A REVISION OF THE LECANORA DISPERSA COMPLEX 
IN NORTH AMERICA

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Abstract. The Lecanora dispersa group in North America is revised based on about 1900 specimens from 25 herbaria. The following 19 species are recognized in the study area: Lecanora agardhiana Ach., L. albescens (Hoffm.) Flörke, L. cf. andrewii B. de Lesd., L. crenulata Hook., L. dispersa (Pers.) Sommerf., L. flowersiana H. Magn., L. fugiens Nyl., L. hagenii (Ach.) Ach., L. invadens H. Magn., L. juniperina Śliwa, L. percrenata H. Magn., L. perpruinosa Fröberg, L. persimilis (Th. Fr.) Nyl., L. salina H. Magn., L. sambuci (Pers.) Nyl., L. semipallida H. Magn., L. torrida Vain., L. wetmorei Śliwa, and L. zosterae (Ach.) Nyl. The morphology, anatomy, lichen products, and ecology of the species are discussed. Based on the combinations of morphological, anatomical and chemical characters, four distinctive subgroups of species are identified: L. dispersa s.str. gr., L. semipallida gr., L. crenulata gr., and L. hagenii gr. A key for the identification of the species is provided, and all species are illustrated. The North American species have varied distribution patterns, which are illustrated on maps. The taxa differ also in frequency: common species including L. dispersa, L. semipallida and L. hagenii; frequent species but with limited distributional ranges such as L. flowersiana, L. wetmorei, and L. zosterae; relatively rare species including L. albescens, and L. fugiens; and taxa known only from a single locality, such as L. agardhiana, L. perpruinosa, and L. salina. Seven of the species are reported for the first time from the continent: L. agardhiana, L. cf. andrewii, L. fugiens, L. invadens, L. percrenata, L. perpruinosa, and L. semipallida. Nomenclatural and taxonomic clarifications include the typification of L. crenulata, L. persimilis, and L. sambuci, and the synonymy of L. turbinata Poelt & Leuckert with L. zosterae var. beringii. Two new combinations are made: L. zosterae var. beringii (Nyl.) Śliwa comb. nov. (= L. beringii) and L. zosterae var. palanderi (Vain.) Śliwa comb. nov. (= L. palanderi). Moreover, Lecanora elenkii Mereschk., L. flotoviana Spreng., L. thallopila H. Magn., and L. utahensis H. Magn., which at first were considered members of the group, were excluded from the study as they proved not to be related.

Key words: Ascomycota, Lecanorales, lichens, taxonomy, nomenclature, key, distribution, new records, Canada, Mexico, United States

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Dedicated to Clifford M. Wetmore, University of Minnesota, U.S.A. To him I owe my appreciation of lichen taxonomy.
INTRODUCTION

The Lecanora dispersa complex is characterized by thalli that are generally immersed in rock (endolithic) or bark (endophloedal) but are superficial in rare cases, apothecia with a mostly white thalline margin, and either with xanthones or lichen products not being detectable. The group is considered to be the most difficult for taxonomic study in the large genus Lecanora (Laundon 2003).

The present treatment was initiated as a revision of the North American collections of the group in an effort to assess the species diversity of these lichens on that continent. Previously, only a few members of the complex had been reported from the U.S.A., L. dispersa, L. hagennii, and L. sambuci, whereas in the sixth checklist of the lichen-forming, lichenicolous, and allied fungi of the continental United States and Canada (Esslinger & Egan 1995) ten species were listed: L. albescens, L. beringii, L. crenulata, L. dispersa, L. hagennii, L. persimilis, L. salina, L. sambuci, L. torrida, and L. zosterae.

During the course of this study, it became clear that a thorough examination of the taxonomy and nomenclature of the entire group was necessary, and as a result many discoveries and novel observations were made.

The group proved extremely difficult for study as many characters considered diagnostic in previous studies of other Lecanora groups were found to be highly variable, particularly with respect to ecological conditions. The species exhibit considerable intraspecific variability. On the other hand, the differences between species are subtle or difficult to observe if one is not familiar with the taxa. Therefore, a particular effort was made to assess the characters of greatest taxonomic value. As a result, the following features were taken into particular consideration in this revision: thallus and apothecia morphology, apothecial anatomy, pycnidia and conidia, lichen products, ecology, and distribution.

Nevertheless, many problems remain to be resolved in the L. dispersa complex in North America, and much is yet to be learnt about the complex in other continents. This revision is intended as a contribution to the ongoing struggle with the taxonomy of this common yet so difficult species complex.

PREVIOUS INVESTIGATIONS

TAXONOMY

The first attempt towards the modern taxonomy of the complex was that of Poelt et al. (1995), which concerning saxicolous species of the eastern Alps. These authors circumscribed and illustrated a number of species based on combinations of anatomical and chemical characters. They also provided a useful key to aid species identification and recognized 11 species in the region: L. agar-dhiana, L. albescens, L. crenulata, L. dispersa, L. flotoviana, L. perpruinosa, L. ‘roridula’, L. tor-rida, L. turbinata, L. xanthostoma, and L. eury-carpa (unrelated to the group). Poelt et al. (1995) brought the knowledge of the complex up to date, and their treatment served as an excellent basis for discussing the North American species. Those authors, however, did not refer to type or original
collections, and none of the names adopted were

typed in the work.

Fröberg (1997) studied the species on rocks in southern Sweden, and accepted six species: L. *albescens*, L. *crenulata*, L. *dispersa*, L. *flotoviana*, L. *perpruinosa*, and L. *xanthostoma*. He validated the name L. *xanthostoma*, and discussed his new species L. *perpruinosa* proposed earlier (Fröberg 1989) in more detail. However, with respect to other names he did not study the original material. Consequently, despite the progress he made in the understanding of species concepts in the group, the usage of certain names, for instance L. *flotoviana*, remained ambiguous. Moreover, both Poelt et al. (1995) and Fröberg (1997) pointed out some particular problems, as with the circumscription of L. *hagenii*. Additionally, there were some differences in species concepts between the two treatments, such as in the delimitation of L. *dispersa*, which have caused some further confusion.

A neglected member of the complex, L. *zosterae*, was resurrected and lectotypified in a publication on the typification of L. *subfusca*, its varieties, and some related taxa published before 1850 by Brodo and Vitikainen (1984). This species has since been more precisely circumscribed by Laundon (2003), who examined the status of the species in the British Isles. Laundon briefly discussed the whole L. *dispersa* group in this paper, and lectotypified L. *umbrina* which he suggested should be taken up for the species concepts between the two treatments, such as in the delimitation of L. *dispersa*, which have caused some further confusion.

Other observations on the L. *dispersa* complex are included in national or local biogeographical and other studies. Such observations and remarks are often a valuable source of information on members of the complex and their delimitation (e.g., Roux 1976; Clauzade & Roux 1985; Degelius 1986; Hawksworth & Dalby 1992; Nimis 1993; Nimis & Bolognini 1993; Wirth 1995; Thomson 1997; Brodo et al. 2001; Sérusiaux et al. 2003; Ryan et al. 2004).

Here it is worth mentioning J. Motyka’s volumes devoted to the Lecanoraceae family (Motyka 1995, 1996) and supplemented by the atlas of nomenclature types in LBL-L (Motyka-Zglobicka & Zglobicki 2002). They were produced posthumously and have been ruled not to be used as a source of validly published names under the Code (Lumbsch et al. 1999), but the treatment may serve as a source of information on the location of some original collections as well as detailed descriptions of particular species.

In 2001–2002, I conducted research on North American collections of the complex, which were continued in 2004–2006. During this study, it became clear that a thorough examination of the taxonomy and nomenclature of all representatives of the complex was necessary. Since the majority of available names within the group of taxa are based on European collections, it was also necessary, in most cases, for material from both continents to be compared. A particular effort was made to trace available original collections to ensure that names were correctly applied; this led to some interesting discoveries.

The most significant was a reappraisal of the application and taxonomic status of two important but so far poorly understood members of the complex: L. *flotoviana* and L. *xanthostoma*. As a consequence, it was found that the true L. *flotoviana* did not belong to the L. *dispersa* complex at all, from studies of the original material discovered in GOET; L. *semipallida* was shown to be the correct name for the common, widespread member of the L. *dispersa* group to which the name L. *flotoviana* had been misapplied. Further, the recently named L. *xanthostoma* proved to be conspecific with L. *semipallida* and was reduced to synonymy with it (Śliwa 2007).

It was also critical to fix the application of the epithets of the oldest names in the complex, L. *dispersa* and L. *albescens* (Śliwa 2006), and in addition the name L. *hagenii* was saved for usage in its current sense by conservation of the epithet with a conserved type (Śliwa & Hawksworth 2006). Specimens distributed in exsiccates were preferentially selected for typifications in these works, as that means that isotype reference material was thus made available for consultation in many institutions throughout the world.

In the course of the study, two previously unknown corticolous species of the group were
discovered, L. juniperina and L. wetmorei, and these have been formally described elsewhere (Ryan et al. 2004). Further results from the revision of the L. dispersa group in North America are presented here.

CHEMOTAXONOMY
The extracellular chemical products of species of the Lecanora dispersa complex have interested a few lichenologists. Pioneering chemical studies on the complex were performed by Leuckert et al. (1990), who examined the products of both intact thalli and pure cultures of the fungal partner. They reported production of two depsidones, pannarin and dechloropannarin, by cultures of made from single ascospores of a specimen named as L. dispersa which also produced a xanthone pigment as the major secondary compound. Leuckert et al. (1990) analysed further samples with 'the L. dispersa s.l. morphology' and found and characterised two chemotypes containing (1) 2,7-dichlorolichexanthone (major product), traces of chloroxanthones in various combinations in the lichen products of particular members of the complex, and recognized several different chemotypes of some broader-scope mycological/lichenological groups: '0', lichen substances not detected and most of them chemically. TLC analyses were made in water, and ascospore measurements were made in water. Tissue measurements were made in water, and ascospore measure-

MATERIAL AND METHODS
The geographical area of this study includes the continental United States of America and Canada as well as the northernmost part of Mexico. This area is referred to as North America throughout this text.

The study is based on collections named as members of the L. dispersa complex in the following North American herbaria: ASU, CANL, COLO, FH, NY, MICH, MIN, MSC, OMA, OSC, US, WIS, and herb. Spreibille. Additionally, a considerable number of Lecanora names of unknown taxonomic position were investigated and their diagnoses checked for any indication they may belong to the group. As a result, types and historical materials of most of the 32 taxa mentioned in this work were located and examined, along with other reference material from many major European herbaria: B, BM, GOET, GZU, H, KRAM, L, ID, LE, M, S, UPS. In total, about 1900 specimens were examined morphologically, and most of them chemically. TLC analyses were made on representative specimens of all accepted taxa.

For light microscopy, free-hand sections were made with a razor blade and mounted in water. Tissue measurements were made in water, and ascospore measure-
ments in 25% KOH (K). Measurements are rounded to the nearest 0.5 microns, with normal extremes in parenthesis. The structure and coherency of paraphyses were also studied in K, which facilitates their separation. Granulation of tissues was observed in polarized light (pol); pol+ meaning the granules are bright in polarized light, and pol− that they are not prominent. The solubility of granules and/or crystals was tested with 25% KOH (K) and 65% nitric acid (N); these last two reagent tests were always carried out on separate cross sections.

Chemical examination included colour reactions, response to ultraviolet light (UV) and thin-layer chromatography (TLC). Spot test reactions of thalli, apothecial margins and discs were made with KOH [20–30% aqueous solution] (K), sodium hypochlorite [commercial laundry bleach] (C) and paraphenylenediamine [solution in 95% ethyl alcohol] (PD). The TLC analyses was performed in solvent system A and/or C (methods followed Orange et al. 2001).

Scanning electron microscopy (SEM) was applied to study the surface of the apothecial disc and to recognize features of pruina. For SEM examination, apothecia direct from herbarium specimens were affixed to an aluminium stub with double-sided transparent tape. The specimens were not critical-point dried or fixed in any other way. The stubs were sputter-coated with carbon using a CRESSINGTON sputter-coater, and viewed with a Hitachi S-4700 scanning electron microscope at 20.0 kv. Additionally, an elemental analysis of apothecial margins and discs was performed using the NORAN Vantage energy dispersive spectrometer (EDS) microanalysis system.

The terminology used in the descriptions basically follows Brodo (1984) and Purvis et al. (1992). Abbreviations of authors’ names follow Brummitt and Powell (1992). To make specimen citations more uniform, some label data were supplemented with county information (where lacking) based on the Citation World Atlas (Hammond Incorporated 1984). Biogeographical terminology used throughout the text is based on Brodo et al. (2001).

The research was performed in the lichen laboratory and herbarium of the J. F. Bell Museum of Natural History, University of Minnesota (St Paul, U.S.A.; MIN) during the academic year 2001/02, and continued in the Laboratory of Lichenology at the W. Szafer Institute of Botany, Polish Academy of Sciences (Kraków, Poland) in 2004–2006. The SEM studies were made in the Laboratory of Field Emission Scanning Electron Microscope and Microanalysis in the Institute of Geological Sciences, Jagiellonian University (Kraków, Poland) in 2006.

RESULTS

CHARACTERIZATION OF THE GROUP

Thallus morphology

In most species of the Lecanora dispersa group, the thallus is not visible or inconspicuous since it is entirely or partly developed within the substratum. However, there are also species with a clearly visible, crustose, superficial thallus (sometimes also evanescent). The habit of the thallus varies from indistinct, to membranaceous, through thin, crustose and ecoricate, to distinct, relatively thick, and corticate with various structures. No species have soredia or isidia.

The variations in thallus structure include a continuous, smooth or granulose to areolate-rimose crust (e.g., L. juniperina, L. perpruinosa); discontinuous and composed of more or less convex granules or areoles, clearly dispersed or aggregated (e.g., L. fugiens, L. salina); and rarely distinct rosettes (e.g., L. albescens). Depending on the structure of the thallus, the margin is indefinite or definite (i.e., hardly or clearly distinguishable), continuous, sometimes slightly crenulate, or indistinctly lobate. The thallus is often best-developed close to the base of apothecia or may be confined to the region under apothecia and then rarely wider than the apothecia under which they occur (e.g., L. salina, L. torrida, L. zosterae var. beringii).

A prothallus was not observed in any species except L. fugiens, where white dendroid hyphae arise on the edges of thallus areoles.

Thallus colour does not vary a great deal, being some shade of whitish grey to yellowish or greenish grey. The colour may also be more striking in some species, however: for example, chalk white (e.g., L. torrida), ash-grey (e.g., L. perpruinosa), or beige to yellowish brown (e.g., L. fugiens). A diffuse bluish pigment occurs in some species (e.g., L. hagenii, L. invadens), and in others the surface is slightly to moderately pruinose (e.g., L. albescens).

Apothecial morphology

All species in the Lecanora dispersa group have well-developed lecanorine apothecia, with the exception of L. agardhiana, which may also
produce lecideine apothecia (L. agardhiana subsp. sapaudica var. lecideella (Poelt) Leuckert & Poelt; Poelt et al. 1995) and L. persimilis, in which the apothecia are often biatorine. Apothecial size is generally 0.3–1.2 mm diam., but the apothecia of some species do not exceed 0.6 mm (e.g., L. sambuci) or 0.8 mm (e.g., L. fuginis), and those of L. albescens, L. semipallida, L. zosterae and L. wetmorei commonly reach 1.4 mm; moreover L. zosterae can reach 3.5 mm diam. The apothecia may occur singly, in which case they are often evenly distributed or clustered in groups. Lecanora fuginis has, for instance, apothecia arising singly on a discrete, single areole of the thallus, whereas those of L. zosterae var. berthingii or L. persimilis often arise in groups of 2–3. In most taxa the apothecia are sessile, but in some the apothecia are adnate or immersed either in the substratum or thallus areoles. The fruit bodies of L. agardhiana are whole or partly immersed into the substratum, while those of L. torrida are clustered in groups of 2–3 and widely sessile or immersed in single areoles of the thallus. In some species the apothecia are distinctly constricted at the base, as in L. zosterae var. berthingii, in which they are raised on a short stipe, and L. zosterae var. zosterae with pellate apothecia which are apparently adnate but actually narrowly attached at the base and constricted. Several species have apothecia, some of which are constricted and some of which are sessile (e.g., L. albescens, L. semipallida).

