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LAURI SAAG

Taxonomic and ecologic problems
in the genus *Lepraria*
(*Stereocaulaceae*, lichenised *Ascomycota*)



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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications that are referred in the further text by the Roman numerals:

- I** Saag, L., Saag, A. & Randlane, T. 2008. World survey of the genus *Lepraria* (*Stereocaulaceae*, lichenized Ascomycota). Manuscript submitted to *Lichenologist*.
- II** Saag, L., Hansen, E. S., Saag, A. & Randlane, T. 2007. Survey of *Lepraria* and *Leprocaulon* in Greenland. *Mycotaxon* 102: 57–90.
- III** Lõhmus, P., Saag, L. & Lõhmus, A. 2003. Is there merit in identifying leprarioid crusts to species in ecological studies? *Lichenologist* 35(2): 187–190.
- IV** Saag, L. 2007. The substrate preferences of epiphytic *Lepraria* species in old-growth forests in Estonia. *Folia Cryptogamica Estonica* 43: 51–56.

The author has contributed to the co-authored publications as follows: 80% to the surveying and analysing the literature for papers **I–II** and 50% for **III**; 100% to the identification of lichens and 80% to laboratory work for **I–III**; 5% to the statistical analysis and 0% for sampling for **III**; 80% of writing of **I**, 70% of **II** and 20% of **III**.

I. INTRODUCTION

I.1 General

The genus *Lepraria* Ach. (*Stereocaulaceae*, *Ascomycota*) comprises lichen-forming fungi that never develop fruiting bodies and build a morphologically simple lichen thallus. It is distributed worldwide. 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). The taxonomy is largely based on the chemistry of secondary metabolites as these lichens produce a wide variety of lichen substances, and morphological and anatomical characters are often scarce.

I.2. Reproduction strategies and genetic diversity

Being dual organisms, reproduction and dispersal of lichens present challenges since both partners have to be present for the successful development of a new lichen thallus (Dobson 2003). One solution to this is the occurrence of vegetative propagules such as soredia and isidia, which contain both the fungal and photosynthetic partner. Soredia typically consist of photobiont cells enclosed in a (loose) network of hyphae, they lack cortex – as defined by Kirk *et al.* (2001), a soredium is a non-corticate combination of photobiont cells and fungal hyphae having the appearance of a powdery granule, and capable of reproducing a lichen vegetatively; these structures can develop diffusely over the surface of the thallus (Fig. 1), or in specialized areas called soralia. Isidia are small, variously shaped (often cylindrical) structures that project outwards from the thallus surface, being covered with the cortex. Soredia and isidia can be dispersed by wind, rain or small animals (Büdel & Scheidegger 1996, Dobson 2003, Purvis 2000). In the short term, vegetative propagules have the advantage that both the mycobiont and the photobiont are dispersed simultaneously and so can rapidly establish a new thallus (Ott 1987a, b).

However, the most commonly produced lichen propagules are sexually derived ascospores that are exclusively fungal in origin. Whilst ascospores might be effective in long distance dispersal of the fungus, as lichen propagules they have the disadvantage of lacking the photobiont; they must find a suitable photobiont in order to reestablish the symbiosis. Thus, vegetative and sexual reproductive strategies appear to serve two complementary functions: asexual propagules provide a way of rapid spread of locally-adapted genotypes in a local environment, and sexually derived ascospores disperse potentially novel genotypes over long-distances (Seymour *et al.* 2005, Jahns *et al.* 1995).

To ensure the long-term survival and evolution of a species, there is normally a requirement for genetic diversity to be present in a population to facilitate response to environmental change by the selection of genotypes. Sexual reproduction provides a mechanism for generating such genetic diversity within lichen populations. Little variation, associated with extensive clonal development and/or inbreeding, might place lichen populations at risk especially if a widespread genotype was unable to withstand altered abiotic or biotic conditions (Seymour *et al.* 2005; Ott 1987a, b).

However, despite the lack of sexuality, the chemical variation in genus *Lepraria* is surprisingly wide; also the molecular diversity in the markers that have been studied so far is rather great, being similar to the variation between the sexually reproducing species in related groups (Ekman & Tønsberg 2002, Myllys *et al.* 2005, Nelsen & Gargas 2007). Speciation in *Lepraria* seems to be as abundant as in any sexual group, but the mechanisms by which this takes place are yet unknown (Ekman & Tønsberg 2002).

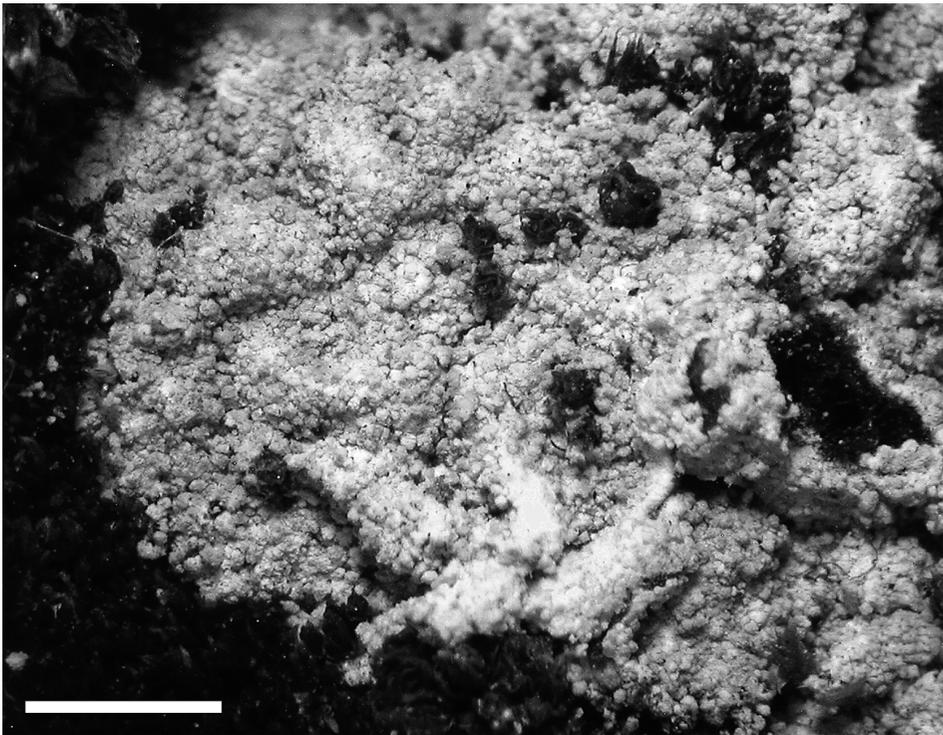


Figure 1. Thallus of *Lepraria gelida* growing on moss. Scale bar 2 mm.

I.3. History, systematics and present situation

The genus *Lepraria* Ach. was described by Acharius (1803) for sterile sorediate lichens. It is a *nomen conservandum* after the proposal by Laundon (1963). Initially the genus included various different species. It 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 history of this genus started when Laundon (1974, 1981) transferred the bright-coloured species producing anthraquinones to *Caloplaca* Th. Fr. and *Leproplaca* (Nyl.) Nyl. ex Hue (now a synonym of *Caloplaca*) and the ones containing pulvinic acid derivatives to *Chrysothrix* Mont. The number of species in *Lepraria* was again decreased when taxa producing dibenzofuranes were placed in *Leproloma* Nyl. ex Cromb. (Laundon 1989, Leuckert & Kümmerling 1991). The concept of the genus was further developed by Laundon (1992) who also moved some species from *Crocynia* (Ach.) A. Massal. to *Lepraria*, and Tønsberg (1992), Lohtander (1995) and Leuckert *et al.* (1995). *L. lesdainii* (Hue) R.C. Harris was transferred to a new monotypic genus *Botryolepraria* Canals, Hern.-Mar., Gómez-Bolea & Llimona in 1997 (Canals *et al.* 1997). The leprose usnic acid producing taxa were placed in *Lecanora* Ach. by all these authors.

Ekman & Tønsberg (2002) first showed the monophyly of *Lepraria* in a molecular study. Additionally, the *Leproloma* species nested in *Lepraria* in their analysis and the clade showed affinities with *Stereocaulaceae*. Today, *Lepraria* is widely accepted as a natural genus and a member of *Stereocaulaceae* (Myllys *et al.* 2005, and many others). Three species – *L. flavescens* Cl. Roux & Tønsberg, *Botryolepraria lesdainii* (Hue) Canals, Hern.-Mar., Gómez-Bolea & Llimona and *Lepraria obtusatica* Tønsberg – position outside the genus (Ekman & Tønsberg 2002). *Leproloma* was formally synonymised with *Lepraria* by Kukwa (2002). *L. flavescens* was transferred to *Lecanora* as *L. rouxii* S. Ekman & Tønsberg (Grube *et al.* 2004).

Sipman (2003, 2004) included also usnic acid containing species in *Lepraria* – an example that was followed by other authors (Kukwa 2006a, 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 (Aptroot 2002; Elix 2005, 2006a; Flakus & Kukwa 2007; Knudsen & Elix 2007, 2008; Lendemer *et al.* 2008; Orange 2001; Slavíková-Bayerová & Orange 2006; Tønsberg 2007; and many others, see the references in I) and 6 species transferred to *Lepraria* from other genera, *Leproloma* and *Lecanora* (Kukwa 2002, 2006a; Sipman 2004). In this publication 58 *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. caesia* (de Lesd.) J.R. Laundon, *L. nivalis* J.R. Laundon), while the presence or absence of a compound is considered to justify the taxonomic rank of species in many other cases. Partly, this is the result of the different amount of effort spent on different species groups but also the concepts used by some authors differ significantly from each other (e. g. Baruffo *et al.* 2006, Bayerová *et al.* 2005, Slavíková-Bayerová & Orange 2006). The practical identification of the species can be obscured by „mechanical hybrids” – the 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 (Nelsen & Gargas 2008, Ekman & Tønsberg 2002). Still, there are molecular data available for about 30 species of *Lepraria*, showing that all these are molecularly distinct, and only few are fairly close to each other in respect to DNA sequences (Bayerová *et al.* 2005; Crespo *et al.* 2006; Ekman & Tønsberg 2002; Myllys *et al.* 2005; Nelsen & Gargas 2006, 2007, 2008; Slavíková-Bayerová & Orange 2006; Slavíková-Bayerová & Fehrer 2007). Nelsen & Gargas (2008) have included the highest number of *Lepraria* species so far in one molecular phylogenetic analyse – 28 species. The genetic variation within species remains less studied, the highest number of specimens from the same species included in an analyse being eight (Crespo *et al.* 2006, see also the references above).

Like in *Lepraria*, the representatives of *Leprocaulon* lack sexual structures. The genus mostly occurs in the Southern Hemisphere and in arctic-alpine to temperate areas in the Northern Hemisphere (Lamb & Ward 1974, Ryan 2002). The thalli are usually dwarf fruticose, with more or less developed pseudopodetia and phyllocladia-like structures that are more or less covered with granules. In some species the pseudopodetial structures are very poorly developed and a crustose powdery, granular or subsquamulose thallus is formed (Lamb & Ward 1974, Brodo *et al.* 2001, Ryan 2002). As in *Lepraria*, the lichen substances are important in the taxonomy of *Leprocaulon*. This genus has been of somewhat lesser interest to taxonomists recently (Lamb & Ward 1974, Alstrup 1979, Leuckert & Kümmerling 1989, Schindler 1990, Golubkova *et al.* 1996, Marcano *et al.* 1997, Brodo *et al.* 2001, Ryan 2002) and its position within the *Lecanoromycetes* is still not settled.

I.4. Geographical distribution

The known diversity of *Lepraria* species is greatest (29 species) in Europe, where sufficient modern data are available for several regions e.g. Fennoscandia (Tønsberg 1992, 2002; Lohtander 1994, 1995; Lindblom 1995; Santesson *et al.*

2004, and many others), Italy (Baruffo *et al.* 2006), Great Britain (Laundon 1989, 1992; Orange 2001; Slavíková-Bayerová & Orange 2006; British Lichens web page, and many others), Poland (Kukwa 2006a, b), Estonia (Saag & Saag 1999, Randlane & Saag 2004). Six taxa have been reported only from Europe, 5 of them rather recently described.

In North America, 25 species are known; seven new species have been described in two recent years that have not reported from elsewhere (Knudsen *et al.* 2007 Knudsen & Elix 2007, 2008; Lendemer *et al.* 2008; Tønsberg 2007, Esslinger 2008, and others). A revision of *Lepraria* in North America is in progress (J. C. Lendemer, pers. comm.).

Twenty species have been reported from South America, four recently described taxa are known only from this region (Aptroot 2002, Flakus & Kukwa 2007, Sipman 2004, and others).

From Australasia, 19 species have been found, two of them (*L. lobata*, *L. toilenae*) possibly endemic (Elix 2005, 2006 a, b; Kantvilas & Kukwa 2006; McCarthy 2008, and others).

Altogether 17 species are known from different parts of Asia, three newer ones of them have not been found elsewhere. (Abbas *et al.* 2002, Han *et al.* 2006, Makarova *et al.* 2006, Orange & Wolseley 2005, Orange *et al.* 2001b, and others).

Fourteen species are registered from Africa, a recent one of them is only known from the Canary Islands (Aptroot *et al.* 1997, Baruffo *et al.* 2006, Crespo *et al.* 2006, Sipman 2004, and others). Many areas of the two latter continents are very poorly studied.

Eleven species had been reported from the panarctic region before the publication of paper **II**, one of them, *L. gelida*, probably has polar distribution only (Geiser *et al.* 1998, Kristinsson *et al.* 2006, Tønsberg & Zhurbenko 2006, and others).

From Antarctic areas, eight species plus few undescribed taxa are known, two species are probably endemic (Øvstedal & Lewis Smith 2001, Elix *et al.* 2005, and others).

The known distribution of the *Lepraria* species in eight major regions of the world is summarised in Table 1.

Despite the intensive taxonomical research mentioned earlier in this introduction, for many regions of the world, modern floristic data are still limited. Also, the available data are often outdated or incorrect due to the rapid increase of the number of species and the difficulties in determination, especially regarding chemical characters.

Greenland has been one of the less studied territories in respect of the genus *Lepraria*. Since the middle of the 20th century, numerous specimens were gathered during botanical fieldwork in various parts of Greenland with the purpose to make representative collections for the visited areas (see the references in **II**). However, the sorediate crusts in most of these collections remained

unstudied by means of the modern methods of identification and form an important source for the investigation presented in paper II. Most of Greenland is located in the Arctic climate zone (Putnins 1970, Frisrup 1981). Two subzones are distinguished, a High and a Low Arctic zone (Heide-Jørgensen & Johnsen 1997). In the southernmost part of Greenland, the Subarctic zone covers a relatively small inland area. The vegetation is mostly confined to more or less coastal areas because about 82% of Greenland is covered by an ice sheet. Leprarioid lichens are more or less common in all zones.

Table 1. The known distribution of the *Lepraria* species in eight major regions of the world. Eur – Europe; N Am – North America; S Am – South and Central America; Aus – Australasia; Asia – Asia; Afr – Africa; Ant – Antarctic region; Arct – Panarctic region, including Greenland; ² – New Guinea only; ³ – Canary Islands only.

Taxon	Eur	N Am	S Am	Asia	Aus	Ant	Arct	Afr
<i>L. achariana</i>			+					
<i>L. adhaerens</i>		+						
<i>L. alpina</i> var. <i>alpina</i>	+	+	+			+	+	
<i>L. alpina</i> var. <i>zeorinica</i>								+
<i>L. atlantica</i>	+				+		+	
<i>L. atrotomentosa</i>				+				
<i>L. aurescens</i>				+				
<i>L. bergensis</i>	+							
<i>L. borealis</i>	+	+				+	+	
<i>L. caesiella</i>		+	+					+
<i>L. caesioalba</i> var. <i>caesioalba</i>	+	+	+	+	+	+	+	+
<i>L. caesioalba</i> var. <i>groenlandica</i>								+
<i>L. celata</i>	+							
<i>L. coriensis</i>				+	+			
<i>L. crassissima</i>	+				+			
<i>L. diffusa</i>	+	+		+				
<i>L. eburnea</i>	+	+			+		+	
<i>L. ecorticata</i>	+	+	+	+				
<i>L. elobata</i>	+	+					+	
<i>L. friabilis</i>		+						
<i>L. gelida</i>							+	
<i>L. goughensis</i>						+		
<i>L. granulata</i>	+							
<i>L. humida</i>	+							
<i>L. impossibilis</i>			+					
<i>L. incana</i>	+	+	+	+	+		+	+
<i>L. isidiata</i>	+							+
<i>L. jackii</i>	+	+		+	+		+	
<i>L. lanata</i>		+						
<i>L. lecanorica</i>		+	+					
<i>L. leprolomopsis</i>					²			
<i>L. leuckertiana</i>	+		+					+

Taxon	Eur	N Am	S Am	Asia	Aus	Ant	Arct	Afr
<i>L. lobata</i>					+			
<i>L. lobifcans</i>	+	+	+	+	+		+	+
<i>L. membranacea</i>	+	+	+	+	+		+	+
<i>L. multiacida</i>			+					
<i>L. neglecta</i>	+	+	+	+	+	+	+	
<i>L. neojackii</i>			+					
<i>L. nigrocincta</i>			+		+ ²			+
<i>L. nivalis</i>	+	+		+	+ ²		+	
<i>L. normandinoides</i>		+						
<i>L. nylanderiana</i>	+							+
<i>L. obtusatica</i>	+				+			
<i>L. pallida</i>			+					+
<i>L. pulchra</i>				+				
<i>L. rigidula</i>	+	+		+		+		+
<i>L. salazinica</i>		+						
<i>L. santamonicae</i>		+						
<i>L. santosii</i>								+ ³
<i>L. sipmaniana</i>			+	+				+
<i>L. squamatica</i>			+		+			
<i>L. straminea</i>						+		
<i>L. sylvicola</i>	+							
<i>L. texta</i>		+						
<i>L. toensbergiana</i>	+							
<i>L. toilenae</i>					+			
<i>L. umbricola</i>	+							+
<i>L. usnica</i>			+	+	+			+
<i>L. vouauxii</i>	+	+	+	+	+	+	+	+
<i>L. xerophila</i>	+	+						

I.5. Ecological studies

During the past few decades many ecological studies have explored the diversity of temperate forest lichens on different substrata, and the majority of such studies have treated *Lepraria* species collectively, possibly due to unclear taxonomy or difficulties in field identification (Muhle & LeBlanc 1975, Anonby 1994, Laaka 1995, Kuusinen 1996, Johansson 1997, Forsslund & Koffman 1998, Holien 1998, Kuusinen & Siitonen 1998, Kivisto & Kuusinen 2000, Lõhmus & Lõhmus 2001). Although *L. incana*, one of the most frequent species of the genus in northern Europe, has sometimes been reported (Rose 1978, Istomina 1993; Cieslinski *et al.* 1995; Ohlson *et al.* 1997), it is likely that the other species have been overlooked or (partly) included in the former.

Most taxonomic and floristic treatments mention the substrate preferences of the *Lepraria* species (e. g. Laundon 1989, 1992; Tønsberg 2004, and many others), but the quantitative ecological studies are scarce (Wirth & Heklau

1995, Baruffo *et al.* 2006). Wirth & Heklau (1995) have presented extensive quantitative data on substratum use by different species, but they did not test the differences statistically. Baruffo *et al.* (2006) used cluster analysis to group the species according to their preferred substrates but the information on the statistical significance of these preferences was not given.

According to present taxonomy (see the references in **I**), there are about 12 European species of *Lepraria* that grow mainly on bark and wood. Given the problems described above, the ecology of *Lepraria* species is still insufficiently known, especially for the corticolous species.

I.6. The aims of the thesis

As shown above, over the recent years numerous new taxa have been described by many authors and very intensive taxonomic work continues in the genus *Lepraria*. At the same time, the species concepts vary significantly between different authors and species. The literature on many taxa is rather fragmented. As the result of such situation, often many *Lepraria* species are misinterpreted or ignored by the lichenologists who are not specialised on sterile sorediate crusts. This means that the diversity of these species in most areas in the world is actually higher than reported in general floristic publications and that a special study is needed to clarify the situation. The ecological requirements of the species are not sufficiently studied, often being regarded as fairly similar. Considering these aspects, the aims of this thesis are defined as follows:

- To provide a comparative review of all species currently accepted in the genus *Lepraria* in a standardized manner, summing up the present taxonomic situation, also being of practical help to the lichenologists who are not specialists in this relatively fast developing genus.
- Contribute to the understanding of the diversity and taxonomy of *Lepraria* by a survey in Greenland, one of the lichenologically most rich Arctic areas, where the sterile sorediate crusts have been less studied.
- Investigate the ecological niches, particularly substrate needs of *Lepraria* species, using the old growth forests of Estonia as a model.

2. MATERIAL & METHODS

2.1. Material

Altogether, about 2000 specimens of *Lepraria* have been examined for compiling this thesis.

Paper **I** is mainly based on literature (see the references in **I**), but also on original observations in many cases. Material from B, C, H, LD, NMW, PH, TU, TUR, UPS, private herbarium of Š. Slavíková was examined to refine the species descriptions.

Paper **II** is based on collections from the Botanical Museum, University of Copenhagen (C). Altogether about 700 specimens from various localities of Greenland were analysed. Additional material from other herbaria (H, LD, TU, TUR, UPS) was analysed for comparison.

The ecological studies (**III–IV**) are based on herbarium specimens from the lichenological herbarium of the Natural History Museum of the University of Tartu (TU), particularly the collections of Piret Lõhmus from Alam-Pedja Nature Reserve and of Inga Jüriado from Valgamaa, Pärnumaa, Ida-Virumaa and Saaremaa counties. About 300 specimens were examined for papers **III–IV**.

2.2. Morphology, anatomy and chemistry

Morphology and anatomy were studied using a stereomicroscope Olympus SZ40 equipped with additional objectives and a camera mounting kit, and a light microscope Olympus CH40.

All specimens were analysed by means of thin layer chromatography (TLC). TLC was carried out according to Orange *et al.* (2001a). Mostly solvent A, sometimes also B and C, rarely E were used. For the evaluation of the plates, photographs were taken in UV 254 and 366 nm before sulphuric acid treatment and in visible light and UV 366 nm afterwards (Fig. 2), using a digital camera Olympus C4040. The availability of digital images of the UV fluorescence adds to the sensitivity of the method and makes processing the chemical information easier. Some fatty acids which 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 porphyritic 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” and “porphyritic acid and accessories.”

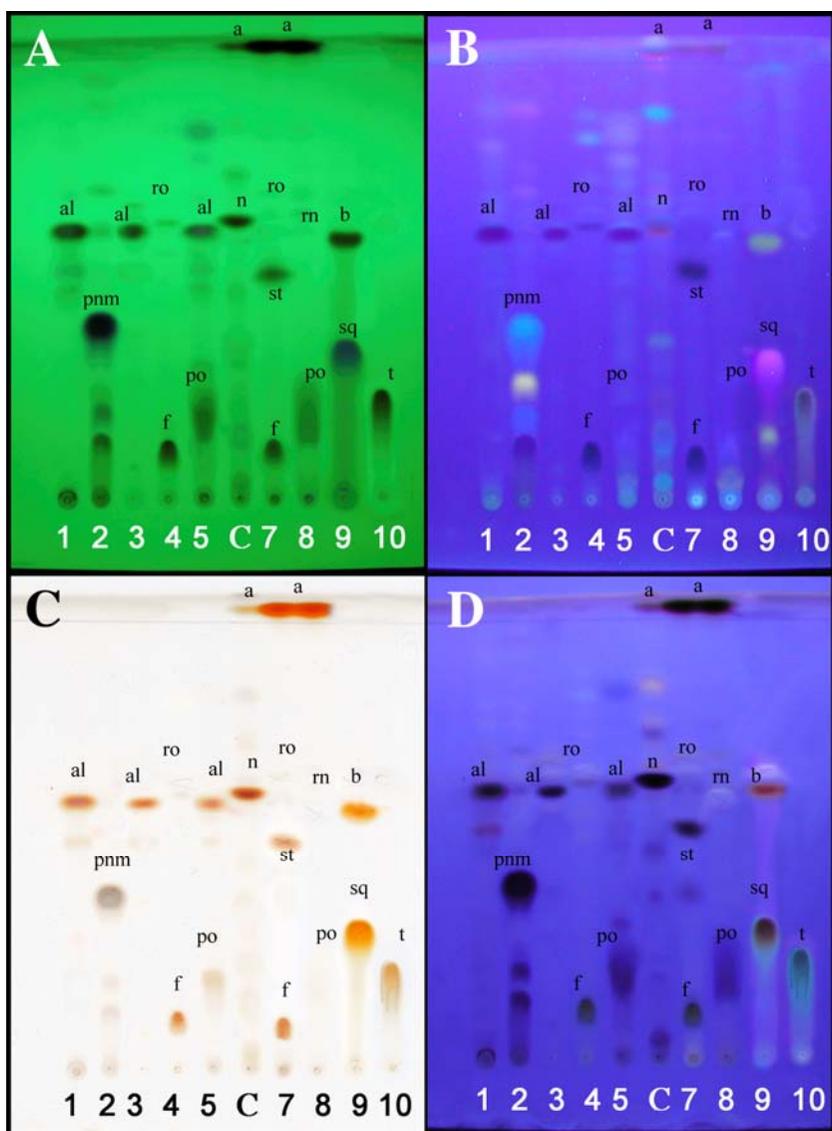


Figure 2. TLC chromatograms (in solvent A) of *Lepraria* species. A – UV254, before charring; B – UV366, before charring; C – visible light, after charring; D – UV366, after charring. 1 – *Lepraria neglecta*; 2 – *L. vouauxii*; 3 – *L. eburnea*; 4 – *L. caesioalba*; 5 – *L. gelida*; C – control (*Platismatia glauca* + *Pleurosticta acetabulum*); 7 – *L. caesioalba* (mixture of 2 chemotypes); 8 – *L. alpina*; 9 – *Leprocaulon albicans*/*L. subalbicans*; 10 – *L. umbricola*. a – atranorin; al – alectorialic acid; b – baecomycetic acid; f – fumarprotocetraric acid; n – norsietic acid; pnm – pannaric acid-6-methylester; po – porphyrillic acid; rm – rangiformic acid; ro – roccellic acid; sq – squamatic acid; st – stictic acid; t – thamnolic acid.

2.3. Study areas and data collection (papers III–IV)

In paper III, the data of Lõhmus & Lõhmus (2001) were re-analyzed, where the genus *Lepraria* had been treated collectively. This study was carried out in old peatland forests (age of dominant trees >60 years for deciduous and >80 years for coniferous species) of the Alam-Pedja Nature Reserve in east-central Estonia. A slightly modified method of Kuusinen (1996) was used. In randomly selected plots the occurrence of *Lepraria* specimens was recorded on four tree species – the coniferous *Picea abies* and *Pinus sylvestris* and the deciduous *Betula pubescens* and *Alnus glutinosa* – as these are the most common in the studied habitats. Two types of trunks from each tree species were selected – living trees and snags without bark. In each plot two pairs of trunk types from each tree species were analysed. The closest snag from the centre of the plot, and the nearest living tree of the same species and age class, made up a description unit. Whenever possible, all combinations of tree species and snag-type were studied in duplicate in a plot, but for statistical analysis, only the first replicate was used. For further details of sampling design, see Lõhmus & Lõhmus (2001). All probable specimens of *Lepraria* were collected and identified using microscopic characters and TLC.

In paper IV, the specimens gathered during the lichenological inventories of old-growth forests from different parts of Estonia were used in addition to the ones analysed in paper III. The old growth forest was defined as having the age of dominant trees >50 years for deciduous and >80 years for coniferous species. Besides *Picea abies*, *Pinus sylvestris*, *Betula* spp. and *Alnus glutinosa*, also *Populus tremula* was among the common tree species in the studied stands, although much less frequent in the analysed dataset. Other tree species were represented by few records only in this study (IV, Appendix 1). The trunks of different tree species were selected at random within the sampled forest stands. For further details, see Viilma *et al.* (2001) and Jüriado *et al.* (2003).

2.4. Data processing (papers II–IV)

The localities of the taxa were mapped using the software DMAP (Morton 2003) for the paper II. Localities based on literature records only were not included.

In paper III, the data on 77 *Lepraria* specimens were used in statistical analysis. The distribution of species amongst substrata was tested with χ^2 -tests, one of which compared substratum use by species, while the others explored the species selectivity by comparing observed and expected frequencies (Neu *et al.* 1974). To meet the sample size requirements of χ^2 -tests (Sokal & Rohlf 1995), data was pooled as follows: (1) all species into two groups (*L. incana* as the

commonest species vs. four rare species), and (2) deciduous and coniferous snags (they have similar wood pH and lichen communities, Lõhmus & Lõhmus 2001).

Two datasets were compiled for the statistical analyses in paper **IV**. The first dataset contained data from the paper **III** and Lõhmus & Lõhmus (2001). The data matrix contained entries for 114 specimens on 288 trunks, including the trunks that had no *Lepraria* thalli on them. In paper **III** and Lõhmus & Lõhmus (2001), some data from this dataset were omitted from the statistical analyses. The first dataset was used to test the tree species preference of the genus *Lepraria* as a whole. The Chi-square test was used in STATISTICA 6.0 (StatSoft, Inc. 2001).

