of *Lepraria* in a molecular study. In addition, the former *Leproloma* species nested in *Lepraria* in their analysis and the clade showed affinities with *Stereocaulaceae.* However, three species, *L. flavescens, L. obtusatica* and *Botryolepraria lesdainii*, were positioned outside the genus in the analysis by Ekman & Tønsberg. Later, *L. flavescens* was transferred to *Lecanora* as *L. rouxii* S. Ekman & Tønsberg (Grube *et al.* 2004) but the position of *Lepraria obtusatica* remains unclear.

L. Saag, A. Saag and T. Randlane: University of Tartu, Institute of Ecology and Earth Sciences, Department of Botany, Lai st. 38, 51005, Tartu, Estonia. Email: lauri.saag@ut.ee

Sipman (2003, 2004) also included usnic acid-containing species in *Lepraria;* an example that was followed by other authors (Kukwa 2006*a*; Knudsen & Elix 2008).

Sterile crustose lichens have recently been rather intensely studied and the number of *Lepraria* species is constantly increasing. Since the year 2000, 35 taxa have been newly described (Orange 2001; Orange *et al.* 2001*b*; Aptroot 2002; Tønsberg 2002, 2004, 2007; Sipman 2003, 2004; Wirth *et al.* 2004; Bayerová *et al.* 2005; Orange & Wolseley 2005; Elix 2005, 2006*a*; Elix *et al.* 2005; Lendemer 2005; Crespo *et al.* 2006; Kantvilas & Kukwa 2006; Slavíková-Bayerová & Orange 2006; Tønsberg & Zhurbenko 2006; Flakus & Kukwa 2007; Knudsen & Elix 2007, 2008; Knudsen *et al.* 2007; Lendemer & Harris 2007; Saag *et al.* 2007; Slavíková-Bayerová & Fehrer 2007; Lendemer *et al.* 2008) and 6 species have been transferred to *Lepraria* from the genera, *Leproloma* and *Lecanora* (Kukwa 2002, 2006*a*; Sipman 2004). In this paper 57 *Lepraria* species and 2 varieties are included.

Today, the species concept is not uniform for different *Lepraria* species. Several chemotypes have been included in some species (e.g. *L. caesioalba, L. nivalis)*, while the presence or absence of a compound is considered to justify the taxonomic rank of species in many other cases. The practical chemotaxonomy can be obscured by 'mechanical hybrids' i.e. specimens consisting of mixed soredia from more than one species, that are not rare in the genus. Additionally, chemical similarities may not necessarily indicate close phylogenetic relationships, as the production of the compounds can be phylogenetically homoplasious (Ekman & Tønsberg 2002; Nelsen & Gargas 2008).

The purpose of this publication is to provide a comparative review of all 57 species and two varieties currently accepted in the genus in a standardized manner. We aim to summarize the present taxonomic situation, and hope the review will also be of practical help to lichenologists who are not specialists in *Lepraria* and the relatively rapid taxonomic changes in this genus.

Material and Methods

The current review is mainly based on literature, but in many cases also on original observations. Material from B, C, H, LD, NMW, PH, TU, TUR, UPS, and the private herbarium of Š. Slavíková was examined to refine the species descriptions. Morphology and anatomy were studied using a stereomicroscope (Olympus SZ40) equipped with additional objectives and a camera mounting kit. Thin layer chromatography (TLC) was carried out according to Orange *et al.* (2001*a*).

Some fatty acids that cannot be distinguished by TLC are reported as pairs, for instance 'roccellic/angardianic acid'. Stictic acid is usually accompanied by constictic and cryptostictic acids, while both pannaric acid 6-methylester and porphyrilic acid often occur together with related dibenzofurans (Elix & Tønsberg 2004). These complexes are referred to as 'stictic acid complex', 'pannaric acid 6-methylester and accessories', etc.

The Species

Lepraria Ach., nom. cons.

Methodus Lichenum: 3 (1803); type species: *Lepraria incana* (L.) Ach.

Thallus crustose to subfoliose or squamulose, with a powdery, granular, cottony, membranous or subsquamulose to subfoliose appearance; variously coloured, but not very bright, greyish, greenish and creamy hues prevalent; thin to thick, soft or hard; firmly or loosely attached to the substratum, sometimes parts of the thallus free from substratum, revealing lower surface; shape irregular or rosette-shaped (especially young thalli), individual thalli usually from few mm to 10 cm diam., thalli may fuse to form more or less continuous covers up to several metres diam.; margin diffuse or delimited, *lobes* absent or present, obscure to well-developed, mostly not wider than 2 mm, raised marginal rim may be present; cortex predominantly absent, but subcorticate areas may be present in a few species; *medulla* absent or present, thin to thick, sometimes soredia below the upper surface of sorediate thallus may be discoloured and/or poorly separated, forming a pseudomedulla; *hypothallus* absent or present, sometimes forming thick conspicous weft, white, grey or brown to black or orange in patches; *prothallus* rarely present; *areoles* sometimes present in thick specimens;

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marginal lobes can be squamulose; thallus surfaces without soredia sometimes present, medulla or hypothallus may be exposed or soredia may be poorly differentiated to form an almost smooth surface, or be distinguishable but not well separated from each other; *soredia* usually abundant, rarely absent, sometimes scarce on some parts of thallus or sparsely and evenly distributed throughout the thallus, often aggregated in consoredia; very fine to coarse, 10 μm to 1–3 mm diam., convex, ellipsoidal or irregular, loosely or densely packed; wall absent or present; hyphae projecting from soredia often present, very short (few μm) to very long (120 μm); *isidia-like structures* (large granules, warts or lobules) may be present, sometimes becoming sorediate. *Photobiont* trebouxioid green alga, most often *Asterochloris* (Hildreth & Ahmadjian 1981; Nelsen & Gargas 2006, 2008).

Ascomata and *conidiomata* absent.

Chemistry. Aliphatic acids, anthraquinones, benzyl esters, biphenyls, depsides, depsidones, dibenzofurans, terpenoids and usnic acids.

Ecology and *distribution*. On various substrata, most often bark, mosses and rock; most species prefer places sheltered from rain and shaded from direct sunlight, often with high humidity, but several taxa grow on exposed and/or dry surfaces. Worldwide; according to current knowledge the highest number of species is found in temperate areas.

Lepraria achariana Flakus & Kukwa

Lichenologist **39:** 464 (2007); type: Bolivia (KRAM-L—holotype).

Thallus leprose, powdery; margin diffuse, *lobes* absent; true *medulla* absent; *hypothallus* usually well-developed, lax, white or orange in places; *soredia* abundant, fine, up to 45 μm diam.; consoredia prevalent, up to 75(−150) μm diam. For more details see Flakus & Kukwa (2007).

Chemistry. Lecanoric acid, roccellic/angardianic acid ±, and 2–4 unidentified anthraquinones ± (2 of them major). K− or underside K+ purple in patches, C+ carmine red, KC+ red, PD− (Flakus & Kukwa 2007).

Ecology and distribution. On humus, terricolous mosses, and rocks. Found in open areas of high Andean Puna vegetation and upper montane cloud forest. South America (Bolivia).

Discussion. *Lepraria neojackii* sometimes has a very similar morphology but lacks lecanoric acid. Species that can produce lecanoric acid are discussed under *L. cupressicola*.

Lepraria adhaerens K. Knudsen, Elix & Lendemer

Opuscula Philolichenum **4:** 5 (2007); type: USA (UCR—holotype; ASU, CANB, PH, SD, UGDA—isotypes).

Thallus leprose, granular; margin diffuse, *lobes* absent; *medulla* absent, but older thalli forming a lower necral layer of gelatinized granules; *soredia* abundant, fine to medium, 40–100 μm diam., projecting hyphae absent, but frequently with thin colourless hyphae acting as anchors or rhizines; soredia clumped together. For further details see Knudsen *et al.* (2007).

Chemistry. Pannarin and zeorin (major to trace, very rarely absent) and trace accessories including norpannarin, dechloropannarin, hypopannarin and atranorin. K−, C−, KC−, Pd+ orange (Knudsen *et al.* 2007).

Ecology and distribution. On rocks (usually on mosses and lichens), rarely soil, in open habitats exposed to rain and sunlight, but in sheltered places in snowy areas. North America.

Discussion. The occurrence of small attaching hyphae and the tendency of granules to adhere to one another and the substratum is characteristic (Knudsen *et al.* 2007). Unstratified, diffuse thalli are found in several other species, but *L. santamonicae* (argopsin and norargopsin) is the most similar.

Lepraria alpina (B. de Lesd.) Tretiach & Baruffo var. alpina

in Baruffo *et al.*, *Nova Hedwigia* **83:** 395 (2006); type: USA (UPS—neotype; GZU, ASU—isoneotypes; distributed in Weber, *Lichenes exsiccati*, distr. by the Univ. of Colorado, Fasc. 16: no. 609).

Crocynia alpina B. de Lesd., *Bull. Soc. Bot. France* **61:** 85 (1914).

Lepraria angardiana Øvstedal, *Nova Hedwigia* **37:** 687 (1983).

Lepraria caerulescens (Hue) Botnen & Øvstedal, *Polar Research* **6:** 130 (1988).

Leproloma cacuminum sensu J.R. Laundon, *Lichenologist* **24:** 345 (1992).—*Lepraria cacuminum sensu* Loht. *Ann. Bot. Fennici* **32:** 52 (1995)—non *Diploicia cacuminum* A. Massal., *Symm. Lich. Nov.:* 52 (1855).

Thallus leprose, granular; margin usually delimited, *lobes* sometimes present, minute, often obscure, without raised rims; *medulla* usually present, not conspicuous, white; *hypothallus* sometimes present, poorly developed; *soredia* abundant, coarse or variably sized, typically 100–150 μm diam., projecting hyphae sometimes present, short; consoredia present from few to abundant, typically 200–300 μm. For further details see Lohtander (1995), Baruffo *et al.* (2006) and Saag *et al.* (2007).

Chemistry. Atranorin, porphyrilic acid and a fatty acid (roccellic/angardianic or rarely rangiformic acid); very rarely fatty acids and/or atranorin can be absent (Leuckert *et al.* 1995; Saag *et al.* 2007), or another, unidentified fatty acid present (Flakus & Kukwa 2007). K− or + yellow, C−, KC− or + yellow, Pd− or + yellow.

Ecology and distribution. On rock and saxicolous mosses, also on soil, lichens and rarely bark; mostly acidic substrata; usually exposed but also in shaded places, mostly cool climate.

Europe, North and South America, Antarctica, Greenland.

Discussion. According to molecular studies, *L. alpina* belongs to a monophyletic '*L. neglecta* group' together with *L. atlantica, L. borealis, L. caesioalba, L. elobata, L. granulata, L. humida* and *L. neglecta* (Ekman & Tønsberg 2002; Slavílová-Bayerová & Fehrer 2007). Morphologically similar species with a coarsely granular appearance include *L. borealis, L. caesioalba, L. granulata* and *L. neglecta*, but these taxa differ chemically. The chemotype with angardianic/roccellic acid only was included in *L. alpina* (sub. nomine *L. cacuminum)* by Lohtander (1994, 1995), but in *L. borealis* by Kukwa (2006*b*); specimens with atranorin only or fatty acids only were placed in *L. borealis* by Saag *et al.* (2007). Thus specimens with a deficient chemistry can be identified as either *L. alpina* or *L. borealis* as there are no distinctive morphological differences between these two species (Prigodina-Lukošienë *et al.* 2003; Kukwa 2006*b*; see also Lohtander 1995). *Lepraria atlantica* has a similar chemistry but is usually powdery to cottony, and is only very rarely morphologically similar to *L. alpina* (Saag *et al.* 2007).

Lepraria alpina var. zeorinica L. Saag

Mycotaxon **102:** 68 (2007); type: Greenland (C—holotype, TU—isotype).

Thallus and *chemistry* as *L. alpina* var. *alpina*, but also produces zeorin. K− or + yellow, C−, KC− or + yellow, Pd− or + yellow.

Ecoloy and distribution. On soil and mosses, and sometimes lichens. Greenland.

Lepraria atlantica Orange

Lichenologist **33:** 462 (2001); type: Ireland (NMW—holotype, BG—isotype).

Thallus leprose, powdery; margin diffuse or delimited, *lobes* absent; true *medulla* absent; *hypothallus* present in patches, of usually sparse, white to dull orange hyphae; *soredia* abundant, fine to rarely coarse, 40–100 (160–220) μm diam., projecting hyphae rarely present, short; consoredia rare. For further details see Orange (2001), Slavíková-Bayerová & Orange (2006) and Saag *et al.* (2007).

Chemistry. The two common chemotypes contain (1) atranorin, porphyrilic acid and

accessories, rangiformic acid; (2) atranorin, porphyrilic acid and accessories, roccellic/angardianic acid. In addition, rare chemotypes have been reported with (3) porphyrilic acid and accessories only and (4) both fatty acids (rangiformic and roccellic/angardianic acids) besides atranorin and porphyrilic acid. The subthalline hyphae usually produce unidentified anthraquinones (Orange 2001; Slavíková-Bayerová & Orange 2006; Saag *et al.* 2007). K+ yellow, C−, Pd− or + yellow.

Ecology and distribution. On siliceous rock (also on mosses), sometimes on soil and rarely bark; sheltered from rain. Europe, Australia, Greenland.

Discussion. According to molecular studies, *L. atlantica* belongs to the monophyletic '*L. neglecta* group' (Ekman & Tønsberg 2002; Slavíková-Bayerová & Fehrer 2007; see also the discussion under *L. alpina*). Fehrer *et al.* (2008) used a narrower definition of the '*L. neglecta* group' and distinguished the '*L. atlantica* group' including *L. atlantica*, *L. humida* and *L.* sp. H (discussed under *L. humida)*. Other morphologically similar species are mentioned under *L. jackii*. *Lepraria atlantica* is chemically and morphologically rather similar to *L. neojackii*, which is described as having fine soredia only, and containing both roccellic/angardianic and rangiformic acids together but no atranorin (Flakus & Kukwa 2007). See also the discussion under *L. jackii*. *Lepraria atlantica* is also chemically very similar to *L. alpina* (discussed under *L. alpina* var. *alpina*).

Lepraria aurescens Orange & Wolseley

Lichenologist **37:** 247 (2005); type: Thailand (BM—holotype).

Thallus leprose, powdery; margin usually diffuse, rim absent, *lobes* absent; *medulla* absent; *hypothallus* present in places, brown, well developed, lax; *soredia* abundant to sparse in few places, fine to medium, 40–100 µm diam., projecting hyphae usually absent, but present on marginal or solitary granules, long, downward, mostly dark. For more details see Orange & Wolseley (2005).