The discs of the apothecia of most species are more or less flat (Fig. 1), but may also be concave and cup-like. They are generally regular in outline, but may become flexuose (Fig. 2), especially when crowded.

Apothecial margins, that is exciples, are predominantly persistent and usually prominent and thick. In some species the margin becomes level with the disc, thin, and very rarely almost excluded as the species matures. Sometimes, when the thalline exciple is excluded, a dark parathecial ring becomes evident (e.g., L. torrida). In L. zosterae the margin may occasionally become raised above the disc and involuted. In some specimens of several species, a heavily flexuose margin is observed, while others have an even margin (e.g., L. semipallida). The texture of the margin varies from predominantly smooth to rough (e.g., L. flowersiana) or rarely to wax-like (e.g., L. salina). The margins are most often white or whitish (e.g., L. flowersiana, L. hagenii) or concolorous with the thallus (e.g., L. albescens, L. salina), or more occasionally concolorous or almost so with the disc (e.g., L. persimilis, some morphs of L. dispersa). The margin may be epruinose or slightly to moderately white pruinose. In many species the margins are uniform, but they may also be differentiated, that is concolorous with the thallus below (close to the base of the apothecia) and whitish, sometimes also apparently pruinose at the top (e.g., L. zosterae). In some species a bluish pigment appears on the uppermost part of the margin and they become darkened (e.g., L. semipallida, L. torrida, occasionally L. dispersa).

Margin morphology, and especially its crenulation, is often used to distinguish and/or characterize some species in the L. dispersa group. Although this character is very variable in some species, it may well define some others. To use it as a diagnostic character, however, some terminological clarification is necessary, as the term ‘crenulate’ is used in different ways by different authors. Here, the following distinctions are used: (i) margin entire (= continuous, Figs 3 & 4), e.g., L. wetmorei, L. zosterae, sometimes also L. semipallida; (ii) margin cracked (= discontinuous, fissured, Figs 5 & 6), e.g., L. flowersiana, L. percrenata; (iii) margin crenate (= undulate, with rounded marginal segments, Figs 7 & 8), e.g., L. cremulata, L. juniperina, L. semipa-
lida, sometimes also L. zosterae; and (iv) margin incised (= dentate, with sharp marginal segments), e.g., L. hagenii (especially young apothecia).

The discs are predominantly plane, smooth, and without umbos, but may also be concave, and in a few species, convex. However, in L. agardhiana some specimens were found to be umbonate (i.e. with a sterile column in the centre of the apothecial disc). The colour of the discs varies from yellowish to pale brown, brown, reddish brown or blackish, but can also be pale greenish yellow, or yellow-orange (e.g., L. semipallida), orange or maroon (e.g., L. hagenii), chocolate brown (e.g., L. flowersiana), or lead-coloured (e.g., some morphs of L. juniperina). When infected by lichenicolous fungi, the disc may become dark brown or black in colour. Exposure to intense insolation also influences the colour of the disc, which can become darkened or blackish. The discs are bare or slightly, moderately, or heavily pruinose (scabrose to almost frosted). Pruina are characteristically present in some species and absent in others, but this feature may perhaps also be modified by habitat conditions. When abundant, the pruina may impart a somewhat plumbeous or bluish appearance of the disc (e.g., L. invadens, L. perpruinosa, L. wetmorei). The pruina of the apothecial discs was studied by SEM. These investigations showed, the pruinosity in most species was caused by non-crystalline, fine granular (Fig. 9) or coarse granular (Fig. 10) material. Crystalline material was observed on the disc surface of only a few species (e.g., L. hagenii, L. flowersiana) (Figs 11 & 12).
Apothecial anatomy

An amphithecium, that is, a thalline exciple, is always present, contains trebouxioid algae, and is rather thick, averaging mostly 100–200(–270) μm in height at the base of the apothecia. In a few species (e.g., L. agardhiana) the amphithecium may be reduced or is considerably thinner and rarely exceeds ± 60 μm. The amphithecium is always corticate and the algal more or less densely fill the area below the cortex. The algal layer is most often continuous below the hypothecium, but may also be frequently discontinuous in some species (e.g., L. dispersa, L. torrida). In several species the algae tend to be clustered into groups and may also be sometimes restricted to the apothecial base (e.g., L. agardhiana, L. persimilis).

The amphithecial cortex varies from indistinctly to well delimited; however, some variation was also observed between different specimens of a single species. The cortex is characteristically thickened at the base in some species, but more or less uniform in thickness in others. The structure of the cortex is various and somewhat depends on the species, and may be composed of (i) adglutinated hyphae (sometimes apparently cellular), gelatinous, e.g., L. dispersa; (ii) paraplectenchyma (lumina of cells distinct, irregular), not gelatinous, e.g., L. perpruinosa; (iii) prosoplectenchyma (interwoven, ± regularly arranged hyphae), gelatinous, e.g., L. semipallida; or (iv) amorphous (cell walls and lumina indistinct), gelatinous, e.g., L. floweriana, L. zosterae. Sometimes the structure of the cortex is hard to be defined due to the presence of especially dense cortical granules. The majority of species of the L. dispersa group have the cortex more or less densely obscured by cortical granules, which are especially prominent in polarized light (pol+) and indicate the same solubility features; they are insoluble in K and slowly soluble in N. The abundance of the granules seems related to substratum properties. Species occurring in calcium-rich habitats have the cortex filled with the granules, which may also spread into the area below the cortex. An example of infraspecific variation in the abundance of cortical granules is L. dispersa, which has very abundant cortical granules when growing on calcareous rock, but much less abundant to almost absent granules in specimens originating from bark or wood. In a few species cortical granules are sparse (often located mostly in the top of the margin) or lacking (e.g., L. hagenii, L. persimilis, L. zosterae). In several species of the group, additional K-soluble granules occur in the amphithecial cortex (e.g., L. salina). In the species of the L. dispersa group, the cortical area is also inspersed with very fine granules (the same kind as in the epithecium), which are insoluble in K and insoluble in N. These granules are best observed after application of the reagents and the disappearance of the soluble granules.

A parathecium, that is, a true exciple, is indistinct in the majority of species, but may also be well-delimited and up to 30 μm wide. A distinct parathecium, which may be narrow or wide, characteristically overlaps the amphithecium in L. agardhiana and L. torrida. A distinct prosoplectenchymatous parathecium is seen in a few species, especially L. crenulata and L. semipallida.

An epithecium (i.e., an epihymenium), the uppermost part of the hymenium and including the granules between and directly above the paraphyses, is usually coloured or rarely hyaline. It tends to be pale in some species and dark in some others, although it is probably modified by habitat conditions, especially insolation. The colour of the epithecium is most often shades of yellow or brown (e.g., L. dispersa, L. hagenii, L. semipallida) but may also be reddish (e.g., L. floweriana, L. zosterae) or shades of olive, green, bluish green or blackish (e.g., L. invadens, L. percrenata). The colour disappears, remains unchanged, or becomes more intense with K. It may be unchanged, turning more intense, or pink to purple in N (often part of the hymenium below also turning pink). In a few species the epithecium is deeply pigmented, and the pigment extends through up to a third of the upper hymenium (e.g., L. floweriana, L. percrenata). The granulation of the epithecium is an important character within the L. dispersa complex, and its features can be used to diagnose and to distinguish species and/or species groups. Four basic types of epithelial structures occur in the group: (i) granular (pol+), granules superficial
and between paraphyses tips, or also inspersed in the whole hymenium, fine, insoluble in K and insoluble in N (in some specimens the granules may partly be soluble but most remain prominent in K and prominent in N), Figs 13–16, e.g., *L. dispersa*, *L. albescens*, *L. juniperina*; (ii) granular (pol+), granules superficial and between the paraphyses tips, coarse, soluble in K and insoluble in N, Figs 17–20, e.g., *L. semipallida*, *L. fugiens*, *L. invadens*; (iii) indistinctly granular (pol±), rarely not at all granular, granules superficial, coarse, insoluble in K and soluble in N (those epithecial granules have identical features as the epipsamma usually has, see below), Figs 21–24, e.g., *L. hagenii*, *L. sambuci*; (iv) not at all granular but usually distinctly pigmented (epipsamma sometimes insoluble in N), Figs 25–26, e.g., *L. flowersiana*, *L. percrenata*.

A different situation exists in the epithecium of *L. torrida*, which is often not at all granular but shows shades of brown, or shades of olive, green or bluish (becoming more intensely green with K and turning pink or red in N). Although the epithecium itself is not at all granular, fine granules (pol+) may be interspersed through the whole hymenium and are insoluble in K and insoluble in N, as in *L. dispersa*. *Lecanora wetmorei* has a granular epithecium (pol±), with granules insoluble in K and soluble in N. In some specimens, however, additional coarse granules are present in or above the epithecium (pol+) which are soluble in K but insoluble in N. *Lecanora zosterae* usually has an epithecium that is not at all granular, but it may very rarely be granular (pol+) with granules soluble in K but insoluble in N.

An epipsamma is defined here as the most superficial part of the epithecium, that is, present above the tips of the paraphyses. It may be ± granular (usually pol±, rarely pol+) with an undifferentiated structure. The epipsamma is generally insoluble in K and soluble in N, although in a few species it was occasionally N-insoluble, e.g., *L. flowersiana*, *L. percrenata*. It is always present in some species but is entirely lacking in some others. The presence of an epipsamma may be correlated with the pruinosity of the apothecial disc.
The hymenium is hyaline in the majority of species, and only in a few is the hymenium yellowish. The height of the hymenium is (30–)45–70(–90) μm. A subhymenium is indistinct in most species, but may also be more or less distinct and averages 15–20(–30) μm in height, hyaline or not transparent (and then usually ± granular). The hypothecium is hyaline or almost so, or rarely yellowish, and varies between 20–50 μm and 100–120 μm in height. The hypothecium is composed of adglutinated hyphae which form a pseudoparenchyma or prosoplectenchyma. It is most often clear and without granules, but in a few species it is darkened by granules (pol–) and/or oil droplets, e.g., L. flowersiana, L. percrenata.

The width of the paraphyses varies between species. They may be slender (averaging less than 2 μm wide) or thick (averaging more than 2 μm wide). In some species the paraphyses are somewhat branched throughout, with few anastomoses, not expanded apically, and coherent in K (e.g., L. dispersa, L. juniperina, L. salina). Most often, however, they are simple or sparsely branched (frequently only in the uppermost part), not or slightly to moderately expanded apically (rarely capitate) and ± free in K (e.g., L. hagenii, L. invadens, L. semipallida). The tips of the paraphyses may be pigmented or not. The pigment is rarely sharply delimited as a cap (e.g., L. torrida). Unusual paraphyses occur in L. perpruinosa which are submoniliform, that is, appearing as chains of swollen cells. Lecanora flowersiana and L. percrenata have thick and adglutinated paraphyses which are distinctly septe with extraordinarily

enlarged apical cells; they are apparently submo-
niliform as well.

The asci are clavate or broadly clavate, with
the thickened ascus tips staining blue in iodine
(K/I), and with a distinct projection from below
*(Lecanora*-type). The asci are eight-spored in the
majority of species. The only species with mul-
tispored asci is *L. sambuci*, which has (12–)16
or more spores per ascus. Specimens with four-
spored asci occur occasionally in *L. persimilis*
and *L. semipallida*.

The ascospores are always hyaline, non-sep-
tate and ellipsoid. Although the shape of spores is
rather variable in most species, in some they seem
broadly ellipsoid (Fig. 27) or more distinctly nar-
rowly ellipsoid (Fig. 28). To provide more objec-

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tive spore shape descriptions the following scale is used here: (i) broadly ellipsoid – mean spore length to width ratio (Q) averaging 1.2–1.8; (ii) ellipsoid – mean spore length to width ratio (Q) averaging 1.9–2.3; and (iii) narrowly ellipsoid – mean spore length to width ratio (Q) averaging 2.4–3.5. Additionally, for the length and width of spores between their minimum and maximum values recorded, the arithmetic mean of all observations is given in squared parentheses. In several species, extreme values (recorded once and never repeated) are also indicated. Unusual in the group are the narrowly ellipsoid (sometimes apparently fusiform) spores of *L. percrenata*, and the broadly ellipsoid (sometimes apparently sub-globose) spores of *L. semipallida*.

Pycnidia and conidia

Pycnidia were seen in a few specimens of two species, *L. percrenata* and *L. semipallida*. They are black, not abundant, and inconspicuous since buried in locally thickened parts of the thallus. Conidia are falcate, consistently filiform and characteristically curved. They are about 16–19 μm long and ±1 μm thick in *L. percrenata*, and 10–17–18 μm long and ±1 μm thick in *L. semipallida*. Pycnidia may occur more frequently and been overlooked in the species complex.

Chemistry

**LICHEN PRODUCTS.** Although several members of the group do not produce any characteristic lichen compounds (e.g., *L. hagenii* and related species), the chemistry plays an important role in the identification of certain taxa. Examples include *L. dispersa* (refers predominantly to its chemical race with pannarin), *L. semipallida* (which consistently contains vinetorin), and *L. salina* (gyrophoric acid present). In these cases, the segregation is made on the grounds of morphological and anatomical characters, and is supported by the chemical data. The identification of other species within the group by chemical features, however, has serious restrictions. This is due to the need for sophisticated protocols for chromatographic studies of xanthones, the main constituents of many species, and severe limitations as to their determination on the basis of such characters. Consequently, lichexanthones are difficult to use in identification keys, and in this treatment attention was paid to identification of the xanthones most frequently detected and able to be recognized with available standards, 2,7-dichlorlichexanthone and vinetorin (5-chloro-3-O-methylnorlichexanthone). Detailed chemical characterizations of most species can be found in published reports discussed above (see ‘Previous investigations’ section).

**REAGENT AND UV-TESTS.** The most common patterns of chemical reagent tests in the complex are consistently negative responses to spot tests and also to UV light (10 species). The apothecial
margin and sometimes also the disc of species producing pannarin may give a PD-positive orange reaction (e.g., *L. albescens*, *L. fugiens*, *L. dispersa*, *L. torrida*). The reaction may be more or less distinct in different parts of the same specimen. The species containing xanthones usually give positive, yellow or weakly orange reactions with C, and sometimes also with K; they usually are also UV-positive (e.g., *L. fugiens*, *L. semipallida*). The presence of gyrophoric acid in *L. salina* is manifested by a C+ pink reaction.

**ELEMENT CONTENT.** When undertaking SEM examinations of the morphology of the apothecia, the element content of apothecial disc and margin was also analyzed. This study revealed differences between species in the element composition of particular parts of the apothecia. There are species that have the same element content and more or less the same element ratios in both the disc and margin, e.g., *L. wetmorei* (Fig. 29). In some other species, however, the ratio of particular elements varies between the disc and margin, e.g., *L. semipallida* (Fig. 30). The preliminary data obtained are interesting, and further study may yield more information on variation in this aspect of the *L. dispersa* complex, and especially on the location of particular chemical constituents.

**Ecology**

The members of the complex are generally regarded as occupying primarily calcareous substrata, and the majority of taxa do occur directly on calcareous rocks, often on limestone, and also on concrete and mortar. Several of the saxicolous
species grow exclusively on calcareous rocks: *L. agardhiana*, *L. crenulata*, *L. perpruinosa*, and *L. torrida*. Others, although tending to favour calcium-containing substrata, may also inhabit weakly or non-calcareous rocks (e.g., *L. dispersa*, *L. flowersiana*). Siliceous rock is occupied by such species as *L. andrewii*, *L. fugiens*, and *L. salina*.