The second dataset was compiled using the first matrix and the results of lichenological inventories of old-growth forests from different parts of Estonia. The entries of uninhabited trunks were excluded. The abundance of species on trunks was not evaluated. The matrix included 220 specimens. The second dataset was used to investigate the substrate preferences of *Lepraria* species individually. The Dufrene-Legendre indicator species analysis was carried out using PC-ORD 4.0 and the significance values were calculated with Monte Carlo test (Legendre & Legendre 1998, McCune & Mefford 1999). For tree species preference analysis, infrequent substrata with up to 4 records were excluded. When analysing corticolous specimens, the records on wood were omitted.

3. RESULTS

3.1. Description of the genus

A comprehensive description of the genus *Lepraria* was compiled for paper I. *Lepraria* Ach., nom. cons.

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

Thallus crustose to subfoliose or squamulose, with 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 substrate, sometimes parts of the thallus free from substrate, revealing lower surface; shape irregular or rosette-shaped (especially young thalli), individual thalli usually from few mm to 1 dm in diam., thalli may fuse to form more or less continuous covers up to several meters in 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 on 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 conspicuous weft, white, grey or brown to black or orange in patches; **prothallus** rarely present; **areoles** sometimes present in thick specimens; 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 in 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** trebouxoid green alga, most often *Asterochloris* (Hildreth & Ahmadjian 1981; Nelsen & Gargas 2006, 2007). **Ascomata** and **conidiomata** absent.

Substrate and ecology: 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.

Distribution: worldwide; according to current knowledge, highest number of species is found in temperate areas.

Chemistry: aliphatic acids, anthraquinones, benzyl esters, biphenyls, depsides, depsidones, dibenzofuranes, terpenoids, usnic acids.

3.2. New taxa and combinations

Two new varieties, *Lepraria alpina* var. *zeorinica* L. Saag and *L. caesioalba* var. *groenlandica* L. Saag were described in paper II.

L. alpina var. *zeorinica* is morphologically identical to the *L. alpina* (de Lesd.) Tretiach & Baruffo var. *alpina*, but differs in producing a terpenoid, zeorin, in addition to the substances that are present in the main variety (atranorin, porphyrilic acid are diagnostic). Three chemotypes are distinguished, differing in the content of fatty acids. The new variety is found only from Greenland, growing on soil and bryophytes, sometimes overgrowing other lichens. Its distributional pattern is similar to that of the typical variety; it is less frequent in the High Arctic region (II, Fig. 3A).

L. caesioalba var. *groenlandica*, too, is morphologically not distinguishable from the typical variety *L. caesioalba* (de Lesd.) J.R. Laundon var. *alpina*, but differs in producing zeorin in addition to other substances (atranorin, stictic acid complex, fatty acids). It is known only from Greenland where it is scattered across the Low Arctic (II, Fig. 4A), growing on soil and bryophytes, sometimes other lichens.

Lecanora leuckertiana is transferred to *Lepraria* in paper I as *Lepraria leuckertiana* (Zedda) L. Saag. No new information is added on chemistry, morphology or other characters of the species.

3.3. World key of *Lepraria*

In paper I, a comparative review of 58 *Lepraria* species and 2 varieties is provided together with standardized species descriptions and a key. For the first time, all taxa that are currently accepted in the world can be identified using a single key. The key is mainly based on the contents of secondary substances, however, morphological characters are used as well, where possible (in some cases they are necessary). The following taxa are included: *Lepraria achariana*, *L. adhaerens*, *L. alpina* var. *alpina*, *L. alpina* var. *zeorinica*, *L. atlantica*, *L. atrotomentosa*, *L. aurescens*, *L. bergensis*, *L. borealis*, *L. caesiella*, *L. caesioalba* var. *caesioalba*, *L. caesioalba* var. *groenlandica*, *L. celata*, *L. coriensis*, *L. crassissima*, *L. diffusa*, *L. eburnea*, *L. ecorticata*, *L. elobata*, *L. friabilis*, *L. gelida*, *L. goughensis*, *L. granulata*, *L. humida*, *L. impossibilis*, *L. incana*, *L. isidiata*, *L. jackii*, *L. lanata*, *L. lecanorica*, *L. leprolomopsis*, *L. leuckertiana*, *L. lobata*, *L. lobificans*, *L. membranacea*, *L. multiacida*, *L. neglecta*, *L. neojackii*, *L. nigrocincta*, *L. nivalis*, *L. normandinoidea*, *L. nylanderiana*, *L. obtusatica*, *L. pallida*, *L. pulchra*, *L. rigidula*, *L. salazinicola*, *L. santamonicae*, *L. santosii*, *L. sipmaniana*, *L. squamatica*, *L. straminea*, *L. sylvicola*, *L. texta*, *L. toensbergiana*, *L. toilenae*, *L. umbricola*, *L. usnica*, *L.*

vouauxii, *L. xerophila*. Additionally some previously published but unnamed taxa by different authors are discussed (paper I).

3.4. Floristic and taxonomic studies in Greenland

Species of *Lepraria* and *Leprocaulon* grow intermixed in Greenland, sometimes being hard to separate in the field. They are not inconspicuous and often occur abundantly in their habitats, forming extensive crusts on the ground or on rock faces. In many ways, leprarioid lichens are analogous to the soil-crust organisms that have only recently received particular attention among biologists (Belnap & Lange 2001). Some of them are members of the Greenland soil-crust communities described by Hansen (2001).

Altogether, six species of *Lepraria* and *Leprocaulon* had been previously reported from Greenland: *Lepraria alpina* [sub nomine *L. cacuminum*]; *L. eburnea* (sub nomine *L. frigida*); *L. lobifigans*; *L. membranacea*; *L. neglecta*; *L. vouauxii* (sub nomine *L. arctica*); *Leprocaulon subalbicans*.

Thirteen species (plus two new varieties) of *Lepraria* and three species of *Leprocaulon* were recorded from Greenland in paper II, ten of them new to the territory. *Leprocaulon subalbicans*, *Lepraria alpina* var. *alpina* and *L. borealis* are the most abundant taxa (II, Fig. 1). New to Greenland are: *L. atlantica*, *L. borealis*, *L. caesiella*, *L. caesioalba*, *L. elobata*, *L. gelida*, *L. jackii*, *L. nivalis*, *Leprocaulon albicans* and *L. gracilescens*. New to the panarctic region are: *Lepraria atlantica*, *L. caesiella*, *L. elobata*, *L. jackii* and *Leprocaulon gracilescens*. Altogether, 15 *Lepraria* species are known from the arctic areas after publication of paper II, two of them, *L. incana* and *L. membranacea*, were not found from Greenland during the present investigation.

Lepraria alpina var. *zeorinica* var. nov. and *L. caesioalba* var. *groenlandica* var. nov. were described. For all taxa information on thallus morphology, secondary chemistry, substrata and distribution together with distribution maps was given and a key was provided.

The distribution of *Lepraria* and *Leprocaulon* species in Greenland is summarized on the coincidence map (Fig. 3). The areas richest in species are mainly situated in the Low Arctic zone, including most of the west coast from Nuussuaq and Qeqertarsuaq (Disko) down to southernmost Greenland and the east coast around Tasiilaq. In the High Arctic, only in the Qaanaaq (Thule) area in the northwest were ten or more taxa found. A considerable part of the north coast is without records.

The numerous chemotypes found in the studied taxa are summarized in Table 2. The concept of chemotypes used here is quite narrow: addition or absence of any secondary compound is regarded as marker of a separate chemotype in order to get an overview of the whole chemical variation of the studied taxa.

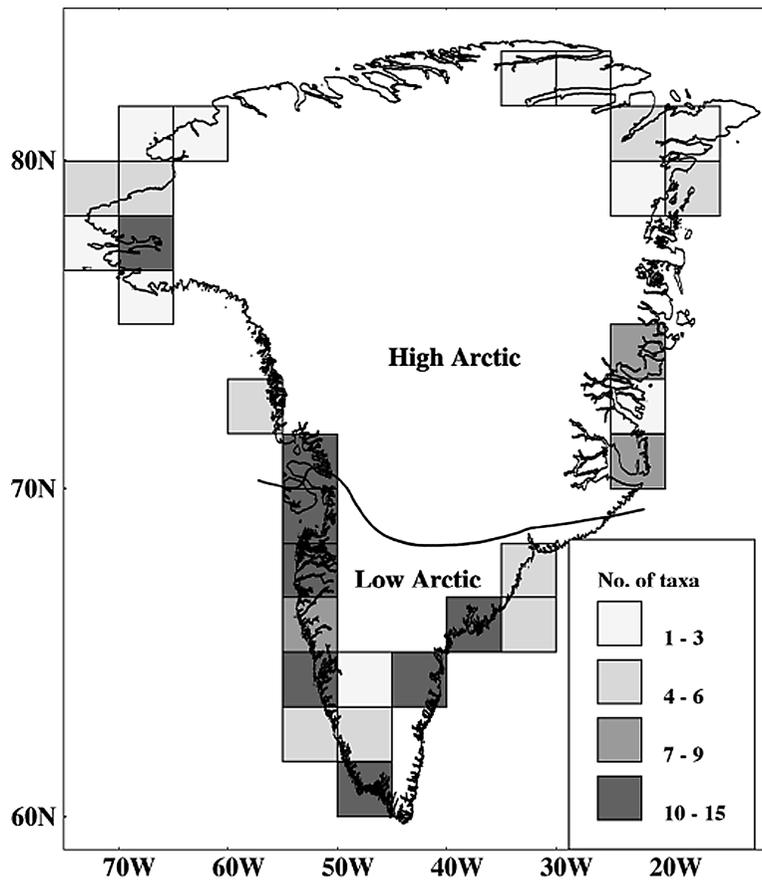


Figure 3. The distribution of *Lepraria* and *Leprocaulon* species in Greenland. Coincidence map.

Table 2. Chemotypes of the studied taxa in Greenland. Diagnostic substances are in bold. alec – alectoralic acid; atr – atranorin; baeom – baeomycesic acid; fumar – fumarprotocetraric acid; jack/rang – jackinic or rangiformic acid; pn6me+accs – pannaric acid 6-methylester and accessory dibenzofurans; porph+accs – porphyrylic acid and accessory dibenzofurans; prot – protocetraric acid; rang – rangiformic acid; roc – roccellic acid; roc/ang – roccellic or angardianic acid; sq – squamatic acid; stict compl – stictic acid complex; thamn – thamnolic acid; unid – unidentified fatty acid; zeo – zeorin.

Taxon	Chemotype	No. of specimens	P-depsids β- orcinol series	M-depsids β- orcinol series	Depsidones β- orcinol series	Benzylesters β- orcinol series	Dibenzofuranes	Terpenoids	Higher aliphatic acids
<i>L. alpina</i> var. <i>alpina</i>	(1)	60	atr				porph + accs		roc/ang
	(2)	6	atr				porph + accs		rang
	(3)	7	atr				porph + accs		
	(4)	2					porph + accs		roc/ang
	(5)	10					porph + accs		
<i>L. alpina</i> var. <i>zeorinica</i>	(1)	10	atr				porph + accs	zeo	roc/ang
	(2)	1	atr				porph + accs	zeo	rang
	(3)	4	atr				porph + accs	zeo	
<i>L. atlantica</i>	(1)	6	atr				porph + accs		roc/ang
	(2)	6	atr				porph + accs		rang
	(3)	1	atr				porph + accs		roc/ang, rang
	(4)	17					porph + accs		
<i>L. borealis</i>	(1)	23	atr						roc/ang
	(2)	18	atr						rang
	(3)	3	atr						roc/ang, rang
	(4)	8	atr						
	(5)	4							roc/ang
<i>L. caesiella</i>	(1)	2	atr					zeo	roc/ang
	(2)	2	atr					zeo	
<i>L. caesioalba</i> var. <i>caesioalba</i>	(1)	11	atr		fumar				roc/ang
	(2)	17	atr		stict compl				roc/ang
	(3)	8	atr		stict compl				rang
	(4)	1	atr		stict compl				roc/ang, rang
	(5)	14	atr		stict compl				
<i>L. caesioalba</i> var. <i>groenlandica</i>	(1)	4	atr		stict compl			zeo	roc/ang
	(2)	1	atr		stict compl			zeo	rang
	(3)	1	atr		stict compl			zeo	

Taxon	Chemotype	No. of specimens	P-depsids β- orcinol series	M-depsids β- orcinol series	Depsidones β- orcinol series	Benzylesters β- orcinol series	Dibensofuranes	Terpenoids	Higher aliphatic acids
<i>L. eburnea</i>	(1)	1			prot	alec			
	(2)	2				alec			roc/ang
	(3)	11				alec			
<i>L. elobata</i>		3	atr		stict compl			zeo	
<i>L. gelida</i>		46				alec	porph		
<i>L. jackii s. lat.</i>	(1)	9	atr						roc
	(2)	7	atr						jack/rang
	(3)	2	atr						jack/rang, roc
	(4)	2	atr						unid
<i>L. lobificans</i>	(1)	8	atr		stict compl			zeo	
<i>L. neglecta</i>	(1)	23				alec			roc/ang
	(2)	13				alec			
	(3)	4	atr			alec			roc/ang
	(4)	2	atr			alec			
<i>L. nivalis</i>	(1)	2	atr		stict compl				rang
	(2)	2	atr		stict compl				
<i>L. vouauxii</i>	(1)	44					pn6me + accs		
	(2)	4					pn6me + accs		roc/ang
	(3)	1	atr				pn6me + accs		
<i>Leprocaulon albicans</i>		40			sq, baecom				roc/ang
<i>Leprocaulon gracilescens</i>	(1)	1	atr						roc/ang
	(2)	1	atr						rang
<i>Leprocaulon subalbicans</i>	(1)	118			sq, baecom				roc/ang
	(2)	3			sq, baecom				
	(3)	2	atr		thamn				roc/ang
	(4)	11			thamn				roc/ang

Several species had distinctive distribution patterns in Greenland (see the distribution maps in II).

Mostly Low Arctic – *Lepraria alpina* var. *alpina*, *L. alpina* var. *zeorinica*, *L. atlantica*, *L. borealis*, *L. caesioalba* var. *caesioalba*, *L. caesioalba* var. *groenlandica*, *L. eburnea*, *L. jackii*, *L. neglecta*, *Leprocaulon albicans*, *L. subalbicans* (except thamnolic acid chemotypes).

Only Low Arctic – *Lepraria caesiella*, *L. elobata*, *L. lobificans*.

Relatively even – *L. gelida*, *L. vouauxii*.

Uncertain (rare) – *Lepraria* cf. *nivalis*, *Leprocaulon gracilescens*.

In paper **II**, new information was presented or novel concepts introduced concerning chemistry, morphology and taxonomy of several studied species in Greenland.

The first detailed description of *Lepraria gelida* Tønsberg & Zhurb. was provided. *L. gelida* was recently rather briefly described as new by Tønsberg & Zhurbenko (2006) from Svalbard and the Russian arctic islands near the Taimyr peninsula. The contents of the lichen substances reported in original description was confirmed. New information on thallus morphology, growth habit, substrate and distribution is presented. Two morphotypes were recognised – a common one which is soft, cottony, with evident medulla and smaller soredia with distinct projecting hyphae (**II**, Fig. 5); and a rare morphotype with more granular appearance, thin and not evident medulla, slightly larger soredia and very short and scarcely projecting hyphae on the soredia.

Lepraria alpina var. *alpina* and *L. atlantica* – Almost a continuum in morphology between *L. alpina* and *L. atlantica* is reported in Greenland. *L. atlantica* was separated from *L. alpina* by Orange (2001) on the basis of a powdery or almost cottony thallus constitution. Its distinctiveness has also been shown by DNA studies (Ekman & Tønsberg 2002, Slavíková-Bayerová & Fehrer 2007). Several thalli studied in paper **II** were intermediate between these two species; more granular specimens were assigned to *L. alpina*, more powdery ones to *L. atlantica*. Previously only a few intermediate specimens were known and the two species were considered to be morphologically strictly distinct (Orange 2001, Baruffo *et al.* 2006). Chemically, presence of porphyritic acid and accessories is diagnostic for *L. alpina* var. *alpina* in Greenland (**II**, Table 1).

Lepraria borealis – Specimens with atranorin only or fatty acids only were tentatively placed in this taxon; they can alternatively be considered deficient representatives of *L. alpina* as there are no distinctive morphological differences between these two species (Prigodina-Lukošienė *et al.* 2003, Kukwa 2006b; see also Lohtander 1995).

Lepraria caesiella – Few specimens contain roccellic acid as an accessory to atranorin and zeorin. Roccellic acid was not reported in original description by Lendemer (2005).

Lepraria eburnea – *L. eburnea* often has a thick, soft and cottony appearance. In Greenland, however, thalli are usually a bit more densely packed, a few being almost granular, but still clearly different from the chemically similar *L. neglecta* (alectorialic acid is considered a diagnostic substance in both these taxa – **II**, Table 1).

Lepraria lobificans – Large and prominent thalli are often common for this widely distributed species elsewhere in the world. In Greenland *L. lobificans* forms only small woolly patches, often in cracks and crevices between other lichens and mosses. Roccellic/angardianic acid was additionally detected in one specimen from Greenland which was morphologically very similar to *L. lobificans*. The fatty acids are normally not encountered in that species. The

specimen with roccellic/angardianic acid is chemically identical with another recently described species *L. santosii* Argüello & A.Crespo (Crespo *et al.* 2006) which is morphologically distinct by the raised rim at the thallus margin and lobate, often subsquamulose growth form.

Lepraria nivalis – In paper II, specimens containing atranorin, stictic acid complex and optionally rangiformic acid, are tentatively assigned to *L. nivalis*. *L. nivalis* is distributed in Europe, North America and Asia, the stictic acid chemotypes being most common in Mediterranean Europe and Macaronesia (Baruffo *et al.* 2006, Leuckert *et al.* 1995, 2004). The Greenland localities are the northernmost so far. A fatty acid rangiformic acid has not been reported from this species before. It is possible that the Greenland specimens represent another undescribed taxon but more collections and investigation are needed to establish that. Material from Greenland is leprose, cottony, soft, usually thick; white to light grey; thallus margin delimited, with obscure sublobes or diffuse; medulla present, white; soredia loosely packed, variably sized, sometimes coarse, usually with projecting hyphae present.

Leprocaulon subalbicans – The chemotypes with squamatic and baeomycetic acids are dominant in Greenland; specimens containing thamnolic acid are much less frequent. Squamatic acid chemotypes are relatively rare on the world scale (Lamb & Ward 1974, Brodo *et al.* 2001, McCune 2004), whereas thamnolic acid chemotypes are known to be common in USA and Canada. The different chemotypes have distinct distribution patterns also in Greenland: thamnolic acid chemotypes are widespread, although scattered, having more localities in High Arctic, while the squamatic acid chemotypes occur in the south and west, mostly in the Low Arctic (II, Fig. 7B).

3.5. The substrate preferences of epiphytic *Lepraria* species in old-growth forests in Estonia

In paper III, a total of six species of *Lepraria* were identified (III, Table 1). The most common species on all the studied substrata was *L. incana*, the rarest species were *L. eburnea* and *L. umbricola*. The occupancy by *Lepraria* seemed to depend on tree species, since living trees and snags of each of the four tree species were ranked similarly in terms of their apparent suitability as habitats: *Picea*>*Alnus*>*Betula*>*Pinus*. The distribution of *L. incana* and other *Lepraria* species among substrata differed statistically significantly. Although *L. incana* tended to inhabit conifers slightly more frequently and deciduous trees less frequently than expected (III, Fig. 1), this tendency was not statistically significant. In contrast, the observed and expected distributions of the other *Lepraria* species among substrata were significantly different due to their pronounced preference for living deciduous trees (III, Fig. 1).

In paper **IV**, eight *Lepraria* species were found from the studied trunks: *L. borealis*, *L. eburnea*, *L. elobata*, *L. incana*, *L. jackii*, *L. lobificans*, *L. umbricola* and *L. vouauxii* (**IV**, Appendix 1). *L. incana* was by far the most frequent (141 records of total 220), which is sometimes not the case in other Estonian forests, where *L. lobificans* can also be dominant (Saag & Saag 1999, L. Saag, unpublished).

In the first dataset, 40% of trunks (115 of 288) were inhabited by *Lepraria*. *Picea abies* was significantly favoured as substrate on the genus level (**IV**, Table 1), in accordance with paper **III**.

The second dataset and the indicator species analysis was used to discover the preferences of studied species for different substrate classes: (1) tree species; (2) bark of coniferous trees and bark of deciduous trees; (3) bark of coniferous trees, bark of deciduous trees and wood of all trees. No distinction was made between the wood of coniferous and deciduous tree species as their pH and the composition of lichen flora are considered to be similar (Lõhmus & Lõhmus 2001).

L. incana prefers norway spruce and the bark of coniferous trees in general (Table 3). This species is overwhelming on wood, compared to other taxa, although majority of thalli grow on bark (**IV**, Fig. 1, 2). Notably most of the wood samples came from coniferous trees, mainly spruce (**IV**, Appendix 1). *L. elobata* is a species of deciduous bark in studied forests. *L. lobificans* mostly grows on the bark of deciduous trees but this preference was statistically significant only in corticolous specimens. *L. jackii* does not have a preference for any substrate analysed. *L. borealis*, *L. eburnea*, *L. umbricola* and *L. vouauxii* also did not show any affinities in this study, probably due to low number of records.

Table 3. Substrate preferences of studied species according to indicator species analysis (the method of Dufrene and Legendre), the significance values calculated with Monte Carlo test.

	Coniferous bark / Deciduous bark	Tree species	Total no. of specimens
<i>Lepraria incana</i>	coniferous p=0.000	<i>Picea abies</i> p=0.024	141
<i>Lepraria jackii</i>	–	–	30
<i>Lepraria lobificans</i>	deciduous p=0.003	–	21
<i>Lepraria elobata</i>	deciduous p=0.003	–	16

4. DISCUSSION

4.1. New taxa and combinations

The new varieties, *Lepraria alpina* var. *zeorinica* and *L. caesioalba* var. *groenlandica*, were described in paper II. The rank of variety has not been used in other modern works on the genus. In some species, several quite different chemotypes have been included (e.g. *L. caesioalba*, *L. nivalis*, see Baruffo *et al.* 2006, Leuckert *et al.* 2004, Tønsberg 2004). At the same time, the presence or absence of a single compound is considered to justify the taxonomic rank of the species in some cases (Bayerová *et al.* 2005, Flakus & Kukwa 2007, Slavíková-Bayerová & Orange 2006). The infraspecific rank of the variety is used here, in agreement with the botanical code (McNeill *et al.* 2007), to describe different types of chemical variation within the population.

Zeorin represents the substance class of terpenoids that have not been reported from *L. alpina* or *L. caesioalba* before, and its content in the collections from Greenland seems to be constant enough to justify this subspecific rank. We describe these taxa on the level of variety because they are not morphologically distinguishable from the rest of the specimens of these species. Chemically *L. caesioalba* var. *groenlandica* is similar to *L. elobata* which is morphologically different in the following aspects: *L. elobata* has thin powdery thallus composed of mostly fine soredia (consoredia are rare) and diffuse thallus margin, unlike *L. caesioalba*. *L. caesioalba* may be a collective species (Ekman & Tønsberg 2002, Tønsberg 2004) but without a comprehensive molecular study the separation on species level is not justified.

Lecanora leuckertiana is transferred to *Lepraria* in paper I as *Lepraria leuckertiana*. Zedda (2000a) described *Lecanora leuckertiana* as very similar to *Lepraria vouauxii*, but provisionally included the new species in *Lecanora* because of its chemistry – usnic acid and zeorin. At that time the genus *Lepraria* did not comprise any usnic acid producing species, following the concept of Laundon (1992, 2003). However, Sipman (2003) placed the newly described *L. usnica* with usnic acid in *Lepraria* arguing that this character alone is not sufficient for determination at generic level. Subsequently *L. coriensis*, *L. ecorticata* were transferred from *Lecanora* (Sipman 2004, Kukwa 2006a) to *Lepraria* and *L. texta* described in the latter genus (Knudsen & Elix 2008). Taking into account these developments, the authors consider the transfer of *L. leuckertiana* appropriate. Still, the phylogenetic relationships of the aforementioned species should be clarified using molecular methods in the future.

4.2. Chemical similarities of the taxa

As the taxonomy in *Lepraria* is traditionally largely based on the chemistry of the lichen substances, the chemically similar taxa can sometimes be a source of confusion. Such groups and the delimiting characters of the taxa are discussed below. As a rule, secondary substances are phylogenetically widespread in *Lepraria* and thus the sets of species discussed below do not represent phylogenetic entities (Ekman & Tønsberg 2002, Nelsen & Gargas 2008). Still, the distinctiveness of most species has been confirmed using molecular methods (Bayerová *et al.* 2005; Crespo *et al.* 2006; Ekman & Tønsberg 2002; Myllys *et al.* 2005; Nelsen & Gargas 2006, 2007, 2008; Slavíková-Bayerová & Orange 2006; Slavíková-Bayerová & Fehrer 2007). However, no molecular data have been published for many species.

The species that may contain **protocetraric and/or fumarprotocetraric acids** include *L. caesioalba*, *L. eburnea*, *L. friabilis*, *L. isidiata*, *L. lanata*, *L. nivalis*, *L. normandinoides*, *L. squamatica*, *L. toilenae*. *L. caesioalba* has granular thallus of *L. neglecta* type morphology. *L. eburnea* contains alectorialic acid besides protocetraric acid and usually has soft powdery to cottony thallus. *L. friabilis* has thin finely powdery thallus, often with sparse individual soredia on the substrate. *L. isidiata* has lobed and isidia like structures on thallus. *L. lanata* has characteristic very large consoredia surrounded by woolly anastomosing hyphae. *L. nivalis* has thick whitish thallus with medulla, may be morphologically similar to *L. eburnea* in some cases but chemically lacks alectorialic acid. *L. normandinoides* has membranous thallus usually with wide lobes, dark thick hyphae on the lower side. *L. squamatica* may sometimes have protocetraric acid only as trace accessory to squamatic acid. *L. toilenae* produces the uncommon malonprotocetraric acid as main substance, has very well developed light hypothallus.

Species with **stictic acid and atranorin** include *L. caesioalba*, *L. elobata*, *L. leprolomopsis*, *L. lobificans*, *L. multiacida* (stictic acid complex mostly in traces), *L. nivalis* (some chemotypes), *L. santosii*. *L. caesioalba* has granular *L. neglecta*-type thallus, the widespread main variety does not produce zeorin. *L. elobata* has thin greenish thallus of relatively compact soredia without medulla or lobes, produces zeorin. *L. leprolomopsis* has thick whitish thallus with medulla, no lobes and white even lower surface, produces an unknown terpenoid. *L. lobificans* has greenish loosely packed soredia with long projecting hyphae and well developed white medulla, produces zeorin. *L. multiacida* contains stictic acid complex mostly in traces and additionally produces salazinic acid (minor to trace), strepsilin derivatives (minor to trace) and usually zeorin together with 1–2 unknown terpenoids; often has minute lobes. *L. nivalis* has thick whitish thallus with medulla, does not produce zeorin (see also discussion under *L. nivalis* in **II**). *L. santosii* has membranous thallus with well developed lobes.

Species that may contain **atranorin and different fatty acids** as only major substances include *L. bergensis*, *L. borealis*, rare chemotypes of *L. caesiella* (Flakus & Kukwa 2007, paper II), a rare chemotype of *L. caesioalba* (chemotype III sensu Tønsberg 2004), *L. celata*, *L. granulata*, *L. humida*, *L. jackii*, *L. lobata*, a chemotype of *L. nivalis* (sensu Zedda 2000b), *L. normandinoides* (rare chemotype III sensu Lendemer & Harris 2007), *L. pallida*, *L. rigidula*, *L. sylvicola*, *L. toensbergiana*. These taxa have the following dissimilarities. *L. bergensis* has delimited thallus margin with lobes and always contains anthraquinones; *L. borealis*, *L. caesioalba* and *granulata* have a granular (*L. neglecta* type) thallus; *L. jackii* has relatively thin thallus, is relatively loosely packed and usually unstratified, lacks lobes. *L. lobata* has a thick delimited thallus with lobes and white medulla, contains anthraquinones; *L. nivalis* is usually thicker, cottony and has a delimited thallus margin often with lobes; *L. normandinoides* has marginal lobes and dark hyphae; *L. pallida* has lobes and well developed dark hypothallus; *L. rigidula* contains a unique fatty acid – nephrosteranic acid – and has lax cottony thallus with long projecting hyphae from soredia. *L. toensbergiana*, *L. celata*, *L. humida* and *L. sylvicola*, related to *L. jackii*, have recently been separated from *L. jackii* (Bayerová *et al.* 2005, Bayerová & Haas 2005, Slavíková-Bayerová & Orange 2006). Their chemical separation is mainly based on the contents of atranorin, different fatty acids and anthraquinones in the subthalline hyphae (see the key).

L. atlantica is chemically identical to *L. alpina* var. *alpina*, producing **atranorin, porphyritic acid and fatty acids**. *L. alpina* differs in its granular (*L. neglecta* type) thallus; still, in paper II, some specimens with intermediate morphology between these species are reported. *L. atlantica* is chemically and morphologically rather similar to *L. neojackii*, which is described as containing both roccellic/angardianic and rangiformic acids at the same time but no atranorin. *L. alpina* and *L. atlantica* belong to the „extended *L. neglecta* group“, supported by the molecular analyses (Ekman & Tønsberg 2002; Nelsen & Gargas 2008; Slavíková-Bayerová & Fehrer 2007, see also the discussion of the morphological *L. neglecta* group below).