Chemistry. Thamnolic acid (Orange & Wolseley 2005). K+ bright yellow, C−, KC−, Pd+ orange-yellow.

Ecology and distribution. On bark; in sheltered places in dry forest. Asia (Thailand).

Discussion. Lepraria yunnaniana also has fine granules and a dark loose hypothallus, but produces divaricatic acid. *Lepraria cupressicola* develops a dark hypothallus but the thallus is blue-grey and has lobes, and it contains lecanoric acid, zeorin and atranorin.

Species producing thamnolic acid include *L. aurescens* (usually thin pale grey to yellowish thallus with a brown well-developed hypothallus and a diffuse margin), *L. nylanderiana* (usually thick whitish thallus with a well-developed greyish hypothallus and a delimited margin, contains roccellic acid), *L. pulchra* (thin whitish to pale bluish grey thallus with a whitish medulla, delimited margin with a rim, and characteristic very short projecting hyphae on the soredia) and *L. umbricola* (usually thin green thallus with diffuse margin and no medulla or hypothallus).

Lepraria bergensis Tønsberg

Graphis Scripta **14:** 47 (2002); type: Norway (BG—holotype; B, H, NMW—isotypes).

Thallus leprose, membranous; margin usually delimited, sharply raised (in saxicolous specimens), *lobes* usually distinct, up to a few mm wide; *medulla* distinct in places, white; *hypothallus* absent or orange-brown to brown, inconspicuous, hyphae below thallus orange-brown to brown or colourless; lower surface present, white (at least along margin), pale yellowish or brown; *soredia* abundant, very fine, up to 25 µm diam., projecting hyphae present or absent, short; consoredia abundant, up to 200 (−340) µm. For more details see Tønsberg (2002).

Chemistry. Atranorin, rangiformic acid, norrangiformic acid (trace), fragilin,

7-chloroemodin, emodin, parietin and A01-anthrone; the anthraquinones are located mostly in the subthalline hyphae. K+ faint yellow, subthalline hyphae K+ purple (in patches), C−, Pd− (Tønsberg 2002).

Ecology and distribution. On siliceous rock (also on mosses); on shaded surfaces. Europe – Norway, Great Britain, Germany (Spribille & Tønsberg 2007).

Discussion. The phylogenetic placement of this and other taxa with distinct lobes are mentioned under *L. membranacea*. Morphologically the most similar species include *L. membranacea* (pannaric acid), *L. normandinoides* (usually protocetraric acid and/or fumarprotocetraric acid in addition to roccellic acid and atranorin) and *L. sipmaniana* (pannaric acid 6-methylester and usually also anthraquinones). Anthraquinone producing species apart from *L. bergensis* and *L. sipmaniana* include *L. goughensis* (obscure minute lobes, lecanoric acid) and non-lobate *L. atlantica* (porphyrilic acid), *L. incana* chemotype 2 (divaricatic acid) and *L. humida* (atranorin and fatty acids).

Lepraria borealis Loht. & Tønsberg

in Lohtander, *Ann. Bot. Fennici* **31:** 224 (1994); type: Norway (BG—holotype, H—isotype).

Thallus leprose, granular; margin usually delimited, sometimes diffuse, obscure minute *lobes* sometimes present, without raised rim; *medulla* sometimes present, inconspicuous, white; *hypothallus* usually absent; *soredia* abundant, coarse or variably sized, typically 100–200 μm diam., projecting hyphae often present, usually short; consoredia sometimes present, typically 200–300 μm, sometimes larger. For further details see the references below.

Chemistry. The commonest chemotype (1) comprises atranorin, rangiformic and ± norrangiformic acid; rarely in (2) rangiformic acid is replaced by roccellic/angardianic acid or in (3) both fatty acids are present (Lohtander 1994; Tønsberg 2004; Kukwa 2006*b* and others). Saag *et al.* (2007) tentatively also included specimens with fatty acids only (4) and atranorin only (5). K− or + faint yellow, C−, KC−, Pd−.

Ecology and distribution. On acidic rock (also on mosses), rarely on soil and lichens; mostly exposed but also shaded places, mostly cool climate. Europe, North America, Antarctica, Greenland.

Discussion. See the discussion under *L. alpina*.

Lepraria caesiella R.C. Harris

in Lendemer, *Opuscula Philolichenum* **2:** 51 (2005); type: USA (NY— holotype; isotypes distributed as *Lichens of Eastern North America Exsiccati*, no. 172).

Thallus leprose, powdery; margin diffuse to poorly delimited, *lobes* absent; *medulla* absent; *hypothallus* absent; *soredia* abundant, very fine, 20–30 μm diam., projecting hyphae present, short, 25–30 μm; consoredia present, up to 100 μm diam. For more details see Lendemer (2005).

Chemistry. Atranorin and zeorin (Lendemer 2005). K− or + faint yellow, C−, KC−, Pd−. Saag *et al.* (2007) and Flakus & Kukwa (2007) included a few specimens with atranorin, zeorin and roccellic/angardianic acid or an unidentified fatty acid.

Ecology and distribution. On bark, rarely on rock, lignum, soil and mosses. North America, South America (Chile), Greenland.

Discussion. Lepraria caesiella was previously known as ''*Lepraria* sp. 3'' from North America (Harris 1977). Morphologically similar species include *L. incana* (divaricatic acid) and *L. elobata* (stictic acid complex). *Lepraria pallida* also contains atranorin and zeorin but always produces fatty acid(s) and possesses lobes; *L. jackii* s. lat. has been reported to contain zeorin as a rare accessory (Leuckert *et al.* 1995; Baruffo *et al.* 2006). Lendemer (2005) referred to an undescribed species that also produces atranorin and zeorin.

Lepraria caesioalba (B. de Lesd.) J. R. Laundon var. caesioalba

Lichenologist **24:** 324 (1992).—*Crocynia caesioalba* B. de Lesd., *Bull. Soc. Bot. France* **61:** 84 (1914); type: France (E—holotype; BM, GL, PC—topotypes).

Thallus leprose, granular; margin usually delimited, sometimes diffuse, obscure minute *lobes* sometimes present, without raised rims; *medulla* present, inconspicuous, white; *hypothallus* usually absent; rarely small patches with exposed medulla present; *soredia* abundant, coarse or variably sized, typically 100–150(−200) µm diam., projecting hyphae sometimes present, usually short; consoredia frequent, typically 200–300 µm. For further details see Laundon (1992), Lohtander (1994), Saag *et al*. (2007).

Chemistry. This species comprises several chemotypes, e.g. Leuckert *et al*. (1995) distinguished three and Tønsberg (2004) five. In this paper, the classification of Leuckert *et al.* (1995), with additions, is followed, and specimens containing only atranorin and fatty acid(s) without depsidones are placed in *L. borealis* as described by Lohtander (1994) and Prigodina-Lukošienë *et al*. (2003). Tønsberg (2004) recognized such specimens as an additional chemotype of *L. caesioalba.* Chemotype (1): atranorin, fumarprotocetraric acid, protocetraric acid ± (in variable amounts), roccellic/angardianic or rangiformic acid; rare modifications of this chemotype include 1a) both fatty acids, 1b) no fatty acids, 1c) no fumarprotocetraric acid, protocetraric acid present and 1d) no atranorin. K− or + yellow, C−, KC−or + faint yellow, Pd+ orange. Chemotype (2): atranorin, stictic acid plus constictic and cryptostictic acids (in variable amounts, mostly minor), rangiformic or roccellic/angardianic acid; rare modifications include 2a) both fatty acids and 2b) no fatty acids. K− or + yellow, C−, KC− or + faint yellow, Pd+ orange. Chemotype (3): atranorin, psoromic acid, roccellic/angardianic or rangiformic acid. K− or + yellow, C+ red, KC−, Pd+ sulphur yellow. Chemotype (1) is the most frequent, (2) common and (3) is rare, but still widespread.

Ecology and distribution. On acidic rock (usually on mosses) and soil, rarely on bark, epiphytic mosses and lichens; in exposed places, mostly cool climate, montane-alpine in tropics. Europe, North and South America, Asia, Australasia, Antarctica, Greenland.

Discussion. The phylogenetic placement of this and morphologically similar species is discussed under *L. alpina*. *Lepraria caesioalba* is not monophyletic (Ekman & Tønsberg 2002; Slavíková-Bayerová & Fehrer 2007), but no nomenclatural segregation has been proposed.

Species producing stictic acid and atranorin include *L. caesioalba* (granular *L. neglecta*-type thallus), *L. elobata* (thin greenish thallus of relatively compact soredia, no medulla or lobes, contains zeorin), *L. leprolomopsis* (thick whitish thallus with medulla, no lobes, even lower surface, an unknown terpenoid), *L. lobificans* (greenish loosely packed soredia with long projecting hyphae, well-developed medulla, contains zeorin), *L. multiacida* (stictic acid complex mostly in traces, also salazinic acid and strepsilin derivates in minor to trace amounts and usually zeorin plus 1–2 unknown terpenoids), *L. nivalis* (some chemotypes; thick whitish thallus with medulla, no terpenoids), *L. santosii* (some chemotypes; membranous to granular thallus with well-developed lobes and marginal rim) and *L.* sp. 2 *sensu* Flakus & Kukwa (for this taxon, see Flakus & Kukwa 2007).

The species that may contain protocetraric and/or fumarprotocetraric acids include *L. caesioalba* (granular *L. neglecta*-type thallus), *L. eburnea* (alectorialic acid, usually soft powdery to cottony thallus), *L. friabilis* (thin finely powdery thallus, often of only sparse soredia), *L. isidiata* and *L. santosii* (lobes with thick raised marginal rims and coarse, more or less isidia-like structures, discussed under *L. isidiata*), *L. lanata* (characteristic very large consoredia surrounded by woolly anastomosing hyphae), *L. nivalis* (thick whitish thallus with medulla, may be similar to *L. eburnea* but lacks alectorialic acid), *L. normandinoides* (dark thick hyphae on the lower side, lobes usually wide), *L. squamatica*

(contains squamatic acid, protocetraric acid trace accessory), *L. toilenae* (malonprotocetraric acid, thick light hypothallus).

Lepraria caesioalba var. groenlandica L. Saag

Saag *et al. Mycotaxon* **102:** 73 (2007); type: Greenland (C—holotype; TU—isotype).

Thallus identical to the main variety. For more details see Saag *et al.* (2007).

Chemistry. Atranorin, stictic acid complex, zeorin (in variable amounts), roccellic/angardianic acid; rarely roccellic/angardianic acid is replaced by rangiformic acid, or fatty acids are absent.

Ecology and distribution. On soil and mosses, sometimes on lichens, rarely on rocks. Greenland.

Discussion. Chemically similar to *L. elobata*, which differs in its thin powdery thallus composed of mostly fine soredia, rare consoredia and diffuse thallus margin.

Lepraria celata Š. Slavíková

in Slavíková & Orange *Lichenologist* **38:** 504 (2006); type: Ukraine (PRA— holotype; BG, NMW—isotypes; GenBank accession no. DQ401100).

Thallus leprose, powdery; margin diffuse or delimited, *lobes* absent; true *medulla* absent; *hypothallus* of sparse patches of white hyphae; *prothallus* absent; *soredia* abundant, fine, (20−)35–50(−60) µm diam., projecting hyphae rarely present, short. For further details see Slavíková-Bayerová & Orange (2006).

Chemistry. Atranorin ± (major to minor) and roccellic/angardianic acid (Slavíková-Bayerová & Orange 2006). K− or + faint yellowish, C−, Pd−.

Ecology and distribution. Terricolous (soil and debris) and on mosses; open habitats, often in rock cervices. Europe (Bulgaria and Ukraine), montane; probably wider.

Discussion. According to molecular studies, *L. celata* is a distinct monophyletic taxon (Fehrer *et al.* 2008). Morphologically similar species are mentioned under *L. jackii.* Chemically similar taxa include *L. borealis* (granular thallus), *L. jackii* s. lat. (discussed under *L. jackii*) and *L. normandinoides* (lobes, usually contains protocetraric or fumarprotocetraric acid).

Lepraria coriensis (Hue) Sipman

Herzogia **17:** 28 (2004).—*Crocynia coriensis* Hue, *Bull. Soc. Bot. France* **71:** 386 (1924); type: South Korea (KYO—isotype).

Thallus leprose, powdery to membranous; margin delimited, *lobes* present, obscure or more often well-developed (0·5–2 mm wide) and with raised marginal rim; *medulla* usually present, thin to medium, white; *hypothallus* sometimes present, thin, brown to black; sometimes soredia sparse in places, exposing smooth ecorticate surface especially near margins; *soredia* fine to coarse, up to 300 µm diam., projecting hyphae usually absent. For more details see Laundon (2003) and Sipman (2004).

Chemistry. Three chemotypes were distinguished by Elix (2006*b*): (1) usnic acid, zeorin, protodehydroconstipatic and constipatic acids (major to minor), isousnic acid ± (minor to trace), and atranorin ± (trace); (2) usnic acid, zeorin, protodehydroconstipatic and constipatic acids (minor to trace), argopsin (minor), norargopsin (minor to trace), isousnic acid ± (minor to trace) and atranorin ± (minor to trace); and (3) usnic acid, zeorin, protodehydroconstipatic and constipatic acids (minor to trace), caloploicin (minor), fulgidin (minor to trace), isousnic acid ± (minor to trace) and atranorin ± (trace). The third chemotype was considered rare. Laundon (2003) reported that rarely zeorin can be missing. K−, C−, KC−, Pd−.

Ecology and distribution. On rock (mostly siliceous), wood, bark, mosses and soil; shaded and sheltered places. Asia (India, South Korea), Australia; tropical to subtropical.

Discussion. Some authors have doubted the distinctiveness of *L. usnica* from *L. coriensis* (Orange & Wolseley 2005), however, chemical differences between these taxa were shown by Elix (2006*b*). In a molecular study Nelsen *et al.* (2008, in press) confirmed that *L. coriensis* and *L. usnica* are distinct species distant from one another and do not belong to *Lepraria*. *Lepraria coriensis* had an uncertain position outside *Lecanorales* in their analysis, while the placement of *L. usnica* in *Pilocarpaceae* (*Lecanorales*) was well-supported.

Other lobate species are discussed under *L. membranacea* and *L. bergensis*. *Lepraria santamonicae* also produces argopsin, but it has no medulla or lobes, does not contain usnic acid, and argopsin is produced in large amounts.