The corticolous members of the complex are *L. hagenii*, *L. juniperina*, *L. persimilis*, *L. sambuci*, and *L. wetmorei*. They inhabit a wide range of tree species but frequently occur also on wood. Some of them are collected mostly on the trunks of trees, but others (e.g., *L. persimilis*, *L. sambuci*) are collected mainly on branches and twigs.

Many species of the complex are less substratum-specific than previously considered. The most spectacular examples are *L. dispersa* and *L. hagenii*. The usually saxicolous *L. dispersa* may occur on tree bark or wood (especially in urban environments) and the predominantly corticolous *L. hagenii* may also occur on calcareous rock, concrete and mortar. The two species frequently accompany each other, especially on constructed substrata such as fences, walls, and tombstones. Some species may rather occasionally be collected on other than typical substrata, for example *L. semipallida* on calcareous rock (limestone, calcium-rich sandstone) and concrete, and may rarely be found on other substrata such as bark or wood. *Lecanora percrenata* grows primarily on calcium-containing rocks (sandstone, caliche, limestone) but may also occur on volcanic ash or on wood.

The least selective species in substratum choice in the whole complex is *L. dispersa*, which occurs
on a wide range of substrata including calcareous and siliceous rocks, concrete and mortar, dusty bark, wood, and many manufactured substrata including asbestos-cement, metal, leather, and rubber. It may also grow commensally on other lichens, as L. semipallida often does. Another species of a wide ecological spectrum is L. zosterae, which inhabits a large variety of organic substrata, that is, wood, detritus, bryophytes, vascular plant debris, bones, and caribou antlers, but it may also grow directly on calcareous rock.

The habitats of the L. dispersa complex representatives include a range from sea level to considerably high elevations, up to 3150 m in the case of L. wetmorei, and close to that in L. flowersiana (2870 m). However, the majority of species preferentially occur at lower altitudes in nature and in natural situations, although a few commonly grow also in urban environments (e.g., L. dispersa, L. hagenii, L. semipallida). Several taxa occur predominately in particularly exposed environments, such as deserts (e.g., L. flowersiana), tundra (e.g., L. zosterae), or the seashore (e.g., L. salina).

Distribution

The North American species show different distribution patterns. A few species of the complex are widespread on the continent and occur in arctic, boreal and temperate regions, with the main distribution in the temperate zone, notably L. crenulata, L. dispersa, L. hagenii, and L. semipallida. Some scattered species, such as L. albenscens, L. persimilis, and L. sambuci, have a boreal to temperate range. The arctic-alpine to boreal element is represented by L. torrida and L. zosterae. A typical western temperate species is L. flowersiana (and perhaps L. juniperina), and western temperate to western montane species are L. percrenata and L. wetmorei. Lecanora andrewii and L. fugiens have an oceanic distributional pattern, whereas L. salina is maritime.

The taxa differ also in frequency. Common species are L. dispersa, L. semipallida and L. hagenii. Frequent species, but with various distribution ranges, include L. crenulata, L. flowersiana, L. wetmorei, and L. zosterae. Relatively rare species include L. albenscens and L. fugiens. Lecanora agardhiana, L. perpruinosa, and L. salina represent the rarest taxa in the continent, currently being known only from single localities.

Species Groups

Based on morphological and anatomical features, four distinctive groups of species can be recognized within the L. dispersa complex. Chemical study showed they are correlated with the presence of certain chemical compounds.

1. Lecanora dispersa group s.str.

Diagnostic Characters. Epithecial granules fine, on top and between paraphyses tips (inspersed in the whole hymenium), K-insoluble, N-insoluble; paraphyses slender, somewhat branched throughout, with few anastomoses, coherent in K; amphithecial cortex composed of adglutinated hyphae; ascospores ellipsoid; chemistry – 2,7-dichlororichexanthone or other xanthones, ± pannarin, or no lichen substances detected; thallus distinct in some species. Included species: L. andrewii, L. albenscens, L. dispersa, L. juniperina, L. salina, and probably L. torrida.

2. Lecanora semipallida group

Diagnostic Characters. Epithecial granules coarse, on top and between paraphyses tips, K-soluble, N-insoluble; paraphyses slender, rarely dichotomously branched at top, sometimes with the apical cells slightly expanded, free in K; amphithecial cortex prosoplectenchymatous; ascospores broadly ellipsoid; chemistry – 5-chloro-3-O-methylnorlichexanthone or other xanthones, ± pannarin, or no lichen substances detected; thallus distinct in some species. Included species: L. invadens, and L. semipallida. Note: L. fugiens has the same anatomical features but differs in chemistry.

3. Lecanora crenulata group

Diagnostic Characters. Epithecial granules coarse, on top and between paraphyses tips, K-insoluble, N-soluble or absent; paraphyses slender, apical cells expanded to capitate, often pigmented,
coherent in K (adglutinated); amphithecial cortex gelatinous or distinctly paraplectenchymatous; ascospores ellipsoid to narrowly ellipsoid; chemistry — no lichen products detected; disc abundantly pruinose or margin distinctly crenate or cracked; primarily saxicolous species. Included species: L. crenilata, L. flowersiana, L. percrenata, L. perpruinosa, and probably L. agardhiana.

4. Lecanora hagenii group

DIAGNOSTIC CHARACTERS. Epithecial granules absent (only an epipsamma observed, K-insoluble and N-soluble) or coarse, on top and between the paraphyses tips, K-soluble, N-insoluble; paraphyses slender, apical cells expanded to capitulate, often pigmented, free in K; amphithecial cortex gelatinous, or rarely composed of adglutinated hyphae; ascospores ellipsoid to narrowly ellipsoid; chemistry — no lichen products or unknown substance detected; margin of young apothecia often slightly crenate or incised, in older apothecia often flexuose; inhabits a large variety of organic substrata. Included species: L. hagenii, L. persimilis, L. sambuci, and probably L. wetmorei and L. zosterae.

KEY TO THE SPECIES

1. Asci 12- to 16-spored .................. L. sambuci
1’. Asci up to 8-spored ...................... 2

2. Epithecial granules (pol+), coloured or not; epipsamma if present soluble in N .............................. 3
2’. Epithecial granules not granular or granules not prominent in polarized light (pol-), coloured; epipsamma if present soluble or insoluble in N .............................. 14

3. Granules in epithecium coarse or fine, insoluble in K and insoluble in N (the same kind of granules dispersed through the whole hymenium and sometimes also the hypothecium, prominent even if sparse or lacking in the epithecium); paraphyses somewhat branched throughout, sometimes with a few anastomoses; apothecia UV+ dull greenish or yellowish, or UV- .............................. 4

3’. Granules in epithecium coarse, solubility different than above; paraphyses simple or branched only at the top, never with anastomoses; apothecia UV+ yellow to dark orange or UV- .............................. 9

4. Thallus inconspicuous or immersed and not apparent, endolithic or endophloedal .......................... 5

4’. Thallus distinct, well developed or scarcely visible, epilithic .......................... 6

5. Apothecia 0.3–0.9 mm diam.; apothecial margin entire, often PD+ (pannarin); disc very variable in color, yellowish grey, brownish to dark brown or almost black, mostly pruinose; thallus endolithic or visible as a very thin superficial layer or inconspicuous granules (distinct coarse granules sometimes observed are usually those that will produce apothecia); on all kinds of substrata, also commensally on other lichens; widespread ........................ L. dispersa

5’. Apothecia 0.3–1.2 mm diam.; apothecial margin crenate, PD-; disc pale, or yellowish (often turning lead-colored), moderately to heavily pruinose; thallus granulous to areolate-rimose; corticulous species; occurs in western North America .... L. juniperina

6. Thallus white, cream or pale grey yellowish, C-; arctic-alpine or widespread .............................. 7

6’. Thallus yellow, yellowish green to pale brownish, C+ pink or yellow to orange; rare, maritime or oceanic .............................. 8

7. Thallus forming rosettes with many apothecia on top, usually slightly lobate at the margin; apothecial disc pale to brown and often pruinose; widespread ........................ L. albescens

7’. Thallus forming areoles around or restricted only to closest vicinity of apothecia; apothecial disc brown to black and usually epruinose; arctic-alpine to boreal .............................. L. torrida

8. Thallus and apothecial margin PD-, often C+ pink (gyrophoric acid); apothecial margin almost concolorous with the disc or slightly paler .............................. L. albovirens

8’. Thallus and apothecial margin PD+ (pannarin), C+ yellow to orange (arthrothelin); apothecial margin paler than disc, often whitish ... L. cf. andrewii

9. Epithecial and/or epipsamma granules soluble in K and insoluble in N (sometimes sparse!) .............................. 10

9’. Epithecial and/or epipsamma granules insoluble in K and soluble or insoluble in N .............................. 14

10. Thallus within the substrate, endolithic or endophloedal .............................. 11

10’. Thallus partly superficial (sometimes evanescent), more evident around the apothecia, epilithic ............ 13

11. Apothecial disc moderately to heavily white pruinose, K-, C- and UV- (sometimes traces of an unknown lichen product present); corticulous or lignicolous; continental North America .............................. L. wetmorei

11’. Apothecial disc epruinose or faintly yellowish
pruinose, K+ and/or C+, UV+ all yellow to orange (xanthones present); predominately calcicolous; distribution not only continental 12.

12. Apothecia widely sessile, rarely constricted at the base; apothecia flat, only rarely flexuose; apothecia margin thick, prominent; ascospores broadly ellipsoid; often commensally on other lichens; widespread ............... L. semipalida

12’. Apothecia constricted at the base, sometimes apparently stipitate; apothecia often flexuose; apothecia margin thin or partly excluded; ascospores narrowly ellipsoid; often on bones; arctic-alpine [chemotype with a high concentration of xanthone] L. zostereae var. beringii

13. Apothecial margin distinctly cracked; hymenium deeply coloured (up to 1/3 of the height); paraphyses distinctly adglutinated, expanded at the top to capitate, sometimes apparently submoniliform apically .......................... 18

17. Apothecial margin entirely or slightly crenate; only uppermost part of hymenium colored; paraphyses ± loose, faintly expanded at top ............... 19

18. Apothecia widely attached or base immersed in rock; apothecial margin cracked; disc brown, black or almost black; epithecium brown or olive-green, or bluish green; ascospores 12–18 × 4–6 μm; pycnidia sometimes present; continental part of North America and Asia ............... L. percrenata

19. Apothecia marginally or constricted at the base; apothecial margin cracked but often only faintly crenate or continuous in older apothecia; disc reddish brown, dark brown to blackish; epithecium brown or reddish; ascospores 10.5–16.5(−18) × 4–6 μm; pycnidia not observed; continental part of North America ............... L. flowersiana

20. Apothecia epruinose, clustered in groups and	.......

18. Apothecia widely sessile or constricted at the base; apothecial margin cracked but often only faintly crenate or continuous in older apothecia; disc reddish brown, dark brown to blackish; epithecium brown or reddish; ascospores 10.5–16.5(−18) × 4–6 μm; pycnidia not observed; continental part of North America ......... L. percrenata

20. Apothecia marginally or constricted at the base; apothecial margin cracked but often only faintly crenate or continuous in older apothecia; disc reddish brown, dark brown to blackish; epithecium brown or reddish; ascospores 10.5–16.5(−18) × 4–6 μm; pycnidia not observed; continental part of North America ............... L. percrenata

21. Apothecia 0.4–1.0 mm diam., constricted below; disc yellowish to black, plane to convex; apothecial margin C– or C± yellow, PD– (± vinetorin); on siliceous maritime rocks ............... L. agardhiana

22. Apothecia 0.4–1.2(–1.5) mm diam., widely sessile; on various kinds of organic substrata, also calcicolous ............... L. perpruinosa

23. Apothecial margin and/or disc yellow or reddish brown, lead-brown to blackened; arctic-alpine ............... 20

19. Apothecia sessile or detached; disc pale to reddish brown; hypothecium pale brown; cortex thin, composed of paraplectenchyma; ascospores narrowly ellipsoid, up to 13.5 μm long; mostly on wood and bark but also calcicolous ............... L. flowersiana

20. Apothecia epruinose, clustered in groups and raised on a short stipe; calcicolous, primarily on bones [chemotype with no lichen substances] ............... L. zostereae var. beringii

20’. Apothecia faintly to moderately pruinose, scattered and sessile; on various kinds of organic substrata, also on bones ............... L. zostereae var. palanderi

21. Apothecia 0.4–1.6(−3.5) mm diam., constricted at the base, often peltate; epithecium brown or reddish; hypothecium yellowish, prosoplectenchymatous; ascospores narrowly ellipsoid, up to 16.5 μm long; occurs also on all kinds of organic substrata ............... L. zostereae

21’. Apothecia 0.4–1.2(−1.5) mm diam., widely sessile; epithecium brown; hypothecium hyaline; ascospores ellipsoid or narrowly ellipsoid, less than 13.5 μm long; mostly on wood and bark but also calcicolous ............... L. percrenata

22. Apothecial disc epruinose; margin concolorous or paler than disc; young apothecia often in groups of 2–3 ............... L. persimilis
22. Apothecial disc moderately to heavily pruinose; margin paler than disc or whitish; apothecia scattered, evenly distributed  23
23. Margin faintly incised, at least in some apothecia; cortex thin, ± uniform in thickness or faintly thickened at base; no lichen substances detected; widespread  L. *hagenii*
23. Margin entire; cortex thick, expanded at the base; sometimes traces of unknown lichen product present; continental North America  L. *wetmorei*

THE SPECIES


*Lecanora agardhiana* Ach.  Figs 31 & 32


Thallus within the substratum, immersed and not apparent, endolithic, rarely superficial and then whitish and inconspicuous. Apothecia lecanorine or lecanideae or lecanorine, occurring singly, sessile, flat when mature, whole or partly immersed in the rock, 0.3–1.2 mm diam.; disc plane, dark brown, black or almost black, epruinose, or slightly to heavily pruinose, sometimes umbonate (with sterile columns in apothecial disc); margin level with the disc, thin, smooth, entire, even, or flexuose, uniform, epruinose, or pruinose, paler than disc, or the same colour, or sometimes thalline margin excluded and then the dark true exciple usually distinct. Amphithecium 70–180 μm thick, corticate, with a discontinuous algal layer, algae sparse, in groups, often restricted to the base; cortex indistinctly delimited, clearly expanded at the base, ±80 μm thick laterally and 120–150 μm thick at the base, composed of adglutinated hyphae (lumina of cells irregular), not gelatinous, usually more or less obscured by crystals (pol+, insoluble in K, soluble in N); parathecium distinct, thin, overlapping the margin; epithecium shades of brown, olive, greenish or blueish black, not at all granular, unchanged with K, N+ pink or purple (part of the hymenium below also often turning pink), epipsamma absent, or present and undifferentiated (pol±, insoluble in K and soluble in N); hymenium hyaline, 60–70 μm high; subhymenium indistinct; hypothecium hyaline or almost so, 40–130 μm high, composed of pseudoparenchyma, without granules. Paraphyses slender, simple, not expanded or thick and adglutinated, pigmented, free in K. Asci clavate, 8-spored; ascospores hyaline, simple, mostly ellipsoid (broadly ellipsoid to ellipsoid), 10.5–11.1 × 5–5.8 × 7.5 μm, Q = 1.6–1.9–2.4. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C–, KC–, PD–; disc plane, dark brown, black or almost black, epruinose, or slightly to heavily pruinose, sometimes umbonate (with sterile columns in apothecial disc); margin level with the disc, thin, smooth, entire, even, or flexuose, uniform, epruinose, or pruinose, paler than disc, or the same colour, or sometimes thalline margin excluded and then the dark true exciple usually distinct. Amphithecium 70–180 μm thick, corticate, with a discontinuous algal layer, algae sparse, in groups, often restricted to the base; cortex indistinctly delimited, clearly expanded at the base, ±80 μm thick laterally and 120–150 μm thick at the base, composed of adglutinated hyphae (lumina of cells irregular), not gelatinous, usually more or less obscured by crystals (pol+, insoluble in K, soluble in N); parathecium distinct, thin, overlapping the margin; epithecium shades of brown, olive, greenish or blueish black, not at all granular, unchanged with K, N+ pink or purple (part of the hymenium below also often turning pink), epipsamma absent, or present and undifferentiated (pol±, insoluble in K and soluble in N); hymenium hyaline, 60–70 μm high; subhymenium indistinct; hypothecium hyaline or almost so, 40–130 μm high, composed of pseudoparenchyma, without granules. Paraphyses slender, simple, not expanded or thick and adglutinated, pigmented, free in K. Asci clavate, 8-spored; ascospores hyaline, simple, mostly ellipsoid (broadly ellipsoid to ellipsoid), 10.5–11.1 × 5–5.8 × 7.5 μm, Q = 1.6–1.9–2.4. Pycnidia not seen.