L. coriensis, *L. ecorticata*, *L. straminea*, *L. texta*, *L. usnica* and *L. leuckertiana* contain **usnic acid and usually zeorin**, but differ in the following aspects. *L. ecorticata* has no lobes or medulla (or rarely medulla is weakly developed and present in patches), its soredia are well separated from each other. Some soredia of *L. texta* are not well separated, that species also has no medulla but can develop a hypothallus and rarely obscure minute lobes. *L. leuckertiana* is only obscurely lobed and has a cottony appearance with well developed medulla, additionally the soredia of *L. leuckertiana* are not well separated from one another. *L. coriensis* and *L. usnica* have lobes and medulla. The lobes of *L. coriensis* are usually well developed (0.5–2 mm), round and with marginal rim; that species produces protodehydroconstipatic and constipatic acids (in variable amounts) and lacks contortin. The lobes of

L. usnica are usually small (<0.5 mm), irregular and without marginal rim; that species produces minor amounts of contortin and lacks protodehydroconstipatic and constipatic acids. The chemical differences between *L. coriensis* and more recent *L. usnica* were demonstrated by Elix (2006b). Some authors have raised the question of the distinctiveness of *L. usnica* (Orange and Wolseley 2005). *L. straminea* has corticate granules and no lobes.

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

Species containing **pannaric acid 6-methylester** as major substance include *L. impossibilis*, *L. sipmaniana*, *L. vouauxii*, *L. xerophila*. *L. impossibilis* may also be morphologically quite similar to some morphs of *L. vouauxii*. The differences are as follows. *L. impossibilis* produces lecanoric acid, has distinct lobes, lacks isidia-like structures, soredia present, thallus relatively soft. *L. sipmaniana* has well developed lobes, lacks isidia-like structures, soredia present, thallus relatively soft. *L. vouauxii* lacks lobes or develops small and obscure lobes, lacks isidia-like structures, soredia present, thallus relatively to very soft. *L. xerophila* has well developed lobes, has isidia-like structures, soredia absent or few, thallus hard.

Species producing **alectorialic acid** include *L. eburnea*, *L. gelida* and *L. neglecta*. *L. eburnea* and *L. gelida* both have soft light-coloured thallus, but *L. gelida* contains porphyritic acid that never occurs in *L. eburnea* which sometimes produces protocetraric acid instead. *L. neglecta* is easily recognisable by its characteristic granular thallus, it lacks both porphyritic and protocetraric acids.

Species producing **divaricatic acid and zeorin** include *L. crassissima*, *L. incana* and *L. nigrocincta*, but differ in following aspects. *L. incana* and *L. nigrocincta* contain nordivaricatic acid in trace amount or it is absent, unlike *L. crassissima*. *L. incana* is mostly composed of soredia (powdery), lower surface not distinct, thallus never folded and rarely delimited. *L. nigrocincta* has cottony appearance like *L. crassissima*, but develops dominant blackish hypothallus and partly scarce soredia.

Species that can produce **lecanoric acid** include *L. achariana*, *L. atrotomentosa*, *L. goughensis*, *L. impossibilis*, *L. lecanorica*. These species differ in the following aspects. *L. achariana* produces only roccellic/angardianic (not always present) acid besides lecanoric acid and has stratified thallus with fine soredia and diffuse margin. *L. atrotomentosa* contains atranorin and

zeorin and has well developed layer of dark hyphae on the lower side of thallus. *L. goughensis* contains gyrophoric acid and strepsilin (minor to trace amounts) and has very fine soredia and no hypothallus. *L. impossibilis* contains pannaric acid 6-methylester, otherwise being similar to some lobate morphs of *L. atrotomentosa*. *L. lecanorica* contains atranorin and has usually thick thallus without dark hypothallus.

L. salazinica and *L. multiacida* produce **salazinic acid**, and can be similar in morphology. However, *L. salazinica* contains large quantities of salazinic acid and less other substances than *L. multiacida*. *L. multiacida* contains only minor amounts of salazinic acid in addition to other substances.

Argopsin may be found in *L. santamonicae* and *L. coriensis*. In *L. santamonicae* it is the major substance but in *L. coriensis* an occasional minor accessory to usnic acid and zeorin.

4.3. Morphological similarities of the taxa

Despite the relative scarcity of morphological characters useful for species delimitation, few groups of morphologically similar taxa can be outlined.

Species that can form **prominent lobes** include *L. atrotomentosa*, *L. bergensis*, *L. coriensis*, *L. impossibilis*, *L. isidiata*, *L. lobata*, *L. membranacea*, *L. nivalis*, *L. normandinoides*, *L. pallida*, *L. santosii*, *L. sipmaniana*, *L. squamatica* (rarely), *L. xerophila*; *L. vouauxii* may also be lobate to lesser extent. All these species are relatively easily distinguishable using chemical and morphological characters combined (see the discussion under these species in **I**). 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 according to Crespo *et al.* (2006). An analysis by Nelsen & Gargas (2008) added *L. nigrocincta* and *L. nylanderiana* to this molecular clade, although only a subclade containing *L. bergensis*, *L. isidiata*, *L. nylanderiana* and *L. santosii* was significantly supported; at a broader supported level, also *L. umbricola*, *L. incana* and *L. sylvicola* belonged to the group.

The following species exhibit the **granular thallus appearance**, developing coarse soredia and consoredia: *L. adhaerens*, *L. alpina*, *L. borealis*, *L. caesioalba*, *L. granulata*, *L. neglecta*, *L. pallida*, *L. straminea* and to lesser extent also *L. lobata*, *L. multiacida* and sometimes *L. leuckertiana*. Chemical and often additional morphological characters can be used for distinguishing these species (see the key in **I**). *L. alpina*, *L. borealis*, *L. caesioalba*, *L. granulata* and *L. neglecta* are morphologically and ecologically fairly uniform, being commonly referred to as „*L. neglecta* group“. According to molecular studies, *L. neglecta* belongs to a monophyletic group together with *L. alpina*, *L. atlantica*, *L. borealis*, *L. caesioalba*, *L. elobata*, *L. granulata* and *L. humida*

(Ekman & Tønberg 2002, Nelsen & Gargas 2008, Slavíková-Bayerová & Fehrer 2007).

Species producing very **coarse isidia-like granules** include *L. isidiata*, *L. santosii*, *L. xerophila* and sometimes *L. crassissima*, and the first three species are also morphologically similar. All these taxa are easily distinguishable chemically by main diagnostic substances (see the species descriptions in **I**).

The species that can have **well developed dark hypothallus** include *L. atrotomentosa*, *L. aurescens*, *L. multiacida*, *L. nigrocincta* and *L. membranacea*, *L. normandinoides*, *L. pallida*. Three latter species almost always develop lobes, *L. atrotomentosa* can be lobate or not. *L. multiacida* has coarser soredia than the rest. *L. nigrocincta* usually looks different from other *Lepraria* species because of the very thick, very loose, brownish hypothallus is the dominant part, with a loose cover of scattered soredia. All these species also have different chemistry (see the species descriptions in **I**).

Numerous species have **powdery** (e. g. *L. elobata*, *L. umbricola*, also *L. incana*, *L. jackii* etc.), or **cottony thallus** (e. g. *L. eburnea*, *L. lobificans*, *L. nivalis*, *L. nylanderiana* etc.).

4.4. The substrate preferences of the epiphytic species in old-growth forests in Estonia

In paper **III**, the first attempt was made to explore the substrate use of different *Lepraria* species in the old-growth forests in Estonia. The results suggested that at least some degree of substratum specificity exists among the *Lepraria* species and it should be explored in a more detailed manner. In paper **III**, the different habitat use of *L. incana* compared to other *Lepraria* species treated collectively was reported. After the publication of paper **III**, more data became available and a more detailed treatment was thus possible in paper **IV**.

The treatment of *Lepraria* on generic level – the usual practice in ecological studies would be justified if the species had similar requirements for the substrate or if the samples were likely to contain only one species. Although *L. incana* was by far the most abundant species in these studies, being the main cause for g. *Lepraria* (if treated collectively) preferring spruce, 36% of thalli in the randomly collected samples belonged to other taxa with different substrate uses. In paper **III**, six *Lepraria* species were found from only one habitat type in a relatively small area.

15% of the specimens which were determined as *Lepraria* in the field by collectors were demonstrated to belong to other genera. Such percentage of initial misidentifications has also been mentioned in other studies (e.g. Baruffo 2006). This further demonstrates the need for more detailed determination.

The low frequency of *L. lobificans* compared to *L. incana* in the studied old growth forests is unexpected as *L. lobificans* is very common across Estonia in

different habitats (Saag & Saag 1999). The old spruce dominated forests may be especially suitable for *L. incana* because of the shade, relatively high humidity and low pH of spruce bark. This species often grows abundantly on the bases of norway spruce in Estonia. Also Baruffo *et al.* (2006) consider that it prefers acid substrata in humid places, other authors report it from various substrates (Laundon 1992, Tønsberg 1992, Lohtander 1994, Wirth & Heklau 1995, Kukwa 2006b). Additionally, Baruffo *et al.* (2006) report that in Italy both *L. eburnea* and *L. lobificans* are substratum indifferent on broader scale but corticolous specimens of the latter are still more frequent on neutral bark; that *L. jackii* is mainly epiphytic, also preferring neutral substrate and that *L. elobata* belongs to the epiphyte group together with *L. jackii* but is more often acidophytic. The present study was designed to compare coniferous and deciduous trees rather than acidic and neutral substrata. Nevertheless, given that conifers and birch have lower bark pH than other studied trees (Kuusinen 1996, Lõhmus & Lõhmus 2001), our data from Estonian old forests are in accord with the results of Baruffo *et al.* from Italy as far as *L. eburnea* and *L. lobificans* are concerned (IV, Appendix 1). Paper III noted that *L. incana* inhabited conifers slightly more frequently than deciduous trees, but this tendency was not statistically significant – unlike in the paper IV. Other *Lepraria* species were treated collectively in paper III, documenting the preference of this group for deciduous trees. This result is only partly supported in paper IV as *L. jackii* does not share this feature.

Finally, there is an open question as to how ecologists should sample *Lepraria* species if they cannot distinguish them from each other in the field. For most lichens, the sampling unit has traditionally been an individual tree, rock or even larger object, where the species abundance can be measured. In contrast, a *Lepraria* species from a collected piece of bark or wood is probably not representing the whole tree, as witnessed by the accidental co-existence of two or even three species in the 'specimens' analysed in the paper III. This means that the coverage of individual species cannot be measured unless a great number of samples are collected from each object. Further studies of the species coexistence should answer whether such multiple sampling is reasonable, given the large amount of additional work.

5. CONCLUSIONS

- ◆ A comparative review of 58 *Lepraria* species and 2 varieties is provided together with species descriptions and a key. For the first time, all taxa that are currently accepted in the world can be identified using a single key. The key is mainly based on the contents of secondary substances, however, morphological characters are used as well. Also, a comprehensive description of the genus *Lepraria* was compiled for paper I. The descriptions contain detailed information on morphology, chemistry, substrate and distribution. An overview is given of the taxonomic problems in the genus and chemically or morphologically similar groups of taxa. Some previously published but unnamed taxa by different authors are discussed. Today, the species concept is not uniform for different *Lepraria* taxa. Several chemotypes have been included in some species, while the presence or absence of a compound is considered to justify the taxonomic rank of species in many other cases. Partly, this is the result of the different amount of taxonomic effort spent on different species groups but also the concepts used by some authors differ significantly from each other. There are DNA sequences available for about 30 species, mostly supporting the distinctiveness of these taxa.
- ◆ Two new varieties are described: *Lepraria alpina* var. *zeorinica* and *L. caesioalba* var. *groenlandica* (paper II). Both taxa are morphologically identical to the typical varieties of the species, but differ in producing zeorin which belongs to the substance class of terpenoids, that has not been found from these species before. Neither of the new varieties has been found outside of Greenland. The rank of variety has not been used in other modern works on the genus. However, this taxonomic rank seems justified in these cases because of the presence of the new substance class, but absence of other discriminating characters indicates that the level of species may not be appropriate.
- ◆ *Lecanora leuckertiana* is transferred to *Lepraria* as *Lepraria leuckertiana* (Zedda) L. Saag (paper I). *Lecanora leuckertiana* was originally described as very similar to *Lepraria vouauxii*, but provisionally included in *Lecanora* because of its chemistry – usnic acid and zeorin. At that time the genus *Lepraria* did not comprise any usnic acid producing species. However, recently several species with usnic acid have been placed in *Lepraria* arguing that this character alone is not sufficient for determination at generic level.
- ◆ In a floristic study in Greenland, also the species of *Leprocaulon* were included (paper II). These are relatively similar to the *Lepraria* taxa, frequently growing intermixed and forming extensive soil-crusts, sometimes being hard to separate in the field. Thirteen species (plus two new varieties)

of *Lepraria* and three species of *Leprocaulon* were recorded from Greenland in paper II, ten of them new to the territory. Five species are new for the whole panarctic region. Altogether, 15 *Lepraria* species are known from the arctic areas after publication of paper II. Despite of the intensive taxonomic work that has been done especially in recent years, the modern data on many regions in the world are limited. Often many *Lepraria* species are misinterpreted or ignored by the lichenologists who are not specialised on sterile sorediate crusts. This means that the diversity of these species in most areas in the world is actually higher than reported in general floristic studies and lichen checklists.

- ◆ For several species found from Greenland, especially the recently described *Lepraria gelida*, new and interesting information was presented concerning morphology and chemistry. The *Leprarias* have distinctive distribution patterns in Greenland – few species are evenly distributed, while others grow mainly or only in southern Low Arctic subzone, being on the northern border of their world distribution.
- ◆ The *Lepraria* species have different substrate preferences in old growth forests in Estonia (papers III–IV). Also, the species diversity is rather great in local level. Eight species were found from old growth forests in Estonia. When their frequencies on different tree species and substrate types were analysed, the following statistically significant preferences were found. On the genus level, norway spruce is favoured as a substrate. *L. incana* was shown to prefer norway spruce, *L. elobata* and *L. lobificans* the bark of deciduous trees and *L. jackii* is not associated with any substrate group analysed. Other species did not show any affinities in this study probably due to low number of records. The ecological requirements of the species are not sufficiently studied until now in ecological studies, often being regarded as fairly similar. The treatment of *Lepraria* on generic level – the usual practice – would be justified if the species had similar requirements for the substrate or if the samples were likely to contain only one species. These conditions are not fulfilled, so the often tedious work of identifying *Lepraria* species should be completed to obtain exact results from ecological investigations of forest lichens.

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Web pages

- British Lichens – List of Lichens & Lichenicolous Fungi
(<http://www.thebls.org.uk/content/checklist.html>), British Lichen Society.

SUMMARY IN ESTONIAN

Taksonoomia ja ökoloogia probleemid perekonnas *Lepraria* (sugukond *Stereocaulaceae*, lihheniseerunud kottseened)

Löövesamblike perekonda *Lepraria* Ach. (*Stereocaulaceae*, *Ascomycota*) kuuluvad lihheniseerunud seened, kellel puudub suguline paljunemine ja kelle moodustatud samblikutallus on morfoloogiliselt lihtsa ehitusega. Perekond *Lepraria* on levinud üle maailma. Enamiku liikide tallus koosneb üksnes soreedidest. Taksonoomia selles rühmas põhineb suures osas sekundaarse ainevahetuse keemilistel tunnustel, kuna liikide eristamiseks kasutatavaid morfoloogilisi tunnuseid on napilt, küll aga toodavad need samblikud palju erinevaid samblikuaineid.

Samblikutallus koosneb tavaliselt kahest sümbiondist (müko- ja fotobiondist). Seetõttu on levimisel oluliseks piiranguks asjaolu, et uue talluse arenguks peab seen uues kasvukohas leidma sobiva fotobiondi. Evolutsiooni käigus on selle probleemi lahendamiseks tekkinud spetsiaalsed vegetatiivse paljunemise vahendid – soreedid ja isiidid. Soreedid on väikesed (läbimõõt enamasti alla 1 mm) koorkihita kehakesed, mis koosnevad fotobiondi rakkudest, mille ümber on mähkunud seenehüüfid. Isiidid on soreedidest pisut suuremad koorkihiga kaetud talluse väljakasved, mis talluse küljest lahti murdudes on levimisvõimelised. Soreede ja isiide levitavad tuul, vesi või loomad. Kui need levised satuvad sobivasse kasvukohta, siis saab kohe areneda samblikutallus, sest sümbioosi mõlemad partnerid on kohal.

Siiski toodab enamik samblikke moodustavaid seeni sugulisi eoseid, mis levivad üksi, ilma fotobiondita. Üldtunnustatud arvamuse kohaselt täiendavad vegetatiivne ja suguline paljunemine teineteist: suguta paljunemisevahendid võimaldavad antud kasvukohas edukate genotüüpide kiiret levimist suhteliselt väikesel alal; suguline paljunemine toodab uusi genotüüpe ja võimaldab neil kaugele levida. Liigi pikaajaliseks ellujäämiseks ja evolutsiooniks peab populatsioon reeglina olema geneetiliselt küllalt mitmekesine. Klonalse arenguga tavaliselt kaasnev geneetiline ühetaolisus võib elutingimuste muutumise korral põhjustada väljasuremise.

Hoolimata sugulise paljunemise puudumisest on geneetiline (ja keemiline) varieeruvus perekonnas *Lepraria* üllatavalt suur. Seni uuritud DNA regioonide molekulaarne mitmekesisus on võrreldav sugulisel teel paljunevate liikide omaga lähedastes süstemaatilistes rühmades. Liigiteke uuritavas perekonnas näib olevat sama tavaline, kui teistes rühmades, kuigi pole teada, millised mehhanismid seda võimaldavad.

Perekonna *Lepraria* kirjeldas E. Acharius aastal 1803. See kuulus kaua suguta (teis)seente kunstlikku rühma *Fungi Imperfecti*, mõned autorid paigutasid selle ka kottseente alla, asendit täpsustamata. Aastal 2002 näitasid

Ekman ja Tønsberg molekulaarsete meetodite abil perekonna valdava enamiku liikide monofüleetilisust ja kuulumist sugukonda *Stereocaulaceae* hõimkonnas *Ascomycota* klassis *Lecanoromycetes*. Praegu on see seisukoht üldtunnustatud.

Viimasel ajal on *Lepraria* perekonna uurimine olnud väga intensiivne ja liikide arv on pidevalt kasvanud. Näiteks alates aastast 2000 on kirjeldatud 35 uut liiki ja 6 liiki on üle toodud perekondadest *Lepruloma* ja *Lecanora*. Perekonnas on praegu kokku 58 liiki ja 2 varieteeti.

Liigikontseptsioon uuritavas rühmas ei ole ühtne. Mõni liik sisaldab mitut täiesti erinevat kemotüüpi, samas kui mitmel juhul peetakse ainult ühe aine esinemist või puudumist liiki eristavaks tunnuseks. Osalt on see eri liigirühmade erineva uurituse taseme tulemus, aga ka mõnede autorite liigikontseptsioonid on üsna erinevad. Molekulaarsed uuringud on näidanud, et keemilised sarnasused ei pruugi tähendada lähedast evolutsioonilist sugulust. Siiski, molekulaarseid andmeid leidub ligikaudu 30 *Lepraria* liigi kohta ja need näitavad, et kõik nad on üksteisest molekulaarselt erinevad, ja ainult üksikute taksonite DNA järjestused on omavahel väga sarnased. Enamasti toetavad molekulaarsed uuringud samblikuainetel ja morfoloogial põhinevat liikide eristamist.

Hoolimata intensiivsest taksonoomilisest uurimistööst, on mitmete maailma paikade kohta vähe kaasaegseid floristilisi andmeid. Olemasolevad andmed on sageli ekslikud liikide arvu kiire kasvu ja määramise keerukuse tõttu, eriti keemiliste tunnuste osas.

Gröönimaa on üks piirkondi, kus *Lepraria* on olnud vähem uuritud. Alates 20. sajandi keskpaigast on enamasti Taani teadlased sealt põhjalike botaaniliste inventuuride käigus korjanud mahukad kollektioonid, kuid steriilsed soredioossed kooriksamblikud neis kogudes on tavaliselt jäänud piisava analüüsita.

Viimastel kümnenditel on palju uuritud parasvöötme metsasamblike ökoloogiat. *Lepraria* liike on sellistes töödes peaaegu alati käsitletud kollektiivselt perekonna tasemel. Mõnikord esineb ka üks perekonna tavalisemaid, *L. incana*, liigini määratuna, kuid suure tõenäosusega on ka neis uurimustes teisi liike ignoreeritud. Seetõttu on *Lepraria* liikide ökoloogiast, näiteks substraadi-eelistustest, väga vähe teada.

Praktilist liikide määramist on raskendanud keemilise analüüsi töömahukus, kiire uue info lisandumine, taksonoomiliste kontseptsioonide muutumine ja kirjandusallikate fragmenteeritus. Lihhenoloogid, kes pole spetsialiseerunud steriilsetele soredioossetele kooriksamblikele, mõistavad seetõttu sageli *Lepraria* liike valesti või ignoreerivad neid. See omakorda on tekitanud olukorra, kus nende liikide tegelik mitmekesisus on enamikus maailma paigus tunduvalt suurem kui näidatud üldistes floristilistes töödes ja liiginimekirjades.

Ülalöeldust lähtuvalt on käesoleva töö eesmärgid püstitatud järgmiselt: (1) koostada võrdlev ülevaade kõigist perekonna *Lepraria* liikidest maailmas; (2) anda panus *Lepraria* mitmekesisuse ja taksonoomia mõistmisele, uurides seda

perekonda rikka lihhenoflooraga Gröönimaal, mis esindab mitmeid soredioosete pisisamblike poolest vähetuntud arktilisi elupaiku; (3) uurida *Lepraria* liikide ökonisše, täpsemalt substraadieelistusi Eesti vanade metsade näitel.

Käesoleva töö käigus on läbi vaadatud ligikaudu 2000 *Lepraria* eksemplari. Kasutatud on eksemplare järgmistest herbaariumitest: B, C, H, LD, NMW, PH, TU, TUR, UPS ja Š. Slavíková erakogu. Artikkel II põhineb peamiselt Kopenhageni Ülikooli Botaanikamuuseumi kogudel, artiklid III ja IV Tartu Ülikooli kogudel.

Koostati perekonna *Lepraria* kaasajastatud kirjeldus ja võrdlev ülevaade kõigist perekonna liikidest maailmas. Artikkel I aitab saada ülevaadet taksonoomilistest ja süstemaatilistest probleemidest perekonnas, esitatud on kõigi liikide standardiseeritud kirjeldused, mis sisaldavad infot morfoloogia, keemia, leviku ja substraadi kohta; samuti määramistabel. See tabel on esimene, mille abil saab määrata kõiki *Lepraria* liike; liikide eristamine lähtub peamiselt samblikuainete sisaldusest, kuid enamiku liikide puhul kasutatakse ka morfoloogilisi tunnuseid. Käsitletud on 58 liiki ja 2 varieteeti, lisaks arutletakse mõnede eristatud, kuid formaalselt kirjeldamata taksonite üle. Antakse ülevaade paljudest morfoloogiliselt, keemiliselt või molekulaarselt sarnaste liikide rühmadest.

Liik *Lecanora leuckertiana* Zedda paigutati ümber perekonda *Lepraria* nime all *Lepraria leuckertiana* (Zedda) L. Saag. Juba selle liigi originaalkirjelduses märgitakse tema suurt morfoloogilist sarnasust liigiga *Lepraria vouauxii*, kuid usniinhappe sisalduse tõttu paigutati uus takson perekonda *Lecanora*. Sel ajal valitses uurijate seas arvamus, et usniinhapet sisaldavad liigid on iseloomulikud *Lecanora* perekonnale ning ei esine perekonnas *Lepraria*. Viimasel ajal on aga *Lepraria* perekonda kirjeldatud mitmeid uusi usniinhapet sisaldavaid liike.

Gröönimaa uuringusse kaasati ka perekonna *Leprocaulon* liigid, mis on *Lepraria* liikidega võrdlemisi sarnased. Mõlemad perekonnad on Gröönimaal väga tavalised, sageli moodustades ulatuslikke „pinnase-koorikuid“, kus liigid kasvavad läbisegi ja on halvasti eristatavad. Leiti 13 liiki ja 2 varieteeti *Lepraria* perekonnast ning 3 perekonna *Leprocaulon* liiki, kokku 10 liiki esmakordselt Gröönimaa jaoks, 5 liiki olid uued tervele panarktilisele regioonile. Koostati liigikirjeldused, levikukaardid ja määramistabel. Mitmete taksonite, eelkõige hiljuti kirjeldatud arktilise liigi *Lepraria gelida* kohta esitati uut ja olulist morfoloogilist ja keemilist informatsiooni. Leitud liikidel on Gröönimaal erinevad levikumustrid – mõned liigid on levinud ühtlaselt, teised peamiselt või ainult lõunapoolsetel aladel, olles oma leviku põhjapiiril.

Kirjeldati kaks uut varieteeti: *Lepraria alpina* var. *zeorinica* ja *L. caesioalba* var. *groenlandica*. Mõlemad taksonid ei ole oma liigi põhivarieteedist morfoloogiliselt eristatavad, kuid sisaldavad lisaks teistele samblikuainetele neist liikidest varem leidmata terpenoidide aineklassi esindajat tseoriini. Kumbagi uut varieteeti pole leitud väljastpoolt Gröönimaad. Liigisisest taksonit varieteeti pole *Lepraria* perekonnas viimasel ajal kasutatud. Siiski tundub see antud

juhtudel asjakohane, kuna uue aineklassi esinemine annab põhjust taksoni kirjeldamiseks, kuid teiste eristavate tunnuste puudumise tõttu ei ole liigi tase põhjendatud.

Ökoloogilistes uurimustes (III–IV) leiti Eesti vanadest metsadest 8 epifüütset *Lepraria* liiki. Analüüsi nende esinemissagedusi erinevatel substraatidel. Võrreldud substraatideks olid puuliigid või okaspuud ja lehtpuud, uuriti eelistusi ka puidu suhtes. Valdavad puuliigid analüüsis olid harilik kuusk, harilik mänd, kask ja hall lepp. Statistiliselt analüüsi andmeid kokku 220 samblikueksamplari kohta. Kasutati Dufrene-Legendre indikaatorliikide analüüsi ja χ^2 -testi. Uuriti substraadieelistusi nii perekonna kui liigi tasemel. Perekonna tasemel osutus statistiliselt oluliselt eelistatud kasvupinnaks harilik kuusk. Liigi tasemel selgus, et *Lepraria incana* eelistab harilikku kuuske ja üldisemalt okaspuude koort. *L. elobata* ja *L. lobificans* eelistavad lehtpuude koort. Liigil *L. jackii* ei ole võrreldud substraatide suhtes eelistusi. Ülejäänud liigid olid analüüsis esindatud liiga väheste eksemplaridega, et nende kohta usaldusväärseid järeldusi teha.

Selgus, et *Lepraria* liikidel on erinevad ökonišid substraadinõudluse osas. Samuti leidis kinnitust võrdlemise suur lokaalne liigiline mitmekesisus. Lisaks kuulus ligikaudu 15% välitingimustes kogujate poolt *Lepraria* esindajateks peetud eksemplaridest teistesse perekondadesse; sellist esialgsete valemäärangute osakaalu on märkinud ka teised autorid. Ökoloogilistes töodes liikide perekonna tasemel käsitlemine oleks õigustatud, kui liikidel oleks sarnased nõudmised keskkonnale või kui oleks tõenäoline ainult ühe liigi esinemine materjali hulgas. Seega võib *Lepraria* perekonna tasemel käsitlemine ilma täpsema liigini määramiseta moonutada uuringute tulemusi.

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

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Abstract: A comparative review of 58 *Lepraria* species and 2 varieties is provided together with species descriptions and a key. *Lecanora leuckertiana* is transferred to *Lepraria*. The following taxa are included: *Lepraria achariana*, *L. adhaerens*, *L. alpina* var. *alpina*, *L. alpina* var. *zeorinica*, *L. atlantica*, *L. atrotomentosa*, *L. aurescens*, *L. bergensis*, *L. borealis*, *L. caesiella*, *L. caesioalba* var. *caesioalba*, *L. caesioalba* var. *groenlandica*, *L. celata*, *L. coriensis*, *L. crassissima*, *L. diffusa*, *L. eburnea*, *L. ecorticata*, *L. elobata*, *L. friabilis*, *L. gelida*, *L. goughensis*, *L. granulata*, *L. humida*, *L. impossibilis*, *L. incana*, *L. isidiata*, *L. jackii*, *L. lanata*, *L. lecanorica*, *L. leprolomopsis*, *L. leuckertiana*, *L. lobata*, *L. lobificans*, *L. membranacea*, *L. multiacida*, *L. neglecta*, *L. neojackii*, *L. nigrocincta*, *L. nivalis*, *L. normandinoides*, *L. nylanderiana*, *L. obtusatica*, *L. pallida*, *L. pulchra*, *L. rigidula*, *L. salazinica*, *L. santamonicae*, *L. santosii*, *L. sipmaniana*, *L. squamatica*, *L. straminea*, *L. sylvicola*, *L. texta*, *L. toensbergiana*, *L. toilenae*, *L. umbricola*, *L. usnica*, *L. vouauxii*, *L. xerophila*. Additionally some previously published but unnamed taxa by different authors are discussed.