Species producing usnic acid and usually zeorin include *L. coriensis* (usually well-developed lobes with a marginal rim, protodehydroconstipatic and constipatic acids), *L. usnica* (usually small lobes without a marginal rim and minor amounts of contortin), *L. ecorticata* (no lobes, predominantly no medulla, soredia regular and convex, well-separated from each other), *L. leuckertiana* (obscurely and minutely lobed, cottony thallus with thick medulla, soredia not well-separated from one another), *L. straminea* (granular, granules corticate, no lobes), *L. texta* (sometimes obscurely and minutely lobed, powdery thallus with hypothallus, some soredia not well-separated).

Lepraria crassissima (Hue) Lettau

Feddes Repert. **61:** 125 (1958).—*Crocynia crassissima* Hue, *Bull. Soc. Bot. France* **71:** 393 (1924); type: France (B—isotype).

Thallus leprose, membranous to cottony; margin usually delimited, *lobes* sometimes present, poorly defined; *medulla* present, very thick, white; lower surface distinct, folded (if whole thallus folded), smooth to tomentose, white to brownish; often eroded patches with exposed medulla on older specimens; *soredia* abundant, mostly coarse, up to 300(−400) µm diam., projecting hyphae present, short to long; large granules or warts slightly resembling isidia but lacking cortex may be present in well-developed thalli, may become sorediate. For more details see van den Boom *et al.* (1994).

Chemistry. Divaricatic acid, nordivaricatic acid (major, rarely trace), zeorin ± (major to minor) (Laundon 1992; Tønsberg 1992; van den Boom *et al.* 1994). K−, C+ rose-red, KC−, Pd−.

Ecology and distribution. On siliceous rock and epilithic mosses, also sometimes on bark or calcareous rock; shaded, humid. Europe, Australia.

Discussion. Species producing divaricatic acid and zeorin include *L. crassissima* (thallus membranous to cottony, thick white medulla, nordivaricatic acid usually major), *L. incana* (thallus powdery, nordivaricatic acid ± trace) and *L. yunnaniana* (thallus cottony, dominant dark hypothallus, nordivaricatic acid ± trace). In addition, Baruffo *et al.* (2006) reported divaricatic acid as a very rare accessory in *L. rigidula* (lax cottony thallus, very long projecting soredial hyphae, atranorin and nephrosteranic acid).

Lepraria multiacida, *L. lobificans*, and sometimes *L. nivalis* and *L. vouauxii*, may be morphologically similar, but differ in their chemistry and spot reactions (see descriptions of these species). *Lepraria isidiata* was historically described as a variety of *L. crassissima*, but today it is defined as differing in chemistry, morphology and ecology (see under *L. isidiata*). *Lepraria crassissima* was synonomized with *L. incana* by Kümmerling *et al.* (1991) and Leuckert *et al.* (1995), but was shown to be a distinct species by van den Boom *et al.* (1994) and Ekman & Tønsberg (2002). Other species producing isidia-like structures are mentioned under *L. isidiata*.

Lepraria cupressicola (Hue) J. R. Laundon

Lichenologist **40:** 412 (2008).—*Crocynia cupressicola* Hue, *Bull. Soc. Bot. France* **71:** 395 (1924); type: Japan (KYO—holotype).

Lepraria atrotomentosa Orange & Wolseley, *Biblioth. Lichenol.* **78:** 328 (2001); type: Sri Lanka (BM—holotype, PDA—isotype).

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Thallus leprose, powdery to membranous; margin delimited, *lobes* absent or present, sometimes well-developed, 0·5-2 mm wide, with raised marginal rim, sometimes irregular and less than 0·5 mm wide, without a rim; *medulla* present, thin, white; *hypothallus* usually thick, sometimes thin, lax, dark brown, forms a tomentum under lobes; *soredia* abundant to sparse in places, fine to medium, sometimes coarse, 60–200 µm diam., projecting hyphae rarely present, short. For further details see Orange *et al.* (2001*b*) and Sipman (2004).

Chemistry. Lecanoric acid, atranorin, zeorin and unidentified fatty acids (Orange *et al.* 2001*b*; Sipman 2004). K+ yellowish, C+ pink to red, KC+ more or less red, Pd+ yellow.

Ecology and distribution. On siliceous rock or soil and bark; shaded, sheltered, damp. Japan, China (Hong Kong), Taiwan, Sri Lanka.

Discussion. Other lobate species are discussed under *L. membranacea* and *L. bergensis*. Non-lobed specimens of *L. cupressicola* may resemble *L. incana* in appearance but *L. cupressicola* has a dark tomentum below the thallus and a different chemistry. A similar dark tomentum is also present in *L. yunnaniana* (divaricatic acid) and *L. aurescens* (thamnolic acid, tomentum less extensive).

Species that can produce lecanoric acid include *L. achariana* (stratified thallus with fine soredia and a diffuse margin, roccellic acid ±), *L. cupressicola* (dark tomentose hypothallus, atranorin and zeorin), *L. goughensis* (very fine soredia, no hypothallus, gyrophoric acid and strepsilin in minor to trace amounts), *L. impossibilis* (pannaric acid 6-methylester) and *L. lecanorica* (usually thick thallus, no dark hypothallus).

Lepraria diffusa (J. R. Laundon) Kukwa

Ann. Bot. Fennici **39:** 226 (2002).—*Leproloma diffusum* J. R. Laundon, *Lichenologist* **21:** 16 (1989); type: Finland (BM—holotype).

Lepraria diffusa var. *chrysodetoides* (J. R. Laundon) Kukwa, *Ann. Bot. Fennici* **39:** 226 (2002).—*Leproloma diffusum* var. *chrysodetoides* J. R. Laundon, *Lichenologist* **21:** 18 (1989).

Thallus leprose, powdery to cottony; margin diffuse, rarely delimited, *lobes* absent; *medulla* present, usually thick, sometimes thin, white; *hypothallus* sometimes present, weakly developed, whitish grey to brownish; medulla exposed but only in small patches or fissures, *soredia* abundant, coarse, up to 100 µm diam., projecting hyphae sometimes present, short. For more details see Laundon (1992) and Kukwa (2006*b*).

Chemistry. 4-oxypannaric acid 2-methylester; accessories are 4-oxypannaric acid (minor to trace), pannaric acid methylester, pannaric acid 2-methylester, pannaric acid and other dibenzofurans (traces) (Elix & Tønsberg 2004); rarely also atranorin and/or roccellic acid or very rarely rangiformic acid (Baruffo *et al.* 2006). K− or + yellow slowly becoming orange, C− or + yellow, KC− or + yellow, Pd+ reddish orange.

Ecology and distribution. On calcareous rock (often on mosses), rarely on bark or soil; mostly in shaded and sheltered places. Europe, North America, Asia.

Discussion. Lepraria diffusa var. *chrysodetoides* was subsumed within var. *diffusa* by Kukwa (2006*b*). *Lepraria eburnea* and *L. lobificans* and to a lesser extent also *L. leprolomopsis*, *L. nivalis* and *L. nylanderiana* may have a similar morphology but do not produce dibenzofurans. *Lepraria vouauxii* produces dibenzofurans and is sometimes also morphologically similar, but *L. diffusa* is more powdery, with less or no patches of exposed medulla and the diagnostic substance is different.

Lepraria eburnea J. R. Laundon

Lichenologist **24:** 331 (1992); type: United Kingdom (BM—holotype).

Lepraria frigida J. R. Laundon, *Lichenologist* **24:** 332 (1992).

Thallus leprose, powdery to cottony; margin diffuse, rarely delimited, *lobes* usually absent; *medulla* usually present, mostly thick, white; *hypothallus* usually not distinct; thallus surfaces without soredia often present, also

soredia often embedded in a hyphal weft; *soredia* abundant, mostly fine, up to 60 µm diam., projecting hyphae usually present, short to long (to 100 µm); consoredia present, up to 200(−400) µm. For further details see Orange (1997).

Chemistry. Orange (1997) distinguished 3 chemotypes: (1) alectorialic acid, protocetraric acid; (2) alectorialic acid, psoromic acid, 2'-*O*-demethylpsoromic acid; and (3) alectorialic acid only; accessories reported by other authors include barbatolic acid and other satellites of alectorialic acid (e.g. 5,7-dihydroxy-6-methylphthalide) and very rarely atranorin (all major to trace, Laundon 1992; Baruffo *et al.* 2006) or roccellic/angardianic acid (Saag *et al.* 2007). K− or + yellow, C− or + reddish orange, KC+ pink or reddish orange, Pd+ lemon yellow or orange.

Ecology and distribution. Substratum indifferent; on mosses, bark, wood, rock, soil and lichens. Europe, North America, Australasia, Greenland.

Discussion. Lepraria frigida was synonymized with *L. eburnea* by Orange (1997) who showed chemical and morphological continuity between these taxa. Other morphologically similar species are discussed under *L. leprolomopsis*, and the species producing protocetraric and/or fumarprotocetraric acids under *L. caesioalba* (none of them produces alectorialic acid).

Species producing alectorialic acid include *L. eburnea* (soft thallus, see chemistry above), *L. gelida* (usually soft thallus, porphyrilic acid) and *L. neglecta* (granular thallus, ± fatty acids and atranorin).

Lepraria ecorticata (J. R. Laundon) Kukwa

Mycotaxon **97:** 64 (2006).—*Lecanora ecorticata* J. R. Laundon, *Nova Hedwigia* **76:** 100 (2003); type: United Kingdom (BM—holotype).

Thallus leprose, powdery; margin diffuse, *lobes* absent; *medulla* rarely present in places, weakly developed; *soredia* abundant, mostly fine to medium, 10–100 µm diam., well separated from each other. For further details see Laundon (2003) and Kukwa (2006*a*).

Chemistry. Usnic acid, zeorin ±, atranorin (in variable amounts) and unidentified terpenoids ±. Laundon (2003) reported that rarely zeorin can be missing and/or unidentified fatty acids present; Flakus & Kukwa (2007) detected porphyrilic acid in a few specimens. K± faint yellow, C−, KC−, Pd−.

Ecology and distribution. On siliceous rock (also on mosses) and sometimes on lichens; in mostly shaded and sheltered places. Europe, North America, South America, Asia (China).

Discussion. Taxa containing usnic acid and zeorin are compared under *L. coriensis.*

Lepraria elobata Tønsberg

Sommerfeltia **14:** 197 (1992); type: Norway (BG—holotype).

Thallus leprose, powdery; margin diffuse, *lobes* predominantly absent; *medulla* predominantly absent; *hypothallus* absent; *soredia* abundant, mostly fine, 20–45 µm diam., projecting hyphae absent, soredia well separated from one another; consoredia sometimes present, up to 100 µm. For more details see Tønsberg (1992).

Chemistry. Atranorin, stictic acid, constictic acid, cryptostictic acid, zeorin and very rarely an unidentified fatty acid (major to trace) (Tønsberg 1992, 2004 and others). K− or + yellow, C−, KC−, Pd+ orange.

Ecology and distribution. On bark, sometimes soil, wood, siliceous rock and mosses; in shady, humid places. Europe, North America, Greenland.

Discussion. The phylogenetic placement is recorded under *L. alpina. Lepraria lobificans* (cottony appearance) and the rare *L. caesioalba* var. *groenlandica* (granular thallus) have similar chemistry to *L. elobata.* Morphologically, *L. caesiella* (atranorin and zeorin) and

L. incana (divaricatic acid and zeorin) may be similar to *L. elobata;* further morphologically similar species are mentioned under *L. jackii.* Species producing stictic acid complex are compared under *L. caesioalba.*

Lepraria friabilis Lendemer, K. Knudsen & Elix

Opuscula Philolichenum **5:** 64 (2008); type: USA (NY— holotype; B, CANB, UCR, UDGA, hb. Lendemer— isotypes).

Thallus leprose, powdery; margin diffuse, *lobes* absent; *medulla* absent; *hypothallus* present, thin, colourless, inconspicuous; *soredia* sparse to abundant, very fine, (10−)20–30 µm diam., projecting hyphae usually present, short; consoredia present, up to 60 µm. For more details see Lendemer *et al.* (2008).

Chemistry. Two chemotypes: (1) fumarprotocetraric acid with minor amounts of protocetraric, succinprotocetraric and confumarprotocetraric acids; and (2) fumarprotocetraric acid only. Both chemotypes K−, C−, KC−, Pd+ orange or red (Lendemer *et al.* 2008).

Ecology and distribution. On bark of conifers; in humid habitats. Southern North America.

Discussion. Morphologically the most similar species is *L. caesiella* (thinner thallus, slightly smaller soredia, atranorin and zeorin). Species that may contain protocetraric and/or fumarprotocetraric acids are discussed under *L. caesioalba.*

Lepraria gelida Tønsberg & Zhurb.

Graphis Scripta, **18:** 64 (2006); type: Svalbard (BG— holotype; NMW— isotype).

Thallus leprose, powdery to cottony; margin diffuse to delimited, *lobes* usually absent; *medulla* present, thick, rarely thin, white; thallus surfaces without soredia present, can be relatively large, medulla exposed; *soredia* abundant to sparse in places, variable in size, mostly 65–100(−200) µm diam., projecting hyphae present, short to medium. For more details see Tønsberg & Zhurbenko (2006) and Saag *et al.* (2007).

Chemistry. Alectorialic and porphyrilic acids. K+ yellow or orange, C−, KC+ red, Pd+ yellow or orange (Tønsberg & Zhurbenko 2006; Saag *et al.* 2007).

Ecology and distribution. On soil, mosses and sometimes lichens, rarely bark; in open habitats. Greenland, Svalbard and the Russian Arctic islands near the Taimyr peninsula (Tønsberg & Zhurbenko 2006; Saag *et al.* 2007).

Discussion. Species producing alectorialic acid are compared under *L. eburnea.* Porphyrilic acid is also produced by *L. alpina, L. atlantica* and *L. neojackii*, which never contain alectorialic acid. *Lepraria vouauxii* is often morphologically quite similar but produces pannaric acid 6-methylester and atranorin.

Lepraria goughensis Elix & Øvstedal

Mycotaxon **93:** 274 (2005); type: Gough Island (BG— holotype).

Thallus leprose, powdery; margin delimited, usually poorly defined *lobes* present; *medulla* absent; *hypothallus* absent; *soredia* abundant, very fine, 20–26 µm diam., projecting hyphae present, numerous. For further details see Elix *et al.* (2005).

Chemistry. Lecanoric acid, gyrophoric acid (minor to trace), strepsilin (minor to trace), fragilin (trace), 7-chloroemodin (trace), flavo-obscurin C (trace). K−, C+ red, KC+ red, Pd–(Elix *et al.* 2005).