HABITAT. Growing directly on calcareous rock, often on limestone.
DISTRIBUTION. Europe, New Zealand, and North America, but in the U.S.A. recognized from only one locality in Oklahoma.

DISCUSSION. The species is most likely to be confused with *Lecanora crenulata*, which also occurs on limestone, but is much more frequent. However, the apothecia of *L. crenulata* are sessile to constricted at the base and always located on the rock surface, and are not wholly or partly immersed in the rock as are the apothecia of *L. agardhiana*. The apothecial disc of the last species is often epruinose or only slightly pruinose, and the thalline margin is thinner and never distinctly crenate or cracked, as it is in case of *L. crenulata*. Moreover, algae in the amphithecium of *L. crenulata* are much more abundant in comparison to the sparse algae, often clustered into group of *L. agardhiana*.

REMARKS. The following taxa of lower rank have been recognized in Europe: subsp. *spadicea* Clauzade & Cl. Roux with var. *spadicea* and var. *lecidella* (Poelt) Leuckert & Poelt. Full characteristics and discussion of the taxa are provided by Poelt *et al*. (1995). The North American specimen represents the typical subspecies, subsp. *agardhiana*.


Specimens have also been seen from Austria (ASU, COLO, FH, GZU), Balkan Peninsula (FH), Belgium (FH), Germany (GZU), Italy (GZU), New Zealand (MSC: Campbell Island), Switzerland (FH), and UK (NY).

*Lecanora albescens* (Hoffm.) Flörke


Thallus clearly visible, often forming distinct rosettes, thick or thin, areolate, usually slightly lobate at margins, surface pruinose; white, yellowish, cream or pale grey. Apothecia clustered in groups on thallus areoles, sessile or slightly immersed, flat when mature, 0.4–1.4 mm diam.; disc plane, smooth, yellowish to pale brown, slightly to heavily pruinose; margin prominent,
or level with the disc, smooth, sometimes slightly crenate, even, uniform, epruinose, concolorous with thallus. Amphithecium 90–270 μm thick, corticate, algae fill the area below the cortex or algae sparse, algal layer continuous below hypothecium; cortex indistinctly delimited, or distinctly delimited, ± uniform in thickness, or slightly thicker at the base than at the sides, ca 30 mm thick laterally and ca 60 μm thick at the base, prosoplectenchymatous, gelatinous, obscured by granules and larger crystals (pol+, insoluble in K, slowly soluble in N); parathecium indistinct to well delimited and up to 30 μm wide; epithecium shades of yellow or brown, granular (pol+), granules superficial and between paraphyses tips, also inspersed in the whole hymenium, coarse, or fine (insoluble in K and insoluble in N), usually with an epipsamma (insoluble in K and soluble in N); hymenium hyaline, or yellowish, 60–90 μm high; subhymenium distinct; hypothecium hyaline or almost so, 60–130 μm high, composed of prosoplectenchyma, without granules. Paraphyses slender, somewhat branched throughout, with few anastomoses, not expanded and not pigmented, ± coherent in KOH. Asci clavate, 8-spored; ascospores hyaline, simple, ellipsoid (broadly ellipsoid to narrowly ellipsoid), 9–[11.2]–13(–15) × 4.5–[5.6]–7.5 μm, Q = 1.4–[2.0]–2.7. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C–, KC–, PD– or PD+ orange; disc K–, C–, KC–, PD–; apothecia UV-negative or UV+ dull greenish. Lichen products: 2,7-dichlorlichexanthone, ± pannarin; or no lichen products detected by TLC.

HABITAT. Growing directly on calcareous rock, also on concrete and mortar.

DISTRIBUTION. Europe and North America. In North America the species is scattered on the north-eastern coast. It represents perhaps a boreal and temperate element.

DISCUSSION. Lecanora albescens is closely related to L. dispersa and corresponds to the latter in anatomical and chemical characters. It has a much more abundant thallus, however, which is often indistinctly lobate at the margin. Distinct rosettes of the thallus bear numerous, usually pruinose apothecia. Lecanora dispersa never has a distinct thallus, and its apothecia are usually epruinose. Another related species is L. torrida. For differences, see under the species.

NOMENCLATURAL NOTES. As no original Hoffmann collection could be located in B, GOET or MW, the herbarium in Helsinki was checked to trace any relevant material appropriate for typification. No authentic L. albescens was found there, although original collections of its later synonyms, L. galactina and L. urbana, were located. The nomenclature, citation and typification of the names are discussed, and the neotype of L. albescens is designated in Śliwa (2006). Additionally, Flörke is shown in the paper to be the correct author of the combination, according to Art. 34.1 Ex. 3 of the Vienna Code.


Fig. 33. Lecanora albescens (Hoffm.) Flörke (Arnold, Lich. Monac. Exsicc. 212, H – neotype). Scale bar = 1 mm.
Newfoundland. Island of Newfoundland: Bay of Islands, Coal River, 18 Sep. 1896, Waghover 616 (MIN), Shoal Point near Bay of Islands, 17 July 1895, Waghover 322 (BM, US); St. John’s City, along Empire Av., S of Carpasian Road, 6 Aug. 1978, Ahti & Hamet-Ahti 34902b (H); s.loc., 1897, Waghover s.n. (MICH); s.loc., s.d. Arnold s.n. (MICH). Ontario. Carleton Co., Ottawa region Rockcliffe Park, 2 mi. E of Ottawa, at the base of limestone cliffs at river’s edge, 31 May 1978, Brodo et al. 22789 (CANL); Lincoln Co., Winona, Niagara Escarpment, 26 June 1978, Wong 2579 (CANL). — U.S.A. New York. Greene Co., Catskill Park, Blackhead Range Trail, from E of Barnum Road just S of Maplecrest to Camel’s Hump, 13 May 1996, Buck 30206 (NY).

Specimens have also been seen from Austria (ASU, GZU, MIN), Canada (CANL, H, MICH, MIN, US), Denmark (MIN, WIS), Estonia (KRAM), Finland (COLO), Germany (GOET), Luxembourg (herb. Diederich), Malta (NY), Poland (KRAM), Romania (KRAM), Sweden (COLO, LD, MIN, WIS), Switz-

zerland (NY), UK (COLO, KRAM, MSC, NY), and Ukraine (KRAM).

Lecanora cf. andrewii B. de Lesd.

Figs 35 & 36


Thallus clearly visible, thin, areolate, areoles dispersed to aggregated (especially in vicinity of apothecia), pale yellow to yellowish brown, sometimes slightly pruinose. Apothecia occurring in groups, rarely single, broadly sessile to constricted at the base, 0.3–1.1 mm diam.; disc plane, smooth, pale brown to reddish brown or blackish, epruinose or slightly pruinose; margin level with the disc or slightly prominent, smooth, entire, even, or sometimes flexuose, uniform, slightly to moderately white pruinose, paler than thallus and disc, often whitish. Amphitheciun ± 60 μm thick, corticate, with sparse algae; cortex indistinctly or ± well delimited, uniform and ± 30 μm thick or slightly thicker at the base than at the sides and then 25–30 μm thick laterally, 30–45 μm thick at the base, composed of adglutinated hyphae or gelatinous, cortical granules sparse and mostly at top of margin (pol+, insoluble in K, soluble in N); paratheciun indistinct to well delimited and 10–30 μm wide; epithecium shades of yellow or brown, granular (pol+), granules superficial and between paraphyses tips, some also in hymenium (partly soluble in K but most insoluble in K and insoluble in N), epipsamma absent or present (insoluble in K and soluble in N); hymenium hyaline, 60–70 μm high; subhymenium indistinct, 15–20 μm high; hypothecium hyaline or yellowish, 100–120 μm high, composed of adglutinated hyphae, clear, without granules. Paraphyses slender, somewhat branched throughout, with few anastomoses, not or slightly expanded and usually not pigmented, coherent in K. Asci clavate, 8-spored; ascospores hyaline, simple, ellipsoid (broadly ellipsoid to narrowly ellipsoid), 10.5–[12.2]–15 × 4.5–[5.4]–6 μm, Q = 1.8–[2.3]–2.6. Pycnidia not seen.

CHEMISTRY. Thallus and apothecial margin K+ yellow, C+ yellow to orange or rarely C–, KC+
yellow to orange, PD+ orange; disc K+ yellow, C+ orange, KC+ orange, PD+ orange; apothecia UV+ yellowish or rarely UV–. Lichen products: unknown xanthone (Rf 4–5, UV+ reddish, cf. arthrothellin), ± pannarin detected by TLC.

HABITAT. On siliceous rock (granite, rhyolite) along seashore.

DISTRIBUTION. The species is known from northern Europe. It is scattered on the west and east coasts of North America and is also noted in the area of the Great Lakes. It represents a temperate oceanic element.

DISCUSSION. The species seems most closely related to *L. fugiens*. It has similar spot test reactions and ecology but differs in some morphological and anatomical details. *Lecanora andrewii* has, for example, a more abundant thallus and larger, aggregated apothecia. The presence of *dispersa*-like granules in the epithecium is also distinctive for the species. It is worth noting that European material is mentioned as having a white thallus and indicating a distinct C+ orange-red reaction of the thallus; the North American material seems to differ somewhat. The application of the name to North American material may require reconsideration after comparison with more material from Europe.

NOMENCLATURAL NOTES. The name *L. andrewii* B. de Lesd. was chosen as most appropriate for the material. However, typification of the species is needed after more European material is studied, or if further searches of European herbaria for any original collection prove unsuccessful.


Specimen has also been seen from Sweden (WIS).

Fig. 35. *Lecanora andrewii* B. de Lesd. (Ryan 31286b, ASU). Scale bar = 1 mm.

Fig. 36. Known North American distribution of *Lecanora andrewii* B. de Lesd.
Lecanora crenulata Hook. Figs 37 & 38


Thallus within the substratum, immersed and not apparent (endolithic), rarely partly epilithic and then thin, granulose, chalky white, ecorticate. Apothecia occurring singly, sessile or constricted at the base, concave, cup-like, or flat when mature, 0.4–1 mm diam.; disc plane, smooth, pale brown, brown, rarely blackish brown, slightly or heavily pruinose to scabrose; margin prominent and usually thick, cracked (with 3–5 fissures) or crenate, even, uniform, epruinose or pruinose, white. Amphithecium 90–190 μm thick, corticate, algae fill the area below the cortex; cortex distinctly delimited, expanded at the base, 30–70 μm thick laterally and 50–130 μm thick at the base, with gelatinous hyphae, ± obscured by granules (pol+, insoluble in K, slowly soluble in N); parathecium distinct, prosoplectenchymatous, with granules on top, up to 20 μm wide; epithecium shades of brown (more intense in N), granular (pol±), rarely not at all granular, granules superficial, coarse (insoluble in K and soluble in N); epipsamma usually present (insoluble in K and soluble in N); hymenium hyaline or pale yellow, 50–60(–80) μm high; subhymenium distinct, hyaline; hypothecium hyaline or almost so, composed of prosoplectenchyma, clear, without granules but often with numerous droplets of oil, 45–80 μm high. Paraphyses slender to moderately thick, somewhat branched, mostly in upper part, slightly expanded apically, not pigmented or pigmented brown, coherent in K. Asci clavate, 8-spored; ascospores hyaline, simple, ellipsoid (broadly ellipsoid to narrowly ellipsoid), 7.5–10.0–13(–15) × 4–5.2–6 μm, Q = 1.3–2.0–2.7. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C–, KC–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. No lichen products detected by TLC.

HABITAT. On calcareous rock, mostly limestone, occasionally also on mortar.

DISTRIBUTION. The species is widespread in Europe and in North America. It is also known from Australia. In North America it represents a boreal to temperate element with its main distribution in temperate regions.

DISCUSSION. Lecanora crenulata has distinctive apothecia with a white, crenate margin and usually a heavily pruinose apothecial disc. A similar species is L. flowersiana, which has a more distinctly cracked (tissured) apothecial margin; however, the apothecial disc is epruinose, or rarely and only slightly pruinose. The two taxa are easily distinguished by their spores, which are much longer in L. flowersiana, and by the paraphyses, which are thicker, capitate and often submoniliform in the uppermost part in L. flowersiana. Another related taxon is L. hagenii, which has smaller apothecia with a much thinner, entire to incised rather than cracked apothecial margin. The latter species also has a much thinner amphithecial cortex than in L. crenulata.

NOMENCLATURAL NOTES. The authorities’ citation of the species was cleared up by Laundon (1984).

Although some general indications pertaining to the collection area were given in Hooker’s work (southern England localities, as Glasgow, on limestone rocks) there is little chance of tracing the original collection to use as a lectotype. No
original material could be located in BM (Scott LaGreca, in letter); although W. Mudd’s allegation of Lecanora caesioalba β dispersa from Bilsdale, Yorkshire, labeled ‘Neotype specimen, Lecanora crenulata (Dicks.) Hook.’ by an unknown investigator and, to my knowledge, not published elsewhere, has been found there. Therefore I decided to choose a neotype, giving priority, as in previous cases of species typification within the L. dispersa complex, to an exsiccate collection as the most appropriate. The selected neotype represents a typical and well-developed specimen of the species.

EXSICCATES SEEN. Arnold, Lich. Exsicc. 931a (as L. crenulata) (M); Arnold, Lich. Exsicc. 931b (as L. crenulata) (M; types); Arnold, Lich. Exsicc. 1808 (as L. crenulata) (M, MIN); Hasse, Lich. Exsicc. 240 (as L. hagenii) (FH); Pišut, Lich. Slovakiæ Exsicc. 290 (as L. albenscens) (KRAM); Tobolewski, Lichenoth. Polon. 187 (as L. crenulata) (COLO, KRAM, WIS).


NEW MEXICO. Otero Co., Lincoln National Forest, near Cloudcroft, above The Pines Campground, 10 June 1966, Wetmore 14388 (MIN), Wetmore 14385 (KRAM, MIN). SOUTH DAKOTA. Lawrence Co., Limestone Plateau Region, 4 mi. WSW of Savoy, 11 mi. W of Lead, 4 June 1960, Anderson S20501 (COLO). WISCONSIN. Iowa Co., 6 mi. W of Arena, Mill Creek Bluff, 19 Aug. 1965, Foote s.n. (CANL); Richland Co., T9N R1W Sec. 20, 29 July 1960, Foote 60799a (WIS); Sauk Co., Spring Green Reserve State Natural Area, Baraboo Hills, off Jones Road, 4 Sep. 1998, Buck 34505 (NY); Vernon

Fig. 38. Known North American distribution of Lecanora crenulata Hook.
Lecanora dispersa (Pers.) Sommerf.