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

Introduction

The genus *Lepraria* Ach. (*Stereocaulaceae*, *Ascomycota*) comprises morphologically simple lichen-forming fungi that never develop fruiting bodies. It is distributed worldwide. 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). The 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* Ach. was described by Acharius (1803) for sterile sorediate lichens. It is a *nomen conservandum* after the proposal by Laundon (1963). Initially the genus included various different species. It 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 history of this genus started when Laundon (1974, 1981) transferred the bright-coloured species producing anthraquinones to *Caloplaca* Th. Fr. and *Leproplaca* (Nyl.) Nyl. ex Hue (a synonym of *Caloplaca*) and the ones containing pulvinic acid derivatives to *Chrysothrix* Mont. The number of species in *Lepraria* was again decreased when taxa producing dibenzofuranes were placed in *Leproloma* Nyl. ex Cromb. (Laundon 1989, Leuckert & Kümmerling 1991). The concept of the genus was further developed by Laundon (1992) who also moved some species from *Crocynia* (Ach.) A. Massal. to *Lepraria*, and Tønsberg (1992), Lohtander (1995) and Leuckert et al. (1995). *L. lesdainii* was transferred to a new monotypic genus *Botryolepraria* Canals, Hern.-Mar., Gómez-Bolea & Llimona in 1997 (Canals et al. 1997). The leprose usnic acid producing taxa were placed in *Lecanora* Ach. by all these authors.

Ekman & Tønsberg (2002) first showed the monophyly of *Lepraria* in a molecular study. Additionally, the *Leproloma* species nested in *Lepraria* in their analysis and the clade showed affinities with *Stereocaulaceae*. Three species – *L. flavescens*, *Botryolepraria lesdainii*, *Lepraria obtusatica* – positioned outside the genus in Ekman & Tønsberg's analyse. *Leproloma* was formally synonymised with *Lepraria* by Kukwa (2002). *L. flavescens* was transferred to *Lecanora* as *L. rouxii* (Grube et al. 2004).

Sipman (2003, 2004) included also usnic acid containing species in *Lepraria* – an example that was followed by other authors (Kukwa 2006a, 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 (Aptroot 2002; Bayerová et al. 2005; Crespo et al. 2006; Elix 2005, 2006a; Elix et al. 2005; Flakus & Kukwa 2007; Kantvilas & Kukwa 2006; Knudsen & Elix 2007, 2008; Knudsen et al. 2007; Lendemer 2005; Lendemer & Harris 2007; Lendemer et al. 2008; Orange & Wolseley 2005; Orange 2001; Orange et al. 2001b; Saag et al. 2007; Sipman 2003, 2004; Slavíková-Bayerová & Fehrer 2007; Slavíková-Bayerová & Orange 2006; Tønsberg 2002; Tønsberg 2004; Tønsberg 2007; Tønsberg & Zhurbenko 2006; Wirth et al. 2004) and 6 species transferred to *Lepraria* from other genera, *Leproloma* and *Lecanora* (Kukwa 2002, 2006a; Sipman 2004). In this publication 58 *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. caesiocalba*, *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” – the 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 (Nelsen & Gargas 2008, Ekman & Tønsberg 2002).

The purpose of this publication is to provide a comparative review of all species currently accepted in the genus in a standardized manner, summing up the present situation, and also be of practical help to the lichenologists who are not specialists in the relatively fast developing genus *Lepraria*.

Material and methods

The current review is mainly based on literature, but also on original observations in many cases. Material from B, C, H, LD, NMW, PH, TU, TUR, UPS, 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. (2001a).

Some fatty acids which 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 porphyritic 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”.

Results

Lepraria Ach., nom. cons.

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

Thallus crustose to subfoliose or squamulose, with 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 substrate, sometimes parts of the thallus free from substrate, revealing lower surface; shape irregular or rosette-shaped (especially young thalli), individual thalli usually from few mm to 1 dm in diam., thalli may fuse to form more or less continuous covers up to several meters in 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 on 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 conspicuous weft, white, grey or brown to black or orange in patches; **prothallus** rarely present; **areoles** sometimes present in thick specimens; 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 in 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** trebouxiod green alga, most often *Asterochloris* (Hildreth & Ahmadjian 1981; Nelsen & Gargas 2006, 2008). **Ascomata** and **conidiomata** absent.

Substrate and ecology: 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.

Distribution: worldwide; according to current knowledge, highest number of species is found in temperate areas.

Chemistry: aliphatic acids, anthraquinones, benzyl esters, biphenyls, depsides, depsidones, dibenzofuranes, terpenoids, usnic acids.

***Lepraria achariana* Flakus & Kukwa**

Lichenologist 39(5): 464 (2007); type: Bolivia, Dept. La Paz, Prov. Manco Kapac, Mt. Horca del Inca near Copacabana village, 16°10'15"S, 69°05'05"W, 18 June 2006, A. Flakus 8670 (KRAM-L-holotype).

Thallus crustose, leprose, with powdery appearance; greenish grey to grey; thin; margin diffuse, **lobes** absent; cortex absent; true **medulla** absent but hypothallus may look like medulla; **hypothallus** usually well developed but hyphae loosely packed, white or orange in places (anthraquinones); **areoles** absent; **squamules** absent; **soredia** abundant, fine, up to 45 µm in diam., round; wall rather well developed but not complete; projecting hyphae usually absent, rarely few present, more common on lower side of marginal and single soredia on substratum, short, up to 10 µm, long on lower side of marginal and single soredia on substratum; consoredia prevalent, up to 75(–150) µm in diam.; **isidia-like structures** absent. **Photobiont** chlorococcoid, cells up to 13 µm in diam., sometimes with autospores visible inside.

Substrate and ecology: humus, terricolous mosses, rocks; found in open areas of high Andean Puna vegetation and upper montane cloud forest.

Distribution: South America (Bolivia).

Chemistry: lecanoric acid, roccellic/angardianic acid \pm , 2 to 4 unidentified anthraquinones \pm (2 of them major). K⁻ or lower surface K⁺ purple in patches, C⁺ carmine red, KC⁺ red, PD⁻.

Discussion. *L. neojackii* sometimes has very similar morphology to *L. achariana* but does not contain lecanoric acid. Chemically similar species that can produce lecanoric acid include *L. atrotomentosa*, *L. goughensis*, *L. impossibilis*, *L. lecanorica*. See the discussion under *L. atrotomentosa*.

Lepraria adhaerens K. Knudsen, Elix & Lendemer

Opuscula Philolichenum, 4: 5 (2007); type: U.S.A. California, San Diego Co., Torrey Pines State Park, 32° 54' 58"N, 117° 19' 56"W, 13. Apr. 2005, K. Knudsen et al. 2700 (UCR-holotype; ASU, CANB, PH, SD, UGDA-isotypes).

Thallus crustose, leprose, with granular appearance; light blue-grey, sometimes with a dull brownish tinge; thin to thick (up to 1 mm), relatively hard; shape irregular, individual colonies up to 2 cm, fused patches up to several meters; margin diffuse, **lobes** absent; cortex absent; **medulla** absent, but older thalli forming a lower necral layer of gelatinized granules; lower surface absent; **areoles** present in well developed thalli, divided by deep fissures; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant, fine to medium, 40–100 μm in diam., densely packed; wall present; projecting hyphae absent, but frequently with thin colourless hyphae acting as anchors or rhizines; soredia clumped together; **isidia-like structures** absent. **Photobiont** chlorococcoid, 10–14 μm in diam., often aggregating.

Substrate and ecology: mosses and lichens on different types of rock, rarely directly on soil or rock; open habitats, also those exposed to rain and sunlight, but sheltered places in snowy areas. **Distribution:** North America.

Chemistry: pannarin and zeorin (major to trace, very rarely absent), accessories include norpannarin \pm (trace), dechloropannarin \pm (trace), hypopannarin \pm (trace), atranorin \pm (trace). K⁻, C⁻, KC⁻, Pd⁺ orange.

Discussion. *L. santamonicae* and *L. coriensis* produce chlorodepsidones argopsin and norargopsin that are biosequentially related to pannarin, but otherwise these species differ chemically and morphologically. The morphology of *L. adhaerens* is most similar to that of *L. santamonicae* (Knudsen & Elix 2007), but is not radically different from other unstratified *Lepraria* species with indeterminate thalli which lack lobes. The most characteristic feature of *L. adhaerens* is the small attaching hyphae and the tendency of granules to adhere to one another and the substrate.

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

in Baruffo et al., Nova Hedwigia 83: 395 (2006); type: Weber, Lichenes exsiccati no. 609 (UPS-neotype, GZU, ASU-isoneotypes)

Crocynia alpina de Lesd., Bull. Soc. Bot. France 61: 85 (1914). – *Leproloma cacuminum* sensu J.R. Laundon, Lichenologist 24: 345 (1992). – *Leproloma angardianum* (Øvstedal) J.R. Laundon, Lichenologist 21(1): 19 (1989). – *Lepraria angardiana* Øvstedal, Nova Hedwigia 37: 687 (1983). – *Lepraria caerulescens* (Hue) Botnen & Øvstedal, Polar Research 6: 130 (1988). – *Lepraria cacuminum* sensu Loht., Ann. Bot. Fennici 32: 52 (1995). – non *Diploicia cacuminum* A. Massal., Symm. Lich. Nov.: 52 (1855).

Thallus crustose, leprose, with coarsely granular, rarely slightly powdery appearance; usually dark grey, sometimes light grey to almost white, often with bluish tinge; thick, rarely thin, usually hard, hyphae densely packed, firmly attached to the substrate; usually growing in irregular patches, young thalli often in rosettes, up to several cm in diam., rosettes up to c. 2 cm; margin usually delimited, sometimes diffuse, **lobes** sometimes present, minute, often obscure, without raised rims; cortex absent; **medulla** usually present, not evident, white; **hypothallus** sometimes present, poorly developed, whitish grey to brown or colourless, lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; rarely small patches with exposed medulla present, **soredia** abundant, coarse or variably sized, sometimes largest along margin, typically 100–150 µm in diam., convex or ellipsoidal, densely packed; wall distinct, with pruinose appearance; projecting hyphae sometimes present, short; consoredia present from few to abundant, typically 200–300 µm, convex or ellipsoidal; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 20 µm in diam.

Substrate and ecology: rock and saxicolous mosses, also soil, lichens, rarely bark; mostly acidic substrata, mostly exposed but also shaded places, mostly cool climate. **Distribution:** Europe, North and South America, Antarctica, Greenland.

Chemistry: atranorin, porphyritic 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.

Discussion. According to molecular studies, *L. alpina* belongs to a monophyletic group together with *L. atlantica*, *L. borealis*, *L. caesioalba*, *L. elobata*, *L. granulata* *L. humida* and *L. neglecta* (Ekman & Tønsberg 2002, Slavíková-Bayerová & Fehrer 2007). Morphologically similar species include *L. borealis*, *L. caesioalba*, *L. neglecta*, *L. granulata*, 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 (2006b), specimens with atranorin only or fatty acids only were placed in *L. borealis* by Saag et al. (2007); they can alternatively be considered deficient

representatives of *L. alpina* as there are no distinctive morphological differences between these two species (Prigodina-Lukošienė et al. 2003, Kukwa 2006b; see also Lohtander 1995). *L. alpina* var. *alpina* and *L. atlantica* have the same chemistry, see the discussion under *L. atlantica*. Very rarely *L. atlantica* may be morphologically similar to *L. alpina* (Saag et al. 2007).

***Lepraria alpina* var. *zeorinica* L. Saag**

Mycotaxon 102: 68 (2007); type: Greenland, Qingertivaq, alt. 550 m (66°06'N, 37°13'W), 30 July 1970, E. S. Hansen ESH-70.0032 (C-holotype, TU-isotype).

Thallus identical to *L. alpina* var. *alpina*.

Substrate and ecology: on soil and bryophytes, sometimes overgrowing other lichens. **Distribution:** Greenland.

Chemistry: contains the same diagnostic substances as *L. alpina* var. *alpina*, but also produces zeorin. K– or + yellow, C–, KC– or + yellow, Pd– or + yellow.

Discussion. Zeorin had not been reported from *L. alpina* before Saag et al. (2007) described this new variety.

***Lepraria atlantica* Orange**

Lichenologist 33(6): 462 (2001); type: Ireland, West Donegal (V.C. H35), southeast of Glenties, Owenbhan river, 1 April 1998, A. Orange 11829 (NMW-holotype, BG-isotype).

Thallus crustose, leprose, with powdery, rarely almost cottony appearance; usually pale bluish grey, sometimes whitish to greyish cream, sometimes greenish; thin to thick, not very firmly attached to the substrate; shape usually irregular, diameter variable; margin diffuse or delimited, **lobes** absent; cortex absent; true **medulla** absent but hypothallus may look like medulla; **hypothallus** present in patches, growing into cavities of substratum, hyphae below thallus usually sparse, white, lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; **soredia** abundant, fine to rarely coarse, 40–100(160–220) µm in diam., mostly convex, relatively densely, rarely loosely packed; wall indistinct; projecting hyphae rarely present, short; consoredia rare; **isidia-like structures** absent. **Photobiont** green, coccoid, 7–13 µm in diam.

Substrate and ecology: siliceous rock, mosses on siliceous rock, sometimes soil, rarely bark; sheltered from rain. **Distribution:** Europe, Australia, Greenland.

Chemistry. The common chemotypes contain (1) atranorin, porphyrilic acid and accessories, rangiformic acid; (2) atranorin, porphyrilic acid and accessories, roccellic/angardianic acid. Additionally, 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 (Saag et al. 2007). K+ yellow, C–, Pd– or + yellow.

Discussion. According to molecular studies, *L. atlantica* belongs to a monophyletic group together with *L. alpina*, *L. borealis*, *L. caesioalba*, *L.*

elobata, *L. granulata*, *L. humida* and *L. neglecta* (Ekman & Tønsberg 2002, Slavíková-Bayerová & Fehrer 2007). Morphologically similar species characterized by diffuse and powdery appearance include *L. celata*, *L. jackii*, *L. neojackii*, *L. sylvicola*, *L. toensbergiana*, and especially *L. humida* and *L. elobata*. *L. atlantica* is chemically distinct from these taxa by the content of porphyrilic acid and usually one or two fatty acids. This species is chemically identical to *L. alpina*, which differs in its granular (*L. neglecta* type) thallus; still, Saag et al. 2007 reported some specimens with intermediate morphology between these species. *L. atlantica* is chemically and morphologically rather similar to *L. neojackii*, which is described as containing both roccellic/angardianic and rangiformic acids at the same time but no atranorin. See also discussion under *L. jackii*.

Lepraria atrotomentosa Orange & Wolesey

Biblioth. Lichenol. 78: 328 (2001); type: Sri Lanka, Central Province, Nuwara Eliya District, Ramboda, 07°03'30"N, 80°42' E, 12. Jan. 2000, V. Karunaratne, K. Bombuwala & S. Mendis (BM-holotype, PDA-isotype).

Thallus crustose, leprose; with powdery, partly membranous, sometimes cottony appearance; pale blue-grey to greenish grey; thin to moderately thick, relatively soft, not very firmly attached to the substrate, partly loose; shape irregular, often fusing with other thalli, creating patches of individual and often scattered lobes together with non-lobate parts intermixed, up to several cm in diam.; 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; cortex absent; **medulla** present, thin, white; **hypothallus** usually thick, sometimes thin, lax, dark brown, forms a tomentum under lobes; **prothallus** absent; **areoles** absent; **squamules** absent; **soredia** abundant to sparse in places, sometimes exposing smooth ecorticate membranous surface, fine to medium, sometimes coarse, 60–200 µm in diam., usually relatively densely packed; without distinct wall; projecting hyphae rarely present, not abundant, short, up to 40 µm; **isidia-like structures** absent. **Photobiont** green, cells more or less spherical, 6–15 µm in diam.

Substrate and ecology: siliceous rock or soil, bark, shaded, sheltered, damp.

Distribution: China (Hong Kong), Taiwan, Sri Lanka, Japan.

Chemistry: lecanoric acid, atranorin, zeorin, unidentified fatty acids. K+ yellowish, C+ pink to red, KC+ more or less red, Pd+ yellow.

Discussion. *L. impossibilis* and *L. pallida* are similar morphologically. *L. impossibilis* contains pannaric acid 6-methylester in addition to lecanoric acid, *L. pallida* produces atranorin, zeorin and fatty acids. Unlobed specimens of *L. atrotomentosa* may resemble *L. incana* in appearance but *L. atrotomentosa* has a dark tomentum below the thallus and a different chemistry. *L. nigrocincta* and *L. aurescens* also have dark tomentum below thallus. *L. nigrocincta* contains divaricatic acid, *L. aurescens* produces thamnolic acid and the tomentum is less

extensive. Several species can develop well developed lobes, see the discussion under *L. membranacea*.

Species that can produce lecanoric acid include *L. achariana*, *L. atrotomentosa*, *L. goughensis*, *L. impossibilis*, *L. lecanorica*, but these species differ in the following aspects. *L. achariana* produces only roccellic/ angardianic (not always present) acid besides lecanoric acid and has stratified thallus with fine soredia and diffuse margin. *L. atrotomentosa* contains atranorin and zeorin and has well developed layer of dark hyphae on the lower side of thallus. *L. goughensis* contains gyrophoric acid and strepsilin (minor to trace amounts) and has very fine soredia and no hypothallus. *L. impossibilis* contains pannaric acid 6-methylester, otherwise being similar to some lobate morphs of *L. atrotomentosa*. *L. lecanorica* contains atranorin and has usually thick thallus without dark hypothallus.

***Lepraria aurescens* Orange & Wolseley**

Lichenologist 37(3): 247 (2005); type: Thailand, Chiang Mai Province, Doi Suthep, 18°48'N, 99°56'E, 25 Nov. 1991, P. A. Wolseley & B. Aguirre-Hudson 5001 (BM-holotype).

Thallus crustose, leprose; pale grey to pale yellowish grey; usually thin, c. 200 µm; margin diffuse, rarely partly weakly delimited, rim always absent, **lobes** absent; cortex absent; **medulla** absent; **hypothallus** present in places, brown, well developed, forming a loose weft; **areoles** absent; **squamules** absent; **soredia** abundant to sparse in few places, then dark tomentum visible between soredia, fine to medium, 40–100 µm in diam.; surface covered by weft of colourless hyphae; projecting hyphae usually absent, but present on marginal or solitary granules, long, projecting downwards, to 150(–300) µm, mostly dark, grey-brown; **isidia-like structures** absent. **Photobiont** green, coccoid.

Substrate and ecology: bark, sheltered places, dry forest. **Distribution:** Thailand.

Chemistry: thamnolic acid. K+ bright yellow, C–, KC–, Pd+ orange-yellow.

Discussion. *L. nigrocincta* is morphologically similar in fine granules, abundant weft of dark hyphae and sometimes yellowish colour; *L. atrotomentosa* also develops dark hypothallus. *L. nigrocincta* differs in producing divaricatic acid, *L. atrotomentosa* has blue-grey thallus with small lobes, contains lecanoric acid, zeorin, atranorin.

Species producing thamnolic acid include *L. aurescens*, *L. nylanderiana*, *L. pulchra*, *L. umbricola*. *L. aurescens* has usually thin pale grey to yellowish thallus with brown well developed hypothallus, diffuse margin. *L. nylanderiana* has usually thick whitish thallus with well developed greyish hypothallus, delimited margin, contains roccellic acid. *L. pulchra* has thin whitish to pale bluish grey thallus with whitish medulla, delimited margin with a rim, characteristic very short projecting hyphae on soredia. *L. umbricola* has usually

thin green thallus with predominantly no medulla or hypothallus, diffuse margin.

Lepraria bergensis Tønsberg

Graphis Scripta 14: 47 (2002); type: Norway. Hordaland: Bergen, Haukeland/Landaås, Vognstølen, 60°22.2'N, 5°21.8'E, 25 Nov. 2000, Tønsberg 28875 (BG-holotype; B, H, NMW-isotypes).

Thallus crustose, leprose, with membranous appearance; pale bluish grey; relatively thin, up to 220 µm excluding loose soredia, relatively soft, not very firmly attached to the substrate; young thalli form small rosettes up to few mm in diam., later fused patches 1 cm or more in diam. form; margin usually delimited, sharply raised (in saxicolous specimens), **lobes** usually distinct, up to few mm wide; cortex absent; **medulla** distinct in places, white; **hypothallus** not evident or orange-brown to brown, never conspicuous and not visible from above, hyphae below thallus projecting, orange-brown to brown or colourless, lower surface present, white (at least along margin), pale yellowish or brown; **prothallus** absent; **areoles** absent; **squamules** absent; **soredia** abundant, very fine, up to 25 µm in diam., mostly loosely packed; projecting hyphae present or absent, short; consoredia abundant, up to 200(–340) µm; **isidia-like structures** absent. **Photobiont** trebouxoid, to 16 µm in diameter.

Substrate and ecology: on siliceous rock, also on mosses on rock, shaded surfaces. **Distribution:** Europe – Norway, Great Britain, Germany (Spribille & Tønsberg 2007).

Chemistry: atranorin, rangiformic acid, norrangiformic acid (trace), fragilin, 7-chloroemodin, emodin, parietin, A01-anthrone; the anthraquinones are located mostly in the subthalline hyphae. K+ faint yellow, subthalline hyphae K+ purple (in patches), C–, Pd–.

Discussion. The morphologically similar species include *L. bergensis*, *L. membranacea*, *L. normandinoides*, *L. sipmaniana* that all have different diagnostic substances. *L. bergensis* produces atranorin, rangiformic acid and anthraquinones. *L. membranacea* always contains pannaric acid. *L. normandinoides* usually produces protocetraric acid and/or fumarprotocetraric acid besides constant roccellic acid and atranorin. *L. sipmaniana* is distinguished by pannaric acid 6-methylester and usually also anthraquinones. *L. humida*, too, produces anthraquinones, but lacks lobes. Several additional taxa can develop well developed lobes, see the discussion under *L. membranacea*.

Lepraria borealis Loht. & Tønsberg

in Lohtander, Ann. Bot. Fennici 31: 224 (1994); type: Norway, Nord-Trøndelag, Namsskogan, Børgefjell Natl. Park, Namskroken, 6. Jun. 1977, Tønsberg 1519 (BG-holotype, H-isotype).

Thallus crustose, leprose, with coarsely granular appearance; white or light grey, rarely dark grey, often with bluish tinge; thick, rarely thin, usually hard,

hyphae densely packed, sometimes relatively soft, firmly attached to the substrate; shape rosette-forming or irregular, rosettes to c. 2 cm in diam., fused patches up to c. 4 cm; margin usually delimited, sometimes diffuse, obscure minute **lobes** sometimes present, without raised rim; cortex absent; **medulla** sometimes present, not evident, white; **hypothallus** usually absent, lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant, coarse or variably sized, sometimes largest along margin, typically 100–200 µm in diam., convex, relatively loosely to densely packed; wall indistinct to distinct, with pruinose appearance; projecting hyphae often present, short, can be long in marginal soredia; consoredia sometimes present, typically 200–300 µm, sometimes larger; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 20 µm in diam.

Substrate and ecology: mosses on acidic rock, acidic rock, rarely soil, lichens, mostly exposed but also shaded places, mostly cool climate. **Distribution:** Europe, North America, Antarctica, Greenland.

Chemistry: commonest chemotype comprises (1) atranorin, rangiformic and ± norrangiformic acid; rarely (2) rangiformic acid is replaced by roccellic/angardianic acid or (3) both fatty acids are present. Saag et al. (2007) tentatively included specimens with (4) fatty acids only and (5) atranorin only in *L. borealis*.

Discussion. According to molecular studies, *L. borealis* belongs to a monophyletic group together with *L. alpina*, *L. atlantica*, *L. caesiocalba*, *L. elobata*, *L. granulata*, *L. humida* and *L. neglecta* (Ekman & Tønsberg 2002, Slavíková-Bayerová & Fehrer 2007). Morphologically similar species include *L. alpina*, *L. caesiocalba*, *L. neglecta*, *L. granulata*, 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 (2006b), specimens with atranorin only or fatty acids only were placed in *L. borealis* by Saag et al. (2007); they can alternatively be considered deficient representatives of *L. alpina* as there are no distinctive morphological differences between these two species (Prigodina-Lukošienė et al. 2003, Kukwa 2006b; see also Lohtander 1995).

Lepraria caesiella R.C. Harris

in Lendemer, *Opuscula Philolichenum* 2: 51 (2005); type: U.S.A., Pennsylvania, Monroe Co., Community Drive Wetlands, 41° 04' 43"N, 75° 00' 24"W, 24. Apr. 2004, J.C. Lendemer 2304 & R.C. Harris et al. (NY- holotype; isotypes distributed as *Lichens of Eastern North America Exsiccati*, no. 172).

Thallus crustose, leprose, with powdery appearance; pale bluish to greenish grey (fades to white in the herbarium); thin, 0.1–0.2 mm, firmly attached to the substrate; shape irregular, usually forming continuous patches, thallus diameter very variable in diam.; margin diffuse to poorly delimited, **lobes** absent; cortex

absent; **medulla** absent; **hypothallus** absent, lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant, very fine, 20–30 µm in diam., loosely to densely packed; projecting hyphae present, irregular, short, 25–30 µm; consoredia present, up to 100 µm; **isidia-like structures** absent. **Photobiont** green, coccoid.

Substrate and ecology: tree bark, rarely rock, lignum, soil, mosses.

Distribution: North America, South America (Chile), Greenland.

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

Discussion. *L. caesiella* was known earlier as “*Lepraria* sp. 3” from North America (Harris 1977). *L. incana* and *L. elobata* may be morphologically similar to this species. However, *L. incana* contains divaricatic acid, *L. elobata* stictic acid. *L. pallida* also contains atranorin and zeorin but always produces fatty acid(s) and has lobes; *L. jackii* s. lat. has been reported to contain zeorin as a rare accessory (Leuckert et al. 1995, Baruffo et al. 2006). Lendemé (2005) referred to an undescribed *Lepraria* from North America different from *L. caesiella*, that also produces atranorin and zeorin.

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

Lichenologist 24(4): 324 (1992); type: France, Seine-et-Maine, Forêt de Fontainebleau, July 1913, M. Bouly de Lesdain (E-holotype, BM, GL, PC-topotypes).

Crocynia caesioalba de Lesd., Bull. Soc. Bot. France 61: 84 (1914). – *Leproloma caesioalba* (de Lesd.) M. Choisy, Bull. mens. Soc. linn. Lyon II 19: 12 (1950) – *Crocynia henrici* de Lesd., Bull. Soc. Bot. France 61: 84 (1914). – *Lepraria zonata* Brodo, New York State Mus. & Sci. Service Bulletin 410: 263.

Thallus crustose, leprose, with coarsely granular appearance; light grey to almost white or dark grey, predominantly with bluish tinge; thick, very rarely thin, usually hard, hyphae densely packed, rarely somewhat softer, firmly attached to the substrate; shape rosette-forming or irregular, often concentric zones visible, up to several cm in diam., rosettes up to c. 2 cm; margin usually delimited, sometimes diffuse, obscure minute **lobes** sometimes present, without raised rims; cortex absent; **medulla** sometimes present, not evident, white; **hypothallus** usually absent, lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; rarely small patches with exposed medulla present, **soredia** abundant, coarse or variably sized, sometimes largest along margin, typically 100–150(–200) µm in diam., convex, densely packed; wall distinct, often with pruinose appearance; projecting hyphae sometimes present, short, can be long in marginal soredia; consoredia frequent, typically 200–300 µm, sometimes larger especially at margin, convex or ellipsoidal; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 19 µm in diam.

Substrate and ecology: mosses on acidic rock, acidic rock, soil, rarely bark, epiphytic mosses, lichens; exposed places, mostly cool climate, montane-alpine in tropics. **Distribution:** Europe, North and South America, Asia, Australasia, Antarctica, Greenland.

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) are placed in *L. borealis* as described by Lohtander (1994) and Prigodina-Lukošienė et al. (2003). Tønsberg (2004) recognised an additional chemotype with atranorin and roccellic acid without depsidones.

Chemotype (1): atranorin, fumarprotocetraric acid, protocetraric acid \pm (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, (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, (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 most frequent, 2 common and 3 rare but also found from different parts of the world.

Discussion. According to molecular studies, *L. caesioalba* belongs to a monophyletic group together with *L. alpina*, *L. atlantica*, *L. borealis*, *L. elobata*, *L. granulata*, *L. humida* and *L. neglecta*. In itself, *L. caesioalba* is not monophyletic (Ekman & Tønsberg 2002, Slavíková-Bayerová & Fehrer 2007), but no nomenclatural segregation has been proposed. Morphologically similar species include *L. alpina*, *L. borealis*, *L. neglecta*, *L. granulata*, but these taxa differ chemically.

Species with stictic acid and atranorin include *L. caesioalba*, *L. elobata*, *L. leprolomopsis*, *L. lobificans*, *L. multiacida* (stictic acid complex mostly in traces), *L. nivalis* (some chemotypes), *L. santosii*, *L. sp. 2* sensu Flakus & Kukwa (for this taxon, see Flakus & Kukwa 2007).

L. caesioalba has granular *L. neglecta*-type thallus, the widespread main variety does not produce zeorin. *L. elobata* has thin greenish thallus of relatively compact soredia without medulla or lobes, produces zeorin. *L. leprolomopsis* has thick whitish thallus with medulla, no lobes and white even lower surface, produces an unknown terpenoid. *L. lobificans* has greenish loosely packed soredia with long projecting hyphae and well developed white medulla, produces zeorin. *L. multiacida* contains stictic acid complex mostly in traces and additionally produces salazinic acid (minor to trace), strepsilin

derivates (minor to trace) and usually zeorin together with 1–2 unknown terpenoids; often has minute lobes. *L. nivalis* has thick whitish thallus with medulla, does not produce zeorin (see also discussion under *L. nivalis*). *L. santosii* has membranous thallus with well developed lobes.