Ecology and distribution. On mosses and debris, peat; in shady, humid places. Gough Island (South Atlantic).

Discussion. Species that can produce lecanoric acid are discussed under *L. cupressicola. Lepraria multiacida* and *L. xerophila* can produce strepsilin, but these taxa differ in both

their morphology and chemistry. Anthraquinone producing species are mentioned under *L. bergensis*.

Lepraria granulata Slav.-Bay.

In Slavíková-Bayerová & Fehrer, *Lichenologist* **39:** 321 (2007); type: Bulgaria (PRA—holotype; BG—isotype; GenBank accession no. DQ914539).

Thallus leprose, granular; margin delimited to diffuse, *lobes* sometimes present, obscure; *medulla* absent; *hypothallus* usually scarce, usually grey; *soredia* abundant, coarse, up to 0–2(–0·3) mm diam., projecting hyphae usually absent. For more details see Slavíková-Bayerová & Fehrer (2007).

Chemistry. Atranorin ±, 'granulata unknown 1', 'granulata unknown 2' ±, unidentified anthraquinones ± (hyphae below thallus only). K+ yellowish, coloured hyphae below thallus K+ purple-red, other hyphae below thallus K−, C−, Pd− or + faint yellowish. The diagnostic feature of this recently described species is the production of two unknown fatty acids, 'granulata unknown 1 & 2' (Slavíková-Bayerová & Fehrer 2007).

Ecology and distribution. On mosses on siliceous rock, sometimes also on soil. So far known from Central and Eastern Europe.

Discussion. The phylogenetic placement is reported under *L. alpina*. In addition, Slavíková-Bayerová & Fehrer (2007) characterized *L.* sp. G that is chemically identical to *L. granulata*, and also is very close to that species in ITS sequences, but is morphologically more similar to *L. humida*. Morphologically similar species include *L. alpina, L. caesioalba, L. neglecta* and especially *L. borealis*, but *L. granulata* is chemically distinct by producing unknown fatty acids 'granulata unknown 1 & 2'.

Lepraria humida Slav.-Bay. & Orange

Lichenologist **38:** 505 (2006); type: United Kingdom (PRA—holotype; BG, NMW—isotypes; GenBank accession no. DQ401101).

Thallus leprose, powdery; margin diffuse or delimited, *lobes* absent; true *medulla* absent; *hypothallus* weakly developed, sparse, pale orange-brown; *soredia* abundant, mostly fine to medium sized, 40–100(−160) μm diam., projecting hyphae absent. For more details see Slavíková-Bayerová & Orange (2006).

Chemistry. The usual chemotype contains (1) atranorin, jackinic/rangiformic acid, norjackinic/norrangiformic acid ± (minor), angardianic/roccellic acid ± (minor) and unknown anthraquinones ± (minor, in subthalline hyphae only); sometimes (2) stictic and constictic acids have also been found, but were interpreted as contamination by Slavíková-Bayerová & Orange (2006). K+ yellowish, hyphae below thallus K+ purple-red, C−, Pd− or + yellow.

Ecology and distribution. On siliceous rocks, often between mosses; on rain-sheltered damp surfaces. Europe (British Isles).

Discussion. According to molecular studies, *L. humida* is a distinct taxon with considerable intraspecific variability. It is related to *L. atlantica*, thus, belonging to the extended *L. neglecta* group (Fehrer *et al.* 2008). Morphologically similar species are mentioned under *L. jackii*. *Lepraria humida* is distinguished by its chemistry, especially anthraquinones in subthalline hyphae, and ecology. Anthraquinone producing species are discussed under *L. bergensis*.

Slavíková-Bayerová & Orange (2006) also reported *L.* sp. H which was said to be morphologically and chemically identical to *L. humida* but distinct in ITS sequences; according to Fehrer *et al.* (2008), it is monophyletic, closely related to *L. humida* and forms '*L. atlantica* group' together with *L. atlantica* and *L. humida*. *Lepraria* sp. H has been reported growing on rain-sheltered siliceous rocks, moss and rarely bark in Western to Central Europe. Slavíková-Bayerová & Fehrer (2007) also added *L.* sp. BG with the same morphological and chemical features, growing on damp siliceous rock in Bulgaria. See also discussion under *L. jackii*.

Lepraria impossibilis Sipman

Herzogia **17:** 30 (2004); type: El Salvador (B—holotype; LAGU—isotype).

Thallus leprose, powdery to membranous; margin delimited, *lobes* present, *c.* 1 mm wide and long, with raised marginal rim; *medulla* present, thin, white; *hypothallus* grey; *soredia* abundant, medium sized, *c.* 0·1 mm diam., projecting hyphae absent. For more details see Sipman (2004).

Chemistry. Diagnostic substances are lecanoric acid and pannaric acid 6-methylester; accessories include 4-oxypannaric 6-methylester, atranorin (trace), unidentified anthraquinones and 'vouauxii unknown 1'. K− or + faint yellow, hyphae below thallus K+ purplish, C+ more or less red, KC+ more or less red, Pd− or + orange (Sipman 2004; Flakus & Kukwa 2007).

Ecology and distribution. On bark, also on terricolous and saxicolous mosses, soil, siliceous rock and schist; in forest or open areas. South and Central America, Asia – Iran (M. Sohrabi, pers. comm.).

Discussion. Lepraria cupressicola may be morphologically very similar but lacks pannaric acid 6-methylester and contains fatty acids. Species that can produce lecanoric acid are discussed under *L. cupressicola.* Species containing pannaric acid 6-methylester as major substance are compared under *L. vouauxii.* Distinctly lobate species are discussed under *L. membranacea* and *L. bergensis.*

Lepraria incana (L.) Ach.

Meth. Lich.: 4 (1803).—*Byssus incana* L., *Sp. Pl.* **2:** 1169 (1753); type: United Kingdom, drawing in Dillenius, *Hist. Musc.* tab. I fig. 3 (1742) (holotype); typotype: hb Hist. Muse: tab. I no 3 (OXF).

Thallus leprose, powdery; margin diffuse, *lobes* absent; *medulla* sometimes present, usually poorly developed; *hypothallus* scarce; *soredia* abundant, mostly fine, up to 50 µm diam., projecting hyphae sometimes present, short; consoredia sometimes present, up to 110 µm. For further details see Laundon (1992) and Tønsberg (1992).

Chemistry. Common chemotype (1): divaricatic acid, nordivaricatic acid ± (trace), zeorin (rarely absent – Baruffo *et al.* 2006; Leuckert *et al.* 1995) and atranorin ± (major to trace); K− or + faint yellow, C−, KC−, Pd−. Rare chemotype (2): with anthraquinones in addition to the aforementioned substances: parietin, fallacinal, parietinic acid and citreorosein; K+ purple-red, C−, KC+ purple-red, Pd+ orange (Laundon 1992; Tønsberg 1992). Very rare accessories include gyrophoric acid, lecanoric acid, thamnolic acid and an unknown terpenoid (Laundon 1992; Leuckert *et al.* 1995; Baruffo *et al.* 2006; Makarova *et al.* 2006).

Ecology and distribution. On bark, acidic rock, and sometimes on mosses, wood and soil; in more or less shaded places. Worldwide, except Arctic and Antarctic.

Discussion. Lepraria incana can be morphologically quite variable, sometimes forming relatively loose cottony cushions and sometimes consisting of sparse or denser separate soredia only. Species producing divaricatic acid are discussed under *L. crassissima. Lepraria caesiella* and *L. elobata* are sometimes morphologically similar but both these species lack divaricatic acid.

Lepraria isidiata (Llimona) Llimona & A. Crespo

in Wirth *et al.*, *Guía de Campo de los Líquenes, Musgos y Hepáticas:* 309 (2004).—*L. crassissima* var. *isidiata* Llimona, in Vězda, *Lich. Sel. Exs. Fasc.* **47:** 7 (1973); type: Spain (BCC—holotype; isotypes distributed in Vězda, *Lich. Sel. Exs. Fasc.* **47:** 7 (1973).

Thallus crustose to subfoliose, membranous to granular; margin delimited, *lobes* present, usually well-developed, margin raised; *hypothallus* sometimes present, light brownish; subcorticate patches may be present; *granules similar to true isidia* abundant, sometimes not well separated at margin, very coarse, 0·32–0·54(−3) mm diam.,

compact outer layer present, projecting hyphae rare and short, granules often become sorediate. For more details see Wirth *et al.* (2004), Baruffo *et al.* (2006), Tretiach *et al.* (2008).

Chemistry. Chemotype (1) with atranorin, fumarprotocetraric and protocetraric acids and roccellic acid ±; chemotype (2) with atranorin and fumarprotocetraric acid and roccellic acid ±; and chemotype (3) with atranorin, protocetraric acid and roccellic acid ± (Wirth *et al.* 2004; Crespo *et al.* 2006; Baruffo *et al.* 2006). Chemotype (3) is rare (Baruffo *et al.* 2006). K− or + yellow, C−, KC− or + yellow, Pd+ reddish orange, hypothallus Pd−.

Ecology and distribution. On calcareous soil and rock (sometimes on mosses); in shaded but well-lit places. Europe (Mediterranean countries).

Discussion. The phylogenetic placement of this taxon is mentioned under *L. membranacea*. *Lepraria isidiata* was historically described as *L. crassissima* var. *isidiata* Llimona (Vězda 1973). Specimens of *L. isidiata* have also been included in *L. nivalis* (Laundon 1992; Leuckert *et al.* 2004; Sipman & Raus 1999; Sipman 2004).

Species that can produce structures more or less similar to isidia include *L. crassissima* (divaricatic and nordivaricatic acids), *L. xerophila* (pannaric acid 6-methylester or rarely norascomatic acid), *L. isidiata* and *L. santosii*. *Lepraria isidiata* and *L. xerophila* produce structures similar to true isidia having a compact outer layer. Some chemotypes of *L. santosii* are chemically distinguishable by the stictic acid complex, while others are chemically similar to *L. isidiata*. *Lepraria santosii* differs from *L. isidiata* morphologically (coarse soredia without compact outer layer) and ecologically (siliceous substrata).

Species producing protocetraric and/or fumarprotocetraric acids are compared under *L. caesioalba*. Distinctly lobate species are discussed under *L. membranacea* and *L. bergensis*.

Lepraria jackii Tønsberg

Sommerfeltia **14:** 200 (1992); type: Norway (BG—holotype; BM—isotype).

Lepraria toensbergiana Slav.-Bay & Kukwa, *Bryologist* **108:** 132 (2005).

Thallus leprose, powdery; margin diffuse or delimited, *lobes* absent; true *medulla* absent; *hypothallus* sparse to continuous and thick (epibryotic specimens), white; sometimes hypothallus exposed in places; *soredia* abundant, fine to coarse, up to 160 µm diam., projecting hyphae sometimes present, short; consoredia sometimes present, up to 160 µm diam. For further details see Tønsberg (1992), Bayerová *et al.* (2005) and Slavíková-Bayerová & Orange (2006).

Chemistry. *Lepraria jackii sensu* Slavíková-Bayerová & Orange (2006) comprises specimens with atranorin and jackinic/rangiformic acid as main compounds, and accessories roccellic acid, norjackinic/norrangiformic acid (minor) and toensbergianic acid (minor). *Lepraria toensbergiana sensu* Bayerová *et al.* (2005) contains atranorin and toensbergianic acid. In the earlier, broader sense, *L. jackii* included all chemotypes with atranorin and any of the fatty acid(s) mentioned above, plus rarely also zeorin and/or minor amounts of anthraquinones (Tønsberg 1992; Leuckert *et al.* 1995; Baruffo *et al.* 2006, and others). K− or + faint yellow, C−, KC−, Pd−.

Ecology and distribution. On bark, sometimes mosses, wood, siliceous and neutral rock, rarely on soil, plant debris or lichens; mostly acidic substrata; usually in more or less sheltered, relatively humid places. Europe, North America, Asia, Australia (*L. toensbergiana* – Central Europe).

Discussion. Recently *L. toensbergiana* was separated from the morphologically identical *L. jackii* on the basis of its chemistry (atranorin together with the newly described fatty acid toensbergianic acid), ITS sequences and montane distribution (Bayerová *et al.* 2005; Bayerová & Haas 2005). However, Baruffo *et al.* (2006) did not regard the differences

sufficient and *L. toensbergiana* was reduced to a synonym of *L. jackii*. Further evidence for synonymizing *L. toensbergiana* with *L. jackii* comes from the molecular phylogeny by Fehrer *et al.* (2008). The monophyly of *L. toensbergiana* and the small sequence difference between these taxa was confirmed (similar to the intraspecific variability of some other *Lepraria* species), however, the two taxa formed a single clade on a highly supported long branch of the phylogenetic tree. Three further species, *L. celata, L. humida*, and *L. sylvicola* were segregated from *L. jackii* by Slavíková-Bayerová & Orange (2006). According to molecular studies, these taxa are distinct and not closely related to *L. jackii* or to each other (Fehrer *et al.* 2008). They are all morpologically similar to *L. jackii*, the chemical separation being based on the contents of atranorin, different fatty acids and anthraquinones in the subthalline hyphae.

Other morphologically similar species include *L. atlantica, L. elobata* and *L. neojackii* which are chemically easily separable (see the descriptions of these taxa).

Lepraria jackii s. lat. can be chemically similar to several species: *L. bergensis* and *L. lobata* (delimited thallus margin with lobes, anthraquinones); *L. borealis, L. caesioalba* and *L. granulata* (granular *L. neglecta* type thallus); *L. caesiella* (zeorin, only rarely with fatty acids); *L. nivalis* (one chemotype, usually thicker, cottony and has a delimited thallus margin often with lobes); *L. normandinoides* (rare chemotype, marginal lobes, thick dark hyphae below thallus); *L. pallida* (lobes and well-developed dark hypothallus); *L. rigidula* (nephrosteranic acid, lax cottony thallus with long projecting hyphae from soredia).

Lepraria lanata Tønsberg

Opuscula Philolichenum **4:** 51 (2007); type: USA (BG—holotype; ASU, DUKE, NMW, NY—isotypes).

Thallus leprose, with characteristic woolly consoredia; margin diffuse, *lobes* absent; *medulla* absent; *soredia* abundant, all soredia aggregated into consoredia, surrounded by lax network of branching and anastomosing but mostly not projecting hyphae, colourless or in external parts often brown; consoredia large, to 1 mm. For more details see Tønsberg (2007).