Fig. 39 & 40


Thallus within the substratum, immersed and not apparent, mostly endolithic, or superficial but indistinct, very thin, ecorticate, or composed of inconspicuous granules (distinct coarse granules sometimes observed are usually those producing apothecia); pale grey, yellowish or whitish. Apothecia occurring singly, or clustered in groups, sessile, or constricted at the base, concave, flat when mature, or soon convex, 0.3–0.9 mm diam.; disc plane, smooth, yellowish grey, pale brown, dark brown or almost black, epruinose or rarely slightly pruinose; margin prominent, or level with the disc, smooth, entire, even, or slightly flexuose, uniform, epruinose or pruinose, white, or concolorous with thallus, rarely concolorous with disc. Amphithecial (60–)90–200 μm thick, corticate, algae fill the area below the cortex or algae sparse, algal layer often discontinuous below hypothecium; cortex indistinctly delimited, ± uniform in thickness, or slightly thicker at the base than at the sides, 30–80 μm thick laterally and 35–120 μm thick at the base, composed of adglutinated hyphae to apparently cellular, ± obscured by granules (pol+, insoluble in K, soluble in N); paraparaphyses indistinct to well delimited and up to 30 μm wide; epithecium shades of yellow or brown, granular (pol+), granules superficial and between paraphyses tips, or also inspersed in the part or whole hymenium (often the same kind of granules dispersed also through the hypothecium), fine (insoluble in K and insoluble in N), sometimes with an epipsamma (insoluble in K and soluble in N); hymenium hyaline, or pale yellow, 45–70 μm high; subhymenium indistinct; hypothecium hyaline or almost so, 40–120 μm high, composed of adglutinated hyphae to apparently cellular, often with some granules. Paraphyses slender, somewhat branched throughout, with few anastomoses, not expanded and usually not pigmented, coherent in K. Asci clavate, 8-spored; ascospores hyaline, simple, ellipsoid (broadly ellipsoid to narrowly ellipsoid), 8–[10.3]–12 × 4.5–[5.3]–6 μm, Q = 1.5–[2.0]–2.7. Pycnidia not seen.

**CHEMISTRY.** Apothecial margin K–, C–, KC–, PD– or PD+ orange (± 75%); disc K–, C–, KC–, PD–; apothecia UV-negative or ± pale yellow or
under the species. For comparison with diagnostic (C+ yellow or orange, UV+ yellow-orange), the latter is well distinguishable by its K-soluble epithecial granules, often inspersed in part of the thalline margin (detectable especially on the inner side of the thalline margin) are also significant diagnostic characters in many specimens. Lecanora dispersa is one of the most widely distributed species of the complex, apart from L. semipallida, from which it differs both anatomically and chemically. The presence of pannarin in K and insoluble in N. The presence of pannarin and the PD+ orange reaction of the apothecial hymenium or the whole of it, which are insoluble, is one of the most widely distributed species of the complex, apart from L. semipallida, from which it differs both anatomically and chemically. The latter is well distinguishable by its K-soluble epithelial granules. The presence of vinetorin is also diagnostic (C+ yellow or orange, UV+ yellow-orange). For comparison with L. albenscens, see under the species.

NOMENCLATURAL NOTES. In the Persoon herbarium in L there is now no collection of L. dispersa. Nor could any Persoon specimen of the taxon be traced in the Acharius herbarium in Helsinki. Other herbaria supposedly holding Persoon’s material were contacted, also unsuccessfully. Apparently all original material has been lost. Thus the neotype was designated and exsiccate collections were chosen to supply an easily accessible reference collection (Śliwa 2006).


Fig. 40. Known North American distribution of Lecanora dispersa (Pers.) Sommerf.


Thallus within the substratum, immersed and not apparent (endolithic or endophloedal) or rarely crustose and composed of dispersed inconspicuous areoles, greyish. Apothecia occurring singly, widely sessile or constricted at the base, concave, cup-like or flat to slightly convex when mature, 0.3–1.0 mm diam.; disc plane to slightly convex, smooth, reddish brown, dark brown to blackish, epruinose; margin prominent or level with the disc, thick, smooth, distinctly cracked (with 3–10 fissures) when young then thin and entire or slightly crenate in older apothecia, even, uniform, epruinose, white or rarely slightly brownish on inner side (close to the disc), paler than the disc. Amphitheicum 100–170 μm thick, corticate, algae fill the area below the cortex and reach the top of margin; cortex indistinctly delimited, ±uniform in thickness, 30–50(–70) μm thick laterally and at the base, amorphous (cell walls and lumina indistinct), gelatinous, more or less obscured by granules (pol+, insoluble in K, soluble in N); parathecium ±distinct, 10–15 μm wide; epithecium deeply pigmented (up to 1/3 of the upper hymenium), shades of brown or reddish (colour disappearing or unchanged with K and more intense red with N), not at all granular, epipsamma absent, or rarely present and then undefined (insoluble in K, soluble in N); hymenium partly coloured by extended epithecial pigment, hyaline below, 40–60 μm high; subhymenium distinct, granular, not transparent, 20–30 μm high; hypothecium hyaline or almost so, 50–90 μm high, composed of adglutinated hyphae, darkened by granules (pol–) and oil droplets. Paraphyses simple or scarcely branched in upper part, thick and adglutinated, uppermost part (2–3 highest segments) apparently submoniliiform and pigmented, distinctly separte, expanded to capitate apically, coherent in K. Ascii clavate,
8-spored; ascospores hyaline, simple, mostly narrowly ellipsoid (broadly ellipsoid to narrowly ellipsoid), 10.5–[13.0]–16(–18) μm, Q = 1.8–[2.6]–3.7. Pycnidia not observed.

CHEMISTRY. Apothecial margin K–, C–, KC–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. No lichen products detected by TLC.

HABITAT. On dry, exposed sandstone and granite rock, occasionally also on wood; in desert to montane habitats. Mostly at elevation of above 1000 m and up to 2870 m.

DISTRIBUTION. The species occurs exclusively in central and western North America. It represents western temperate element.

DISCUSSION. *Lecanora flowersiana* is characterized by a reddish brown, dark brown to black, usually epruinose apothecial disc and a white, distinctly cracked apothecial margin. It is also easily distinguishable by its pigmented upper part of the hymenium, its thick adglutinated paraphyses which may become submoniliform apically, and its narrowly ellipsoid spores. The taxon was first recognized by W. A. Weber in the 1950s (label information) but was subsequently neglected and for a long time not even considered a member of the *L. dispersa* complex. The species is closely related to *L. percrenata* H. Magn., a taxon described from Central Asia (Magnusson 1940). The type collection of the latter species is too poor a specimen to elucidate potential differences, but part of the North American collections vary from typical *L. flowersiana* and were recognized as conspecific with *L. percrenata*. *Lecanora percrenata* differs in epithecium colour and in having a more distinct thallus. Epithecium colour can be influenced by habitat conditions such as isolation, and is also altered by parasitic fungi; thus it is not very reliable as a diagnostic character. The taxonomic relationship between the two species needs more attention since their separation from each other is open to question. Further investigations in Asia might yield an explanation. For further comparison with *L. percrenata*, *L. cremilata* and *L. hagennii*, see under those species.


**Lecanora fugiens** Nyl. Figs 43 & 44


Thallus partly superficial (evenascent), crustose, indistinct, thin, effuse, consisting of very small dispersed areoles, more evident around the apothecia or occasionally thicker, granulose to irregularly areolate, ecoricate but sometimes corticate with a loose unorganised alga-free layer, beige or pale yellow to yellowish brown, sometimes slightly to moderately pruinose, with distinct prothallus as white dendroid hyphae. Apothecia arising each on a discrete, single areole of thallus, sessile, flat or soon convex, 0.3–0.8 mm diam.; disc plane to slightly convex, smooth, pale brown to reddish brown, pruinose; margin level with the disc, smooth, entire, even, uniform, slightly to moderately white pruinose, paler than thallus and disc. Amphithecium ± 60 μm thick, corticate, with sparse algae; cortex indistinctly or ± distinctly delimited, uniform or slightly thicker at the base than at the sides, 25–30 μm thick laterally, 30–45 μm thick at the base, composed of adglutinated hyphae, gelatinous, cortical granules sparse and mostly at top of margin (pol+, insoluble in K, soluble in N); parathecium indistinct to well delimited and 10–30 μm wide; epithecium shades of yellow or brown to reddish brown, granular (pol+), granules coarse, superficial and between the paraphyses tips (soluble in K and insoluble in N), unchanged with K and unchanged with N, epipsamma present (insoluble in K and soluble in N); hymenium hyaline, 50–60(–70) μm high; subhymenium indistinct, ± granular, 15–20 μm high; hypothecium hyaline or yellowish, more intense in K, 100–120 μm high, composed of adglutinated hyphae, clear, without granules. Paraphyses slender (averaging less than 2 μm wide), simple or scarcely branched in upper part, slightly or not expanded, usually not pigmented, free in K. Ascii clavate, 8-spored; ascospores hyaline, simple, mostly ellipsoid (broadly ellipsoid to narrowly ellipsoid), 9–10.4–13(–15) × 4.5–5.0–6 μm, Q = 1.5–2.2–3.1. Pycnidia not seen.

**CHEMISTRY.** Thallus and apothecial margin K+ yellow, C+ orange, KC+ orange, PD– or PD+ orange; disc K+ yellow, C+ orange, KC+ orange, PD+ orange; apothecia UV+ yellowish to yellow-orange. Lichen products: unknown xanthone (Rf 4–5, cf. arthrothellin), ± pannarin detected by TLC.

**HABITAT.** On siliceous rock, predominantly on coastal cliffs, very likely also on vegetation detritus.

**DISTRIBUTION.** The species is known from northern Europe and it is scattered on eastern and western seashores of North America. Inland locations are noted in the Great Lakes area. The species has a distinctly temperate oceanic distribution.

**DISCUSSION.** The species is distinguished from *L. dispersa* by the positive K and C reactions of its thallus and apothecia and by the distinct PD+ orange reaction of its apothecial disc. It also has
smaller, regular and pruinose apothecia, which each arise on a discrete, single areole of the thallus. The characteristic prothallus and K-soluble epithecial granules of *L. fugiens* distinguish it further. *Lecanora fugiens* is a typical oceanic species. The most closely related species that occurs in a similar habitat is *L. andrewii*. The latter, however, has a much more abundant thallus and larger apothecia, with a mostly prominent thalline margin and epruinose disc. *Lecanora andrewii* also differs by the presence of *dispersa*-like epithecial granules which are absent in *L. fugiens*. The epithecial granule properties also distinguish *L. fugiens* from the maritime species *L. salina*, which additionally differs in chemistry: it indicates a C− positive reaction, but its C+ pink reaction reveals the presence of gyrophoric acid and not xanthones (C+ orange). *Lecanora conferta* is similar to *L. fugiens* in its spot test reactions, pruinose apothecial disc and epithecial granule properties, but has much more abundant apothecia which often become angular by compression. *Lecanora conferta* also occupies a different habitat; it occurs on hard limestone.

**REMARKS.** The history of the species as well as its detailed characteristics are provided by James (1960).

**EXSICCATES SEEN.** Malme, *Lich. Suecici Exsicc.* 897 (as *L. hagenii*) (MIN, WIS); Norrlin, *Herb. Lich. Fen-niae* 144 (as *L. dispersa f. atrynella*) (COLO); Räsänen, *Lichenoth. Fennica* 15 (as *L. crenulata*) (MIN).


Specimens have also been seen from Finland (COLO, MIN) and Norway (ASU, WIS).

**Lecanora hagenii** (Ach.) Ach. Figs 45 & 46


Thallus within the substratum, immersed and not apparent (endophloedal or endolithic), very rarely inconspicuous, greenish with bluish pigment. Apothecia occurring singly, evenly distributed, when young apparently immersed in the substratum, later widely sessile, flat when mature, 0.3–0.9 mm diam.; disc smooth, plane, brown with some orange to reddish tint, maroon to brown, slightly, moderately to heavily pruinose (almost frosted) or rarely epruinose, smooth; margin prominent or level with the disc, thin, smooth or rough, entire or incised (especially in young apothecia), even, uniform, epruinose or pruinose, paler than the disc or most often white. Amphithecium 75–90 μm thick, corticate, algae more or less densely fill the area below the cortex, algal layer continuous and extending below the hypothecium; cortex indistinctly delimited, ± uniform in thickness (± 30 μm) or differentiated (15–20 μm thick laterally and 20–60 μm thick at the base), composed of adglutinated, gelatinous hyphae, obscured with granules throughout or granules sparse, more abundant only on top of margin (pol+, insoluble in K and soluble in N); hymenium hyaline, 35–60 μm high; subhymenium hyaline, indistinct; hypothecium hyaline or almost so, 20–50 μm high, composed of adglutinated hyphae, without granules. Paraphyses simple, thick, slightly expanded or capitate, brown pigmented at tips, usually free in K. Ascii clavate, 8-spored; ascospores hyaline, simple, mostly ellipsoid (broadly ellipsoid to narrowly ellipsoid), 9–[11.1]–13(–15) × 4.5–[4.8]–6 μm, Q = 1.8–[2.3]–3.0. Pycnidia not seen.

**CHEMISTRY.** Apothecial margin K–, C–, KC–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. No lichen products detected by TLC.

**HABITAT.** On a wide range of organic substrata (bark of trees, wood, bones, bryophytes, vegetation or other lichens), often also directly on rock or concrete and bricks.

**DISTRIBUTION.** This is a widespread species in Europe and North America. It is also known from Asia. In North America the species occurs in boreal and temperate regions but its main distribution is in temperate areas.

**DISCUSSION.** *Lecanora hagenii* is closely related to *L. crenulata* but is distinguished by its smaller apothecia with a much thinner apothecial margin, which is entire to incised rather than distinctly crenate. *Lecanora hagenii* also has a considerably thinner amphithecial cortex, lower hymenium, and paraphyses that are ± free in K. Another similar species, *L. flowersiana*, differs from *L. hagenii* in having larger, epruinose apothecia and longer spores. Additionally *L. flowersiana* seems restricted in its occurrence to central and western North America, whereas *L. hagenii* is a widespread species.

*Lecanora hagenii* was previously assumed to be most closely related to *L. dispersa* from which it was differentiated as having a thin, neat, regular apothecial margin surrounding a small brown disc and growing on bark and wood (Laundon 2003). In the present treatment, *L. hagenii* was observed to differ from *L. dispersa* additionally by the following anatomical characters: (i) the lack of *L. dispersa*-type epithecial granules, (ii) having paraphyses that are simple, thicker, expanded in K and soluble in N); hymenium hyaline, 35–60 μm high; subhymenium hyaline, indistinct; hypothecium hyaline or almost so, 20–50 μm high, composed of adglutinated hyphae, without granules. Paraphyses simple, thick, slightly expanded or capitate, brown pigmented at tips, usually free in K. Asci clavate, 8-spored; ascospores hyaline, simple, mostly ellipsoid (broadly ellipsoid to narrowly ellipsoid), 9–[11.1]–13(–15) × 4.5–[4.8]–6 μm, Q = 1.8–[2.3]–3.0. Pycnidia not seen.

**CHEMISTRY.** Apothecial margin K–, C–, KC–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. No lichen products detected by TLC.

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Fig. 45. *Lecanora hagenii* (Ach.) Ach. (Spribille 8812, herb. Spribille). Scale bar = 1 mm.
apically and + free in K, and (iii) usually having more narrowly ellipsoid spores. In contrast to *L. dispersa*, *L. hagenii* does not produce any lichen substances. Some authors regarded *L. hagenii* as a corticolous form of *L. dispersa* (Poelt et al. 1995) or suggested that intermediate forms are frequent (Laundon 2003). This cannot be confirmed, based on the above-listed anatomical and chemical differences between the two species. The taxa do not on the above-listed anatomical and chemical differences between the two species. This could cause some confusion since they were regarded by some authors. Although *L. dispersa* is generally saxicolous and *L. hagenii* corticolous, both can occupy various kinds of substrata. This could cause some confusion since the two species occasionally grow close to each other or may even form mechanical hybrids. For comparison of *L. hagenii* with *L. persimilis* and *L. wetmorei*, see under those species.