The species that may contain protocetraric and/or fumarprotocetraric acids include *L. caesioalba*, *L. eburnea*, *L. friabilis*, *L. isidiata*, *L. lanata*, *L. nivalis*, *L. normandinoides*, *L. squamatica*, *L. toilenae*.

L. caesioalba has granular thallus of *L. neglecta* type morphology. *L. eburnea* contains alectorialic acid besides protocetraric acid and usually has soft powdery to cottony thallus. *L. friabilis* has thin finely powdery thallus, often with sparse individual soredia on the substrate. *L. isidiata* has lobes and isidia-like structures on thallus. *L. lanata* has characteristic very large consoredia surrounded by woolly anastomosing hyphae. *L. nivalis* has thick whitish thallus with medulla, may be morphologically similar to *L. eburnea* in some cases but chemically lacks alectorialic acid. *L. normandinoides* has membranous thallus usually with wide lobes, dark thick hyphae on the lower side. *L. squamatica* may sometimes have protocetraric acid only as trace accessory to squamatic acid. *L. toilenae* produces the uncommon malonprotocetraric acid as main substance, has very well developed light hypothallus.

***Lepraria caesioalba* var. *groenlandica* L. Saag**

Mycotaxon 102: 73 (2007); type: Greenland. Qaanaaq, Thule, alt. (77°29'N, 69°12'W), 28 June 1986, E. S. Hansen ESH-86.0321 (C-holotype, TU-isotype).

Thallus identical to the main variety.

Substrate and ecology: on soil and bryophytes, sometimes overgrowing other lichens, rarely on rocks. **Distribution:** Greenland.

Chemistry: (1) atranorin, stictic acid plus constictic and cryptostictic acids (in variable amounts, mostly minor), zeorin (in variable amounts), roccellic/angardianic acid; rarely (1a) roccellic/angardianic acid is replaced by rangiformic acid, or (1b) fatty acids are absent.

Discussion. Zeorin had not been reported from *L. caesioalba* before Saag et al. (2007) described this new variety. *L. caesioalba* var. *groenlandica* is chemically identical with *L. elobata* which is morphologically different in the following aspects: *L. elobata* has thin powdery thallus composed of mostly fine soredia (consoredia are rare) and diffuse thallus margin.

***Lepraria celata* Š. Slavíková**

Lichenologist 38(6): 504 (2006); type: Ukraine, the East Carpathians, north of Rachiv (Račov), west slope of Terentin Mt., 48°6'26.3"N, 24°12'20.4"E, 19 July 2004, Š. Bayerová 3448 (PRA-holotype; BG, NMW-isotypes; GenBank accession no. DQ401100).

Thallus crustose, leprose, with powdery appearance; grey-green to whitish green; thin to thick, relatively soft, not very firmly attached to the substrate;

shape usually irregular; margin diffuse or delimited, **lobes** absent; cortex absent; true **medulla** absent but hypothallus may look like medulla; **hypothallus** of sparse patches of hyphae growing into cavities of substratum, hyphae below thallus usually sparse, white, lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; **soredia** abundant, fine, (20-)35–50(–60) μm in diam., mostly convex, loosely packed; projecting hyphae rarely present, short; **isidia-like structures** absent. **Photobiont** chlorococcoid.

Substrate and ecology: terricolous – soil and debris, mosses; open habitats, often in rock crevices. **Distribution:** Europe (Bulgaria and Ukraine), montane; probably wider.

Chemistry: atranorin \pm (major to minor), roccellic/angardianic acid. K– or + faint yellowish, C–, Pd–.

Discussion. According to molecular studies, *L. celata* is close to but still different from *L. jackii* (Slavíková-Bayerová & Orange 2006, Fehrer et al. unpublished). Morphologically similar species include *L. atlantica*, *L. humida*, *L. elobata* and especially *L. jackii*, *L. neojackii*, *L. toensbergiana* and *L. sylvicola* but all these taxa can be distinguished chemically. *L. celata* is chemically identical to a chemotype of *L. borealis* (sensu Prigodina-Lukošienė et al. 2003, Kukwa 2006b, Saag et al. 2007), *L. caesioalba* (chemotype III sensu Tønsberg 2004), *L. jackii* sensu lato, and *L. normandinoides* (rare chemotype III sensu Lendemer & Harris 2007). *L. borealis* and *L. caesioalba* are distinct in their granular (*L. neglecta* type) thallus, *L. normandinoides* has marginal lobes and dark rhizohyphae. See also discussion under *L. jackii*.

Lepraria coriensis (Hue) Sipman

Herzogia 17: 28 (2004); type: South Korea, Cheju-do, Hongno, Oct. 1906, R. P. Faurie 645 (KYO-isotype).

Crocynia coriensis Hue, Bull. Soc. Bot. France 71: 386 (1924). – *Lecanora coriensis* (Hue) J.R. Laundon, Nova Hedwigia 76: 97 (2003).

Thallus crustose, leprose, with powdery to membranous appearance; greenish to whitish or yellowish grey; thin to moderately thick, relatively soft, not very firmly attached to the substrate, sometimes partly loose; shape irregular or rosette-forming, often fusing with other thalli, usually up to 10 cm; margin delimited, **lobes** present, obscure or more often well developed (0.5–2 mm wide) and with raised marginal rim; cortex absent; **medulla** usually present, thin to medium, white; **hypothallus** sometimes present, thin, brown to black; **areoles** absent; **squamules** absent; sometimes soredia sparse in places, exposing smooth ecorticate surface, especially near margins, **soredia** abundant to sparse in places, fine to coarse, up to 300 μm in diam., relatively loosely packed; projecting hyphae usually absent; **isidia-like structures** absent. **Photobiont** chlorococcoid, up to 13 μm in diam.

Substrate and ecology: rock (mostly siliceous), wood, bark, mosses, soil; shaded and sheltered places. **Distribution:** Australia, Eastern Asia, India; tropical to subtropical.

Chemistry: Three chemotypes were distinguished in a detailed chemical survey by Elix (2006): (1) usnic acid, zeorin, protodehydroconstipatic and constipatic acids (major to minor), isousnic acid \pm (minor to trace), atranorin \pm (trace); (2) usnic acid, zeorin, protodehydroconstipatic and constipatic acids (minor to trace), argopsin (minor), norargopsin (minor to trace) isousnic acid \pm (minor to trace), atranorin \pm (minor to trace); (3) usnic acid, zeorin, protodehydroconstipatic and constipatic acids (minor to trace), caloploicin (minor), fulgidin (minor to trace), isousnic acid \pm (minor to trace), atranorin \pm (trace); the third chemotype was considered rare. Laundon (2003) reported that rarely zeorin can be missing. K-, C-, KC-, Pd-.

Discussion. *L. sipmaniana* can resemble *L. coriensis* in having well developed lobes with smooth surface and scarce granules, but is more intensely yellow and has different chemistry. Very strongly lobate specimens of *L. coriensis* may be similar to *L. membranacea* that is also different chemically, see the discussion under *L. membranacea*. *L. ecorticata*, *L. straminea*, *L. texta*, *L. usnica* and *L. leuckertiana* contain usnic acid and usually zeorin like *Lepraria coriensis*, but differ in the following aspects. *L. ecorticata*, *L. straminea* and *L. texta* have no lobes and *L. straminea* has corticate granules; *L. leuckertiana* is only obscurely and minutely lobed. The lobes of *L. usnica* are usually small (<0.5 mm), irregular and without marginal rim; that species produces minor amounts of contortin and lacks protodehydroconstipatic and constipatic acids. The chemical differences between *L. coriensis* and more recent *L. usnica* were demonstrated by Elix (2006). Some authors have raised the question of the distinctiveness of *L. usnica* (Orange and Wolseley 2005). *L. santamonicae* produces argopsin, like *L. coriensis*, but it has no medulla nor lobes, does not contain usnic acid and argopsin is major secondary substance.

Lepraria crassissima (Hue) Lettau

Feddes Repert. 61: 125 (1958). – *Crocynia crassissima* Hue, Bull. Soc. Bot. France 71: 393 (1924); type: France, Dépt. Vosges: Docelles, Claudel et Harmand, Lich.Gall. 400 (B-isotype).

Thallus crustose, leprose, with cottony to powdery or membranous appearance; bluish, greyish or greenish, brownish patches of dying parts often present; thick, relatively soft, sometimes weakly attached to the substrate; shape usually rosette-forming, uneven, often folded, usually several cm in diam.; margin usually delimited, **lobes** sometimes present, poorly defined; cortex absent; **medulla** present, very thick, white; lower surface distinct, folded (if whole thallus folded), smooth to tomentose, white to brownish; **prothallus** absent; **areoles** absent; **squamules** absent; often eroded patches with exposed medulla on older specimens, **soredia** abundant, mostly coarse, up to

300(–400) µm in diam., loosely packed; projecting hyphae present, short to long; large granules slightly **resembling isidia** that become sorediate may be present in well developed thalli. **Photobiont** green, coccoid.

Substrate and ecology: mostly siliceous rock and epilithic mosses, sometimes bark or calcareous rock; shaded, humid. **Distribution:** Europe, Australia.

Chemistry: divaricatic acid, nordivaricatic acid (major, rarely trace), zeorin ± (major to minor). K–, C+rose-red, KC–, Pd–.

Discussion. Species producing divaricatic acid and zeorin include *L. crassissima*, *L. incana* and *L. nigrocincta*, but differ in following aspects. *L. incana* and *L. nigrocincta* contain nordivaricatic acid in trace amount or it is absent, unlike *L. crassissima*. *L. incana* is mostly composed of soredia (powdery), lower surface not distinct, thallus never folded and rarely delimited. *L. nigrocincta* has cottony appearance like *L. crassissima*, but develops dominant blackish hypothallus and partly scarce soredia. Additionally, Baruffo et al. (2006) reported divaricatic acid in *L. rigidula* as a very rare accessory. That species is distinct by its lax cottony thallus and very long projecting hyphae from soredia, and producing atranorin and nephrosteranic acid.

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

Lepraria diffusa (J.R. Laundon) Kukwa

Ann. Bot. Fennici 39(3): 226 (2002); type: Finlandia, Oulu, Paltamo, Melalahti, Viilonkallio, 11. Oct. 1959, A. J. Huuskonen & L. Heikkinen (BM-holotype).

Leproloma diffusum J.R Laundon, Lichenologist 21(1): 16 (1989). – *Lepraria diffusa* var. *chrysodetoides* (J.R. Laundon) Kukwa, Ann. Bot. Fennici 39(3): 226 (2002). – *Leproloma diffusum* var. *chrysodetoides* J. R. Laundon, Lichenologist 21(1): 18 (1989).

Thallus crustose, leprose, with powdery, rarely slightly cottony appearance; greenish white, sometimes greenish yellow with occasional orange-yellow patches; medium to thick, soft, firmly attached to the substrate; shape irregular; margin diffuse, rarely delimited, **lobes** absent; cortex absent; **medulla** present, usually thick, sometimes thin, white; **hypothallus** sometimes present, weakly developed, whitish grey to brownish; **areoles** absent; **squamules** absent; thallus surfaces without soredia rarely present, medulla exposed but only in small patches or fissures, **soredia** abundant, coarse, up to 100 µm in diam., rather

loosely packed; projecting hyphae sometimes present, short; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 15 µm in diam.

Substrate and ecology: mosses on calcareous rock, calcareous rock, rarely bark or soil; mostly shaded and sheltered places. **Distribution:** Asia, Europe, North America.

Chemistry: 4-oxypannaric acid 2-methylester, 4-oxypannaric acid ± (minor to trace), pannaric acid methylester ± (trace), pannaric acid 2- methylester ± (trace), pannaric acid ± (trace) and other dibenzofurans ± in traces (see Elix & Tønsberg 2006), 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.

Discussion. *L. eburnea*, *L. lobificans* may have similar morphology but do not produce dibenzofuranes. *L. diffusa* var. *chrysodetoides* was subsumed within var. *diffusa* by Kukwa (2006b). It was described based on yellow pigment by Laundon (1989) but detection of this is problematic, and the substance, possibly the diagnostic dibenzofurane itself, appears to be present also in main variety (Kukwa 2006b). *L. vouauxii* produces dibenzofuranes and is sometimes also morphologically similar. However, *L. diffusa* is more powdery, with less or no patches with exposed medulla, contains 4-oxypannaric acid 2-methylester as major substance. Sometimes *L. leprolomopsis*, *L. eburnea*, *L. lobificans*, *L. nivalis*, *L. nylanderiana* and *L. vouauxii* may be morphologically similar to *L. diffusa*, see the discussion under *L. leprolomopsis*.

Lepraria eburnea J.R. Laundon

Lichenologist 24(4): 331 (1992); type: United Kingdom, England, London Borough of Hammersmith and Fulham (V.C. 21, Middlesex), 30 June 1987, J. R. Laundon 3185 (BM-holotype).

Lepraria frigida J.R. Laundon, Lichenologist 24(4): 332 (1992).

Thallus crustose, leprose, with powdery, often cottony appearance; white to light grey, often cream or greenish, sometimes with rose tinge (herbarium specimens, caused by alectorialic acid); usually thick and soft, firmly or sometimes partly weakly attached to the substrate; shape irregular, up to 1 dm or more in diam.; margin diffuse, rarely delimited, **lobes** absent or very rarely obscure lobes present; cortex absent; **medulla** usually present, usually thick, white; **hypothallus** usually not distinct but sometimes small patches of grey-brown hyphae in cavities below thallus, lower surface not distinct; **areoles** absent; **squamules** absent; thallus surfaces without soredia often present, also soredia often embedded in hyphal weft, **soredia** abundant, mostly fine, up to 60 µm in diam., loosely packed; wall indistinct to distinct; projecting hyphae usually present, usually short (to 40 µm), sometimes long (to 100 µm) particularly on margin; consoredia present, up to 200(–400) µm, loosely packed; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 20 µm in diam.

Substrate and ecology: substratum indifferent - mosses, bark, wood, rock, soil, lichens. **Distribution:** Australasia, Europe, Greenland, North America.

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

Discussion. Species producing alectorialic acid include *L. eburnea*, *L. gelida* and *L. neglecta*. *L. eburnea* and *L. gelida* both have soft light-coloured thallus, but *L. gelida* contains porphyrilic acid that never occurs in *L. eburnea* which sometimes produces protocetraric acid instead. *L. neglecta* is easily recognisable by its characteristic granular thallus, it lacks both porphyrilic and protocetraric acids. *L. frigida* was synonymised with *L. eburnea* by Orange (1997), showing that there is chemical and morphological continuity between these species. Sometimes *L. leprolomopsis*, *L. diffusa*, *L. lobificans*, *L. nivalis*, *L. nylanderiana* and *L. vouauxii* may be morphologically similar to *L. eburnea*, see the discussion under *L. leprolomopsis*. Several species produce protocetraric and/or fumarprotocetraric acids, see the discussion under *L. caesiocalba*.

Lepraria ecorticata (J.R. Laundon) Kukwa

Mycotaxon 97: 64 (2006); type: United Kingdom, England, Devon, Ilfracombe, Torrs Walks, 1. Sept. 1971, J. R. Laundon 2851 (BM-holotype).

Lecanora ecorticata J.R. Laundon, Nova Hedwigia 76: 100 (2003).

Thallus crustose, leprose, with powdery appearance; greyish green to greenish grey, often with yellowish tinge; usually thick, firmly attached to the substrate; shape usually irregular, thallus diameter can be extensive; margin diffuse, **lobes** absent; cortex absent; **medulla** rarely present in places, weakly developed; **prothallus** absent; **areoles** sometimes present on thick specimens; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant, mostly fine to medium, 10–100 µm in diam.; soredia well separated from each-other; **isidia-like structures** absent. **Photobiont** chlorococcoid, up to 15 µm in diam.

Substrate and ecology: siliceous rock, mosses on rock, sometimes lichens; mostly shaded and sheltered places. **Distribution:** Europe, North America, South America, Asia (China).

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

Discussion. Chemically similar taxa include *L. coriensis*, *L. straminea*, *L. texta*, *L. usnica* and *L. leuckertiana* which produce usnic acid and usually

zeorin, but differ in following aspects. *L. coriensis* and *L. usnica* have lobes and medulla. *L. straminea* has corticate granules. *L. leuckertiana* has cottony appearance with well developed medulla and the soredia are not well separated from one another. Some soredia of *L. texta* are also not well separated, that species also can develop a hypothallus. Usually the appearances of *L. texta* and *L. ecorticata* are different.

Lepraria elobata Tønsberg

Sommerfeltia 14: 197 (1992); type: Norway, Vest-Agder, Krisiansand, Hamresand, 28. Sept. 1991, T. Tønsberg 17404 (BG-holotype).

Thallus crustose, leprose, with powdery appearance; bluish grey or greenish grey; usually thin, sometimes thick, firmly attached to the substrate; shape irregular, up to 1 dm or more in diam.; margin diffuse, **lobes** absent, very rarely flattened aggregations of densely packed hyphae up to 1 mm in diam. present; cortex absent; **medulla** absent or very rarely present, weakly developed; **hypothallus** absent, lower surface absent; **areoles** absent; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant, mostly fine, 20–45 µm in diam., loosely to relatively densely packed; wall usually not complete; projecting hyphae absent; consoredia sometimes present, up to 100 µm; soredia well separated from one another; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 18 µm in diam.

Substrate and ecology: bark, sometimes soil, wood, siliceous rock, mosses; shaded, humid places. **Distribution:** Europe and North America, Greenland.

Chemistry: atranorin, stictic acid, constictic acid, cryptostictic acid, zeorin, very rarely an unidentified fatty acid (major to trace). K– or + yellow, C–, KC–, Pd+ orange.

Discussion. According to molecular studies, *L. elobata* belongs to a monophyletic group together with *L. alpina*, *L. atlantica*, *L. borealis*, *L. caesioalba*, *L. granulata*, *L. humida* and *L. neglecta* (Ekman & Tønsberg 2002, Slavíková-Bayerová & Fehrer 2007). *L. lobificans* and the rare *L. caesioalba* var. *groenlandica* have the same chemistry as *L. elobata*; *L. lobificans* has well developed medulla and cottony appearance, *L. caesioalba* is granular and mostly with delimited margin, belonging to *L. neglecta* group. Morphologically, *L. caesiella* and *L. incana* may be similar to *L. elobata*, but are easily separable chemically (see the descriptions of these species).

Several species can produce the stictic acid complex and atranorin, see the discussion under *L. caesioalba*.

Lepraria friabilis Lendemer, K. Knudsen & Elix

Opuscula Philolichenum 5: 64 (2008); type: U.S.A. Alabama, Baldwin Co., Splinter Hill Bog Preserve, 12. Apr. 2007, J. C. Lendemer et al. 9063 (NY-holotype; B, CANB, UCR, UDGA, HERB. LENDEMER-isotypes).

Thallus crustose, leprose, with powdery appearance; pale bluish to greenish grey or almost white; thin, less than 0.5 mm thick, relatively soft; shape irregular, usually continuous patches form, variable in diam.; margin diffuse, **lobes** absent; cortex absent; **medulla** absent; **hypothallus** present, thin, colourless, not evident, lower surface absent; **prothallus** not evident, thin, relatively broad, colourless; **areoles** absent; **squamules** absent; thallus surfaces without soredia absent, **soredia** sparse to abundant, very fine, (10-)20–30 µm in diam., relatively densely packed; wall usually distinct; projecting hyphae usually present, short; consoredia present, up to 60 µm; **isidia-like structures** absent. **Photobiont** green, coccoid, c. 7–10 µm in diam.

Substrate and ecology: bark of conifers; humid habitats. **Distribution:** southern North America.

Chemistry. This species comprises two chemotypes: (1) fumarprotocetraric acid with minor amounts of protocetraric acid, succinprotocetraric acid and confumarprotocetraric acid; (2) fumarprotocetraric acid only. Both chemotypes K⁻, C⁻, KC⁻, Pd⁺ orange or red.

Discussion. The species that may contain protocetraric and/or fumarprotocetraric acids include *L. caesiocalba*, *L. eburnea*, *L. friabilis*, *L. isidiata*, *L. lanata*, *L. nivalis*, *L. normandinoides*, *L. squamatica*, *L. toilenae*, see the discussion under *L. caesiocalba*. Morphologically *L. friabilis* is most similar with *L. caesiella*, but differs in slightly smaller soredia that are often sparsely distributed on the substrate, forming thinner thallus. *L. caesiella* produces atranorin and zeorin, while *L. friabilis* contains fumarprotocetraric acid.

Lepraria gelida Tønsberg & Zhurb.

Graphis Scripta, 18: 64 (2006); type: Svalbard, Spitsbergen, SSE of Wijdefjorden, E of Austfjorden, SE of Finnekroken, 78°56.09'N, 16°30.19'E, 5 July 2002, Tønsberg 31049 (BG-holotype, NMW-isotype).

Thallus crustose, leprose, with powdery to cottony, rarely slightly granular appearance; white, cream or light grey, sometimes with rose tinge (herbarium specimens), only very rarely with bluish tinge; usually thick and relatively soft, soredia in cushions, rarely thin and soredia sparsely and evenly distributed, not very firmly attached to the substrate; shape usually growing in irregular patches, sometimes young thalli form rosettes up to 1 cm, 1–3 cm, rarely up to 10 cm in diam.; margin diffuse to delimited, **lobes** usually absent, rarely obscure lobe-like structures present; cortex absent; **medulla** present, rarely not evident, distinct, thick, rarely thin, white; **areoles** absent; **squamules** absent; thallus surfaces without soredia present, variably sized, sometimes relatively large, medulla exposed, **soredia** abundant, may be sparse in places, variably sized, mostly 65–100 µm, occasionally few up to 200 µm in diam., relatively loosely packed; projecting hyphae present, short to medium; **isidia-like structures** absent.

Substrate and ecology: soil and mosses, sometimes lichens, rarely bark; open habitats. **Distribution:** Greenland, Svalbard and the Russian arctic islands near the Taimyr peninsula (Tønsberg & Zhurbenko 2006, Saag et al. 2007).

Chemistry: alectorialic and porphyrylic acids. K+ yellow or orange, C–, KC+ red, Pd+ yellow or orange.

Discussion. Species producing alectorialic acid include *L. eburnea*, *L. gelida* and *L. neglecta*. *L. eburnea* and *L. gelida* both have soft light-coloured thallus, but *L. gelida* contains porphyrylic acid that never occurs in *L. eburnea*. *L. neglecta* is easily recognisable by its characteristic granular thallus, it also lacks porphyrylic acid. Porphyrylic acid is produced by *L. alpina* and *L. atlantica*, which never contain alectorialic acid. *L. vouauxii* is often quite similar to *L. gelida* in morphological features but produces pannaric acid 6-methylester and atranorin.

Lepraria goughensis Elix & Øvstedal

Mycotaxon 93: 274 (2005); type: Gough Island, Seal Beach, 40°20'S, 9°52'W, 22. Sept. 1999, N. Gremmen 99–701 (BG-holotype).

Thallus crustose, leprose, with powdery appearance; grey-green; thin, 0.2–0.3 mm; shape rosette, 1–4 cm in diam.; margin delimited, usually poorly defined **lobes** present; cortex absent; **medulla** absent; **hypothallus** absent, lower surface absent; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant, very fine, 20–26 µm in diam.; projecting hyphae present, numerous; **isidia-like structures** absent. **Photobiont** green, coccoid.

Substrate and ecology: mosses, debris, peat; shaded, humid places. **Distribution:** Gough Island (South Atlantic).

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–.

Discussion. Chemically similar species that can produce lecanoric acid include *L. achariana*, *L. atrotomentosa*, *L. impossibilis*, *L. lecanorica*. See the discussion under *L. atrotomentosa*. *L. multiacida*, *L. xerophila* can produce strepsilin and *L. bergensis*, *L. sipmaniana* and a chemotype of *L. incana* contain anthraquinones, but all these taxa differ in both morphology and chemistry (see descriptions of these species).

Lepraria granulata Š. Slavíková

Lichenologist 39(4): 321 (2007); type: Bulgaria, Rila Mts, Rila National Park, 42°12'1.7"N, 23°19'27.7"E, 23 June 2004, Š. Bayerová 3243 & M. Slavík (PRA-holotype; BG-isotype; GenBank accession no. DQ914539).

Thallus crustose, leprose, with granular appearance; white, whitish grey to grey, sometimes with faint bluish grey tinge, granules below the upper surface sometimes creamy; relatively soft, hyphae quite loosely packed, firmly attached to the substrate; margin delimited to diffuse, **lobes** sometimes present, obscure; cortex absent; **medulla** absent; **hypothallus** usually scarce, whitish grey, grey

to blackish grey, occasionally pale yellowish orange-brown, lower surface absent; **areoles** absent; **squamules** absent; **soredia** abundant, coarse, up to 0.2(–0.3) mm in diam.; projecting hyphae usually absent; **isidia-like structures** absent.

Substrate and ecology: mainly on moss on siliceous rock, sometimes on soil. **Distribution:** so far known from Central and Eastern Europe.

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 recent species is the production of two unknown fatty acids, “granulata unknown 1 & 2”, for TLC characteristics see Slavíková-Bayerová & Fehrer (2007).

Discussion. According to molecular studies, *L. granulata* belongs to a monophyletic group together with *L. alpina*, *L. atlantica*, *L. borealis*, *L. caesioalba*, *L. elobata*, *L. humida* and *L. neglecta* (Ekman & Tønberg 2002, Slavíková-Bayerová & Fehrer 2007). Slavíková-Bayerová & Fehrer (2007) additionally described *L. sp. G* that is chemically identical to *L. granulata*, and also is very close to that species by means of ITS sequence, but morphologically is more similar to *L. humida* than to *L. granulata*. 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” and “granulata unknown 2”.

Lepraria humida Š. Slavíková & Orange

Lichenologist 38(6): 505 (2006); type: United Kingdom, Wales, Merioneth (V.C. 48), Rhyd-y-sarn, south of Clogwyn y Geifr, 25 January 2005, A. Orange 15754 (PRA-holotype, BG, NMW-isotypes; GenBank accession no. DQ401101).

Thallus crustose, leprose, with powdery appearance; grey-green to whitish green; thin to thick; shape usually irregular; margin diffuse or delimited, **lobes** absent; cortex absent; true **medulla** absent; **hypothallus** weakly developed, hyphae below thallus sparse, pale orange-brown, lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; **soredia** abundant, mostly fine to medium sized, 40–100(–160) µm in diam., relatively densely packed; projecting hyphae absent; **isidia-like structures** absent. **Photobiont** chlorococcoid.

Substrate and ecology: siliceous rocks, often between mosses; rain-sheltered damp surfaces. **Distribution:** British Isles.

Chemistry: The usual chemotype contains (1) atranorin, jackinic/rangiformic acid, norjackinic/norrangiformic acid ± (minor), angardianic/roccellic acid ± (minor), unknown anthraquinones ± (minor, in subthalline hyphae only); sometimes (2) stictic and constictic acids have been found in addition to usual substances, but were interpreted as contamination by Slavíková-Bayerová &

Orange (2006). K+ yellowish, hyphae below thallus K+ purple-red, C-, Pd- or + yellow.

Discussion. According to molecular studies, *L. humida* is distinct from *L. jackii* and close to *L. atlantica*, thus belonging to the extended *L. neglecta* group (Ekman & Tønsberg 2002, Slavíková-Bayerová & Orange 2006, Slavíková-Bayerová & Fehrer 2007, Fehrer et al. unpublished). Morphologically similar species include *L. jackii*, *L. neojackii*, *L. toensbergiana*, *L. sylvicola* and especially *L. atlantica* and *L. elobata*. *L. humida* is distinct by its chemistry, especially anthraquinones in subthalline hyphae, and ecology. *L. bergensis* also contains anthraquinones but in that species, anthraquinones are usually abundant in the underside of thallus, while in *L. humida* they are confined to patches of subthalline hyphae (Slavíková-Bayerová & Orange 2006).

Slavíková-Bayerová & Orange (2006) also reported sp. H which was said to be morphologically and chemically identical to *L. humida* but distinct in ITS sequences, growing on rain-sheltered siliceous rocks, over moss, rarely on bark in Western to Central Europe. Slavíková-Bayerová & Fehrer (2007) added sp. BG of 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, Depto. Ahuachapán, P. N. Impossible, sector La Campana, 11. Nov 1988, H. Sipman, E. Sandoval & R. Welz 44851 (B-holotype, LAGU-isotype).

Thallus crustose, leprose, with powdery to membranous appearance; greenish grey to grey-brown with orange tinge; thin, c. 0.1 mm, tightly attached to the substrate at centre, sometimes loose at margins; shape irregular, continuous, up to several cm in diam.; margin delimited, **lobes** present, c. 1 mm wide and long, with raised marginal rim; cortex absent; **medulla** present, thin, white; **hypothallus** grey, visible below upturned marginal lobes; **areoles** absent; **squamules** absent; **soredia** cover all thallus, surface smoother towards the margin, medium sized, c. 0.1 mm in diam.; surface smooth; projecting hyphae absent; **isidia-like structures** absent. **Photobiont** green, coccoid, c. 7–10 µm in diam.

Substrate and ecology: bark, also terricolous and saxicolous mosses, soil, siliceous rock, schist; forest or open areas. **Distribution:** South and Central America.

Chemistry: Diagnostic substances are lecanoric acid and pannaric acid 6-methylester, accessories (not constantly present) include 4-oxypannaric 6-methylester, atranorin (trace), unidentified anthraquinones, “*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.