Chemistry. Protocetraric acid, angardianic/roccellic acid. Thallus K−, C−, KC−, PD+ orange (Tønsberg 2007).

Ecology and distribution. Mostly on rock, and sometimes on soil or mosses; in dry to rather wet overhangs and rock walls. Eastern USA, montane.

Discussion. Several species produce protocetraric and/or fumarprotocetraric acids (discussed under *L. caesioalba)*. However, *L. lanata* can be distinguished by its characteristic consoredia.

Lepraria lecanorica Tønsberg

in Nash, T. H. III, Ryan, B. D., Diederich, P., Gries, C. & Bungartz, F. (eds), *Lichen Flora of the Greater Sonoran Desert Region* **2:** 326 (2004); type: USA (BG—holotype; ASU—isotype).

Thallus leprose, powdery to membranous; margin delimited, *lobes* sometimes present, obscure; *medulla* present, indistinct to distinct, white; lower surface sometimes present, white to pale brown, usually without tomentum; *soredia* abundant, coarse, up to 200 µm diam., projecting hyphae sometimes present, usually short. For more details see Tønsberg (2004).

Chemistry. Lecanoric acid, atranorin (major to minor). K− or + yellowish, C+ red, KC+ red, Pd− (Tønsberg 2004).

Ecology and distribution. On bark, rock, soil; in shaded places. North and South America.

Discussion. Species that can produce lecanoric acid are discussed under *L. cupressicola.*

Lepraria leprolomopsis Diederich & Sérus.

in Aptroot, Diederich, Sérusiaux & Sipman, *Bibl. Lichenol.* **64:** 76 (1997); type: Papua New Guinea (B— holotype; LG, hb. Diederich—isotypes).

Thallus leprose, powdery to cottony; margin usually delimited, *lobes* absent; *medulla* present, distinct, white; *hypothallus* usually present, poorly developed, white, lower surface present, even, white, not or poorly tomentose; *soredia* abundant, mostly medium sized, 75–125 µm diam., projecting hyphae sometimes present; consoredia often present, 150–300 µm. For more details see Aptroot *et al.* (1997).

Chemistry. Atranorin, stictic, constictic, cryptostictic, norstictic and connorstictic acids and an unknown terpenoid. K+ yellow, C−, KC−, Pd+ orange (Aptroot *et al.* 1997).

Ecology and distribution. On bark (also on mosses). Australasia (Papua New Guinea).

Discussion. Species producing the stictic acid complex and atranorin are discussed under *L. caesioalba*. *Lepraria leprolomopsis* may be morphologically similar to *L. diffusa* (4-oxypannaric acid 2-methylester), *L. eburnea* (alectorialic acid), *L. lobificans* (stictic acid complex plus zeorin), *L. nylanderiana* (thamnolic acid), *L. vouauxii* (pannaric acid 6-methylester) and *L. nivalis* (discussed under *L. nivalis*).

Lepraria leuckertiana (Zedda) L. Saag comb. nov.

Lecanora leuckertiana Zedda, *Nova Hedwigia* **71:** 108 (2000); type: Italy (B—holotype).

Thallus leprose, cottony and powdery to granular; margin diffuse or delimited, *lobes* usually minute, often obscure; *medulla* present, well-developed, white; patches with exposed medulla present, also medullary hyphae intermixed with soredia; *soredia* abundant, fine to coarse, up to 500 µm diam., not well-separated from each other. For more details see Zedda (2000*a*).

Chemistry. Usnic acid, zeorin and isousnic acid (trace). K−, C−, KC−, Pd− (Zedda 2000*a*).

Ecology and distribution. On bark, sometimes on soil; in humid, open, well-lit places. Europe, North Africa, South America (Peru).

Discussion. Zedda (2000*a*) described *Lecanora leuckertiana* as very similar to *Lepraria vouauxii* (pannaric acid 6-methylester, no usnic acid), but provisionally included the new species in *Lecanora* because of its chemistry. At that time, following the concept of Laundon (1992, 2003), the genus *Lepraria* did not contain any usnic acid-producing species. However, Sipman (2003) placed the newly described *L. usnica* with usnic acid in *Lepraria* arguing that this character alone is not sufficient for discrimination at the generic level. Subsequently *L. coriensis* and *L. ecorticata* were transferred from *Lecanora* (Sipman 2004; Kukwa 2006*a*), and *Lepraria texta* described as new (Knudsen & Elix 2008). Taking into account these developments, the authors considered the transfer of *L. leuckertiana* appropriate. Even so, the phylogenetic relationships of the aforementioned species should be clarified using molecular methods in the future. Species producing usnic acid and zeorin are compared under *L. coriensis*.

Lepraria lobata Elix & Kalb

in Elix, *Mycotaxon* **94:** 220 (2005); type: Australia (PERTH—holotype).

Thallus leprose, granular, partly membranous; margin usually delimited, *lobes* often present and well-defined, 1–2 mm wide, slightly to distinctly raised at margins; *medulla* present, distinct, white; *hypothallus* absent; sometimes only sparse soredia on exposed medulla; *soredia* sparse to abundant, fine, 20–75 µm diam., projecting hyphae usually present, usually short; consoredia common, up to 350 µm diam. For more details see Elix (2005).

Chemistry. Atranorin, zeorin and a fatty acid (rangiformic/jackinic or roccellic/angardianic acid); rarely zeorin is present in only a minor amount or very rarely it is absent. Accessories include norrangiformic, pallidic, conpallidic and ursolic acids and an unknown dibenzofuran (minors), and

3,7-di-*O*-methylstrepsilin, fragilin, 7-chloroemodin and 3'-demethylatranorin (traces). K+ yellow, C−, Pd+ pale yellow (Elix 2005).

Ecology and distribution. On bark, mosses on rock and on soil; in sheltered places. Australia.

Discussion. Lepraria lobata and *L. pallida* both produce atranorin, zeorin and fatty acids, and have lobes, but *L. pallida* has a more membranous and rough appearance, a well-developed ±dark hypothallus and thin medulla, and contains unidentified fatty acids; whereas *L. lobata* has a slightly thicker thallus with a thicker medulla, is more green in colour and has finer individual soredia and larger consoredia, produces roccellic or rangiformic acid and sometimes small amounts of anthraquinones and unknown dibenzofurans. However, the characters of these species seem relatively similar.

Other species containing atranorin and fatty acids are mentioned under *L. jackii* and taxa with well-developed lobes under *L. membranacea*.

Lepraria lobificans Nyl.

Flora **56:** 196 (1873); type: France (H—lectotype; BM—topotype).

Thallus leprose, cottony to rarely powdery; margin usually diffuse, *lobes* rarely present, weakly developed; *medulla* present, usually thick, white; *hypothallus* rarely present, scarce, pale brown; thallus surfaces without soredia sometimes present, then medulla exposed; *soredia* abundant, fine, up to 60 µm diam., projecting hyphae present, long; consoredia abundant, up to 100(−200) µm. For further details see Laundon (1992).

Chemistry. Atranorin, stictic acid, constictic acid, cryptostictic acid ± (variable amounts, often major), norstictic acid ± (trace) and zeorin; rare accessories include roccellic/angardianic acid, an unidentified fatty acid and an unidentified terpenoid (Laundon 1992; Baruffo *et al.* 2006 and others). Laundon (1992) reported another, rare chemotype that lacks zeorin. K− or + yellow, C−, KC−, Pd+ orange.

Ecology and distribution. On bark or rock (usually on mosses) and various other substrata; in shaded, sheltered places. Worldwide.

Discussion. Species producing the stictic acid complex and atranorin are discussed under *L. caesioalba*. For morphologically similar species, see the discussion under *L. leprolomopsis*. *Lepraria incana* (divaricatic acid) is sometimes also morphologically similar as both species can be quite variable.

Lepraria membranacea (Dicks.) Vain.

Acta Soc. Fauna Flora Fennica **49**(2)**:** 265 (1921).—*Lichen membranaceus* Dicks., *Fasc. Pl. Crypt. Brit.* **2:** 21 (1790); type: United Kingdom (BM ex K ex D Turner—holotype).

Thallus crustose to subfoliose, leprose, membranous; margin delimited, *lobes* present, well-developed, wide, margin raised or flat; *medulla* present, distinct, white; *hypothallus* present, usually well-developed, dark, sometimes white along margin; thallus surfaces without soredia sometimes present; *soredia* abundant, sometimes not well-separated at margin, fine to medium, up to *c.* 100 µm diam., projecting hyphae sometimes present, short; consoredia often present, up to *c.* 200 µm. For more details see Laundon (1989).

Chemistry. Pannaric acid (major) with satellite dibenzofurans (minors to traces), roccellic/angardianic acid (rarely absent), atranorin ± (major to trace) and very rarely norstictic acid or zeorin (Laundon 1989; Baruffo *et al.* 2006 and others). K− or + yellow, C−, Pd+ reddish orange.

Ecology and distribution. On rock (also on mosses), rarely on bark or soil; shaded to sun-exposed, sheltered from rain. Worldwide but scattered.

Discussion. According to molecular studies *L. membranacea, L. vouauxii, L. xerophila, L.*

bergensis, *L. isidiata*, *L. santosii* form a monophyletic group in *Lepraria* based on ITS (Crespo *et al.* 2006; Tretiach *et al.* 2009), most of these species having membranous and lobed thalli (*L. vouauxii* only rarely develops small lobes).

Lepraria membranacea is the oldest name and the most widely distributed of the strongly lobate *Lepraria* species. Species that can form prominent lobes include *L. bergensis* (anthraquinones, relatively small thallus), *L. coriensis* (usnic acid and zeorin), *L. cupressicola* (lecanoric acid, atranorin and zeorin, well-developed dark hypothallus), *L. impossibilis* (lecanoric and pannaric acids), *L. isidiata* (protocetraric and/or fumarprotocetraric acids, coarse granules similar to true isidia), *L. lobata* and *L. pallida* (atranorin, zeorin and fatty acids, see the discussion under *L. lobata)*, *L. membranacea* (pannaric acid), *L. normandinoides* (usually protocetraric and/or fumarprotocetraric acids, soredia fine), *L. sipmaniana* (pannaric acid 6-methylester, thallus usually rather bright yellowish), *L. santosii* (stictic or protocetraric and/or fumarprotocetraric acids, coarse soredia slightly similar to isidia), *L. squamatica* (squamatic acid, only rarely lobate) and *L. xerophila* (usually pannaric acid 6-methylester, very coarse structures similar to true isidia).

Lepraria multiacida Aptroot

Fungal Divers. **9:** 20 (2002); type: Brazil (SP—holotype, ABL—isotype).

Thallus leprose, granular; margin delimited, minute *lobes* often present, up to 0·5 mm wide, thinner than the rest of the thallus, without raised rims; *medulla* present, distinct, white, sometimes blackened; sometimes medullary hyphae also form *hypothallus*, white to black; *soredia* abundant, coarse, *c.* 100–200 μm diam., projecting hyphae present, long. For more details see Aptroot (2002).

Chemistry. Atranorin; usually zeorin together with 1–2 unknown terpenoids; constictic acid (major to minor); stictic, cryptostictic and norstictic acids (all minor to trace); salazinic acid (minor to trace); 3,7-*O*-methylstrepsilin (minor to trace); 7-*O*-methylstrepsilin, strepsilin and an unidentified dibenzofuran (all trace). K+ yellow to orange, C−, KC− (Aptroot 2002; Elix & Tønsberg 2004; Elix 2006*a*).

Ecology and distribution. On sandstone and soil. South America (Brazil).

Discussion. The chemically and morphologically similar *L. salazinica* contains large quantities of salazinic acid and lacks other substances present in *L. multiacida*. *Lepraria crassissima* and sometimes *L. nivalis* and *L. squamatica* may be morphologically similar, but differ in their chemistry. Species producing the stictic acid complex are discussed under *L. caesioalba* (none of them contains salazinic acid).

Lepraria neglecta (Nyl.) Erichsen

in Lettau, *Feddes Repert.* **61:** 127 (1958).—*Lecidea neglecta* Nyl., *Not. Skällsk. Fauna Fl. Fenn. Förh.* **4:** 233 (1859); type: Finland (H—lectotype).

Thallus leprose, granular; margin usually delimited, obscure minute *lobes* sometimes present; *medulla* sometimes present, inconspicuous, white; *hypothallus* sometimes present, poorly-developed, grey to brown; rarely small patches with exposed medulla present; *soredia* abundant, mostly coarse, typically 100–150(−200) μm diam., projecting hyphae usually absent; consoredia frequent, typically 200–300 μm. For more details see Laundon (1992).

Chemistry. Alectorialic acid and roccellic/angardianic acid; rarely rangiformic acid replaces roccellic/angardianic acid or very rarely both fatty acids are present; rarely atranorin (in variable amounts) occurs; other accessories include norrangiformic acid (minor to trace), 5,7-dihydroxy-6-methylphthalide (minor to trace) and barbatolic acid (trace). K− or + yellow, C− or + reddish orange, KC+ pink or reddish orange, Pd+ lemon yellow or orange (Laundon 1992; Leuckert *et al.* 1995 and others). Kukwa (2006*b*) reported a very rare chemotype without alectorialic acid,

containing an unknown substance 'neglecta unknown'.

Ecology and distribution. On acidic rock (usually on mosses), soil and rarely on bark, epiphytic mosses and lichens; in exposed places, mostly cool climate, montane-alpine in tropics. Europe, North and South America, Asia, Australasia, Antarctica, Greenland.

Discussion. According to molecular studies, *L. neglecta* belongs to the monophyletic '*L. neglecta* group', see the discussion under *L. alpina*. Morphologically the most similar species include *L. borealis*, *L. caesioalba* and *L. granulata*, but these all differ chemically. Alectorialic acid-producing species are discussed under *L. eburnea*.

Lepraria neojackii Flakus & Kukwa

Lichenologist **39:** 468 (2007); type: Bolivia (KRAM-L—holotype; LPB, UGDA—isotypes).

Thallus leprose, powdery; margin diffuse, *lobes* absent; *medulla* absent but sometimes with pseudomedulla of bleached soredia mixed with hypothallus hyphae; *hypothallus* usually present, whitish or orange in places; *soredia* abundant, very fine, up to 20 µm diam., projecting hyphae usually absent; consoredia present, not prevalent, up to 40 µm diam. For further details see Flakus & Kukwa (2007).

Chemistry. Porphyrilic acid, roccellic/angardianic acid, rangiformic/jackinic acid and an unidentified anthraquinone (Flakus & Kukwa 2007).

Ecology and distribution. On mosses, humus and rocks; in mountain cloud forest. South America (Bolivia).