**Nomenclatural Notes.** The species epithet *hagenii* has a complicated history. Longstanding confusion over the application of the epithet has recently been clarified by Śliwa and Hawksworth (2006); in order to unequivocally preserve the current usage of the name *L. hagenii*, the authors proposed its conservation on the basis of a conserved type specimen that is well developed and corresponds very well in all microscopic and chemical characters with the current concept of the species.

**Exsiccatcs seen.** Arnold, Lich. Exsiccat. 996b (as *L. hagenii f. umbrina*) (M, MIN); Arnold, Lich. Exsiccat. 1377c (as *L. hagenii*) (KRAM, UPS); Arnold, Lich. Monac. Exsiccat. 31 (as *L. hagenii*) (M, MIN, UPS; types); Arnold, Lich. Monac. Exsiccat. 205 (as *L. hagenii*, saxicolous) (M, UPS); Arnold, Lich. Monac. Exsiccat. 213 (as *L. hagenii f. umbrina*) (M, MIN, UPS; Arnold, Lich. Monac. Exsiccat. 266a (as *L. hagenii*, saxicolous) (M, MIN, UPS); Arnold, Lich. Monac. Exsiccat. 298 (as *L. hagenii f. umbrina*) (M, UPS); Arnold, Lich. Monac. Exsiccat. 346 (as *L. hagenii f. umbrina*) (M, MIN, UPS); Arnold, Lich. Monac. Exsiccat. 378 (as *L. hagenii*) (M, UPS); Arnold, Lich. Monac. Exsiccat. 511 (as *L. hagenii*) (M, MIN, UPS); Cummings, Decad. North Amer. Lich. 132 (as *L. hagenii*) (NY, WIS); Cummings et al., Lich. Boreali-Americ. 50 (as *L. hagenii*) (COLO, FH, MICH); Macoun, Canad. Lich. 117 (as *L. hagenii*) (COLO, FH, MICH, UPS, WIS); Malme, Lich. Suecici Exsiccat. 434 (as *L. hagenii*) (MIN, UPS, WIS); Nowak, Lich. Polon.

**Fig. 46.** Known North American distribution of *Lecanora hagenii* (Ach.) Ach.

Merid. Exsiccat. 178 (as *L. hagenii*) (COLO, KRAM, MIN); Rabenhorst, Lich. Eur. 205 (as *L. hagenii*) (KRAM); Rabenhorst, Lich. Eur. 486 (as *L. umbrina*) (MIN); Räsänen, Lich. Fenn. Exsiccat. 743 (as *L. hagenii f. coerulescens*) (MIN, UPS); Wartmann & Schenk, Schweiz. Krypt. 157 (as *L. hagenii*) (MIN).


Specimens have also been seen from Armenia (NY: Caucasus), Balkan Peninsula (GZU: Montenegro), China (MIN), Denmark (NY, WIS), France (COLO, NY), Germany (GZU, NY), Hungary (US), Luxembourg (herb. Diederich), Poland (KRAM), Portugal (COLO, WIS), Romania (NY), Russia (ASU, COLO: SW Siberia), Sweden (ASU, MIN, NY), Switzerland (NY), UK (NY), and Ukraine (KRAM).

**Lecanora invadens** H. Magn. Figs 47 & 48


Thallus partly superficial (sometimes even-scent), indistinct, crustose, more evident around apothecia, pale grey to greenish grey, often with distinct bluish pigment. Apothecia occurring singly, or clustered in groups, sessile, or constricted at the base to almost raised, flat when mature or flexuose, 0.4–1.0 mm diam.; disc plane to convex, smooth, shades of yellowish, brown to blackish, or ± plumbeous, slightly to heavily pruinose, rarely epruinose; margin level with the disc, or weakly prominent, smooth or rough, entire, even, uniform, pruinose, paler than thallus and paler than disc, white or grey or indistinctly delimited. Amphithecium 160–170 μm thick, corticate, with algae densely filling the area below the cortex; cortex usually distinctly delimited, slightly thicker at the base than at the sides, 15–50 μm thick laterally and 45–60 μm thick at the base, composed of adglutinated hyphae, obscured by granules occasionally interfering into the area below the cortex (pol+ or insoluble in K, soluble in N), thin and bluish-green at the very top of margin – due to coloured tips of marginal hyphae and bluish-green intracellular pigment (this part becoming purple in N); parathecmum usually distinct, prosoplectenchymatous, 10–15 μm wide; epithecium yellowish or shades of brown or olive, sometimes partly bluish-green, granular (pol+), granules usually sparse, between paraphyses tips, coarse (soluble in K and insoluble in N), epipsamma usually present (insoluble in K, soluble in N); hymenium hyaline, 45–65 μm high; subhymenium indistinct; hypothecium hyaline or yellow (more intense in K), 50–100 μm high, composed of adglutinated hyphae, distinct from parathecmum. Paraphyses simple or dichotomously branched at tips, slender or thickened, not expanded, or slightly expanded apically, often pigmented at top, free in K. Asci clavate, 8-spored; ascospores hyaline, simple, broadly ellipsoid (broadly ellipsoid to ellipsoid), 9–10.6 × 6–6.3–7.5 μm, Q = 1.4–1.7–2.0. Pycnidia not seen.

**CHEMISTRY.** Apothecial margin K– or K± yellow, C– or C+ yellow, KC± yellow, PD–; disc K– or K± yellow, C–, KC± yellow, PD–; apothecia UV– or some apothecia UV+ yellowish. Lichen
products: vinetorin (5-chloro-3-O-methylnorl-
chexanthone); sometimes only traces detected by TLC.

HABITAT. Directly on noncalcareous or weakly calcareous rock, often overgrowing or parasitic on other lichens, e.g., *Aspicilia* spp., *Lecanora* spp., *Verrucaria* spp.

DISTRIBUTION. Europe, Asia and North America. In North America the species is scattered in boreal and temperate regions with the main distribution temperate, but it has also several localities in the Arctic region.

DISCUSSION. *Lecanora invadens* is a morphologically variable species. For example, thallus abundance, apothecial disc colour and the presence/absence of pruina vary. Its epithelial granule type and chemistry are consistent, however. The species is closely related to *L. semipal-
ida* but differs in having a dark brown to blackish, epruinose or heavily pruinose apothecial disc and blue-green epithecium, and often a more distinct thallus. Its close relation to *L. semipallida* is indi-
cated by the presence of K-soluble granules in the epithecium (sometimes sparse!) and the presence of vinetorin. The taxonomic status of the species should be reconsidered after more material from Europe is studied, to determine whether it merits species level.

NOMENCLATURAL NOTES. *Lecanora dispersa* var. *coniotropa* is included here as a synonym for *L. invadens* H. Magn. although it was consid-
ered conspecific with *L. perpruinosa* by Fröberg (1989). The author referred to the collection by Magnusson originating from Torne Lappmark (northern Sweden) and to the collection by Poelt, Steiner and Vězda from Switzerland (distributed in Vězda, *Lich. Selecti Exsicc.* 639). Since I was not able to find the original collection by Fries, I referred to the material studied by Fröberg (1989) here. For further discussion, see also under *L. per-
pruinosa*.

REMARKS: The affinities of the material of *L. dispersa* f. *coniotropa* (coniopta?) reported from France need separate study since, as char-
acterized by Roux (1976: 23), it may represent a different taxon.

(as *L. dispersa* f. *coniotropa*) (COLO).


**Fig. 48.** Known North American distribution of *Lecanora invadens* H. Magn.

Specimens have also been seen from China (S: ‘China occidentalis: prov. Kansu, Yü-erh-hung, c. 2800 m, 11.2.1932, Birger Bohlin’ – PARATYPE [not identical]) and Sweden (FH: Torne Lappmark, coll. H. Magnusson).


Thallus indistinct or superficial, inconspicuous, granulose or areolate-rimose, grayish. Apothecia usually clustered in groups, sessile, flat or flexuose when crowded, 0.3–1.2 mm diam.; disc pale, or yellowish (often turning lead-coloured), moderately to heavily pruinose (rarely epruinose), smooth; margin usually prominent, smooth, entire to distinctly crenate or incised, epruinose or pruinose, even, or flexuose, concolorous with thallus, paler than disc. Amphithecium 60–140 μm thick, corticate, algae fill the area below the cortex, algal layer continuous below hypothecium; cortex distinctly delimited, distinctly expanded at the base, 20–30 μm thick laterally and 60–70 μm thick at the base), composed of adglutinated hyphe or gelatinous, cortical granules sparse or obscuring almost entire cortex area (pol+, insoluble in K, soluble in N); parathecium distinct, thin, ca 10 μm; epithexium shades of yellow, granular (pol+), granules superficial and between paraphyses tips, fine (insoluble in K and insoluble in N), epipsamma absent or present (insoluble in K and soluble in N); hymenium hyaline, 45–60 μm high; subhymenium indistinct, granular; hypothecium hyaline or almost so, 20–50 μm high, composed of adglutinated hyphe, clear, without granules. Paraphyses slender, somewhat branched throughout, with few anastomoses, not expanded and usually not pigmented, coherent in K. Asci clavate, 8-spored; hyaline, simple, ellipsoid (broadly ellipsoid to ellipsoid), 9–11.1 × 4.5–5.9–7.5 μm, Q = 1.5–1.9–2.3. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. Lichen products: unknown xanthone(s) detected by TLC.

HABITAT. Corticolous species occurring on tree bark (*Juniperus and Quercus*), also liginicolous; the species appears to occur typically in pinyon-juniper communities, at intermediate elevations.

DISTRIBUTION. The species is hitherto known
only from the western part of the U.S.A. Perhaps it is a western temperate element.

DISCUSSION. Although *L. juniperina* is superficially similar to *L. hagenii* due to its distinctly pruinose apothecia and often incised apothecial margin, it is in fact more closely related to *L. dispersa* due to its epithecial granule type (insoluble in K and N) and slender and branched paraphyses. It differs from the latter by having a more distinctive thallus and large, pale yellow pruinose apothecia with a conspicuously crenate thalline margin.


*Fig. 50. Known North American distribution of Lecanora juniperina Śliwa.*

*Lecanora percrenata* H. Magn. Figs 51 & 52


Thallus within the substratum, immersed and not apparent (endolithic or endophloedal), or crustose, thin, edge indefinite, mostly continuous, more or less smooth or rimose, pale, cream or greyish. Apothecia occurring singly, or clustered in groups, sessile or the base of apothecia slightly immersed in rock, flat when mature, 0.3–0.9 mm diam.; disc plane, smooth, dark brown, black or almost black, epruinose, or slightly pruinose; margin prominent, smooth, cracked (with numerous fissures), even or flexuose, uniform, epruinose, white or grey. Amphitheciun 80–120(–200) μm, corticate, algae fill the area below the cortex and reach the top of margin, bluish pigmented at top; cortex indistinctly delimited, more or less uniform in thickness, 30–35 μm thick laterally and at the base, composed of adglutinated hyphae, gelatinous, more or less obscured by granules (pol+, insoluble in K, soluble in N), with some bluish pigment at top of margin; parathecium indistinct or very thin, ± 10 μm wide; epithecium deeply pigmented (up to 1/3 of the upper hymenium) shades of brown or olive, or partly bluish-green or greenish (colour unchanged or turning more intense or green in K and turning pink or red in N), not at all granular, epipsamma absent or rarely present and then undifferentiated (insoluble in K, soluble in N); hymenium partly coloured by extended epithelial pigment, hyaline below, 30–50 μm high; subhymenium distinct, granular; hypothecium hyaline or almost so, 45–70 μm high, composed of adglutinated hyphae, with droplets of oil. Paraphyses thick and adglutinated, simple but frequently distinctly branched at tips, uppermost part (2–3 highest segments) apparently submoniliform and pigmented, end cell distinctly enlarged to subglobose (up to 6 μm wide), coherent in K. Asci clavate to broadly clavate, 8-spored; ascospores hyaline, simple, narrowly ellipsoid (ellipsoid to narrowly ellipsoid), 12–14.2–18 × 4.0–4.7–6 μm, Q = 2.3–3.1–3.7. Pycnidia...
rare, black, inconspicuous; conidia falcate – consistently filiform and characteristically curved, 16–19 × 1 μm.

**CHEMISTRY.** Apothecial margin K–, C–, KC–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. No lichen products detected by TLC.

**HABITAT.** Growing directly on calcareous rock (sandstone, caliche, limestone) but also on solid field volcanic ash, or on wood. The species occurs at elevation of 610 to 2040 m.

**DISTRIBUTION.** Scattered in central and western North America and in Asia. In North America it is a western temperate to western montane element.

**DISCUSSION.** The species is well characterized by the cracked apothecial margin and narrowly ellipsoid spores. These characters make *L. percrenata* superficially resemble *L. flowersoniana*, but it differs from the latter by having a very dark to black apothecial disc, an epithecium coloured brown, olive, or bluish green, and usually a more distinctive thallus. *Lecanora fowersiana* usually has a reddish brown or dark brown apothecial disc and an epithecium shaded brown or reddish. Some differences in spore shape were also observed; the spores of *L. percrenata* are longer and most often narrowly ellipsoid. The production of pycnidia by the latter may also prove a significant diagnostic character. See also discussion under *L. flowersoniana*.

Lecanora perpruinosa Fröberg Figs 53 & 54


Thallus clearly visible, thin, edge indefinite but mostly continuous, rimose or areolate, ash-grey. Apothecia usually clustered in groups, sessile, concave, cup-like, or flat when mature, 0.3–0.8 mm diam.; disc black or almost black, or dark brown, heavily pruinose, smooth, without umbos; margin prominent, or level with the disc, smooth, uniform, even, pruinose, thallus-coloured (concolorous with thallus). Amphitheciun 130–140 μm thick, corticate, algae densely filling the area below the cortex; cortex indistinctly delimited, more or less uniform in thickness, 15–30 μm thick, paraplectenchymatous, not gelatinous, cells up to 6 μm diam., walls of cells greenish, outer part of cortex N+ purple, cortical granules (pol+) insoluble in K and soluble in N; paratheciun indistinct; epithecium shades of brown or greenish black, not at all granular, unchanged with K and unchanged in N or N+ more intense brown to reddish, epipsammae present, undefined (insoluble in K and soluble in N); hymenium hyaline, 70–75 μm high; subhymenium indistinct; hypothecium hyaline or almost so, 70–80 μm high, composed of discrete hyphae, clear, without granules, confluent with exciple, similar in colour. Paraphyses thick, simple, submoniliform in upper part, capitate and pigmented at top, coherent in K. Asci clavate, 8-spored; ascospores hyaline, simple, ellipsoid (broadly ellipsoid to ellipsoid), 10.5–11.3–12 × 5–6.1–7.5 μm, Q = 1.6–1.9–2.1. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C–, PD–; disc K–, C–, PD–; apothecia UV-negative. No lichen products detected by TLC.

HABITAT. Growing directly on calcareous rock (limestone).

DISTRIBUTION. The species is known from Europe and North America. More data are necessary, however, to describe the species distribution pattern.

DISCUSSION. It is a very distinctive species, characterized by the ash-grey thallus and the bluish-white pruina on the dark apothecial disc. The amphithecial cortex, which is distinctly paraplectenchymatous, and the thick, submoniliform paraphyses, appearing as chains of swollen cells, are also diagnostic. The species seems most similar to L. agardhiana. A comparison of the two species is provided by Poelt et al. (1995). In my opinion...
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L. perpruinosa is unique in the L. dispersa complex due to its distinctive superficial thallus as well as the structure of the amphithecial cortex and paraphyses.