Discussion. *L. atrotomentosa* may be very similar and *L. pallida* quite similar in morphology to *L. impossibilis* but these taxa differ chemically. *L. atrotomentosa* lacks pannaric acid 6-methylester and contains fatty acids; *L. pallida* lacks both lecanoric and pannaric acid 6-methylester, containing atranorin, zeorin, and fatty acids. Chemically similar species that can produce lecanoric acid include *L. achariana*, *L. atrotomentosa*, *L. goughensis*, *L. lecanorica*. See the discussion under *L. atrotomentosa*. Species containing pannaric acid 6-methylester as major substance include *L. impossibilis*, *L. sipmaniana*, *L. vouauxii*, *L. xerophila*, see the discussion under *L. vouauxii*. Several species can develop well developed lobes, see the discussion under *L. membranacea*.

Lepraria incana (L.) Ach.

Meth. Lich.: 4 (1803); type: United Kingdom, drawing in Dillenius, Hist. Musc.: tab. I fig. 3 (1742) (holotype); typotype: herb Hist. Musc.: tab. I no 3 (OXF).

Byssus incana L., Sp. Pl. 2: 1169 (1753).

Thallus crustose, leprose, with powdery to rarely almost cottony appearance; dull greenish grey, sometimes whitish grey, usually with bluish tinge; usually thick, firmly attached to the substrate; shape irregular, up to 1 dm or more in diam.; margin diffuse, **lobes** absent; cortex absent; **medulla** sometimes present, poorly or rarely relatively well developed; **hypothallus** scarce, lower surface absent; **prothallus** absent; **areoles** sometimes present in well developed thalli; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant, mostly fine, up to 50 µm in diam., mostly loosely packed; wall usually not complete; projecting hyphae sometimes present, short; consoredia sometimes present, up to 110 µm; **isidia-like structures** absent.

Photobiont Chlorophyta, coccoid, up to 18 µm in diam.

Substrate and ecology: bark, acidic rock, sometimes mosses, wood, soil; more or less shaded places. **Distribution:** worldwide, except Arctic and Antarctic.

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

Discussion. *L. incana* can be morphologically quite variable, sometimes forming relatively loose cottony cushions and sometimes consisting of sparse or denser separate soredia only. *L. crassissima* and *L. nigrocincta* also produce divaricatic acid, see the discussion under *L. crassissima*. *L. caesiella*, *L. elobata* are often morphologically similar but 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); type: Spain, Catalonia, Prope Igualada loco Coll del Guix dicto, 2. Nov. 1972, X. Llimona (BCC-holotype; isotypes distributed in Vězda, Lich. Sel. Exs. Fasc. 47: 7 (1973)).

L. crassissima var. *isidiata* Llimona, in Vězda, Lich. Sel. Exs. Fasc. 47: 7 (1973).

Thallus crustose to subfoliose, with membranous, slightly granular appearance; geryish white, grey to dark grey in centre; usually thick, relatively hard, central part sometimes loose from substrate attached to the substrate; shape usually rosettes, sometimes irregular fused patches, usually 2–6 cm in diam., fused patches larger in diam.; margin delimited, **lobes** present, usually well developed, very pruinose, margin raised; subcorticate patches may be present; **areoles** absent; sometimes marginal lobes may look like **squamules**; thallus surfaces without soredia often present, **soredia** abundant, sometimes not well separated at margin, very coarse, 1–3 mm in diam.; larger granules or warts of thallus **similar to isidia**, present in places, especially in centre of thallus, can become sorediate; central part of thallus slightly convex.

Photobiont green, coccoid.

Substrate and ecology: terricolous, calcareous soil (marl and gypsum), sometimes calcareous rock or mosses; shaded but well-lit places, arid climate, mostly steppe-like areas of Spain. **Distribution:** Mediterranean countries.

Chemistry: (1) atranorin, fumarprotocetraric and protocetraric acids; (2) atranorin and fumarprotocetraric acid; (3) atranorin and protocetraric acid. The chemotype 3 is rare (Baruffo et al. 2006). K– or + yellow, C–, KC– or + yellow, Pd+ reddish orange, medulla Pd–.

Discussion. According to molecular studies *L. isidiata* is very close to *L. santosii*, close to *L. bergensis* and all these taxa belong to a monophyletic group together with *L. membranacea*, *L. vouauxii* and *L. xerophila* (Crespo et al. 2006). *L. isidiata* was historically described as *L. crassissima* var. *isidiata* Llimona (Vězda 1973). Specimens corresponding to the description of *L. isidiata* have also been included in *L. nivalis* (Laundon 1992, Leuckert et al. 2004, Sipman & Raus 1999, Sipman 2004). These authors did not consider isidioid forms of *L. nivalis* s. lat. distinct taxonomically. Several species produce protocetraric and/or fumarprotocetraric acids, see the discussion under *L. caesioalba*.

Species producing isidia-like structures include *L. crassissima*, *L. isidiata*, *L. santosii*, *L. xerophila*, and the last three species are also morphologically similar. All these taxa are easily distinguishable chemically by main diagnostic substances: divaricatic and nordivaricatic acids in *L. crassissima*, fumarprotocetraric and/or protocetraric acid in *L. isidiata*, stictic acid complex in *L. santosii*, pannaric acid 6-methylester or rarely norascomatic acid in *L.*

xerophila. Many species may form prominent lobes, see the discussion under *L. membranacea*.

***Lepraria jackii* Tønsberg**

Sommerfeltia 14: 200 (1992); type: Norway, Nord-Trøndelag, Grong, W of Abrahamyra, 16. Sept. 1981, T. Tønsberg 6176 (BG-holotype: BM-isotype).

Thallus crustose, leprose, with powdery, sometimes cottony appearance; pale green to light greenish grey to cream or almost white, sometimes with bluish tinge; thin to often thick, relatively soft, not very firmly attached to the substrate; shape irregular, small to large, fused patches can be several dm in diam.; margin diffuse or delimited, **lobes** absent; cortex absent; true **medulla** absent but hypothallus may look like medulla; **hypothallus** sparse to often abundant and thick, cottony patches of hyphae especially in cavities of substratum, white, lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; sometimes cottony hypothallus exposed in places, **soredia** abundant, fine to coarse, 40–160 µm in diam., loosely packed; wall distinct; projecting hyphae sometimes present, not abundant, short; consoredia sometimes present, up to 160 µm in diam.; **isidia-like structures** absent. **Photobiont** chlorococcoid, up to 15 µm in diam.

Substrate and ecology: mostly acid bark, also mosses, sometimes wood, siliceous and neutral rock, rarely soil, plant debris or lichens, usually well lit and more or less sheltered surfaces in relatively humid conditions.

Distribution: Asia, Australia, North America, Europe.

Chemistry: *L. jackii* sensu strictu (Slavíková-Bayerová & Orange 2006) comprises specimens with atranorin, jackinic/rangiformic acid, roccellic acid ±, norjackinic/norrangiformic acid ± (minor), toensbergianic acid ± (minor). In broader sense it includes all chemotypes with atranorin and jackinic/rangiformic and/or roccellic and/or toensbergianic acids, plus rarely also zeorin and/or minor amounts of anthraquinones (Leuckert et al. 1995, Tønsberg 1992, Baruffo et al. 2006, and others). K– or + faint yellow, C–, KC–, Pd–.

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 as sufficient and *L. toensbergiana* was reduced to a synonym of *L. jackii*. Three further species, *Lepraria celata*, *L. humida*, and *L. sylvicola*, related to *L. jackii*, were described by Slavíková-Bayerová & Orange (2006). Their chemical separation is 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.

Furthermore, *L. jackii* s. lat. can be chemically similar to *L. bergensis*, *L. borealis*, rare chemotypes of *L. caesiella* (Flakus & Kukwa 2007, Saag et al.

2007), a rare chemotype of *L. caesioalba* (chemotype III sensu Tønsberg 2004), *L. granulata*, *L. lobata*, a chemotype of *L. nivalis* (sensu Zedda 2000b), *L. normandinoides* (rare chemotype III sensu Lendemer & Harris 2007), *L. pallida*, *L. rigidula*. Still, these species also have some dissimilarities. *L. bergensis* has delimited thallus margin with lobes and always contains anthraquinones; *L. borealis*, *L. caesioalba* and *granulata* have a granular (*L. neglecta* type) thallus; *L. lobata* has a thick delimited thallus with lobes and contains anthraquinones; *L. nivalis* is usually thicker, cottony and has a delimited thallus margin often with lobes; *L. normandinoides* has marginal lobes and dark rhizohyphae; *L. pallida* has lobes and well developed dark hypothallus; *L. rigidula* contains a unique fatty acid – nephrosteranic acid – and has lax cottony thallus with long projecting hyphae from soredia.

Lepraria lanata Tønsberg

Opuscula Philolichenum 4: 51 (2007); type: U.S.A. Tennessee, Sevier Co., Great Smoky Mountains National Park, 35° 39.11' N, 83° 25.76' W, 8. Sept. 2005, T. Tønsberg 36347 (BG-holotype; ASU, DUKE, NMW, NY-isotypes).

Thallus crustose, leprose, with characteristic woolly, arachnoid consoredia appearance; whitish or partially brownish to bluish grey; relatively thick; shape irregular, up to 1 dm or more in diam.; margin diffuse, **lobes** absent; cortex absent; **medulla** absent; **squamules** absent; **soredia** abundant, all soredia aggregated into consoredia, loosely packed; 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, round; **isidia-like structures** absent. **Photobiont** trebouxoid, to 10(–13) µm wide.

Substrate and ecology: mostly rock, sometimes soil or mosses; dry to rather wet overhangs and rock walls. **Distribution:** Eastern USA, montane.

Chemistry: Protocetraric acid, angardianic/roccellic acid. Thallus K–, C–, KC–, PD+ orange.

Discussion. Several species produce protocetraric and/or fumarprotocetraric acids, see the discussion under *L. caesioalba*. *L. lanata* is unique by its characteristic consoredia.

Lepraria lecanorica Tønsberg

in Lichen Flora of the Greater Sonoran Desert Region 2: 326 (2004); type: U.S.A., Arizona, Coconino Co., SSW of Flagstaff, 35°00.3'N, 111°44'W, 18. Apr. 2001, T. Tønsberg 28991 (BG-holotype, ASU-isotype).

Thallus crustose, leprose, with powdery to slightly membranous appearance; pale bluish grey or whitish; medium to thick, up to 0.6 mm, sometimes partly loose from the substrate; shape rosettes, often distinctly wrinkled, up to 2 cm in diam.; margin delimited, **lobes** sometimes obscure lobes present; cortex absent; **medulla** present, indistinct to distinct, white; lower surface sometimes evident, white to pale brown, without tomentum or with scattered tomentose hyphae;

areoles absent; **squamules** absent; **soredia** abundant, coarse, up to 200 µm in diam., densely to loosely packed; projecting hyphae sometimes present, short, can be long in marginal soredia; **isidia-like structures** absent. **Photobiont** green, coccoid.

Substrate and ecology: bark, rock, soil; shaded places. **Distribution:** North and South America.

Chemistry: lecanoric acid, atranorin (major to minor). K– or + yellowish, C+ red, KC+ red, Pd–.

Discussion. Chemically similar species that can produce lecanoric acid include *L. achariana*, *L. atrotomentosa*, *L. goughensis*, *L. impossibilis*, *L. lecanorica*. See the discussion under *L. atrotomentosa*.

Lepraria leprolomopsis Diederich & Sérus.

in Aptroot, Diederich, Sérusiaux, Sipman, *Bibl. Lichenol.* 64: 76 (1997); type: Papua New Guinea, Simbu prov., Mt. Wilhelm area, 9. Aug. 1992, H. Sipman 35901 (B-holotype; LG, herb. Diederich-isotypes).

Thallus crustose, leprose, with powdery to cottony appearance; yellowish white; thick, relatively soft, weakly attached to the substrate; shape more or less continuous, up to few dm in diam.; margin delimited, sometimes almost diffuse, **lobes** absent; cortex absent; **medulla** present, distinct, white; **hypothallus** usually present, poorly developed, white, lower surface present, continuous, even, white, not or poorly tomentose; **areoles** absent; **squamules** absent; **soredia** abundant, mostly medium sized, 75–125 µm in diam.; wall usually poorly developed; projecting hyphae sometimes present; consoredia often present, 150–300 µm; **isidia-like structures** absent. **Photobiont** green, coccoid, cells 13–15 µm in diam.

Substrate and ecology: bark, mosses on bark. **Distribution:** New Guinea.

Chemistry: atranorin, stictic, constictic, cryptostictic, norstictic and connorstictic acids, unknown terpenoid. K+ yellow, C–, KC–, Pd+ orange.

Discussion. Several species can produce stictic acid complex and atranorin, see the discussion under *L. caesioalba*. Morphologically, *L. diffusa*, *L. eburnea*, *L. lobificans*, *L. nivalis*, *L. nylanderiana* and *L. vouauxii* may be similar to *L. leprolomopsis*, but are separable by diagnostic substances, except *L. nivalis* in some cases (see the discussion under *L. nivalis*). *L. diffusa* contains 4-oxypannaric acid 2-methylester; *L. eburnea* alectorialic acid, *L. nylanderiana* thamnolic acid; *L. vouauxii* pannaric acid 6-methylester and *L. lobificans* zeorin (in addition to the stictic acid complex).

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

Lecanora leuckertiana Zedda, *Nova Hedwigia* 71: 107–112 (2000); type: Italy, Sardinia, Prov. Sassari, Illorai, Monte Artu, 1494647E, 4472420N (Gauss-Boaga), 9. Apr. 1997, L. Zedda 1800(2) (B-holotype).

Thallus crustose, leprose, with cottony and powdery to granular appearance; whitish green to greyish green; thick; shape usually irregular; margin diffuse or delimited, **lobes** usually minute, often obscure; cortex absent; **medulla** present, well developed, forming cottony layer, white; **areoles** absent; **squamules** absent; patches with exposed medulla present, also medullary hyphae intermixed with soredia, **soredia** abundant, fine to coarse, up to 500 µm in diam.; soredia not well separated from each-other; **isidia-like structures** absent. **Photobiont** chlorococcoid, 10–12 µm in diam.

Substrate and ecology: tree bark, sometimes soil; humid, open, well-lit places. **Distribution:** Europe, North Africa, South America (Peru).

Chemistry: usnic acid, zeorin, isousnic acid (trace). K–, C–, KC–, Pd–.

Discussion. Zedda (2000b) described *Lecanora leuckertiana* as very similar to *Lepraria vouauxii*, but provisionally included the new species in *Lecanora* because of its chemistry. At that time genus *Lepraria* did not comprise any usnic acid producing species, following the concept of Laundon (1992, 2003). However, Sipman (2003) placed the newly described *L. usnica* with usnic acid in *Lepraria* arguing that this character alone is not sufficient for determination at generic level. Subsequently *L. coriensis*, *L. ecorticata* were transferred from *Lecanora* (Sipman 2004, Kukwa 2006a) and *L. texta* described (Knudsen & Elix 2008). Taking into account these developments, the authors consider the transfer of *L. leuckertiana* appropriate. Still, the phylogenetic relationships of the aforementioned species should be clarified using molecular methods in the future.

Chemically similar taxa to *L. leuckertiana* – *L. coriensis*, *L. ecorticata*, *L. straminea*, *L. texta* and *L. usnica* that produce usnic acid and usually zeorin – differ in following aspects. *L. straminea* has corticate granules. *L. ecorticata* has no medulla (or rarely it is weakly developed and present in patches) and its soredia are well separated from each-other. *L. texta* also has no medulla. *L. coriensis* and *L. usnica* have better developed lobes and thinner or no medulla. *L. vouauxii* may be very similar morphologically but differs in chemistry.

***Lepraria lobata* Elix & Kalb**

in Elix, Mycotaxon 94: 220 (2005); type: Australia, Western Australia, slopes of Angwin Peak, Porongurups Range, Porongurups National Park, 34°40'S, 117°51'E, 16. Sept. 1994, J. A. Elix 41327, H. T. Lumbsch & H. Streimann (PERTH-holotype).

Thallus crustose, leprose, with granular (but not *L. neglecta* type), partly membranous appearance; whitish grey to greenish or bluish grey; usually thin (up to 250 µm); shape irregular or forming rosettes, that later fuse with each other, rosettes 0.5–1 cm in diam., irregular patches to 10 cm; margin usually delimited, **lobes** often present and well defined, 1–2 mm wide, slightly to distinctly raised at margins; cortex absent; **medulla** present, distinct, white; **hypothallus** absent; **areoles** absent; **squamules** absent; sometimes only sparse

soredia on exposed medulla, **soredia** sparse to abundant and forming thick layer, fine, 20–75 µm in diam.; projecting hyphae usually present, short, up to 20 µm, rarely long, to 100 µm; consoredia common, up to 350 µm in diam.; **isidia-like structures** absent. **Photobiont** chlorococcoid, cells 7–12 µm in diam.

Substrate and ecology: bark, mosses on rock, soil; sheltered places.

Distribution: Australia.

Chemistry: The main diagnostic substances are atranorin, zeorin and a fatty acid – either rangiformic/jackinic or roccellic/angardianic acid; rarely zeorin is present only in minor amount or very rarely it is absent. Accessories that are not constantly present include norrangiformic acid (minor), an unknown dibenzofuran (minor), 3,7-di-O-methylstrepsilin (trace), pallidic acid (minor), conpallidic acid (minor), ursolic acid (minor), fragilin (trace), 7-chloroemodin (trace) and 3'-demethylatranorin (trace). K⁺ yellow, C⁻, Pd⁺ pale yellow.

Discussion. *L. pallida* also produces atranorin, zeorin and fatty acids and has lobes. *L. pallida* has more membranous and rough appearance, well developed ±dark hypothallus and thin medulla, contains unidentified fatty acids, *L. lobata* has slightly thicker thallus with 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 dibenzofuranes. However, the characters of these species seem relatively similar.

L. jackii is chemically and morphologically somewhat similar to *L. lobata*. However, *L. jackii* has much thinner thallus, is more loosely packed and usually unstratified, lacks lobes and only rarely contains zeorin. For other species containing atranorin and fatty acids, see discussion under *L. jackii*. Several species can develop well developed lobes, see the discussion under *L. membranacea*.

Lepraria lobificans Nyl.

Flora 56: 196 (1873); type: France, Pyrénées-Orientales, Collioure, 4 Jul. 1872, W. Nylander (H-lectotype); July 1872, H.A. Weddel (BM-topotype).

Crocynia finkii de Lesd. ex Hue, Bull. Soc. Bot. France, 71: (1924). – *Lepraria finkii* (de Lesd.) R.C. Harris in Brodo, Syllogeus 29: 130 (1981). – *Crocynia aliciae* Hue, Bull. Soc. Bot. France, 71: 333 (1924). – *Crocynia americana* de Lesd., Bull. Soc. Bot. France, 71: 333 (1924). – *Lepra plumbeo-virescens* Jatta, Malpighia 8: 18 (1894).

Thallus crustose, leprose, with cottony to rarely powdery appearance; green to light grey, sometimes with bluish tinge; usually thick, soft, tightly attached at centre, sometimes loose at margins attached to the substrate; shape irregular, sometimes wrinkled, up to 1 dm in diam.; margin usually diffuse, sometimes delimited, **lobes** rarely present, weakly developed, less than 0.5 mm wide, usually without the marginal rim; cortex absent; **medulla** always present,

usually thick, white; **hypothallus** rarely present, scarce, pale brown, lower surface usually indistinct; **areoles** absent; **squamules** absent; thallus surfaces without soredia sometimes present, medulla exposed in places, soredia may be embedded in hyphal weft, **soredia** abundant, fine, up to 60 µm in diam., loosely packed; wall not evident or poorly developed; projecting hyphae usually present, sometimes absent on weather-exposed parts of thallus, long, up to 100 µm; consoredia abundant, up to 100(–200) µm; **isidia-like structures** absent. **Photobiont** trebouxoid, up to 21 µm in diam.

Substrate and ecology: mosses on bark, mosses on rock, also bark, rock, various other substrata; shaded, sheltered places. **Distribution:** worldwide.

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

Discussion. Several species can produce stictic acid complex and atranorin, see the discussion under *L. caesia* *alba*. Sometimes *L. leprolomopsis*, *L. eburnea*, *L. diffusa*, *L. nivalis*, *L. nylanderiana* and *L. vouauxii* may be morphologically similar to *L. lobificans*, see the discussion under *L. leprolomopsis*. *L. incana* is rarely morphologically similar as both species are quite variable, but *L. incana* contains divaricatic acid.

***Lepraria membranacea* (Dicks.) Vain.**

Acta Soc. Fauna Flora Fennica 49(2): 265 (1921); type: United Kingdom, Scotland, J. Dickson (BM ex K ex D Turner-holotype).

Lichen membranaceus Dicks., Fasc. Pl. Crypt. Brit. 2: 21 (1790). – *Leproloma membranaceum* (Dicks.) Vain., Term. Füz. 22: 293 (1899).

Thallus crustose to subfoliose, leprose, with membranous appearance; whitish or greyish yellow to pale yellowish green to light green; usually tightly attached to the substrate at centre, loosely at margins; shape more or less rounded patches, often becoming fused with other thalli, up to 5 cm in diam.; margin delimited, **lobes** present, well developed, rounded, wide, margin raised or flat; cortex absent; **medulla** present, distinct, white; **hypothallus** present, usually well developed, brown to greyish black, sometimes white along margin, usually forming thick tomentum; **prothallus** absent; **areoles** absent; **squamules** absent; thallus surfaces without soredia sometimes present, **soredia** abundant, sometimes not well separated at margin, fine to medium, up to c. 100 µm in diam.; wall indistinct to distinct; projecting hyphae sometimes present, short; consoredia often present, up to c. 200 µm; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 15 µm in diam.

Substrate and ecology: mainly rock and mosses on rock, rarely bark or soil; shaded to sun-exposed, sheltered from rain. **Distribution:** worldwide but scattered.

Chemistry: pannaric acid (major) with satellite dibenzofurans (minors to traces), roccellic/angardianic (rarely absent), atranorin \pm (major to trace); very rarely norstictic acid or zeorin have been found (Baruffo et al. 2006, Laundon 1989). K⁻ or + yellow, C⁻, Pd⁺ reddish orange.

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), these species also may all be membranous and lobed (*L. vouauxii* only rarely develops small lobes).

L. membranacea is the oldest name and the most widely distributed species of the strongly lobate Leprarias. *L. bergensis*, *L. membranacea*, *L. normandinoides*, *L. sipmaniana* are morphologically quite similar, see the discussion under *L. bergensis*. Species that can form prominent lobes include *L. atrotomentosa*, *L. bergensis*, *L. coriensis*, *L. impossibilis*, *L. isidiata*, *L. lobata*, *L. membranacea*, *L. normandinoides*, *L. pallida*, *L. santosii*, *L. sipmaniana*, *L. squamatica* (rarely), *L. xerophila*. All these species are relatively easily distinguishable using chemical and morphological characters, except perhaps *L. lobata* and *L. pallida* in some cases (see the discussion under these species). Differences are as follows:

L. atrotomentosa contains lecanoric acid, atranorin and zeorin and has a well developed layer of dark hyphae on the lower side of thallus. *L. bergensis* produces anthraquinones and is relatively small. *L. coriensis* contains usnic acid and zeorin. *L. impossibilis* produces lecanoric and pannaric acid. *L. isidiata* can produce fumarprotocetraric and protocetraric acids, isidia-like structures together with coarse soredia. *L. lobata* and *L. pallida* produce atranorin, zeorin and fatty acids (see the discussion under these species). *L. membranacea* produces pannaric acid and is relatively large. *L. normandinoides* produces protocetraric and/or fumarprotocetraric acids (very rarely only atranorin and roccellic acid), lacks isidia-like structures, soredia fine. *L. santosii* produces stictic acid complex, isidia-like structures together with coarse soredia. *L. sipmaniana* pannaric acid 6-methylester, lacks isidia-like structures, soredia variably sized, thallus colour usually relatively brightly yellowish. *L. squamatica* contains squamatic acid. *L. xerophila* produces pannaric acid 6-methylester or norascomatic acid, has isidia-like structures (lobules) and few or no soredia.

Lepraria multiacida Aptroot

Fungal Divers. 9: 20 (2002); type: Brazil, Minas Gerais, Catas Altas, Serra do Caraça, Parque Natural do Caraça, 15–21, Sept. 1997, A. Aptroot 40640 a 40 (SP-holotype, ABL-isotype).

Thallus crustose, leprose, with granular appearance; creamy white; thick to very thick, up to 2 mm, attached to the substrate; shape mostly irregular, up to several cm in diam.; margin delimited, minute **lobes** often present, up to 0.5 mm wide, thinner than the rest of the thallus, up to 0.2 mm thick, without

raised rims; cortex absent; **medulla** present, distinct, white, sometimes blackened; sometimes medullary hyphae also form **hypothallus**, white to often black; **areoles** absent; **squamules** absent; **soredia** abundant, coarse, c. 100–200 µm in diam., irregular; projecting hyphae present, long, up to 100 µm; **isidia-like structures** absent. **Photobiont** chlorococcoid.

Substrate and ecology: sandstone, soil. **Distribution:** Brazil.

Chemistry: atranorin; usually zeorin together with 1–2 unknown terpenoids; constictic acid (major to minor); stictic, cryptostictic, norstictic acids (all minor to trace); salazinic acid (minor to trace); 3,7-di-O-methylstrepsilin (minor to trace); 7-O-methylstrepsilin, strepsilin, unidentified dibenzofuran (all trace). K+ yellow to orange, C–, KC–.

Discussion. *L. salazinica* produces salazinic acid, like *L. multiacida*, and can be similar in morphology. However, *L. salazinica* contains large quantities of salazinic acid and less other substances than *L. multiacida*. *L. crassissima*, sometimes *L. nivalis*, *L. squamatica*, may be morphologically similar to *L. multiacida*, but differ in chemistry (see descriptions of these species). Several species can produce stictic acid complex and atranorin, see the discussion under *L. caesioalba*.

Lepraria neglecta (Nyl.) Erichsen

in Lettau, Feddes Repert. 61: 127 (1958); type: Finland, Uusimaa, near Helsinki, 1858, W. Nylander (H-lectotype).

Lecidea neglecta Nyl., Not. Skällsk. Fauna Fl. Fenn. Förh. 4: 233 (1859).

Thallus crustose, leprose, with coarsely granular appearance; light grey to almost white or dark grey, predominantly with bluish tinge, often also with rose tinge (herbarium specimens, caused by alectorialic acid); thick, very rarely thin, usually hard, hyphae densely packed, rarely somewhat softer, firmly attached to the substrate; shape rosette-forming or irregular, often concentric zones visible, up to several cm in diam., rosettes up to c. 2 cm; margin usually delimited, sometimes diffuse, obscure minute **lobes** sometimes present; cortex absent; **medulla** sometimes present, not evident, white; **hypothallus** sometimes present, poorly developed, grey to brown, lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; rarely small patches with exposed medulla present, **soredia** abundant, coarse or variably sized, sometimes largest along margin, typically 100–150(–200) µm in diam., densely packed; wall distinct, often with pruinose appearance; projecting hyphae rarely present, short; consoredia frequent, typically 200–300 µm, sometimes larger especially at margin; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 20 µm in diam.

Substrate and ecology: mosses on acidic rock, acidic rock, soil, rarely bark, epiphytic mosses, lichens; exposed places, mostly cool climate, montane-alpine in tropics. **Distribution:** Europe, North and South America, Asia, Australasia, Antarctica, Greenland.

Chemistry: alectorialic acid, 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-methylphthallide (minor to trace) and barbatolic acid (trace). K⁻ or + yellow, C⁻ or + reddish orange, KC⁺ pink or reddish orange, Pd⁺ lemon yellow or orange.

Kukwa (2006b) additionally reported a very rare chemotype without alectorialic acid, containing an unknown substance “*neglecta* unknown”.

Discussion. According to molecular studies, *L. neglecta* belongs to a monophyletic group together with *L. alpina*, *L. atlantica*, *L. borealis*, *L. caesioalba*, *L. elobata*, *L. granulata* and *L. humida* (Ekman & Tønsberg 2002, Slavíková-Bayerová & Fehrer 2007). Morphologically similar species include *L. borealis*, *L. caesioalba*, *L. neglecta*, *L. granulata* but these taxa differ chemically. Alectorialic acid has been found also in *L. eburnea* and *L. gelida*, but these species have softer and powdery to cottony thallus that is clearly different from *L. neglecta* group morphology.

Lepraria neojackii Flakus & Kukwa

Lichenologist 39(5): 468 (2007); type: Bolivia, Dept. Cochabamba, Prov. Chapare, near Incachaca village, 17°14'17"S, 65°48'54"W, 10 June 2006, A. Flakus 7902 (KRAM-L-holotype; LPB, UGDA-isotypes).

Thallus crustose, leprose, with powdery appearance; greenish grey; thin to quite thick; margin diffuse, **lobes** absent; cortex absent; **medulla** absent but sometimes with pseudomedulla of bleached and dead soredia mixed with hypothallus hyphae; **hypothallus** usually present, whitish or orange in places (anthraquinones); **prothallus** absent; **areoles** absent; **squamules** absent; **soredia** abundant, very fine, sometimes formed by only one algal cell surrounded by mycobiont hyphae, up to 20 µm in diam., round, rather densely packed; wall poorly developed, complete; projecting hyphae usually absent, rarely few present, very short, up to c. 5µm; consoredia present, not prevalent, up to 40 µm in diam.; **isidia-like structures** absent. **Photobiont** chlorococcoid, up to 10 µm.

Substrate and ecology: mosses, humus, rocks; found in mountain cloud forest. **Distribution:** South America (Bolivia).