Discussion. Lepraria atlantica is chemically and morphologically the most similar species, but it contains atranorin together with porphyrilic acid. *Lepraria achariana* is also morphologically close but contains lecanoric acid. Other similar species are mentioned under *L. jackii*.

Lepraria nivalis J. R. Laundon

Lichenologist **24:** 327 (1992); type: France (MARSSJ—holotype).

Thallus leprose, cottony to powdery or membranous; margin delimited or diffuse, *lobes* absent or present; sometimes well-developed and with raised marginal rim; *medulla* usually present, often exposed in places, usually thick, white; lower surface sometimes with distinct brown tomentum; *soredia* abundant, variably sized, up to 300 µm diam., projecting hyphae usually present, short to long. For more details see the references below.

Chemistry. Leuckert *et al.* (2004) distinguished 6 chemotypes in *L. nivalis* s. lat; a classification was complemented by Baruffo *et al.* (2006). Chemotype (1) atranorin, protocetraric acid; (2) atranorin, protocetraric acid, roccellic acid; (3) atranorin, fumarprotocetraric acid (major to trace), protocetraric acid (major to trace); (4) atranorin, stictic and constictic acids, cryptostictic acid ± (trace), norstictic acid ± (trace); (5) atranorin, stictic, constictic and roccellic acids, cryptostictic acid ± (trace), norstictic acid ± (trace); (6) atranorin, psoromic acid, 2'-*O*-demethylpsoromic acid (trace). In addition, Zedda (2000*b*) reported a chemotype (7) with atranorin and roccellic acid only. Laundon (1992) reported gyrophoric acid as a very rare accessory; Baruffo *et al.* (2006) detected atranorin, protocetraric acid, virensic acid and strepsilin dimethyl ester in a single specimen; Sipman (2004) reported a specimen with protocetraric and roccellic acid without atranorin. Chemotypes 1–5: K− or + yellow, C−, KC− or + yellow, Pd+ reddish orange; chemotype 6: K− or + yellow, C−, KC− or + yellow, Pd+ yellow; chemotype 7: K− or + yellow, C−, KC−, Pd−.

Ecology and distribution. On limestone (also on mosses), sometimes on soil, rarely on bark or siliceous rock; in mostly shaded places. Europe, North America, Asia, Australasia (Papua New Guinea), Greenland (tentatively reported by Saag *et al.* 2007). Most

common in Mediterranean areas and southern Europe.

Discussion. Lepraria nivalis is very heterogeneous both chemically and morphologically, and possibly includes different taxa (Baruffo *et al.* 2006; Crespo *et al.* 2006). Chemotype (4) represents 'isidioid' morphology and agrees with the description of some chemotypes of *L. santosii*. Chemotype (5) includes both 'isidioid' and 'non-isidioid' morphs and the 'isidioid' morphotype also has an affinity with *L. santosii*. The 'isidioid' representatives of the chemotype (3) belong to *L. isidiata* according to the present taxonomy (Baruffo *et al.* 2006) while the less warted and softer specimens are left in *L. nivalis*.

Lepraria crassissima (divaricatic and nordivaricatic acids), *L. lobificans* (stictic acid complex and zeorin) and especially *L. nylanderiana* (thamnolic acid) are morphologically similar. Chemotype 7 included by Zedda (2000*b*) is chemically identical to *L. borealis*, which has a granular thallus. Morphological characters for separating non-lobate forms of *L. nivalis* and *L. leprolomopsis* seem to be limited. *Lepraria leprolomopsis* has been found on mossy bark, has a white lower surface and produces a terpenoid, whereas *L. nivalis* is associated with calcareous rock and soil, sometimes has a brown tomentum under the thallus and terpenoids are absent. Other similar species are mentioned under *L. leprolomopsis*. Species producing the stictic acid complex and atranorin, or protocetraric and/or fumarprotocetraric acids are discussed under *L. caesioalba*.

Lepraria normandinoides Lendemer & R. C. Harris

Opuscula Philolichenum **4:** 45 (2007); type: USA (NY—holotype; isotypes distributed in *Lichens of Eastern North America* V: 221).

Thallus leprose, membranous; margin delimited, *lobes* usually well developed, with marginal rim; *medulla* present, whitish; lower surface pale, with thick brown tomentum of thick hyphae; *soredia* abundant, fine, 30–60 μm diam., projecting hyphae absent. For more details see Lendemer & Harris (2007).

Chemistry. Common chemotype (1): atranorin, protocetraric acid, virensic acid (trace), roccellic acid; rare chemotype (2): atranorin, fumarprotocetraric acid, protocetraric acid (minor to trace), roccellic acid; very rare chemotype (3): atranorin, roccellic acid. Chemotypes (1) & (2): K+ yellow, C−, KC+ yellowish, Pd+ orange; chemotype (3): K+ yellow, C−, KC+ yellowish, Pd− (Lendemer & Harris 2007).

Ecology and distribution. On acidic rock and bark; in semi-shaded more or less humid places. Eastern North America.

Discussion. Morphologically similar species are discussed under *L. bergensis* and *L. membranacea*. Species producing protocetraric and/or fumarprotocetraric acids are compared under *L. caesioalba*.

Lepraria nylanderiana Kümmerl. & Leuckert

Biblioth. Lichenol. **58:** 250 (1995); type: Italy (B—holotype).

Thallus leprose, cottony to powdery or membranous; margin delimited, minute *lobes* present in well-developed specimens, without raised rims; *medulla* usually present, whitish; conspicuous greyish *hypothallus* present in well-developed specimens; thallus surfaces without soredia often present, then medulla exposed; *soredia* abundant, medium to coarse, up to 300 μm diam., projecting hyphae usually present, short. For more details see Leuckert *et al.* (1995).

Chemistry. Thamnolic acid, decarboxythamnolic acid (trace), roccellic acid and rarely atranorin (trace). K+ lemon yellow, C−, KC−, Pd+ orange-yellow (Leuckert *et al.* 1995; Baruffo *et al.* 2006 and others).

Ecology and distribution. On soil, mosses, siliceous rocks and sometimes bark. Europe (Mediterranean area, Central Europe, Great Britain).

Discussion. Morphologically the most similar species is *L. nivalis* but it contains no thamnolic acid. Further morphologically similar species are discussed under *L. leprolomopsis*. For species producing thamnolic acid, see under *L. aurescens*.

Lepraria obtusatica Tønsberg

Sommerfeltia **14:** 204 (1992); type: Norway (BG—holotype; DUKE, E—isotypes).

Thallus leprose, powdery; margin diffuse, *lobes* absent; *medulla* usually absent; rarely soredia mixed with some medullary hyphae; *soredia* abundant, very fine, up to 35 µm diam., very fragile; consoredia sometimes present, up to 50 µm diam. For more details see Tønsberg (1992).

Chemistry and distribution. Obtusatic acid, an unidentified pigment, barbatic acid ± (trace). K−, C−, KC−, Pd+ yellow (Tønsberg 1992; Makarova *et al.* 2006).

Ecology and distribution. On bark; in shaded places. Europe, Australia; scattered.

Discussion. According to molecular studies, *L. obtusatica* does not belong to the genus *Lepraria* (Ekman & Tønsberg 2002). It is chemically unique by producing obtusatic acid.

Lepraria pallida Sipman

Herzogia **17:** 33 (2004); type: Brazil (B—holotype, SP—isotype).

Thallus leprose, granular to partly membranous; margin usually delimited, *lobes* present in places, often well-developed, 0·5-2 mm wide and long, with raised marginal rim; *medulla* present, thin, white; *hypothallus* sometimes well-developed, tomentose, grey to black; *soredia* sometimes not well-separated from each other, forming a smoother surface towards margin, abundant, medium, *c.* 0·1 mm diam. For more details see Sipman (2004).

Chemistry. Atranorin, zeorin, unidentified fatty acids, unidentified terpenoids ± and unidentified substances ± (traces) (Sipman 2004; Flakus & Kukwa 2007). K+ pale yellow, C−, KC−, Pd+ yellow to orange.

Ecology and distribution. On bark, sandstone and soil. South America, Africa (Seychelles, Madagascar).

Discussion. Lepraria cupressicola (lecanoric acid) and *L. impossibilis* (dibenzofurans) also have a developed hypothallus and lobes but *L. pallida* is more granular and harder. *Lepraria lobata* has a similar chemistry and lobes, see under *L. lobata*. Other species with distinct lobes are discussed under *L. membranacea* and taxa with atranorin, zeorin and fatty acids under *L. jackii*.

Lepraria pulchra Orange & Wolseley

Lichenologist **37:** 249 (2005); type: Thailand (BM—holotype).

Thallus leprose, powdery to membranous; margin delimited, with raised irregularly indented rim, sometimes small and indistinct *lobes* present, without raised rims; *medulla* present, thin to medium, whitish; lower surface smooth, white; *soredia* abundant to sparse in places, medium to coarse, 80–140 µm diam., projecting hyphae usually present, abundant, very short (10–20 µm, rarely to 60 µm), often soredia not separated from each other, especially in thallus centre. For further details see Orange & Wolseley (2005).

Chemistry. Thamnolic acid. K+ bright yellow, C−, KC−, Pd+ orange-yellow (Orange & Wolseley 2005).

Ecology and distribution. On bark; in sheltered places, dry forest. Asia (Thailand).

Discussion. Species producing thamnolic acid are compared under *L. aurescens*.

Lepraria rigidula (B. de Lesd.) Tønsberg

Sommerfeltia **14:** 205 (1992).—*Crocynia rigidula* B. de Lesd., in Hue, *Bull. Soc. Bot. France* **71:** 331 (1924); type: United Kingdom (E—holotype).

Thallus leprose, cottony to powdery; margin diffuse, *lobes* absent; *medulla* sometimes present, poorly to well developed, lax, white; *soredia* abundant, mostly fine, sometimes coarse, up to 60(−100) µm diam., projecting hyphae present, very long or long at least on some soredia (up to 120 µm); consoredia sometimes present, up to 300 µm diam. For more details see Tønsberg (1992) and Kukwa (2006*b*).

Chemistry. Atranorin and nephrosteranic acid (Tønsberg 1992 and others). Very rarely unidentified anthraquinones (Flakus & Kukwa 2007). K− or + faint yellow, C−, KC−, Pd−.

Ecology and distribution. On bark, also on mosses, rarely on rock, soil, wood and lichens; in both shaded and open places. Europe, North America, Asia, northern Africa.

Discussion. Taxa with atranorin, zeorin and fatty acids are discussed under *L. jackii*. *Lepraria rigidula* is unique in producing a rare fatty acid, nephrosteranic acid, and characteristic soredia. It was regarded as a synonym of *L. alpina* [*sub nomine Leproloma cacuminum* by Laundon (1992)], but was resurrected as a separate species by Tønsberg (1992).

Lepraria salazinica Tønsberg

Opuscula Philolichenum **4:** 52 (2007); type: USA (BG—holotype; DUKE—isotype).

Thallus leprose, powdery to granular; margin diffuse, *lobes* absent; *medulla* absent; *soredia* abundant to scattered, very fine, to 30 µm diam., projecting hyphae absent; consoredia present, up to 50 µm, a few aggregations larger. For more details see Tønsberg (2007).

Chemistry. Atranorin, salazinic acid, roccellic/angardianic acid. K+ yellow turning red, C−, KC−, Pd+ orange (Tønsberg 2007).

Ecology and distribution. On rock; under rock overhangs. Eastern USA, montane.

Discussion. Lepraria salazinica is best characterized by the production of salazinic acid. *Lepraria multiacida* also produces salazinic acid (only minor amounts in addition to other substances), but has a thick thallus with a dark hypothallus.

Lepraria santamonicae K. Knudsen & Elix

Bryologist **110:** 115 (2007); type: USA (holotype—UCR; isotypes—ASU, BM, CANB, H, NY, hb. Lendemer).

Thallus leprose, powdery (minutely granular); margin diffuse, *lobes* absent; *medulla* absent, but sometimes a white pseudomedullary layer of gelatinized hyphae present; *soredia* abundant, fine, 30–50 µm diam., projecting hyphae absent, but occasionally with thin colourless hyphae, some soredia not well-separated from each other. For more details see Knudsen & Elix (2007).

Chemistry. Argopsin, norargopsin (major to minor). K−, C−, KC−, Pd− or Pd+ orange to orange-red (Knudsen & Elix 2007).

Ecology and distribution. On rock or soil, mostly siliceous substrata; in open, sometimes exposed places; a pioneer species. North America (California, USA).

Discussion. Lepraria santamonicae is unique in containing argopsin as the major secondary compound. *Leparaia coriensis* may also contain argopsin, but only in minor amounts in addition to usnic acid.

Lepraria santosii Argüello & A. Crespo

in Crespo *et al.*, *Lichenologist* **38:** 218 (2006); type: Canary Islands (MAF—holotype; BG, GZU—isotypes).

Thallus leprose to subfoliose, membranous to granular; margin delimited, *lobes* present, distinct, with raised marginal rim; *hypothallus* sometimes present, usually poorly developed, light brownish; *soredia* abundant, fine to very coarse, (20–)220–340(−650) µm diam., projecting hyphae present, can be long, very coarse soredia slightly *resemble*

isidia but lack compact outer layer and have projecting hyphae instead. For more details see Crespo *et al.* (2006) and Tretiach *et al.* (2008).

Chemistry. Crespo *et al.* (2006) reported chemotype (1) atranorin, stictic acid, constictic and norstictic acids (traces), zeorin and roccellic acid. K+ yellow to brownish, C−, KC−, Pd+ orange. Tretiach *et al.* (2009) added more chemotypes: (2) atranorin, stictic and constictic acids and an unknown substance (UV 366 pink); (3) atranorin, stictic and constictic acids and roccellic acid; (4) atranorin, stictic and constictic acids, protocetraric or fumarprotocetraric acid (not both) and roccellic acid; (5) atranorin, protocetraric acid and roccellic acid; (6) atranorin, protocetraric and fumarprotocetraric acids and roccellic acid; (7) atranorin, fumarprotocetraric acid and roccellic acid. In addition, they found thamnolic and/or gyrophoric acids as rare accessories in chemotype 3.

Ecology and distribution. On siliceous soil and rock and also basalt; in shaded places. Europe (Mediterranean countries) and Canary Islands.