Fröberg considered L. perpruinosa to be likely conspecific with the taxon L. dispersa var. coniotropa (Fr.) Arnold, which was previously mentioned from Sweden by Fries (1831) and later collected from northern Sweden by Magnusson and from Switzerland by Poelt, Steiner and Vězda. In disagreement with Fröberg, Poelt et al (1995) asserted that L. perpruinosa is not identical with L. dispersa var. coniotropa, at least as the taxon was understood by Arnold. Based on investigations of the above-mentioned collections of L. dispersa var. coniotropa (Magnusson, LD!; Vězda, Lich. Selecti Exsicc. 639, LD!) as well as the original material of L. perpruinosa, I concur that the two taxa differ in several details. Lecanora dispersa var. coniotropa lacks such distinct pruina on the apothecial disc (as was actually noted by Fröberg), but also its amphithecial cortex is only apparently cellular, its paraphyses are expanded at the tips but not submoniliform, and above all it contains vinetorin. The presence of the lichen product makes the species most related to L. semi-pallida, and I consider L. dispersa var. coniotropa conspecific with L. invadens H. Magn. For further discussion, see under the species.

NOMENCLATURAL NOTES. In his 1989 paper, Fröberg stated that he was not validly describing the species as this would be dealt with in a later paper, but he did provide the Latin diagnosis and designated the type specimen. Since Santesson (1993: 103) and subsequently Poelt et al. (1995: 322) and Fröberg (1997: 33) himself considered the description legitimate, I follow their intention and accept the name as validly published in 1989 by Fröberg.

SPECIMENS EXAMINED. U.S.A. IOWA. Fayette Co., Apr. 1894, Fink s.n. (MIN).

Lecanora cf. perpruinosa: U.S.A. MONTANA. Flathead Co., Whitefish Range, Trail Creek, near caves close to confluence of Thoma Creek, 17 Oct. 1999, Spribille 9436 (herb. Spribille) – the specimen lacks distinct pruina on the apothecial disc, but other characters agree with the species characteristics.

Specimen has also been seen from Sweden (LD: ’Öland: Vickleby par., 1.1 km NW of Trindkärr, the great karst of Vickleby. On limestone. 56°34′N 16°30′E. RUBIN 4G411329. Alt. 0–50 m, 1988-08-8, Lars Fröberg L863’ – PARATYPE).

Fig. 53. Lecanora perpruinosa Fröberg (Spribille 9436, herb. Spribille). Scale bar = 1 mm.

Fig. 54. Known North American distribution of Lecanora perpruinosa Fröberg.
Lecanora persimilis (Th. Fr.) Nyl.  
Figs 55 & 56


Thallus within the substratum, immersed and not apparent (endophloedal), very rarely superficial, inconspicuous, membranaceous. Apothecia often clustered in groups of 2–3 or occurring singly, widely attached to the substratum, flat when mature, 0.4–0.6 mm diam.; disc plane, smooth, pale brown to chocolate brown, never pruinose, often ± glossy; margin prominent or level with the disc, smooth, entire or slightly crenate, even, uniform, epruinose or rarely slightly pruinose, concolorous with the disc or almost so, often of biatorine appearance. Amphithecium 80–90 μm thick, corticate, algae sparse or concentrated in the lower part of margin (close to the base) and absent on top; cortex distinctly delimited or continuous with parathecium, differentiated in thickness (15–20 μm thick laterally and 20–60 μm thick at the base), composed of adglutinated hyphae or distinctly prosoplectenchymatic (external hyphae enlarged and blue-green coloured), with sparse granules throughout or granules in outer part of cortex (pol+, partly soluble in K, soluble in N); parathecium distinct; epithecium in shades of brown or olive, indistinctly granular, granules superficial (pol+, partly soluble in K and soluble in N), epipsamma absent; hymenium hyaline, 45–50 μm high; subhymenium hyaline, indistinct; hypothecium hyaline, 40–50 μm high, composed of adglutinated hyphae or prosoplectenchymatic, without granules. Paraphyses slender, simple or slightly branched, slightly expanded, brown pigmented, ± coherent in K. Asci clavate, (4-)8-spored; ascospores hyaline, simple, ellipsoid (broadly ellipsoid to ellipsoidoid), 9–[9.9]–13 × 4–[5.3]–6 μm, Q = 1.5–[1.9]–2.3. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C–, KC–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. No lichen products detected by TLC.

HABITAT. On bark of deciduous trees, most often on branches and twigs.

DISTRIBUTION. Known from Europe and North America, where it was recognized from several scattered localities; probably more frequent but overlooked. It is perhaps a boreal to mainly temperate element.

DISCUSSION. The species is most similar to L. sambuci. Lecanora sambuci is easily distinguished, however, by having 12 or more spored asci. Moreover, the apothecia of L. sambuci are smaller and slightly immersed in the substratum. Lecanora persimilis is also likely to be mistaken with slightly pruinose or epruinose forms of L. hagenii. However, the apothecia of L. hagenii are scattered, occurring singly, not clustered in groups of 2–3 as most often the apothecia of L. persimilis are. The apothecial margin is always white and lecanorine in L. hagenii, whereas it may be brownish and biatorine in L. persimilis.

NOMENCLATURAL NOTES. There are five collections quoted in the species protologue: ‘in Suecia ad Ghanshammar Nericiæ (P. J. Hellbom) et Kållandsö Westrogothie (F. Graewe); in Norvegia ad Christianiam (N. G. Moe) et Tromsöe (ipse); in Fennia ad Asikkala (J. P. Norrlin)’. The following three syntypes were located in the Fries herbarium in UPS: [Sweden] ‘Nerike, Glanshammar, Skala gruva, på Salix caprea, 1866, P. J. Hellbom’;
REMARKS. The species was first reported for North America from British Columbia (Liard River Basin: Wakkpash Lake) by Brodo et al. (1987: 103).


Specimens have also been seen from Luxembourg (herb. Diederich), Poland (KRAM), Sweden (ASU), and UK (NY).


Thallus scarcely visible, thin, or thick, of dispersed or rarely contiguous, more or less convex granules or dispersed areolate, most abundant in close vicinity of apothecia, edge definite and slightly crenulate, yellowish grey to greenish grey, or light brownish. Apothecia clustered in groups, sessile, or constricted at the base, flat when mature or irregular in outline to flexuose, 0.3–0.7 mm diam.; disc plane, smooth, pale brown, epruinose; margin prominent, or level with the disc, smooth to waxy in appearance, entire or slightly crenulate, even, uniform, epruinose, concolorous with thallus, paler than disc. Amphithecium 70–160 μm thick, corticate, algae fill the area below the cortex, algal layer continuous below hypothecium; cortex distinctly delimited, brownish, more or less uniform in thickness, 25–30 μm thick laterally and 25–30 μm thick at the base, amorphous (cell walls and lumina indistinct), gelatinous, obscured by two kinds of granules (pol+): coarse, interfering also into parathecium and medullar tissue (soluble in K and insoluble in N) and fine (insoluble in K and insoluble in N); parathecium well delimited, distinct, thin, 15–20 μm; epithecium shades of yellow or brown, granular (pol+), granules superficial and between paraphyses tips, or inspersed in the whole hymenium, fine (insoluble in K and insoluble in N), unchanged in N, epipsamma

Fig. 56. Known North American distribution of Lecanora persimilis (Th. Fr.) Nyl.
absent; hymenium hyaline, 50–60 μm high; subhymenium indistinct; hypothecium hyaline or almost so, 70–80 μm high, composed of prosoplectenchyma (adglutinated hyphae), clear, without granules, confluent with paratheciurn, similar in colour. Paraphyses slender (averaging less than 2 μm wide), somewhat branched throughout, with few anastomoses, expanded or not and sometimes brownish pigmented, coherent in K. Asci clavate, 8-spored; ascospores hyaline, simple, ellipsoid (broadly ellipsoid to ellipsoid), 10.5–[10.8]–12 × 5–[5.9]–7.0 μm, Q = 1.5–[1.9]–2.1. Pycnidia-like structures were rarely observed.

CHEMISTRY. Thallus and apothecial margin K–, C– or C+ pink, KC–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. Lichen products: ± gyrophoric acid and lichenxanthone detected by TLC.

HABITAT. Exclusively on siliceous seashore rocks.

DISTRIBUTION. The species is known from Europe and the east coast of North America. It represents a maritime element.

DISCUSSION. The species occupies the same habitats as *L. fugiens* and *L. andrewii*. The taxa may appear similar in morphology, especially by the presence of a superficial (sometimes scarcely visible) thallus. *Lecanora fugiens* and *L. andrewii* differ from it in having usually pruinose apothecia, as well as in some details of apothecial anatomy (e.g., properties of epithecial and cortical granules) and chemical content (see under the species). Due to the presence of the thallus and dispersa-like epithecial granules, *L. salina* seems closely allied to *L. albescens*. In *L. salina* the thallus is much less developed and is granular-areolate rather than distinctly areolate to lobe at the margin. Moreover, the apothecia of *L. salina* are smaller and always bare, and the hymenium is lower. The presence of gyrophoric acid is also very distinctive for the species, as it is not produced by any other member of the *L. dispersa* complex. The chemistry and the somewhat different granulation of the apothecial cortex (the presence of K-soluble and N-insoluble cortical granules) suggest that the relation of the species to the complex is a matter for future debate.

NOMENCLATURAL NOTES. There were three syntypes quoted in the protologue of the species: ‘Bohuslän: par. Lycke, Elgön, 1921; par. Långelanda, Svanesund, 1924; par. Torslanda, Flygfältet, 1925’. The first one was selected as lectotype by S. Ekman in 1990 (according to the label information) but this lectotypification was never published.

REMARKS. The species was first reported from North America from Maine (Prince’s Point) by Degelius (1940: 42). The chemistry of the species was previously investigated by U. Arup and S. Ekman (label information). They noted that lecanoric acid and a lichenxanthone were detected by TLC. However, due to the faint pink (soon disappearing) rather than carmine red reaction with C indicated on the thallus, gyrophoric acid is more likely. TLC analysis and comparison with the standardized spot originating from *Umbilicaria muhlenbergii* confirmed the determination of the lichen product. Gyrophoric acid was reported from *L. salina* previously by Leuckert et al. (1990).


SPECIMENS EXAMINED. CANADA. NEWFOUNDLAND. Island of Newfoundland, Bay of Islands, Coal River, 18 Sep. 1896, Waghorne 415 (BM). – U.S.A.
MAINE. Hancock Co., Salisbury Cove, 29 July 1922, Plitt 125a, 125b (US); s.loc., s.d. Degelius s.n. (MIN).

Specimens have also been seen from Denmark (ASU) and Sweden (MIN).

Lecanora sambuci (Pers.) Nyl. Figs 59 & 60


Thallus within the substratum, immersed and not apparent (endophloedal). Apothecia occurring singly or clustered in groups, when young slightly immersed in the substratum, later sessile, flat when mature, 0.3–0.6 mm diam.; disc plane, smooth, brown, epruinose; margin prominent or level with the disc, thin, smooth, entire, even, uniform, epruinose or pruinose, paler than the disc or most often white. Amphitheciun ±80 μm thick, corticate, algae more or less densely fill the area below the cortex, algal layer continuous below the hypothecium; cortex distinctly delimited, differentiated in thickness (20–30 μm thick laterally and 30–60 μm thick at the base), composed of adglutinated, gelatinous hyphae, with sparse granules, more abundant only on top of margin (pol+, insoluble in K, soluble in N); paraphycium indistinct; epithecium in shades of brown, mostly not at all granular or indistinctly granular, granules superficial, coarse (pol+, insoluble in K and soluble in N), epipsamma absent; hymenium hyaline, 45–60 μm high; subhymenium hyaline, indistinct; hypothecium hyaline or almost so, 20–50 μm high, composed of adglutinated hyphae, without granules. Paraphyses simple, thick, slightly expanded or capitate, brown pigmented at tips, usually free in K; asci clavate, 16(–32) spored. Ascospores hyaline, simple, broadly ellipsoid (broadly ellipsoid to ellipsoid), 7.5–[9.6]–12 × 4–[5.8]–7.5 μm, Q = 1.5–[1.7]–1.9. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C–, KC–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. No lichen products detected by TLC.

HABITAT. On bark of deciduous trees especially Populus spp., Fraxinus, Acer; most often on branches and twigs.

Fig. 58. Known North American distribution of Lecanora salina H. Magn.

Fig. 59. Lecanora sambuci (Pers.) Nyl. (Ryan 24979b, ASU). Scale bar = 0.5 mm.
DISTRIBUTION. The species is known from Europe and several scattered localities in North America; perhaps more frequent but overlooked. It is probably a boreal to temperate element with the main distribution area in temperate regions.

DISCUSSION. *Lecanora sambuci* is differentiated by having small apothecia with a thin, regular thalline margin and a brown disc, and by growing predominantly on branches and twigs of deciduous trees, preferring *Sambucus*. The following anatomical characters distinguish the species: (i) asci more than 8-spored, (ii) an epithecium not at all granular, and (iii) the absence of lichen products. The two most similar species are *L. hagenii* and *L. persimilis*. However, the number of spores is diagnostic, since *L. sambuci* is the only species of the complex having multispored asci. Additionally, *L. hagenii* has an often pruinose apothecial disc, and *L. persimilis* usually has a darker apothecial margin (often biatorine), sometimes concolorous with the disc.

NOMENCLATURAL NOTES. It is the oldest species in the complex besides *L. dispersa*. No material of *Lecanora sambuci* was found in the Persoon herbarium at Leiden (Gerard Thijsse, in letter), and the original collection must be regarded as lost. Therefore a neotype has been chosen. The selection was made based on an exsiccate collection seen, as was done for typification of other members of the complex.

REMARKS. The multispored species of *Lecanora s.str.* were studied in detail by Guderley and Lumbsch (1999). The authors concluded that the number of ascospores is of minor taxonomic significance in the genus *sensu stricto*. Assessment of the significance of the character within the *L. dispersa* complex requires study of more material from Europe.


Specimens have also been seen from Austria (MIN), Sweden (MIN), and Ukraine (KRAM).
Lecanora semipallida H. Magn.  Figs 61 & 62


Thallus within the substratum, immersed and not apparent, or crustose, indistinct to clearly visible, thin, edge indefinite, ± smooth or rimose, pale grey, or yellowish grey to greenish grey, often with distinct bluish pigment. Apothecia occurring singly, or clustered in groups, sessile, or constricted at the base to almost raised, flat when mature or flexuose, 0.4–1.3(–1.4) mm diam.; disc plane, smooth, yellow, pale greenish yellow, or yellow-orange to pale brown, epruinose, or slightly pruinose; margin prominent or level with the disc, often considerably thick, smooth or rough, entire or distinctly crenate, even, uniform, pruinose or pruinose, paler than thallus and paler than disc, often with bluish pigment. Amphitheciun 70–170(–270) μm thick, corticate, algae densely filling the area below the cortex; cortex usually distinctly delimited, rarely not distinctly delimited, uniform, or slightly thicker at the base than at the sides, 30–50 μm thick laterally and 50–70 μm thick at the base, composed of adglutinated hyphae to prosoplectenchymatous, obscured by granules occasionally interfering into the area below the cortex (pol+, insoluble in K, soluble in N); paraphyses simple or dichotomously branched at tips, slender or thickened, not expanded, or slightly expanded apically, usually not pigmented, free in K. Asci clavate to broadly clavate, 4–8-spored; ascospores hyaline, simple, broadly ellipsoid (broadly ellipsoid to narrowly ellipsoid), 7.5–10.8 × 4.5–6.0–7.5 μm, Q = 1.2–1.8–2.6. Pycnidia rare, black, inconspicuous; conidia falcate – consistently filiform and characteristically curved, 10–17(–18) × 1 μm.

CHEMISTRY. Apothecial margin K+ yellow, C– or C+ yellow, KC+ yellow, PD–; disc K+ yellow or orange, C+ yellow or orange, PD–; apothecia UV+ yellow-orange; conidia UV+ yellow-orange. Lichen products: vinetorin (5-chloro-3-O-methylnorlichexanthone) detected by TLC.