Chemistry: porphyrylic acid, roccellic/angardianic acid, rangiformic/jackinic acid and an unidentified anthraquinone.

Discussion. Morphologically similar species include *L. atlantica*, *L. humida*, *L. elobata* and especially *L. jackii*, *L. celata*, *L. toensbergiana*, *L. sylvicola*, but these can be distinguished chemically, see the discussion under *L. jackii*. *L. atlantica* is chemically and morphologically rather similar to *L. neojackii*, which is described as containing both roccellic/angardianic and rangiformic acids at the same time but no atranorin. *L. achariana* is sometimes morphologically very similar but contains lecanoric acid.

Lepraria nigrocincta Diederich, Sérus & Aptroot

in Aptroot, Diederich, Sérusiaux, Sipman, *Bibl. Lichenol.* 64: 78 (1997); type: Burundi, galerie forestière de la Siguvyaye un peu en aval du pont de la route Rumonge-Bururi, 20. Sept. 1974, J. Lambinon 74/1266 (LG-holotype, herb. Diederich-isotype).

Thallus crustose, leprose, with cottony hypothallus and powdery soredia on it; soredia greenish grey to whitish, hypothallus dark brown or whitish; moderately thick, soft, not very firmly attached to the substrate; shape irregular, up to few cm, rarely larger in diam.; margin usually delimited, **lobes** usually absent, rarely indistinct; cortex absent; **medulla** absent; **hypothallus** thick, very lax, blackish brown or whitish, of thick hphae; **prothallus** absent; **areoles** absent; **squamules** absent; well developed lax cottony hypothallus exposed between soredia, **soredia** scattered, fine, 30–70 μm in diam., relatively loosely packed; projecting hyphae sometimes present if soredial wall poorly developed; consoredia often present, 75–125 μm ; **isidia-like structures** absent. **Photobiont** green, coccoid, cells 6.5–9 μm in diam.

Substrate and ecology: bark and mosses on bark. **Distribution:** Africa (Burundi), New Guinea, South America (Ecuador, Nöske et al. 2007), montane.

Chemistry: divaricatic acid, nordivaricatic acid (trace). K–, C– or + pinkish, KC+ pink, Pd–.

Discussion. Species producing divaricatic acid include *L. crassissima*, *L. incana* and *L. nigrocincta*, see the discussion under *L. crassissima*. *L. atrotomentosa* and *L. aurescens* also have dark tomentum below the thallus. *L. atrotomentosa* contains lecanoric acid, *L. aurescens* produces thamnolic acid and the tomentum is less extensive. *L. nigrocincta* usually looks different from other *Lepraria* species because of the very thick, very loose, brownish hypothallus is the dominant part, with a loose cover of scattered soredia.

Lepraria nivalis J.R. Laundon

Lichenologist 24(4): 327 (1992); type: France, Alpes-Maritimes, Nice, vieux chemin de Gairaut, July 1945, M. Bouly de Lesdain (MARSSJ-holotype). *Crocynia murorum* de Lesd., *Bull. Soc. Bot. France* 95:199 (1948).

Thallus crustose, leprose, with cottony to powdery, sometimes membranous appearance; white to greyish green or yellowish, sometimes with a bluish tinge; usually thick, soft, often weakly attached to the substrate; shape rosettes or irregular patches, sometimes distinctly wrinkled and folded, variable, up to few dm in diam.; margin delimited or diffuse, **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; cortex absent; **medulla** usually present, often exposed in places, usually thick, white; lower surface sometimes with distinct brown tomentum; **areoles** absent; **squamules** absent; thallus surfaces without soredia often present, **soredia** abundant, variably sized, sometimes coarse, up to 300 μm in diam., loosely packed; projecting hyphae

usually present, short to long; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 13 µm in diam.

Substrate and ecology: limestone, mosses on limestone, sometimes soil, rarely bark or siliceous rock; mostly shaded places. **Distribution:** Asia, Europe, North America, Australasia (Papua New Guinea), Greenland (tentatively reported by Saag et al. 2007). Most common in Mediterranean areas and southern Europe.

Chemistry: Leuckert (2004) distinguished 6 chemotypes in *L. nivalis* s. lat., this classification was complemented by Baruffo et al. (2006): (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 acid, constictic acid, cryptostictic acid ± (trace), norstictic acid ± (trace); (5) atranorin, stictic acid, constictic acid, roccellic acid, cryptostictic acid ± (trace), norstictic acid ± (trace); (6) atranorin, psoromic acid, 2'-O-demethylpsoromic acid (trace).

Chemotypes 1–5: K– or + yellow, C–, KC– or + yellow, Pd+ reddish orange; chemotype 6: K– or + yellow, C–, KC– or + yellow, Pd+ yellow.

Additionally, Zedda (2000b) 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 single specimen; Sipman (2004) reported a specimen with protocetraric and roccellic acid without atranorin.

Discussion. *L. nivalis* is very heterogeneous both chemically and morphologically, possibly including different taxa (Baruffo et al. 2006, Crespo et al. 2006). The chemotype 4 represents “isidioid” morphology, agreeing with the description of *L. santosii*, except the lack of zeorin and roccellic acid. Chemotype 5 includes both “isidioid” and “non-isidioid” morphs; the “isidioid” morphotype also having an affinity with *L. santosii*, except for the lack of zeorin. The “isidioid” representatives of the chemotype 3 belong to *L. isidiata* according to the present taxonomy (Baruffo et al. 2006), the less warted and softer ones are left in *L. nivalis*.

L. crassissima and *L. lobificans* sometimes have similar morphology. However, *L. crassissima* contains divaricatic and nordivaricatic acids, *L. lobificans* stictic acid complex and zeorin. The chemotype 7 included by Zedda (2000b) is chemically identical to *L. borealis*, which however has a granular *L. neglecta*-type thallus. *L. nylanderiana* has similar morphology to *L. nivalis* by definition (Leuckert et al. 1995), but it contains thamnolic acid and often has greyish hypothallus.

Morphological characters for separating non-lobate forms of *L. nivalis* and *L. leprolomopsis* seem to be limited. *L. leprolomopsis* has been found on mossy bark, while *L. nivalis* is associated with calcareous rock and soil. *L. leprolomopsis* has white lower surface that is seldom found in *L. nivalis*, which sometimes can have brown tomentum under the thallus. Chemically, *L.*

leprolomopsis produces a terpenoid but terpenoids are missing in *L. nivalis*. Sometimes also *L. eburnea*, *L. lobificans*, *L. diffusa*, *L. nylanderiana* and *L. vouauxii* may be morphologically similar to *L. nivalis*, see the discussion under *L. leprolomopsis*. Several species can produce stictic acid complex and atranorin and more taxa contain protocetraric and/or fumarprotocetraric acids, see the discussion under *L. caesioalba*.

Lepraria normandinoides Lendemer and R.C. Harris

Opuscula Philolichenum, 4: 45 (2007); type: U.S.A. North Carolina, Transylvania Co., Nantahala National Forest, Shower Falls, 35° 09' 34"N, 82° 58' 26"W, 29.v.2006, J. C. Lendemer et al. 7001 (NY-holotype; isotypes distributed in Lichens of Eastern North America V: 221).

Thallus crustose, leprose, with membranous appearance; bluish-white to greenish-blue or yellowish green; medium to thick, relatively soft, weakly attached to the substrate, partly loose attached to the substrate; shape scattered individual thalli consisting of isolated lobes or a continuous well developed crust with marginal lobes, up to several cm in diam.; margin delimited, **lobes** usually well developed, with marginal rim; cortex absent; **medulla** present, whitish, hyphae hyaline; below thallus **rhizohyphae** present, branching, extending from the medulla, brown, lower surface pale, underlain by thick weft of rhizohyphae; **prothallus** absent; **areoles** absent; **squamules** absent; upper surface soredia held together by a network of gelatinized hyaline hyphae, **soredia** abundant, fine, 30–60 µm in diam.; projecting hyphae absent; **isidia-like structures** absent. **Photobiont** green, coccoid, 7–10µm in diam.

Substrate and ecology: acidic rock, bark; semi-shaded sites with moderate to high humidity. **Distribution:** eastern North America.

Chemistry: This species comprises 3 chemotypes (Lendemer 2007). Common (1): atranorin, protocetraric acid, virensic acid (trace), roccellic acid; K⁺ yellow, C⁻, KC⁺ yellowish, Pd⁺ orange. Rare (2): atranorin, fumarprotocetraric acid, protocetraric acid (minor to trace), roccellic acid; K⁺ yellow, C⁻, KC⁺ yellowish, Pd⁺ orange. Very rare (3): atranorin, roccellic acid; K⁺ yellow, C⁻, KC⁺ yellowish, Pd⁻.

Discussion. *L. bergensis*, *L. membranacea*, *L. normandinoides*, *L. sipmaniana* are morphologically quite similar, see the discussion under *L. bergensis*. Several species can develop well developed lobes, see the discussion under *L. membranacea*. Also several species produce protocetraric and/or fumarprotocetraric acids, see the discussion under *L. caesioalba*.

Lepraria nylanderiana Kümmerl. & Leuckert

Biblioth. Lichenol. 58: 250 (1995); type: Italy, Sardinia, Nuoro Province, Catena del Marghine, 18. Jul. 1987, H. Kümmerling (B-holotype).

Thallus crustose, leprose, with cottony to powdery, sometimes membranous appearance; whitish grey to cream; thick, soft, loosely attached to the substrate;

shape irregular, up to several cm in diam.; margin delimited, minute **lobes** present in well developed specimens, without raised rims; cortex absent; **medulla** usually present, whitish; conspicuous greyish **hypothallus** present in well developed specimens; **areoles** absent; **squamules** absent; thallus surfaces without soredia often present, medulla exposed in places, **soredia** abundant, medium to coarse, up to 300 µm in diam., relatively loosely packed; projecting hyphae usually present, short; **isidia-like structures** absent. **Photobiont** green, coccoid, 7–15 mm.

Substrate and ecology: soil, mosses, siliceous rocks, sometimes bark. **Distribution:** Mediterranean area, Central Europe.

Chemistry: thamnolic acid, decarboxythamnolic acid (trace), roccellic acid, rarely atranorin (trace). K⁺ lemon yellow, C⁻, KC⁻, Pd⁺ orange-yellow.

Discussion. *L. nylanderiana* has similar morphology to *L. nivalis* by definition (Leuckert et al. 1995), but it contains thamnolic acid and often has greyish hypothallus. Species producing thamnolic acid include *L. aurescens*, *L. nylanderiana*, *L. pulchra*, *L. umbricola*, see the discussion under *L. aurescens*. Sometimes *L. leprolomopsis*, *L. eburnea*, *L. diffusa*, *L. lobificans* and *L. vouauxii* may be morphologically similar to *L. nylanderiana*, see the discussion under *L. leprolomopsis*.

Lepraria obtusatica Tønsberg

Sommerfeltia 14: 204 (1992); type: Norway, Hordaland, Askøy, S of lake Askvatn, 14. Jun. 1984, T. Tønsberg 8832 (BG-holotype; DUKE, E-isotypes).

Thallus crustose, leprose, with powdery appearance; pale green with grey-yellow tinge, becoming more distinctly grey-yellow in herbarium; thin, firmly attached to the substrate; shape irregular, discontinuous to partly continuous, in diam.; margin diffuse, **lobes** absent; cortex absent; **medulla** rarely present in thicker parts of thallus, indistinct, white; **squamules** absent; rarely soredia mixed with some medullary hyphae, **soredia** abundant, very fine, up to 35 µm in diam., loosely packed, very fragile; wall poorly developed; consoredia sometimes present, loosely packed, to 50 µm; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 10 µm in diam.

Substrate and ecology: bark; shaded places. **Distribution:** Europe, Australia, scattered.

Chemistry: obtusatic acid, an unidentified pigment, barbatic acid ± (trace). K⁻, C⁻, KC⁻, Pd⁺ yellow.

Discussion. According to molecular studies *L. obtusatica* probably is not a member of *Lepraria* (Ekman & Tønsberg 2002). Morphologically similar to several powdery and green species, unique because of obtusatic acid.

Lepraria pallida Sipman

Herzogia 17: 33 (2004); type: Brazil, Minas Gerais, Munip. Catas Altas, Serra do Caraça, 20. Sept. 1997, H. Sipman 40945 (B-holotype, SP-isotype).

Thallus crustose, leprose, with granular (but not *L. neglecta* type) partly membranous appearance; pale grey with slight bluish tinge; thin, c. 0.1 mm, relatively soft to relatively hard, tightly attached to the substrate at centre, sometimes loose at margins attached to the substrate; shape irregular, continuous, up to several cm in diam.; margin delimited to diffuse in places, **lobes** present in places, often well developed, 0.5–2 mm wide and long, with raised marginal rim, sometimes poorly developed; cortex absent; **medulla** present, thin, white; **hypothallus** sometimes well developed, tomentose, grey to black; **areoles** absent; **squamules** absent; **soredia** sometimes not well separated from each-other, forming smoother surface towards margin; abundant, medium, c. 0.1 mm in diam., relatively densely packed; **isidia-like structures** absent. **Photobiont** green, coccoid, cells c. 10–12 µm in diam.

Substrate and ecology: bark, sandstone, soil. **Distribution:** South America, Seyshelles, Madagascar.

Chemistry: atranorin, zeorin, unidentified fatty acids, unidentified terpenoids ±, unidentified substances ± (traces). K+ pale yellow, C–, KC–, Pd+ yellow to orange.

Discussion. *L. atrotomentosa* and *L. impossibilis* are similar to *L. pallida* in morphology. Still, *L. pallida* is more granular and harder; *L. atrotomentosa* produces lecanoric acid and *L. impossibilis* dibenzofuranes. *L. lobata* also produces atranorin, zeorin and fatty acids, lobes. *L. pallida* has more membranous and rough appearance, well developed ±dark hypothallus and thin medulla, contains unidentified fatty acids, *L. lobata* has slightly thicker thallus with 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 dibenzofuranes. However, the characters of these species seem relatively similar.

Several species can develop well developed lobes, see the discussion under *L. membranacea*. Several species contain atranorin, zeorin and fatty acids as diagnostic substances, see the discussion under *L. jackii*.

Lepraria pulchra Orange & Wolseley

Lichenologist 37(3): 249 (2005); type: Thailand, Chiang Mai Province, Doi Suthep chedi, 18°49'N, 99° 54'E, 31. Jan. 1993, P. W. James & P. A. Wolseley 1605a (BM-holotype).

Thallus crustose, leprose, with powdery to partly membranous appearance; whitish grey to pale bluish grey; thin, c. 100 µm, central parts soft, loose and raised from the substrate at the margin attached to the substrate; margin delimited, with raised and thickened irregularly indented rim that is composed of clumped granules, present at least when young, weakly developed if compared to e.g. *L. membranacea* or *L. sipmaniana*, sometimes small and indistinct **lobes** present, up to 0.5 mm wide, without raised rims; cortex absent; **medulla** present, thin to medium, whitish; lower surface smooth, white, without

conspicuous weft of hyphae; **areoles** absent; **squamules** absent; patches in central parts without well defined granules present, **soredia** abundant to sparse in places, medium to coarse, 80–140 µm in diam.; projecting hyphae usually present, abundant, very short, 10–20 µm, some granules with tufts of longer hyphae to 60 µm; very short projecting hyphae give the soredia pruinose appearance; often soredia not separated from each-other, creating minutely warted surface appearance; **isidia-like structures** absent. **Photobiont** trebouxiod, cells 12–18 x 8–14 µm.

Substrate and ecology: bark; sheltered places, dry forest. **Distribution:** Thailand.

Chemistry: thamnolic acid. K+ bright yellow, C–, KC–, Pd+ orange-yellow.

Discussion. Species producing thamnolic acid include *L. aurescens*, *L. nylanderiana*, *L. pulchra*, *L. umbricola*. See the discussion under *L. aurescens*.

Lepraria rigidula (de Lesd.) Tønsberg

Sommerfeltia 14: 205 (1992); type: United Kingdom, Scotland, Perth, Pitlachry, byside of R. Tummel, Jun. 1914, J. McAndrew (E-holotype).

Crocynia rigidula de Lesd., in Hue, Bull. Soc. Bot. France 71: 331 (1924).

Thallus crustose, leprose, with cottony to powdery appearance; whitish grey to pale bluish grey; usually thick, soft, lax, not very firmly attached to the substrate; shape irregular, small to large, fused patches can be several dm in diam.; margin diffuse, **lobes** absent; cortex absent; **medulla** sometimes present, poorly to well developed, lax, white; lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; **soredia** abundant, mostly fine, sometimes coarse, up to 60(–100) µm in diam., loosely or very loosely packed; wall usually distinct; projecting hyphae present, very long or long at least on some soredia, up to 120 µm; consoredia sometimes present, up to 300 µm in diam.; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 20 µm in diam.

Substrate and ecology: mainly tree bark, also mosses on various substrata, rarely rock, soil or wood, very rarely lichens; shaded but usually open situations. **Distribution:** Asia, Europe, North Africa, North America.

Chemistry: atranorin and nephrosteranic acid. Very rarely unidentified anthraquinones have been found (Flakus & Kukwa 2007). K– or + faint yellow, C–, KC–, Pd–.

Discussion. Several species can contain atranorin and fatty acids, see discussion under *L. jackii*. *L. rigidula* is unique among them in having lax cottony thallus, loosely packed soredia, very long projecting hyphae, and containing a rare fatty acid, nephrosteranic acid. *L. rigidula* was regarded as a synonym of *L. alpina* (sub nomine *Lepruloma cacuminum* by Laundon (1992), but was resurrected as a separate species by Tønsberg (1992).

Lepraria salazinicæ Tønsberg

Opuscula Philolichenum 4: 52 (2007); type: U.S.A. North Carolina, Swain Co., Great Smoky Mountains National Park, Balsam Mountain, 35° 36.2' N, 083° 11.5' W, 20. Jun. 2002, T. Tønsberg 30941 (BG-holotype; DUKE-isotype).

Thallus crustose, leprose, with powdery to granular, consisting of relatively sparse individual soredia appearance; greyish white; thin, attached to the substrate; shape irregular, often thalli fused and contiguous, young individual thalli up to few mm, later large fused covers form; margin diffuse, **lobes** absent; cortex absent; **medulla** absent; **areoles** absent; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant to scattered, very fine, to 30 µm in diam., relatively densely packed; with more or less complete wall of colourless hyphae; projecting hyphae absent; consoredia present, up to 50 µm, few aggregations larger; **isidia-like structures** absent. **Photobiont** trebouxiod, cells to 13 µm in diam.

Substrate and ecology: rock; rock overhangs. **Distribution:** Eastern USA, montane.

Chemistry: atranorin, salazinic acid, roccellic/angardianic acid. K+ yellow turning red, C–, KC–, Pd+ orange.

Discussion. *L. multiacida* also produces salazinic acid, but that species is thick, with dark hypothallus and contains only minor amounts of salazinic acid in addition to other substances.

Lepraria santamonicae K. Knudsen & Elix

Bryologist 110(1): 115 (2007); type: U.S.A. California, Los Angeles Co., Los Angeles, Santa Monica Mountains, Griffith Park, 34°09'07"N, 118°18'08"W, 27 Nov 2005, Knudsen 4380 et al. (holotype-UCR; isotypes-ASU, BM, CANB, H, NY, Herb. Lendemer).

Thallus crustose, leprose, with powdery appearance; pale turquoise to dull green or blue-green, granules in uppermost exposed surface sometimes darkened; thin to thick (100–300 µm, sometimes up to 1 mm); shape irregular, contiguous to dispersed in clumps, fused covers up to several meters in diam.; margin diffuse, **lobes** absent; cortex absent; **medulla** absent, but sometimes a white pseudo-medullary layer of gelatinized hyphae and necral matter, is present; lower surface absent; **areoles** present in well developed thalli; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant, fine, 30–50 µm in diam., densely packed; wall present; projecting hyphae absent, but occasionally with thin colourless hyphae acting as anchors or rhizines; some soredia not well separated from each-other; **isidia-like structures** absent. **Photobiont** chlorococcoid, usually 7–11 µm in diam.

Substrate and ecology: rock or soil, mostly siliceous substrate; open habitats, also those exposed to rain and sunlight, a pioneer species.

Distribution: North America (California, USA).

Chemistry: argopsin, norargopsin (major to minor). K–, C–, KC–, Pd– or Pd+ orange to orange-red.

Discussion. *L. adhaerens* produces the chlorodepsidone pannarin that is biosequentially related to argopsin, but otherwise that species differs chemically and morphologically. *L. coriensis* may contain argopsin like *L. santamonicae* but it has medulla and lobes, contains usnic acid.

Lepraria santosii Argüello & Crespo

Lichenologist 38(3): 218 (2006); type: Canary Islands, Tenerife, Las Mercedes, 28. Mar. 2005, A. Crespo (MAF-holotype; BG, GZU-isotypes).

Thallus crustose to subsquamulose, leprose, with granular, slightly squamulose appearance; whitish grey to greenish grey; relatively thin, c. 0.2 mm, relatively hard, tightly attached to the substrate at centre, loosely at margins; shape rosette to irregular fused patches, 0.5–2.5 cm in diam.; margin delimited, **lobes** present, distinct, with raised marginal rim; some granules may be subcorticate; **medulla** absent; **prothallus** absent; **areoles** absent; marginal lobes can be **subsquamulose**; **soredia** abundant, fine to medium, 20–100 µm in diam., round; pruina absent; projecting hyphae present; larger granules or warts of thallus similar to **isidia** in places. **Photobiont** green, coccoid, cells sometimes aggregated, c. 10–16 µm in diam.

Substrate and ecology: soil and basaltic rock; shaded places. **Distribution:** Canary Islands, probably wider in Mediterranean area.

Chemistry: atranorin, stictic acid, constictic acid (trace), norstictic acid (trace), zeorin, roccellic acid. K+ yellow to brownish, C–, KC–, Pd+ orange.

Discussion. According to molecular studies very close to *L. isidiata*, close to *L. bergensis* (Crespo et al. 2006), see the discussion under *L. membranacea*. Earlier specimens more or less corresponding to the description of *L. santosii* were included in *L. nivalis* as a chemo- and morphotype (Leuckert et al. 1995, 2004; Baruffo et al. 2006), see the discussion under *L. nivalis*. Species producing isidia-like structures include *L. crassissima*, *L. isidiata*, *L. santosii*, *L. xerophila*, see the discussion under *L. isidiata*.

Several species can develop well developed lobes, see the discussion under *L. membranacea*. Several species can produce stictic acid complex and atranorin, see the discussion under *L. caesioalba*.

Lepraria sipmaniana (Kümmerl. & Leuckert) Kukwa

Ann. Bot. Fenn. 39: 226 (2002); type: South Africa, Transvaal Province, Pietersburg District, Soutpansberg Mountains, Llewelin Farm, 13. Jan. 1986, H. Sipman 19.839 (B-holotype).

Lepraloma sipmanianum Kümmerl. & Leuckert, Nova Hedwigia 52: 17–32 (1991).

Thallus crustose, leprose, with membranous to subfoliose appearance; cream or light yellow to grey green, usually relatively bright; moderately thick,

soft, lobes can be loose from substrate; shape irregular or rosette, continuous, often fusing with other thalli, sometimes wrinkled, up to 3 cm in diam.; margin delimited to diffuse in places, **lobes** present, often not surrounding all thallus, well developed, often over 2 mm wide, with raised marginal rim; cortex absent; **medulla** present, thin, white; **hypothallus** sometimes present, not conspicuous, brownish, **prothallus** absent; **areoles** absent; **squamules** absent; **soredia** sparse in places, exposing smooth ecorticate membranous surface, especially near margins, soredia fine to coarse, 40–200 µm in diam., loosely packed; projecting hyphae rarely present, not abundant, short, up to 40 µm; **isidia-like structures** absent. **Photobiont** green, coccoid, 4–15 µm in diam.

Substrate and ecology: soil, rock, bark, mosses; mostly exposed, well-lit places. **Distribution:** Africa, South America, Central America, Sri Lanka, Taiwan.

Chemistry: Diagnostic substance is pannaric acid 6-methylester; accessories (not constantly present) include oxypannaric acid 6-methylester, 4-oxypannaric acid 6-methylester, pannaric acid, 7-chloroemodin, fragilin, A01-anthrone, parietin, emodin, “*vouauxii* unknown 1”. Thallus K⁺ reddish brown or yellowish, hyphae below thallus K⁺ purple to brownish red, C[±] yellowish, KC⁺ reddish brown or yellowish, Pd⁺ pink.

Discussion. *L. bergensis*, *L. membranacea*, *L. normandinoides*, *L. sipmaniana* are morphologically quite similar, see the discussion under *L. bergensis*. Species containing pannaric acid 6-methylester as major substance include *L. impossibilis*, *L. sipmaniana*, *L. vouauxii*, *L. xerophila*, see the discussion under *L. vouauxii*. Several species can develop well developed lobes, see the discussion under *L. membranacea*.

Lepraria squamatica Elix

Australasian Lichenology 58: 20 (2006); type: Australia, Northern Territory, Tabletop Range, Lichfield National Park, 31°11'S, 130°50'E, 2. Jun. 1991, J. A. Elix 27513, H. T. Lumbsch & H. Streimann (CANB-holotype).

Thallus crustose, leprose, with powdery appearance; greenish grey to greyish green or cream to greyish white; relatively thin to very thin, up to 250 µm, relatively soft, not very firmly attached to the substrate; shape irregular or rosettes that later fuse with each-other, rosettes 0.5–2 cm, irregular patches to 10 cm in diam.; margin delimited to diffuse, **lobes** absent or present, sometimes well defined, up to 1 mm wide and with raised margin; cortex absent; true **medulla** absent but hypothallus may look like medulla; **hypothallus** sometimes present, thin, lax, white; **areoles** absent; **squamules** absent; thallus surfaces without soredia present, hypothallus exposed in places, **soredia** abundant to sparse in places, very fine, 15–40 µm in diam., relatively densely packed; projecting hyphae present, variable, sometimes very long along margins (up to 600 µm), shorter in centre (20–125 µm); consoredia common to scarce, 150–

200 µm; soredia well separated from each other; **isidia-like structures** absent. **Photobiont** chlorococcoid, cells 7–12 µm in diam.

Substrate and ecology: bark, wood, rock; more or less shaded, mostly humid places. **Distribution:** Australia, South America (Bolivia, Flakus & Kukwa 2007).

Chemistry: Elix (2006a) described a single chemotype (1) with squamatic acid, baeomycesic acid (major to minor), an unknown fatty acid (major to minor) and occasional trace accessories barbatic, protocetraric, subsquamatic, subbaeomycesic and hypothamnolic acids. Flakus & Kukwa (2007) reported specimens with (2) squamatic and baeomycesic acid plus traces of unidentified substances interpreted as contaminations. K⁺ yellow, C⁻, Pd⁺ yellow.

Discussion. *L. squamatica* may be morphologically similar to *L. multiacida*, *L. jackii* and several other powdery species, but is unique in producing squamatic and baeomycesic acids. Many species can develop well developed lobes, see the discussion under *L. membranacea*. Several species produce protocetraric and/or fumarprotocetraric acids, see the discussion under *L. caesioalba*.

Lepraria straminea Vain.

in Résult. Voyage S. Y. Belgica, Botan., p. 40 (1903); Antarctica, Gerlache Strait [Detroit de Gerlache. Ile de Cavellier de Cuverville, 64 36' de latitud sud, sur les vieilles souches de mousses tombees au pied la falaise (12 débarquement)], Exp. Antarct. Belge no: 238, 1898, M. Emile G. Racovitza (TUR-syntypes).

Thallus crustose, with granular appearance; pale yellowish green; very thick (up to 6 mm); shape usually irregular, to c. 5 cm, fused patches up to several meters; **lobes** absent; cortex present on soredia; **medulla** absent; **prothallus** sometimes present, thin, smooth, up to c. 2 mm broad, whitish; **squamules** absent; **soredia** abundant, coarse, 130–160 µm in diam.; projecting hyphae absent; **isidia-like structures** absent.

Substrate and ecology: mosses, peaty soil; open habitats. **Distribution:** Antarctic endemic.

Chemistry: usnic acid, zeorin. K⁻, C⁻, KC⁻, Pd⁻.

Discussion. Chemically similar taxa include *L. coriensis*, *L. ecorticata*, *L. texta*, *L. usnica* and *L. leuckertiana* that produce usnic acid and usually zeorin, but are different morphologically. *L. straminea* is distinguished primarily by its corticate granules and also the thallus without lobes and medulla. It is considered an Antarctic endemic; it dubiously belongs to *Lepraria* (Øvstedal & Lewis Smith 2001).

Lepraria sylvicola Orange

Lichenologist 38(6): 507 (2006); type: Great Britain, Scotland, Westernness (V.C. 97), near Fort William, Loch Linnhe, 27/0507.6724, 15 May 2004,

A. Orange 15013 (NMW-holotype; BG, PRA-isotypes; GenBank accession no. DQ401102).

Thallus crustose, leprose, with powdery appearance; bluish white to greenish white to pale blue-grey; thin to thick, relatively soft, not very firmly attached to the substrate; shape usually irregular; margin diffuse or delimited, **lobes** absent or obscure and poorly developed; cortex absent; true **medulla** absent but hypothallus may look like medulla; **hypothallus** of sparse patches of hyphae growing into cavities of substratum, hyphae below thallus pale orange-brown (K+ purple-red), lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; **soredia** abundant, fine to coarse, 40–160 µm in diam., loosely packed; projecting hyphae rarely present, short; **isidia-like structures** absent. **Photobiont** chlorococcoid.