Discussion. According to molecular studies, *L. santosii* is close to *L. isidiata* and *L. bergensis*, and has considerable intraspecific variability (Crespo *et al.* 2006; Tretiach *et al.* 2009), see also the discussion under *L. membranacea*. Previously, the specimens corresponding to the description of *L. santosii* were included in *L. nivalis* (discussed under *L. nivalis*). Other species producing more or less isidia-like structures are compared under *L. isidiata*. Several species produce the stictic acid complex and atranorin, or protocetraric and/or fumarprotocetraric acids, see under *L. caesioalba*.

Lepraria sipmaniana (Kümmerl. & Leuckert) Kukwa

Ann. Bot. Fenn. **39:** 226 (2002).—*Leproloma sipmanianum* Kümmerl. & Leuckert, in Leuckert & Kümmerling, *Nova Hedwigia* **52:** 27 (1991); type: South Africa (B—holotype).

Thallus leprose to subfoliose, membranous; margin delimited to diffuse in places, *lobes* present, well developed, often over 2 mm wide, with raised marginal rim; *medulla* present, thin, white; *hypothallus* sometimes present, inconspicuous, brownish; *soredia* sparse in places, exposing smooth ecorticate surface, especially near margins, soredia fine to coarse, 40–200 µm diam., projecting hyphae rarely present, short. For more details see Leuckert & Kümmerling (1991).

Chemistry. The diagnostic substance is pannaric acid 6-methylester; accessories include oxypannaric acid 6-methylester, 4-oxypannaric acid 6-methylester, pannaric acid, 7-chloroemodin, fragilin, A01-anthrone, parietin, emodin and 'vouauxii unknown 1' *sensu* Tønsberg (1992) (Leuckert & Kümmerling 1991; Flakus & Kukwa 2007 and others). Thallus K+ reddish brown or yellowish, hyphae below thallus K+ purple to brownish red, C± yellowish, KC+ reddish brown or yellowish, Pd+ pink.

Ecology and distribution. On soil, rock, bark and mosses; in mostly exposed, well-lit places. South America, Central America, Asia (Sri Lanka, Taiwan), Africa.

Discussion. Morphologically similar species are discussed under *L. bergensis* and *L. membranacea*. Species with pannaric acid 6-methylester as a major substance are compared under *L. vouauxii*.

Lepraria squamatica Elix

Australasian Lichenology **58:** 20 (2006); type: Australia (CANB—holotype).

Thallus leprose, powdery; margin delimited to diffuse, *lobes* absent or present, sometimes well-defined, up to 1 mm wide and with raised margin; true *medulla* absent; *hypothallus* sometimes present, thin, lax, white, exposed in places; *soredia* abundant to sparse in places, very fine, 15–40 µm diam., projecting hyphae present, variable, some very long, soredia well separated from each other; consoredia common to scarce, 150–200 µm. For more details see Elix (2006*a*).

Chemistry. Elix (2006*a*) described a chemotype (1) with squamatic and baeomycesic acids (major to minor), an unknown fatty acid (major to minor) and trace accessories barbatic, protocetraric, subsquamatic, subbaeomycesic and hypothamnolic acids. Flakus & Kukwa (2007) reported additional accessory traces of unidentified substances that were interpreted as contamination. K+ yellow, C−, Pd+ yellow.

Ecology and distribution. On bark, wood and rock; in more or less shaded, mostly humid places. South America (Bolivia – Flakus & Kukwa 2007), Australia.

Discussion. Lepraria squamatica does not have very characteristic morphology but is unique in producing squamatic and baeomycesic acids. Species producing protocetraric and/or fumarprotocetraric acids are discussed under *L. caesioalba.* Species with well-defined lobes are compared under *L. membranacea.*

Lepraria straminea Vain.

in *Résult. Voyage S. Y. Belgica, Botan.*: 40 (1903); type: Antarctica (TUR—syntypes).

Thallus crustose-leprose, granular; margin mostly delimited; *lobes* absent; cortex present on soredia; *medulla* absent; *soredia* abundant, coarse, 130–160 μm diam., projecting hyphae absent. For more details see Øvstedal & Lewis-Smith (2001).

Chemistry. Usnic acid and zeorin. K−, C−, KC−, Pd− (Øvstedal & Lewis Smith 2001).

Ecology and distribution. On mosses and peaty soil; in open habitats. Antarctica, endemic.

Discussion. Lepraria straminea is characterized by a granular, *L. neglecta*-like thallus without lobes and medulla, and also by the corticate soredia. According to Øvstedal & Lewis-Smith (2001), it only dubiously belongs to *Lepraria.* Species with usnic acid and zeorin are discussed under *L. coriensis.*

Lepraria sylvicola Orange

in Slavíková-Bayerová & Orange, *Lichenologist* **38:** 507 (2006); type: United Kingdom (NMW—holotype; BG, PRA—isotypes; GenBank accession no. DQ401102).

Thallus leprose, powdery; margin diffuse or delimited, *lobes* absent or obscure and poorly developed; true *medulla* absent; *hypothallus* sparse, pale orange-brown; *soredia* abundant, fine to coarse, 40–160 μm diam., projecting hyphae rarely present, short. For further details see Slavíková-Bayerová & Orange (2006).

Chemistry. Atranorin, roccellic/angardianic acid, toensbergianic acid, an unknown anthraquinone ± (minor, in subthalline hyphae only). K+ yellowish (subthalline hyphae K+ purple-red), C−, Pd− or + yellow (Slavíková-Bayerová & Orange 2006).

Ecology and distribution. On neutral to slightly acidic bark, especially oak, sometimes on rock; on more or less sheltered surfaces, especially in mature well-lit woodland. Europe (British Isles, France) (Kukwa & Diederich 2007).

Discussion. According to molecular studies, *L. sylvicola* is a distinct monophyletic taxon (Fehrer *et al.* 2008). Apart from *L. sylvicola*, only *L. jackii* also produces toensbergianic acid. For other similar species, see the discussion under *L. jackii.*

Lepraria texta K. Knudsen, Elix & Lendemer

in Nash III, T. H., Gries, C. & Bungartz, F. (eds), *Lichen Flora of the Greater Sonoran Desert Region* **3**: 387 (2008); type: USA (UCR—holotype; ASU, B, CANB, H, PH, UGDA—isotype).

Thallus leprose, powdery; margin diffuse, *lobes* absent; *medulla* absent; *hypothallus* sometimes present, distinct, whitish; *soredia* abundant, fine, up to 50 μm diam., projecting hyphae present, short, some soredia not well separated from each other. For more details see Knudsen & Elix (2008).

Chemistry. Usnic acid, zeorin (minor), atranorin (major to minor) and roccellic/angardianic acid (minor). K± yellow, C−, KC± yellow, Pd− (Knudsen & Elix 2008).

Ecology and distribution. On rock. North America (California, USA).

Discussion. Taxa that produce usnic acid and zeorin are discussed under *L. coriensis.*

Lepraria toilenae Kantvilas & Kukwa

Muelleria **23:** 3 (2006); type: Tasmania (HO—holotype; BG, BM, UGDA—isotypes).

Thallus leprose, powdery to cottony; margin diffuse (except young colonies), *lobes* absent; true *medulla* absent; *hypothallus* very well-developed, thick, white or rarely pale greyish; sometimes only sparse soredia on exposed hypothallus; *soredia* sparse to abundant, fine, 16–40 μm diam., projecting hyphae usually absent; consoredia sometimes present, up to *c.* 80 μm diam. More details in Kantvilas & Kukwa (2006).

Chemistry. Malonprotocetraric, fumarprotocetraric and roccellic acids, protocetraric acid (minor) and confumarprotocetraric acid (trace). K−, C−, KC−, Pd+ red (Kantvilas & Kukwa 2006).

Ecology and distribution. On bark, often slightly burnt; in high humidity, old forest, dry bark. Australia (Tasmania).

Discussion. The production of the rare substance malonprotocetraric acid in large quantities makes *L. toilenae* unique. Characteristic morphological features are the fine soredia on thick whitish hypothallus and the lack of lobes. Species producing protocetraric and/or fumarprotocetraric acids are compared under *L. caesioalba.*

Lepraria umbricola Tønsberg

Sommerfeltia **14:** 206 (1992); type: Norway (BG—holotype).

Thallus leprose, powdery; margin diffuse, *lobes* absent; *medulla* very rarely present, thin, white; *hypothallus* absent; *soredia* abundant to scattered, fine, up to 60 μm diam., projecting hyphae rarely present, short. For more details see Tønsberg (1992).

Chemistry. Thamnolic acid, atranorin ±, roccellic/angardianic acid ± (major to trace) and decarboxythamnolic acid ± (trace). K+ lemon yellow, C−, KC−, Pd+ orange-yellow (Tønsberg 1992; Leuckert *et al.* 1995; Baruffo *et al.* 2006 and others).

Ecology and distribution. On bark, rock, mosses and soil, mostly acidic substrata; shaded, sheltered, humid, sometimes extremely shaded. Europe, Africa (Macaronesia).

Discussion. Lepraria umbricola may be similar to several powdery, unstratified and green-coloured species, for example, *L. ecorticata*, but is distinguished by producing thamnolic acid. Species producing thamnolic acid are discussed under *L. aurescens.*

Lepraria usnica Sipman

Biblioth. Lichenol. **86:** 179 (2003); type: Singapore (B—holotype, SINU—isotype).

Thallus leprose, powdery; margin diffuse or delimited, *lobes* sometimes present, mostly less than 0·5 mm wide, usually without a rim; *medulla* usually present, thin to medium, white to pale yellowish; *soredia* abundant, mostly medium sized, 70–100 μm diam., projecting hyphae usually absent. For more details see Sipman (2003, 2004).

Chemistry. Three chemotypes were distinguished by Elix (2006*b*): (1) usnic acid, zeorin, contortin (minor), placodiolic acid (trace), hopane-16β,22-diol (major to minor) and isousnic acid (minor to trace); (2) usnic acid, zeorin, contortin (minor), placodiolic acid (trace), isousnic acid ± (trace) and roccellic acid ± (trace); (3) usnic acid, zeorin, contortin (minor), placodiolic acid (trace), isousnic acid (minor to trace), atranorin

(minor) and chloratranorin (minor). In addition, Sipman (2003) reported 5-chloro-3–*0*-methylnorlichexanthone and 5,7-dichloro-3–*0*-methylnorlichexanthone as trace accessories. K−, C± yellow to orange, KC± yellow to orange, Pd−.

Ecology and distribution. On rock, bark and soil; in shaded places. Central and South America, Australia, southern and south-eastern Asia (Singapore, Sri Lanka), southern Africa, tropical.

Discussion. Taxa that produce usnic acid and zeorin are discussed under *L. coriensis*. In a molecular study Nelsen *et al.* (2008, in press) showed that *L. usnica* belongs to the *Pilocarpaceae* (*Lecanorales*), thus being distant from *Lepraria*.

Lepraria vouauxii (Hue) R. C. Harris

In Egan, *Bryologist* **90:** 163 (1987).—*Crocynia vouauxii* Hue, *Bull. Soc. Bot. France* **71:** 392 (1924); type: France (BM—lectotype).

Thallus leprose, cottony to powdery; margin diffuse to delimited, sometimes obscure *lobes* present, without raised rims; *medulla* usually present, usually thick, white; *hypothallus* sometimes present, brownish, often poorly developed; often medulla exposed between soredia; *soredia* abundant, mostly coarse, up to 100 μm diam., projecting hyphae often present, short; consoredia often present, up to 300 μm; thallus characters rather variable. More details in Laundon (1989) and Tønsberg (2004).

Chemistry. The diagnostic substance is pannaric acid 6-methylester. Accessories include (a) dibenzofurans (mostly minor to trace): oxypannaric acid 6-methylester, 4-oxypannaric acid 6-methylester, 4-oxypannaric acid 2-methylester, pannaric acid, pannaric acid 2-methylester, methyl porphyrilate and porphyrilic acid; (b) fatty acids (major to trace): roccellic/angardianic or rarely rangiformic acid; (c) *p*-depsides: rarely atranorin (major to trace), very rarely gyrophoric or lecanoric acids (mostly minor to trace); (d) terpenoids: very rarely zeorin; (e) very rarely unidentified anthraquinones; (f) 'vouauxii unknown 1' and very rarely 'vouauxii unknown 2' (Tønsberg 1992; Elix & Tønsberg 2004 and others). K− or + faint yellow, C−, KC−, Pd+ reddish orange or Pd− (soredia).

Ecology and distribution. Substratum indifferent, on mosses, bark, rock, soil and lichens; in mostly shaded and sheltered, but also open and exposed places. Worldwide.

Discussion. Phylogenetic placement is mentioned under *L. membranacea.* Several species may have similar thalli, for example, *L. crassissima, L. diffusa, L. eburnea, L. gelida, L. leuckertiana, L. leprolomopsis, L. lobificans, L. nivalis* and *L. nylanderiana*, for differences see under these taxa, especially *L. leprolomopsis.*

Species containing pannaric acid 6-methylester as major substance include *L. impossibilis* (lecanoric acid, distinct lobes, relatively soft thallus), *L. sipmaniana* (distinct lobes, relatively soft thallus), *L. vouauxii* (sometimes obscure lobes, relatively soft thallus) and *L. xerophila* (distinct lobes and isidia-like structures, soredia absent or few, thallus hard).

Lepraria xerophila Tønsberg

In Nash, T. H. III, Ryan, B. D., Diederich, P., Gries, C. & Bungartz, F. (eds.), *Lichen Flora of the Greater Sonoran Desert Region* **2:** 326 (2004); type: Mexico (ASU—holotype; BG, DUKE—isotypes).

Thallus crustose to subfoliose or squamulose, membranous, slightly granular; margin delimited, obscurely to distinctly *lobed*, with marginal rim up to 0·5 mm thick; subcorticate patches may be present; *medulla* usually present, distinct in thick specimens, white; *hypothallus* absent, lower surface whitish grey; *soredia* few or absent; numerous large granules or lobules similar to *isidia* present, compact outer layer present. For more details see Tønsberg (2004).

Chemistry. Common chemotype (1): pannaric acid 6-methylester, rangiformic and/or roccellic acid; atranorin (minor to trace),

methyl porphyrilate ± (minor to trace), porphyrilic acid ± (trace), pannaric acid ± (trace) and an unknown dibenzofuran (trace); K−, C−, KC−, Pd− or + orange; rare chemotype (2): norascomatic acid plus minor to trace amounts of strepsilin, isostrepsilic acid, atranorin and chloratranorin; K− or + pale yellow, C− or + pale yellow, KC− or + green becoming brown, Pd− (Tønsberg 2004, Elix & Tønsberg 2004).

Ecology and distribution. On soil, rarely rock or wood; in dry places. Europe, North America, arid areas.