Substrate and ecology: neutral to slightly acidic bark, especially abundant on oak, sometimes on rock; more or less sheltered surfaces, especially in mature well-lit woodland. **Distribution:** British Isles.

Chemistry: atranorin, roccellic/angardianic acid, toensbergianic acid, an unknown anthraquinone ± (minor, in subthalline hyphae only). K+ yellowish, C–, Pd– or + yellow.

Discussion. According to molecular studies, *L. sylvicola* is close to but still different from *L. jackii* (Slavíková-Bayerová & Orange 2006, Fehrer et al. unpublished). Morphologically similar species include *L. atlantica*, *L. celata*, *L. humida*, *L. elobata* and especially *L. jackii*, *L. neojackii*, and *L. toensbergiana* but all these taxa can be distinguished chemically. Besides *L. sylvicola*, *L. jackii* and *L. toensbergiana* also produce toensbergianic acid. See discussion under *L. jackii*.

Lepraria texta K. Knudsen, Elix & Lendemer

in Lichen Flora of the Greater Sonoran Desert Region 3: 387 (2008); type: U.S.A. California, Ventura Co., Santa Monica Mountains, Party Rock, 34°6'37"N 118°54'22"W, 8. Feb. 2006, K. Knudsen 5153 w/, R. Muertter & T. Sagar (UCR-holotype; ASU, B, CANB, H, PH, UGDA-isotype)

Thallus crustose, leprose, with finely granular appearance; green, slightly yellowish; thin to relatively thick, firmly attached to the substrate; shape irregular, continuous; margin diffuse, **lobes** absent; cortex absent; **medulla** absent; **hypothallus** sometimes present, evident, whitish, lower surface absent; **areoles** absent; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant, fine, up to 50 µm in diam., irregular, relatively densely packed; wall present; projecting hyphae present, short; some soredia not well separated from each-other; **isidia-like structures** absent.

Substrate and ecology: rock. **Distribution:** North America (California, USA).

Chemistry: usnic acid, zeorin (minor), atranorin (major to minor), roccellic/angardianic acid (minor). K± yellow, C–, KC± yellow, Pd–.

Discussion. *L. coriensis*, *L. ecorticata*, *L. straminea*, *L. usnica* and *L. leuckertiana* also contain usnic acid and usually zeorin, but differ from *L. texta* in following aspects. *L. coriensis* and *L. usnica* have lobes and medulla. *L. straminea* has corticate granules. *L. leuckertiana* has cottony appearance with well developed medulla and the soredia are not well separated from one another. Some soredia of *L. texta* are also not well separated, unlike another similar species *L. ecorticata*, which soredia are more regular and convex, additionally *L. texta* can develop hypothallus and obscure minute lobes but *L. ecorticata* is predominantly unstratified and without any lobes. Usually the appearances of *L. texta* and *L. ecorticata* are different.

Lepraria toensbergiana Bayerová & Kukwa

Bryologist 108(1): 132 (2005); type: Poland, Western Carpathians, Eastern Tatra Mts, Dolina Roztoki Valley, near Nowa Roztoka, 21. Aug. 1999, W. Fałtynowicz, s.n. (UGDA-holotype; herb. Š. Bayerová-isotype).

Thallus crustose, leprose, with powdery appearance; yellowish white, whitish yellow or greenish grey; thin to thick, relatively soft, not very firmly attached to the substrate; shape usually irregular; margin diffuse or delimited, **lobes** absent; cortex absent; true **medulla** absent but hypothallus may look like medulla; **hypothallus** sparse (abundant in epibryotic specimens) patches of hyphae growing into cavities of substratum, hyphae below thallus usually sparse, white, lower surface absent; **prothallus** absent; **areoles** absent; **squamules** absent; **soredia** abundant, fine to medium, up to 50(–110) μm in diam., relatively densely packed; wall present, incomplete to complete; projecting hyphae rarely present, short; consoredia sometimes present, up to 110 μm in diam., round; **isidia-like structures** absent. **Photobiont** chlorococoid.

Substrate and ecology: bark of coniferous and deciduous trees, mosses, debris, humus, siliceous rocks; mostly acidic substrata, more or less sheltered surfaces. **Distribution:** Central Europe.

Chemistry: atranorin, toensbergianic acid. Sometimes minor amounts of rangiformic/jackinic and roccellic/angardianic acids have also been detected but were interpreted as contaminations by Bayerová et al. (2005). K⁺ pale yellow, C⁻, Pd⁻.

Discussion. According to molecular studies, *L. toensbergiana* is very close to but still different from *L. jackii* (Slavíková-Bayerová & Orange 2006, Fehrer et al. unpublished, disputed by Baruffo et al. 2006). Morphologically similar species include *L. atlantica*, *L. celata*, *L. humida*, *L. elobata* and especially *L. jackii*, *L. neojackii*, and *L. sylvicola* but all these taxa can be distinguished chemically. Besides *L. toensbergiana*, *L. jackii* and *L. sylvicola* also can produce toensbergianic acid. See discussion under *L. jackii*.

Lepraria toilenae Kantvilas & Kukwa

Muelleria 23: 3 (2006); type: Tasmania, West of Tahune Bridge in the Warra SST, 43°06'S, 146°40'E, 10. May 2005, G. Kantvilas 121/05 (HO-holotype; BG, BM, UGDA-isotypes).

Thallus crustose, leprose, with powdery to cottony appearance; whitish green to greenish grey; thick or thin; shape irregular, up to 50 cm in diam., sometimes colonies 3–5 mm; margin diffuse, young colonies more or less delimited, **lobes** absent; cortex absent; true **medulla** absent but hypothallus may look like medulla; **hypothallus** very well developed, white or rarely pale greyish white, forming thick weft; **areoles** absent; **squamules** absent; soredia-free zone at thallus margins, sometimes only sparse soredia on exposed cottony hypothallus, **soredia** sparse or abundant and forming thick continuous layer, fine, 16–40 µm in diam.; wall incomplete; projecting hyphae very rarely present, sparse, short, up to 15 µm; consoredia sometimes present, up to c. 80 µm in diam.; **isidia-like structures** absent. **Photobiont** chlorococcoid, cells 5–8(–10) µm in diam.

Substrate and ecology: bark of very large and old trees, often slightly burnt; prefers high humidity, old forest, dry bark. **Distribution:** Tasmania.

Chemistry: malonprotocetraric acid, fumarprotocetraric acid, roccellic acid, protocetraric acid (minor), confumarprotocetraric acid (trace). K–, C–, KC–, Pd+ red.

Discussion. Morphologically more or less similar species include *L. achariana*, *L. atlantica*, *L. celata*, *L. humida*, *L. jackii*, *L. lobata*, *L. neojackii*, *L. sylvicola*, *L. toensbergiana*. The production of the rare substance malonprotocetraric acid in large quantities makes *L. toilenae* chemically unique. Characteristic morphological features are fine soredia on well developed whitish hypothallus and the lack of lobes. Several species produce protocetraric and/or fumarprotocetraric acids, see the discussion under *L. caesiaalba*.

Lepraria umbricola Tønsberg

Sommerfeltia 14: 206 (1992); type: Norway, Hordaland, Bergen, Milde, Brandaneset, 25. Sept. 1990, T. Tønsberg 13635 (BG-holotype).

Thallus crustose, leprose, with powdery appearance; usually deep green, sometimes greyish or whitish; usually thin, rarely thick, relatively hard, firmly attached to the substrate; shape irregular, up to 1 dm in diam.; margin diffuse, **lobes** absent; cortex absent; **medulla** very rarely present, thin, white; **hypothallus** absent; **areoles** absent; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant to scattered, fine, up to 60 µm in diam., relatively densely packed; wall indistinct to distinct; projecting hyphae rarely present, short; **isidia-like structures** absent. **Photobiont** green, coccoid, up to 15 µm in diam.

Substrate and ecology: bark, rock, mosses, soil, mostly acidic substrata; shaded, sheltered, humid, sometimes extremely shaded. **Distribution:** Europe, Macaronesia.

Chemistry: thamnolic acid, atranorin \pm , roccellic/angardianic acid \pm (major to trace), decarboxythamnolic acid \pm (trace). K⁺ lemon yellow, C⁻, KC⁻, Pd⁺ orange-yellow.

Discussion. *L. umbricola* may be similar to several powdery, unstratified and green species, e. g. *L. ecorticata*, but is distinct by producing thamnolic acid. Species producing thamnolic acid include *L. aurescens*, *L. nylanderiana*, *L. pulchra*, *L. umbricola*. See the discussion under *L. aurescens*.

Lepraria usnica Sipman

Biblioth. Lichenol. 86: 179 (2003); type: Singapore, Sembawan Park, on N-coast, 25 Nov. 2000, H. Sipman & B. C. Tan 46399 (B-holotype, SINU-isotype).

Thallus crustose, leprose, with powdery appearance; greyish green with yellowish or bluish tinge; thin to thick, relatively soft; shape irregular or of obscure rosettes, usually up to 10 cm in diam.; margin diffuse or delimited, **lobes** sometimes present, irregular, mostly less than 0.5 mm wide, usually without a rim; cortex absent; **medulla** usually present, thin to medium, white to pale yellowish; **areoles** sometimes present on thick specimens; **squamules** absent; thallus surfaces without soredia absent, **soredia** abundant, mostly medium sized, 70–100 μ m in diam., relatively densely packed; projecting hyphae usually absent; **isidia-like structures** absent. **Photobiont** chlorococcoid, usually 10–12 μ m in diam.

Substrate and ecology: rock, bark, soil; shaded places. **Distribution:** Australia, Southeastern Asia, Sri Lanka, Southern Africa, Central and South America; tropical.

Chemistry: Three chemotypes were distinguished in a detailed chemical survey by Elix (2006b): (1) usnic acid, zeorin, contortin (minor), placodiolic acid (trace), hopane-16 β ,22-diol (major to minor), isousnic acid (minor to trace); (2) usnic acid, zeorin, contortin (minor), placodiolic acid (trace), isousnic acid \pm (trace), roccellic acid \pm (trace); (3) usnic acid, zeorin, contortin (minor), placodiolic acid (trace), isousnic acid (minor to trace), atranorin (minor), chloratranorin (minor). Additionally, Sipman (2003) reported 5-chloro-3-0-methylnorlichexanthone and 5,7-dichloro-3-0-methylnorlichexanthone as trace accessories. K⁻, C \pm yellow to orange, KC \pm yellow to orange, Pd⁻.

Discussion. Chemically similar taxa include *L. coriensis*, *L. ecorticata*, *L. straminea*, *L. texta* and *L. leuckertiana* that produce usnic acid and usually zeorin, but differ in the following aspects. *L. ecorticata*, *L. straminea* and *L. texta* have no lobes and *L. straminea* has corticate granules. *L. leuckertiana* is only obscurely lobed and has a cottony appearance with well developed medulla, additionally the soredia of *L. leuckertiana* are not well separated from

one another. Lobes of *L. coriensis* are usually well developed (0.5–2 mm), round and with marginal rim; that species produces protodehydroconstipatic and constipatic acids (in variable amounts) and lacks contortin. The chemical differences between *L. coriensis* and more recent *L. usnica* were demonstrated by Elix (2006b). Some authors have raised the question of the distinctiveness of *L. usnica* (Orange & Wolseley 2005).

Lepraria vouauxii (Hue) R.C. Harris

in Egan, *Bryologist* 90(2): 163 (1987); type: France, Meurthe-et-Moselle, Nancy, Jarville-la-Malgrange, L. Vouaux s.n. in Claudel, Claudel & Harmand, *Lich. Gall. Praec. Exs. no. 300* (BM-lectotype).

Crocynia vouauxii Hue, *Bull. Soc. Bot. France* 71: 392 (1924). – *Leproloma vouauxii* (Hue) J.R. Laundon, *Lichenologist* 21: 13 (1989). – *Crocynia arctica* Lynge, *Skr. om Svalbard og Ishavet* 81: 19 (1940). – *Lepraria arctica* (Lynge) Wetmore, *Publ. Mich. St. Univ. Mus., biol. ser.*, 3: 440 (1968).

Thallus crustose, leprose, with cottony to powdery appearance; white, cream to greyish cream, sometimes greenish; usually thick, soft, sometimes partly weakly attached to the substrate; shape rosettes or irregular patches, sometimes wrinkled, up to several cm in diam.; margin diffuse to delimited, sometimes obscure **lobes** present, without raised rims; cortex absent; **medulla** usually present, usually thick, white; **hypothallus** sometimes present, brownish, often poorly developed; **areoles** absent; **squamules** absent; thallus surfaces without soredia often present and medulla exposed in small to relatively large patches, **soredia** abundant, mostly coarse, up to 100 µm in diam., rather loosely packed; projecting hyphae often present, short; consoredia often present, up to 300 µm; sometimes soredia not well separated from each other in places; **isidia-like structures** absent; thallus characters rather variable. **Photobiont** green, coccoid, up to 18 µm in diam.

Substrate and ecology: substratum indifferent – mosses, bark, rock, soil, lichens; mostly shaded and sheltered, but also open and exposed places. **Distribution:** worldwide.

Chemistry: Diagnostic substance is pannaric acid 6-methylester. Accessories (not constantly present) include (a) several 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, 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; (6) “*vouauxii* unknown 1” and very rarely “*vouauxii* unknown 2”. K– or + faint yellow, C–, KC–, Pd+ reddish orange or Pd– (soredia).

Discussion. According to molecular studies, *L. vouauxii* is most closely related to *L. membranacea* (Ekman & Tønsberg 2002), see also the discussion

under *L. membranacea*. Several species may have thallus similar to *L. vouauxii* – *L. crassissima*, *L. diffusa*, *L. eburnea*, *L. gelida*, *L. leuckertiana*, *L. leprolomopsis*, *L. lobificans*, *L. nivalis*, *L. nylanderiana*, see the discussion under these taxa, especially under *L. leprolomopsis*.

Species containing pannaric acid 6-methylester as major substance include *L. impossibilis*, *L. sipmaniana*, *L. vouauxii*, *L. xerophila*. *L. impossibilis* may also be morphologically quite similar to some morphs of *L. vouauxii*. The differences are as follows. *L. impossibilis* produces lecanoric acid, has distinct lobes, lacks isidia-like structures, soredia present, thallus relatively soft. *L. sipmaniana* has well developed lobes, lacks isidia-like structures, soredia present, thallus relatively soft. *L. vouauxii* lacks lobes or develops small and obscure lobes, lacks isidia-like structures, soredia present, thallus relatively to very soft. *L. xerophila* has well developed lobes, has isidia-like structures, soredia absent or few, thallus hard.

Lepraria xerophila Tønsberg

Lichen Flora of the Greater Sonoran Desert Region 2: 326 (2004); type: Mexico, Baja California, Punta Santo Tomas, 31°33'30"N, 116°40'50"W, 30. Dec. 1995, T. H. Nash 38224 (ASU-holotype; BG, DUKE-isotypes).

Thallus crustose to subfoliose or squamulose, with membranous, slightly granular appearance; whitish grey to pale yellowish grey; usually thick, relatively hard; shape rosettes, later irregular patches, rosettes to 2 cm, irregular patches to 10 or more cm in diam.; margin delimited, obscurely to distinctly **lobed**, rarely placodioid, 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, without tomentum; **prothallus** absent; **areoles** absent; marginal lobes can be **squamulose**; large thallus surfaces without soredia usually present, **soredia** few or absent; large granules or lobules **similar to isidia** present, numerous, shape regular to irregular, sometimes capitate, easily detached, acting as diaspores; morphologically variable, differentiated algal layer beneath upper surface present. **Photobiont** green, aggregated in globose groups 24–50 µm in diam.

Substrate and ecology: soil, rarely rock or wood; dry places. **Distribution:** Europe, North America, arid areas.

Chemistry: This species comprises 2 chemotypes. Common (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), unknown dibenzofuran (trace); K–, C–, KC–, Pd– or + orange. Rare (2): norascomatic acid, strepsilin (minor to trace), isostrepsilic acid (minor to trace), atranorin (minor to trace), chloratranorin (minor to trace); K– or + pale yellow, C– or + pale yellow, KC– or + green becoming brown, Pd–.

Discussion. According to molecular studies belongs to a monophyletic group together with *L. membranacea*, *L. vouauxii*, *L. xerophila*, *L. bergensis*, *L.*

isidiata, *L. santosii* (Crespo et al. 2006), see the discussion under *L. membranacea*. Species containing pannaric acid 6-methylester as major substance include *L. impossibilis*, *L. sipmaniana*, *L. vouauxii*, *L. xerophila*, see the discussion under *L. vouauxii*. Species producing isidia-like structures include *L. crassissima*, *L. isidiata*, *L. santosii*, *L. xerophila*, see the discussion under *L. isidiata*.

Several species can develop well developed lobes, see the discussion under *L. membranacea*.

Key to the species of *Lepraria*

- 1 Protocetraric acid and/or fumarprotocetraric acid present.....2
 Protocetraric acid and/or fumarprotocetraric acid absent.....8
- 2 Isidia-like granules and warts present, may become sorediate; thallus distinctly lobate, with very coarse soredia (1–3 mm). *L. isidiata*
 Isidia-like structures absent, soredia smaller (up to 1 mm in diam.), thallus lobate or diffuse.....3
- 3 Thick weft of brown rhizohyphae on the lower surface of thallus, soredia fine, lobes distinct..... *L. normandinoides*
 Thick weft of brown rhizohyphae absent (however, hypothallus or medulla may be well developed); soredia fine or coarse, lobes absent or present.....4
- 4 All soredia aggregated into coarse consoredia (up to 1 mm in diam.), surrounded by conspicuous lax network of branching and anastomosing but mostly not projecting hyphae..... *L. lanata*
 Soredia different.....5
- 5 Medulla or hypothallus well developed, thallus soft.....6
 Medulla and hypothallus poorly developed or absent, thallus soft or hard.....7
- 6 Malonprotocetraric acid present, soredia and consoredia fine (up to c. 80 µm in diam.)..... *L. toilenae*
 Malonprotocetraric acid absent, soredia variably sized (up to c. 300 µm in diam.)..... *L. nivalis*
- 7(5) Thallus granular, soredia coarse (mostly 100–200, consoredia up to 300 µm)..... *L. caesioalba* var. *caesioalba*
 Thallus not granular, soredia very fine (up to 30 µm, consoredia up to 60 µm)..... *L. friabilis*
- 8(1) Stictic acid complex present.....9
 Stictic acid complex absent.....16
- 9 Terpenoids present.....10
 Terpenoids absent.....15
- 10 Thallus distinctly lobate, with raised marginal rim, lobes over 0.5 mm wide..... *L. santosii*

	Thallus without lobes or lobes poorly developed, without marginal rim.....	11
11	More than one terpenoid and minor amounts of salazinic acid present. Soredia coarse (up to 200 µm in diam.), with long projecting hyphae.	<i>L. multiacida</i>
	Mostly only one terpenoid present, salazinic acid absent. Soredia not coarse or if coarse then projecting hyphae short or absent.	12
12	Medulla distinct, evident.	13
	Medulla absent or not evident.	14
13	Soredia with long projecting hyphae, loosely packed and soft, mostly fine to medium sized (30–100 µm in diam.); thallus greenish. Zeorin present.	<i>L. lobificans</i>
	Projecting hyphae short or absent, soredia harder, medium sized to coarse (75–300 µm in diam.); thallus yellowish. An unknown terpenoid present.	<i>L. leprolomopsis</i>
14(12)	Soredia are mostly fine (20–45 µm in diam.), consoredia are rare, thallus margin diffuse; thallus greenish.	<i>L. elobata</i>
	Soredia are coarse (100–200 µm in diam.), consoredia abundant (up to 300 µm in diam.), thallus margin usually delimited; thallus grey or bluish grey, not greenish.	<i>L. caesioalba</i> var. <i>groenlandica</i>
15(9)	Thallus granular, hard, medulla not evident, lobes absent or obscure.....	<i>L. caesioalba</i> var. <i>caesioalba</i>
	Thallus softer, with well developed medulla, lobes usually distinct or rarely absent.	<i>L. nivalis</i>
16(8)	Alectorialic acid present.	17
	Alectorialic acid absent.	19
17	Porphyritic acid present.	<i>L. gelida</i>
	Porphyritic acid absent.	18
18	Thallus soft, soredia loosely packed, medulla distinct and usually thick. .	<i>L. eburnea</i>
	Thallus hard, granular, soredia densely packed, medulla not evident.	<i>L. neglecta</i>
19(16)	Divaricatic acid present.	20
	Divaricatic acid absent.	22
20	Nordivaricatic acid present as major substance, medulla well developed, lower surface distinct.	<i>L. crassissima</i>
	Nordivaricatic acid absent or in trace amounts, medulla absent or poorly developed, lower surface not distinct.	21
21	Thick lax hypothallus, usually brown, soredia sparsely distributed on hypothallus.	<i>L. nigrocincta</i>
	Hypothallus absent, soredia abundant.	<i>L. incana</i>
22(19)	Pannaric acid or one of pannaric acid derivatives present as main substance.	23

	Pannaric acid and its derivatives absent or present in trace to minor amounts besides other major compound(s).....	28
23	4-oxypannaric acid 2-methylester present as only major dibenzofurane.	<i>L. diffusa</i>
	4-oxypannaric acid 2-methylester absent or present in trace to minor amounts besides other major dibenzofuranes.	24
24	Pannaric acid present as only major dibenzofurane.	<i>L. membranacea</i>
	Pannaric acid absent or present in trace to minor amounts besides other major dibenzofuranes.	25
25	Lecanoric acid present.	<i>L. impossibilis</i>
	Lecanoric acid absent.	26
26	Soredia absent or few, isidia-like structures present, lobes well developed.	<i>L. xerophila</i>
	Soredia numerous, isidia-like structures absent, lobes well or poorly developed or absent.....	27
27	Lobes well developed, with raised marginal rim.....	<i>L. sipmaniana</i>
	Lobes absent or poorly developed, without marginal rim.	<i>L. vouauxii</i>
28(22)	Porphyritic acid present.	29
	Porphyritic acid absent.	31
29	Thallus granular, hard, soredia coarse (100–300 µm in diam.).	<i>L. alpina</i>
	Thallus relatively soft, powdery (or rarely cottony), soredia medium or very fine (20–100, rarely some up to 200 µm in diam.) .	30
30	Atranorin present, one or very rarely two fatty acids present.	<i>L. atlantica</i>
	Atranorin absent, always two fatty acids present.	<i>L. neojackii</i>
31(28)	Lecanoric acid present.	32
	Lecanoric acid absent.	35
32	Zeorin present; dark brown hypothallus present (usually thick, rarely thin).	<i>L. atrotomentosa</i>
	Zeorin absent; hypothallus absent or if present, white or orange in patches.....	33
33	Atranorin present; soredia coarse (up to 200 µm in diam.).	<i>L. lecanorica</i>
	Atranorin absent; soredia fine (up to c. 50 µm in diam.).....	34
34	Thallus margin delimited, hypothallus absent, soredia very fine (up to c. 30 µm in diam.).....	<i>L. goughensis</i>
	Thallus margin diffuse, hypothallus usually present, soredia fine (up to c. 50 µm in diam.).....	<i>L. achariana</i>
35(31)	Thamnolic acid present.....	36
	Thamnolic acid absent.....	39
36	Thallus unstratified – medulla and hypothallus absent, colour green to rarely whitish green.	<i>L. umbricola</i>
	Thallus stratified – medulla or hypothallus present, colour not green. .	37
37	Roccellic acid present; thallus thick, usually with well developed greyish hypothallus.	<i>L. nylanderiana</i>

	Roccellic acid absent; thallus thin, hypothallus absent or present and brown.	38
38	Thallus margin diffuse without raised rim; brown hypothallus present, usually well developed.	<i>L. aurescens</i>
	Thallus margin delimited, with raised rim; hypothallus absent or poorly developed, white.	<i>L. pulchra</i>
39(35)	Usnic acid present together with zeorin.	40
	Usnic acid absent, zeorin absent or present.	45
40	Thallus margin distinctly lobed, lobes with raised rim, predominantly over 0.5 mm wide. Protodehydroconstipatic and constipatic acids present (in major to trace amounts).	<i>L. coriensis</i>
	Thallus margin diffuse or lobed; if lobes present, without the rim, less than 0.5 mm wide. Protodehydroconstipatic and constipatic acids absent.	41
41	Medulla thick and cottony.	<i>L. leuckertiana</i>
	Medulla absent or thin.	42
42	Lobes present, obscure to distinct, small, less than 0.5 mm wide.	<i>L. usnica</i>
	Lobes absent.	43
43	Thallus granules coarse (up to 160 µm in diam.), corticate.	<i>L. straminea</i>
	Cortical granules absent, soredia smaller (up to 100 µm in diam.)	44
44	Soredia regular, spherical, well separated from each other; hypothallus absent.	<i>L. ecorticata</i>
	Soredia irregularly shaped, not well separated from each other in places; whitish hypothallus may be present.	<i>L. texta</i>
45(39)	Squamatic acid present.	<i>L. squamatica</i>
	Squamatic acid absent.	46
46	Argopsin present.	<i>L. santamonicae</i>
	Argopsin absent.	47
47	Pannarin present.	<i>L. adhaerens</i>
	Pannarin absent.	48
48	Psoromic acid present.	49
	Psoromic acid absent.	50
49	Thallus granular, hard, medulla not evident.	<i>L. caesioalba</i> var. <i>caesioalba</i>
	Thallus softer, with well developed medulla.	<i>L. nivalis</i>
50(48)	Salazinic acid present.	<i>L. salazinicica</i>
	Salazinic acid absent.	51
51	Obtusatic acid present.	<i>L. obtusatica</i>
	Obtusatic acid absent.	52
52	Norascomatic acid present; soredia absent or few, isidia-like structures (lobules) present, lobes well developed.	<i>L. xerophila</i>
	Norascomatic acid absent; thallus different.	53

53	Distinct well developed marginal lobes present, over 0.5 mm wide and mostly with marginal rim.	54
	Marginal lobes absent or obscure.	57
54	Zeorin present.	55
	Zeorin absent.	56
55	Hypothallus present, grey to black; unidentified fatty acids present.	<i>L. pallida</i>
	Hypothallus absent (medulla present); rangiformic/jackinic or roccellic/angardianic acid present.	<i>L. lobata</i>
56(54)	Anthraquinones present (mostly in subthalline hyphae).	<i>L. bergensis</i>
	Anthraquinones absent.	<i>L. normandinoides</i>
57(53)	Zeorin present.	58
	Zeorin absent.	60
58	Fatty acids present; medulla or hypothallus present.	59
	Fatty acids absent; medulla and hypothallus absent.	<i>L. caesiella</i>
59	Thallus relatively hard, soredia densely packed, consoredia up to 350 µm in diam.	<i>L. lobata</i>
	Thallus soft, soredia loosely packed, consoredia up to 160 µm in diam.	<i>L. jackii s. lat.</i>
60(57)	Nephrosteranic acid present; soredia with very long projecting hyphae (60–120 µm in diam.), very loosely packed.	<i>L. rigidula</i>
	Nephrosteranic acid absent; projecting hyphae absent or shorter, soredia densely or loosely packed.	61
61	Soredia up to 300 µm in diam., thallus granular (<i>L. neglecta</i> type).	62
	Soredia up to 160 µm in diam., thallus powdery or slightly cottony.	63
62	Fatty acid “granulata unknown 1” present, rangiformic/jackinic and roccellic/angardianic acids absent.	<i>L. granulata</i>
	“Granulata unknown 1” absent, rangiformic/jackinic or roccellic/angardianic acid present.	<i>L. borealis</i>
63(61)	Jackinic/rangiformic acid present as the only major fatty acid.	64
	Other fatty acids present as major compounds (jackinic/rangiformic acid also present in one species).	65
64	Anthraquinones present on subthalline hyphae (local and often inconspicuous).	<i>L. humida</i>
	Anthraquinones absent.	<i>L. jackii s. str.</i>
65(63)	Roccellic/angardianic acid present as only major fatty acid.	<i>L. celata</i>
	Toensbergianic or jackinic/rangiformic acid present as major fatty acids (roccellic acid may be present in addition).	66
66	Toensbergianic acid present as only major fatty acid.	<i>L. toensbergiana</i>
	Other fatty acids present as major substances (toensbergianic acid present in combination with roccellic/angardianic acid).	67
67	Jackinic/rangiformic acid present as major fatty acid, subthalline hyphae (when present) lacking anthraquinones.	<i>L. jackii s. str.</i>

Toensbergianic and roccellic/angardianic acids present as major compounds, subthalline hyphae (when present) with anthraquinones.....
..... *L. sylvicola*

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List of publications

Monographs

1. Randlane, T.; Saag, A. (eds.); Jüriado, I.; Lõhmus, P.; Nilson, E.; Saag, L.; Suija, A. (2004). Eesti pisisamblikud. Tartu: Tartu Ülikooli Kirjastus. In Estonian. 582 pp.

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14. Saag, L. A (TLC) guide to Baltic Lepraria species. "XVI Symposium of Mycologists and Lichenologists of Baltic States" Cesis, Läti, 21–25 september 2005.

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Ede Leppik, Master's Degree, 2007, (sup.) Lauri Saag, Tiina Randlane, Epifüütsete samblike mitmekesisust mõjutavad tegurid Eesti puisniitudel (Factors influencing diversity of epiphytic lichens in wooded meadows of Estonia), Institute of Botany and Ecology, Faculty of Biology and Geography, University of Tartu

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"Lichen Taxonomy" – course organized by University of Uppsala, Sweden, 09–19 mai 2004.

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