Discussion. Phylogenetic placement and other lobate species are mentioned under *L. membranacea.* Species containing pannaric acid 6-methylester as major substances are discussed under *L. vouauxii.* Species producing isidia-like structures are compared under *L. isidiata.*

Lepraria yunnaniana (Hue) Zahlbr.

in Handel-Mazzetti, *Symbolae Sinicae* **3:** 244 (1930).—*Crocynia yunnaniana* Hue, *Bull. Soc. Bot. France* **71:** 396 (1924); type: China (PC−holotype; BM—isotype).

Lepraria nigrocincta Diederich, Sérus & Aptroot, in Aptroot, Diederich, Sérusiaux & Sipman, *Bibl. Lichenol.* **64:** 78 (1997).

Thallus leprose, of cottony hypothallus and powdery soredia; margin usually delimited, *lobes* usually absent, rarely indistinct; *medulla* sometimes present, white; *hypothallus* thick, very lax, blackish brown or whitish, of thick hyphae; hypothallus exposed between soredia; *soredia* scattered, fine, 30–70 µm diam., projecting hyphae sometimes present; consoredia often present, 75–125 µm. For further details see Aptroot *et al.* (1997) and Laundon (2008).

Chemistry. Divaricatic acid and nordivaricatic acid (trace). K−, C− or + pinkish, KC+ pink, Pd− (Aptroot *et al.* 1997).

Ecology and distribution. On bark (also on mosses). South America (Ecuador, Nöske *et al.* 2007), Asia (China), Africa (Burundi), Australasia (New Guinea), montane.

Discussion. Lepraria yunnaniana usually looks different from other *Lepraria* species because of the very thick and loose, dark hypothallus, which is the dominant part of the thallus, with only a loose cover of scattered soredia. Species producing divaricatic acid are discussed under *L. crassissima.* Species with a similar dark hypothallus are mentioned under *L. cupressicola.*

Key to the species of *Lepraria**

1 Protocetraric acid and/or fumarprotocetraric acid present 2
Protocetraric acid and/or fumarprotocetraric acid absent 9

2(1) All soredia aggregated into coarse consoredia (up to 1 mm diam.), surrounded by a conspicuous lax network of branching and anastomosing but mostly not projecting hyphae . . . . . **L. lanata**
Soredia different 3

3(2) Thick weft of thick brown hyphae on the lower surface of thallus; soredia fine (30–60 µm diam.), lobes distinct . . . . . **L. normandinoides** chem. 1 & 2
Thick weft of thick brown hyphae absent (however, hypothallus or medulla may be well developed); soredia fine or coarse, lobes absent or present 4

4(3) Medulla or hypothallus well developed, thallus soft 5
Medulla and hypothallus poorly developed or absent, thallus soft or hard 6

*chem. – chemotype; couplets 68–70 adapted from Slavíková-Bayerová & Orange (2006).

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5(4) Malonprotocetraric acid present, soredia and consoredia fine (up to *c.* 80 µm diam.) . . . . . **L. toilenae**

Malonprotocetraric acid absent, soredia variably sized (up to *c.* 300 µm diam.) . . . . . **L. nivalis** chem. 1–3

6(4) Thallus powdery, soredia very fine (up to 30 µm, consoredia up to 60 µm) . . . . . **L. friabilis**

Thallus granular or membranous, soredia or thallus granules (similar to isidia) mostly coarse (predominantly >100 µm diam.) 7

7(6) Thallus distinctly lobate, with thick raised marginal rim, lobes >0·5 mm wide . . 8

Thallus without lobes or obscure minute lobes present without thick raised rim . . . . . **L. caesioalba var. caesioalba** chem. 1

8(7) Structures similar to true isidia with compact outer layer present, projecting hyphae absent; granules mostly 320–540 µm diam. . . . . **L. isidiata**

Structures slightly similar to isidia may be present but compact outer layer absent, numerous projecting hyphae present, soredia mostly 220–340 µm diam. . . . . **L. santosii** chem. 4–7

9(1) Stictic acid complex present 10

Stictic acid complex absent 18

10(9) Terpenoids present 11

Terpenoids absent 16

11(10) Thallus distinctly lobate, with raised marginal rim, lobes over 0·5 mm wide . . . . . **L. santosii** chem. 1

Thallus without lobes or lobes poorly developed, without marginal rim 12

12(11) More than one terpenoid and minor amounts of salazinic acid present; soredia coarse (up to 200 µm diam.), with long projecting hyphae . . . . . **L. multiacida**

Mostly only one terpenoid present, salazinic acid absent; soredia not coarse or if coarse then projecting hyphae short or absent 13

13(12) Medulla distinct, conspicuous 14

Medulla absent or inconspicuous 15

14(13) Soredia with long projecting hyphae, loosely packed and soft, mostly fine to medium sized (30–100 µm diam.); thallus greenish; zeorin present . . . . **L. lobificans**

Projecting hyphae short or absent, soredia harder, medium sized to coarse (75–300 µm diam.); thallus yellowish; an unknown terpenoid present . . . . . **L. leprolomopsis**

15(13) Soredia are mostly fine (20–45 µm diam.), consoredia are rare, thallus margin diffuse; thallus greenish . . . . . **L. elobata**

Soredia are coarse (100–200 µm diam.), consoredia abundant (up to 300 µm diam.), thallus margin usually delimited; thallus grey or bluish grey, not greenish . . . . . **L. caesioalba var. groenlandica**

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16(10) Well-developed medulla present, thallus with membranous appearance, lobes usually distinct or rarely absent . . . . . **L. nivalis** chem. 4–5
Well-developed medulla absent, thallus with granular or membranous appearance, lobes present or absent 17

17(16) Thallus distinctly lobate, with thick raised marginal rim, lobes over 0·5 mm wide; projecting hyphae from soredia present and mostly long . . . . . **L. santosii** chem. 2 & 3
Thallus without lobes or obscure minute lobes present without thick raised rim; projecting hyphae from soredia mostly short or absent . . . . . **L. caesioalba var. caesioalba** chem. 2

18(9) Alectorialic acid present 19
Alectorialic acid absent 21

19(18) Porphyrilic acid present . . . . . **L. gelida**
Porphyrilic acid absent 20

20(19) Thallus soft, soredia loosely packed, medulla distinct and usually thick . . . . . **L. eburnea**
Thallus hard, granular, soredia densely packed, medulla inconspicuous . . . . . **L. neglecta**

21(18) Divaricatic acid present 22
Divaricatic acid absent 24

22(21) Nordivaricatic acid present as major substance, medulla well-developed, lower surface distinct . . . . . **L. crassissima**
Nordivaricatic acid absent or in trace amounts, medulla absent or less developed, lower surface not distinct 23

23(22) Thick lax hypothallus, usually brown, soredia sparsely distributed on hypothallus . . . . . **L. yunnaniana**
Hypothallus absent, soredia abundant . . . . . **L. incana**

24(21) Pannaric acid or one of pannaric acid derivatives present as main substance . . 25
Pannaric acid and its derivatives absent or present in trace to minor amounts besides other major compound(s) 30

25(24) 4-oxypannaric acid 2-methylester present as only major dibenzofuran . . . . . **L. diffusa**
4-oxypannaric acid 2-methylester absent or present in trace to minor amounts besides other major dibenzofurans 26

26(25) Pannaric acid present as only major dibenzofuran . . . . . **L. membranacea**
Pannaric acid absent or present in trace to minor amounts besides other major dibenzofurans 27

27(26) Lecanoric acid present . . . . . **L. impossibilis**
Lecanoric acid absent 28

28(27) Soredia absent or few, isidia-like structures present, lobes well-developed . . . . . **L. xerophila** chem. 1
Soredia numerous, isidia-like structures absent, lobes well or poorly developed or absent 29

29(28) Lobes well-developed, with raised marginal rim . . . . . **L. sipmaniana**
Lobes absent or poorly-developed, without marginal rim . . . . . **L. vouauxii**

30(24) Porphyrilic acid present 31
Porphyrilic acid absent 34

31(30) Thallus granular, hard, soredia coarse (100–300 μm diam.) 32
Thallus relatively soft, powdery (or rarely cottony), soredia medium to very fine (20–100, rarely some up to 200 μm diam.) 33

32(31) Zeorin present . . . . . **L. alpina var. zeorinica**
Zeorin absent . . . . . **L. alpina var. alpina**

33(31) Atranorin present, one or very rarely two fatty acids present . . . . . **L. atlantica**
Atranorin absent, two fatty acids present . . . . . **L. neojackii**

34(30) Lecanoric acid present 35
Lecanoric acid absent 38

35(34) Zeorin present, dark brown hypothallus present (usually thick, rarely thin) . . . . . **L. cupressicola**
Zeorin absent, hypothallus absent or present and white or orange in patches . 36

36(35) Atranorin present, soredia coarse (up to 200 μm diam.) . . . . . **L. lecanorica**
Atranorin absent, soredia fine (up to *c.* 50 μm diam.) 37

37(36) Thallus margin delimited, hypothallus absent, soredia very fine (up to *c.* 30 μm diam.) . . . . . **L. goughensis**
Thallus margin diffuse, hypothallus usually present, soredia fine (up to *c.* 50 μm diam.) . . . . . **L. achariana**

38(34) Thamnolic acid present 39
Thamnolic acid absent 42

39(38) Thallus unstratified – medulla and hypothallus absent, colour green to rarely whitish green . . . . . **L. umbricola**
Thallus stratified – medulla or hypothallus present, colour not green 40

40(39) Roccellic acid present; thallus thick, usually with well-developed greyish hypothallus . . . . . **L. nylanderiana**
Roccellic acid absent; thallus thin, hypothallus absent or present and brown . . 41

41(40) Thallus margin diffuse without raised rim; brown hypothallus present, usually well-developed . . . . . **L. aurescens**
Thallus margin delimited, with raised rim; hypothallus absent or poorly-developed, white . . . . . **L. pulchra**

42(38) Usnic acid present together with zeorin 43
Usnic acid absent, zeorin absent or present 48

43(42) Thallus margin distinctly lobed, lobes with raised rim, predominantly over 0·5 mm wide; protodehydroconstipatic and constipatic acids present (in major to trace amounts) . . . . . **L. coriensis**
Thallus margin diffuse or lobed; if lobes present, without the rim, less than 0·5 mm wide; protodehydroconstipatic and constipatic acids absent 44

44(43) Medulla thick and cottony . . . . . **L. leuckertiana**
Medulla absent or thin 45

45(44) Lobes present, obscure to distinct, small, less than 0·5 mm wide . . . **L. usnica**
Lobes absent 46

46(45) Thallus granules coarse (up to 160 µm diam.), corticate . . . . . **L. straminea**
Cortical granules absent, soredia smaller (up to 100 µm diam.) 47

47(46) Soredia regular, spherical, well separated from each other; hypothallus absent . . . . . **L. ecorticata**
Soredia irregularly shaped, not well separated from each other in places; whitish hypothallus may be present . . . . . **L. texta**

48(42) Squamatic acid present . . . . . **L. squamatica**
Squamatic acid absent 49

49(48) Argopsin present . . . . . **L. santamonicae**
Argopsin absent 50

50(49) Pannarin present . . . . . **L. adhaerens**
Pannarin absent 51

51(50) Psoromic acid present 52
Psoromic acid absent 53

52(51) Thallus granular, hard, medulla inconspicuous . . . . . **L. caesioalba var. caesioalba** chem. 3
Thallus softer, with well-developed medulla . . . . . **L. nivalis** chem. 6

53(51) Salazinic acid present . . . . . **L. salazinica**
Salazinic acid absent 54

54(53) Obtusatic acid present . . . . . **L. obtusatica**
Obtusatic acid absent 55

55(54) Norascomatic acid present; soredia absent or few, isidia-like structures (lobules) present, lobes well-developed . . . . . **L. xerophila** chem. 2
Norascomatic acid absent; thallus different 56

56(55) Distinct well-developed marginal lobes present, over 0·5 mm wide and mostly with marginal rim 57
Marginal lobes absent or obscure 60

57(56) Zeorin present 58
Zeorin absent 59

58(57) Hypothallus present, grey to black; unidentified fatty acids present . . . **L. pallida**
Hypothallus absent (medulla present); rangiformic/jackinic or roccellic/angardianic acid present . . . . . **L. lobata**

59(57) Anthraquinones present (mostly in subthalline hyphae) . . . . . **L. bergensis**
Anthraquinones absent . . . . . **L. normandinoides** chem. 3

60(56) Zeorin present 61
Zeorin absent 63

61(60) Fatty acids present; medulla or hypothallus present 62
Fatty acids absent; medulla and hypothallus absent . . . . . **L. caesiella**

62(61) Thallus relatively hard, soredia densely packed, consoredia up to 350 µm diam. . . . . **L. lobata**
Thallus soft, soredia loosely packed, consoredia up to 160 µm diam. . . . . **L. jackii s. lat**

63(60) Nephrosteranic acid present; soredia with very long projecting hyphae (60–120 µm), very loosely packed . . . . . **L. rigidula**
Nephrosteranic acid absent; projecting hyphae absent or shorter, soredia densely or loosely packed 64

64(63) Soredia up to 300 µm diam., thallus granular (*L. neglecta* type) 65
Soredia up to 160 µm diam., thallus powdery or slightly cottony 66

65(64) Fatty acid 'granulata unknown 1' present, rangiformic/jackinic and roccellic/angardianic acids absent . . . . . **L. granulata**
'Granulata unknown 1' absent, rangiformic/jackinic or roccellic/angardianic acid present . . . . . **L. borealis**

66(64) Jackinic/rangiformic acid present as the only major fatty acid 67
Other fatty acids present as major compounds (jackinic/rangiformic acid also present in one species) 68

67(66) Anthraquinones present on subthalline hyphae (local and often inconspicuous) . . . . . **L. humida**
Anthraquinones absent . . . . . **L. jackii s. str.**

68(66) Roccellic/angardianic acid present as the only major fatty acid . . . . . **L. celata**
Toensbergianic or jackinic/rangiformic acid present as major fatty acids (roccellic acid may be present in addition) 69

69(68) Toensbergianic acid present as the only major fatty acid . . . .**L. toensbergiana**
Other fatty acids present as major substances (toensbergianic acid present in combination with roccellic/angardianic acid) 70

70(69) Jackinic/rangiformic acid present as major fatty acid, subthalline hyphae (when present) lacking anthraquinones . . . . . **L. jackii s. str.**
Toensbergianic and roccellic/angardianic acids present as major compounds, subthalline hyphae (when present) with anthraquinones . . . . . **L. sylvicola**

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