HABITAT. Directly on calcareous rock (limestone, calcium-rich sandstone) and concrete or overgrowing or commensally on other lichens, e.g., Aspicilia calcarea (L.) Mudd, Caloplaca spp., Lecanora spp., Physcia spp., Phaeophyscia
Lecanora nigricans (Flörke) Moberg, *Verrucaria* spp.; occasionally on bark, bryophytes and plant debris, also on metal.

**Distribution.** It is a widespread species in Europe and North America. It is also known from Asia, Australia and New Zealand. In North America it occurs in the Arctic, alpine, boreal and temperate regions with the main distribution in temperate areas.

**Discussion.** *Lecanora semipallida* is one of the more distinct species of the *L. dispersa* complex. A key character distinguishing *L. semipallida* is the presence of epithelial granules that are soluble in K. The presence of vinetorin, resulting in positive spot tests and UV reactions of the apothecial disc, is also diagnostic. Especially interesting was the discovery of elongate, curved conidia produced by the species. Morphologically, *L. semipallida* is a highly variable species. The size, shape and colouration of the apothecia may vary significantly. The species is consistent in regard to anatomy (properties of epithecial granules) and chemistry (vinetorin always present).

A closely related species is *L. invadens* H. Magn., which differs in having a more distinct thallus than *L. semipallida*, a dark brown to blackish, epruinose or heavily pruinose apothecial disc, and a bluish-green epic theium. For comparison with *L. dispersa*, see discussion under the species.

**Nomenclatural Notes.** *Lecanora semipallida* H. Magn. was shown to be the correct name for the common, widespread member of the *L. dispersa* complex hitherto known as *L. flotoviana* (auct. non Spreng.). Further, *L. xanthostoma* Cl. Roux was shown to be conspecific with *L. semipallida* and therefore was relegated to synonymy (Śliwa 2007). Full details on the status and application of the names are provided in the publication.


MIN); Le Sueur Co., 1.5 mi. SW of Kasota, 17 July 1999, Wheeler 20114 (MIN); Otter Tail Co., Battle Lake, 20 June 1900, Fink 109 (MIN, with conidia); Wabasha Co.: Handshaw Coulee, 11 July 1979, Brako 1678 (MIN), Millville, 14 mi. SW of Wabasha, 26 June 1979, Brako 1485 (MIN); Winona Co.: 0.5 mi. SW of Bear Creek, 10 mi. NW of Winona, 17 June 1979, Brako 921 (MIN), John Latsch State Park, 12 mi. NW of Winona, near Mississippi River, 7 June 1975, Wetmore 244110 (MIN), 17 June 1979, Brako 943 (MIN), White-water Wildlife Management Area, 2 mi. W of Elba, 25 mi. NW of Winona, 13 Oct. 1979, Brako 2424 (MIN).


Specimens have also been seen from Australia (FH), Austria (ASU, GZU, KRAM), Belgium (FH), Czech Republic (NY, US), Denmark (KRAM), Germany (ASU, GOET, L, M), Hungary (FH, KRAM, WIS), Italy (MSC), Mongolia (KRAM, LE), New Zealand (ASU; MSC: Campbell Island), Norway (GOET, NY), Poland (KRAM), Russia (WIS), Sweden (FH, L, LD, MIN, NY, WIS), Switzerland (GOET, NY), UK (H, MSC, NY), and Ukraine (KRAM).

Lecanora torrida Vain. Figs 63 & 64


Thallus clearly visible, dispersed areolate, present only under apothecia or restricted to their close vicinity, rarely wider than apothecia and forming areoles, white. Apothecia occurring singly, or clustered in groups of 2–3, widely sessile on single areole of thallus, sometimes slightly immersed in the areole (areoles often very small, create stalk-like structure under apothecia), flat when mature, 0.3–1.0(–1.3) mm diam.; disc plane to convex, smooth, dark brown, or black or almost black, epruinose; margin prominent, or level with the disc, smooth, entire, even, uniform, epruinose, concocorous with thallus or darkened, paler than disc, or the same colour as the disc, or sometimes thalline margin excluded and then dark true exciple usually distinct. Amphithecium 80–190 μm thick, corticate, algae not abundant in the area below the cortex, algal layer discontinuous below hypothecium; cortex indistinctly delimited, or distinctly delimited, more or less uniform in thickness, 30–40 μm thick, prosoplectenchymatous, gelatinous, filled by abundant or sparse granules (pol+, insoluble in K, soluble in N); paratheciuncm distinct, thick, up to 50 μm, granular, bluish on top, often higher than disc and overlapping margin; epithecium shades of brown, or shades of olive, green or blue (becoming more intensely green with K and turning pink or red in N), not granular or granules scarce, but fine granules (pol+) inspersed in the whole hymenium (insoluble in K and insoluble in N), eprusima absent; hymenium hyaline, 45–60 μm high; subhymenium indistinct; hypothecium hyaline or almost so, 30–40 μm high, composed of thick adglutinated hyphae, clear, without granules. Paraphyses slender, or thick, somewhat branched throughout, with few anastomoses, slightly expanded to capitate, pigmented, with pigment sharply delimited as a cap, coherent in K. Asci clavate, 8-spored; ascospores hyaline, simple, ellipsoid (broadly ellipsoid to narrowly ellipsoid), 9–[10.9]–11 × 4.5–[5.4]–6 μm, Q = 1.5–[2.0]–2.6. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C–, KC–, PD– or PD+ orange; disc K–, C–, KC–, PD–; apothecia UV-negative. Lichen products: 2,7-dichlorlichexanthone, ± pannarin; or no lichen products detected by TLC.

HABITAT. Growing directly on calcareous rock.

DISTRIBUTION. The species occurs in Europe, North America, New Zealand and Antarctica. In North America L. torrida is an arctic-alpine to boreal species.

DISCUSSION. The chemistry and granulation of the apothecial tissues indicate the close relation of
this species to *L. dispersa* and *L. albescens*. Unlike the dispersed areolate thallus of *L. torrida*, *L. dispersa* has a thallus immersed within the substratum and not apparent, and *L. albescens* has a much more abundant thallus, often forming conspicuous rosettes which are indistinctly lobate at the margins. Additionally, the thallus of *L. albescens* bears numerous apothecia, whereas the apothecia of *L. torrida* are clustered in groups of 2–3 per thallus areole. Moreover, both *L. albescens* and *L. dispersa* have a distinctly granular epithecium which is tinged yellow or brown (unlike the dark and often not at all granular epithecium of *L. torrida*), and both are more widely distributed than *L. torrida*.

**REMARKS.** The species was known to occur in the Arctic but has recently been reported also from the Antarctic (Śliwa & Olech 2002), indicating a bipolar range.


**Lecanora cf. torrida**: CANADA. NEW BRUNSWICK. Albert Co., Fundy National Park, Point Wolfe Beach, 5 Sep. 1981, Gowan 4708 (CANL), NEWFOUNDLAND. Island of Newfoundland, Cape Norman, at N tip of the Northern Peninsula, off of Rt. 435 going towards Cook’s Harbor, 26 July 1993, LaGreca 1492 (BM, CANL, KRAM).

Specimens have also been seen from Antarctica (Śliwa & Olech 2002), Austria (GZU), New Zealand (MSC: Campbell Island), Norway (FH), and Sweden (MIN).

**Lecanora wetmorei** Śliwa

Thallus within the substratum, immersed and not apparent (endophloedal). Apothecia sessile and flat when occurring singly, flexuose when mature or crowded, 0.4–1.2(–1.5) mm diam.; disc pale brown to black, heavily pruinose, (therefore disc apparently bluish), smooth; margin prominent or level with the disc, entire, smooth, uniform, pruinose, paler than disc to white. Amphithecium 80–190 μm thick, corticate, algae fill the area below the cortex, algal layer continuous below hypothecium; cortex distinctly delimited, strongly expanded at the base, 16–20 μm thick laterally and 60–100 μm thick at the base, composed of adglutinated hyphae or gelatinous, cortical granules sparse, more abundant at top of margin (pol+, insoluble in K, soluble in N); parathecium indistinct; epithecium in shades of yellow or brown, granular, granules superficial (pol±, insoluble in K, soluble in N), in some specimens additional coarse granules present (pol+, soluble in K, insoluble in N) [those granules are easier to observe in thick cross sections], epipsamma absent or present (insoluble in K and soluble in N); hymenium hyaline, 50–65 μm high; subhymenium distinct, granular; hypothecium hyaline, 40–50 μm high, composed of adglutinated hyphae. Paraphyses simple, rarely branched, slightly expanded or capitate and not pigmented or pale brown, ± free in K. Asci clavate, 8-spored; ascospores hyaline, simple, ellipsoid (ellipsoid to narrowly ellipsoid), 9–[11.9]–13 × 4.5–[5.1]–6 μm, Q = 2.0–[2.4]–2.7. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C–, KC–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. Lichen products: sometimes traces of unknown lichen product detected by TLC (Rf A5, ice blue substance visible in 366 UV before charring).

HABITAT. Inhabits tree bark of Juniperus, Populus, Pseudotsuga, Quercus, Salix, Thuja and wood; occurs mostly at higher elevations (600 m to 3150 m).

DISTRIBUTION. The species is so far known only from the western part of North America, where it represents a western temperate to western montane element.

DISCUSSION. Although L. wetmorei is a distinctive western North American species, it was
previously identified by most collectors as *L. hagenii* due to its heavily pruinose apothecial disc. *Lecanora wetmorei* is distinguished by its considerably larger apothecia, 0.4–1.2(–1.5) mm diam. The apothecia are sessile or constricted at the base, flat to flexuose, with an entire thalline margin and a yellowish, pale brown to black disc. The amphithallic cortex of the species is considerably thickened at the base (60–100 μm). *Lecanora hagenii* has widely sessile, smaller apothecia, 0.3–0.9 mm diam., with a usually incised apothecial margin and a pale to distinctly brown disc, often tinted orange. The amphithallic cortex of the species is of more or less uniform thickness, up to 0.3 mm thick. Moreover, *L. wetmorei* occurs only at higher elevations, mostly over 600 m, whereas *L. hagenii* is a widespread species.

**Exsiccate seen.** Nash, Lich. *Exsicc. ASU* 115 (as *L. populicola*) (KRAM).


*Lecanora zosterae* (Ach.) Nyl. var. *zosterae*


Thallus within the substratum, immersed and not apparent (endophloedal), or evanescent, indistinct, thin of edge indefinite, whitish or greyish brown. Apothecia scattered to clustered, evenly distributed (not crowded), constricted at the base, orbicular at first, flat, later peltate (apparently adnate, nevertheless, narrowly attached at the base and thus regarded as constricted), 0.6–1.6(–3.5) mm diam.; disc plane and smooth initially, becoming concave and sinuous, orange brown, reddish, to lead brown or brown to almost black, epruinose or slightly pruinose; margin prominent (may sometimes be raised and involute above the disc), or level with the disc, rarely becoming excluded, relatively thin, smooth, entire, even or flexuose, uniform, concorlous with thallus or differentiated, concolorus with thallus below but often whitish and apparently pruinose on top.
Amphithecium 60–140 μm thick, corticate, algae not abundant in the area below the cortex, algal layer continuous below hypothecium; cortex distinctly delimited, indistinct or thin (30–40 μm) laterally and clearly expanded at the base (up to 40–80 μm), composed of adglutinated hyphae to apparently paraplectenchymatous, or gelatinous, cortical granules absent or sparse (pol+, insoluble in K, soluble in N); parathecium indistinct, thin, ca 10 μm wide; epithecium shades of yellow, deep orange to brown or reddish (more intense to red in N), not at all granular or rarely with sparse granules (pol+), granules superficial and between paraphyses tips (soluble in K and insoluble in N), epipsamma absent; hymenium hyaline, 45–60 μm high; subhymenium hyaline, indistinct; hypothecium hyaline or yellowish, 60–65 μm high, composed of adglutinated hyphae or prosoplectenchymatous, clear, without granules. Paraphyses slender, simple to sparsely branched, slightly expanded to capitate (up to 3 μm) apically and usually pigmented, adglutinated, coherent or free in K. Asci clavate, 8-spored; ascospores hyaline, simple, ellipsoid (ellipsoid to narrowly ellipsoid), 9–11.0–13(–16) × 4–4.8–6 μm, Q = 2.1–2.3–2.7. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C–, KC–, PD–; disc K–, C–, KC–, PD–; apothecia UV-negative. No lichen products detected by TLC.

HABITAT. On wood, detritus, other organic substrata; described and often quoted as occurring on the eelgrass Zostera.

DISTRIBUTION. It is a widespread taxon of heterogeneous distribution pattern, known from Europe, Asia and North America, including Greenland.

DISCUSSION. Lecanora zosterae is most closely related to L. hagenii. The latter differs in having small, sessile apothecia up to 0.8 mm diam., with a plane disc which is usually pruinose. Laundon (2003) provided an unambiguous and precise circumscription of Lecanora zosterae. The species as defined by the author is morphologically, anatomically and chemically uniform, and Laundon’s concept of the species is accepted here. It is recognized by its characteristic peltate apothecia, with a brown or, more usually, orange-brown to reddish and pruinose disc which becomes sinuous and concave when old, and with a whitish or grey involute margin. It has an amphithecial cortex which is distinctly delimited and clearly thickened at the base, and an epithecium which is not at all granular. The species lacks any lichen products. While studying collections of the species from the Arctic region, however, it became very difficult to keep to such a clear species concept, because of the considerable morphological variability of the species. To cover this variability, which is most likely due to extreme environmental conditions in the Arctic region and does not influence the anatomy, it seems reasonable to delimit infraspecific taxa, as proposed below.

NOMENCLATURAL NOTES. Brodo and co-authors considerably extended our knowledge of the species and related taxa (Brodo 1976; Brodo & Vitikainen 1984; Brodo et al. 2001). Based on examination of the type collections, Brodo (1976) maintained that the distinction between L. palanderi and L. beringii is not clear-cut. Brodo and Vitikainen (1984: 296) studied and lectotypified L. zosterae. In the same paper they regarded L. palanderi as conspecific with the former species and relegated it to synonymy (Brodo & Vitikainen 1984: 297). Brodo et al. (2001) again indicated the close relation of L. zosterae to L. beringii. In the present treatment a new...
taxonomic status is proposed for both *L. palanderi* and *L. beringii* (see below).

**Exsiccate seen.** *Lich. Danici Exsicc. 65 (as *L. dispersa* s.lat.)* (KRAM), with *L. semipallida*.


**Specimens also been seen from Greenland (NY, S), Mongolia (KRAM), Russia (FH: Novaya Zemlya, S: Siberia), and UK (KRAM).**

**Lecanora zosterae var. beringii** (Nyl.) Śliwa, comb. nov.  

**Fig. 69**  


Thallus within the substratum, immersed and not apparent, endolithic or endophloedal or some distinct granules of thallus visible in close vicinity of the base of apothecia. Apothecia usually

![Fig. 68. Known North American distribution of *Lecanora zosterae* (Ach.) Nyl. [including var. zosterae, var. beringii (Nyl.) Śliwa and var. palanderi (Vain.) Śliwa].](image)
clustered in groups of 2–3(–4), raised on a stalk or stipe, concave, cup-like, flat when young to flexuose when mature, 0.3–1.4 mm diam.; disc plane, smooth, reddish brown or dark brown, black or almost black, epruinose; margin prominent, occasionally becoming raised above the disc and involute, or partly excluded, entire or slightly crenate, flexuose, uniform, epruinose, paler than the disc, concolorous with thallus. Amphitheicum 90–140 μm thick, corticate, algal layer very loose, algae sparse in the area below the cortex, more abundant at both sides of apothecia; cortex distinctly delimited, expanded at the base, 30–45 μm thick laterally and 45–70(–80) μm thick at base, gelatinous, or composed of adglutinated hyphae, cortical granules sparse or more abundant, in rows or located mostly on top of margin (pol+, insoluble in K, soluble in N); parathecium indistinct; epithecium shades of yellow or brown, reddish or shades of olive, green or blue, unchanged in N, or turning pink or red in N, not at all granular or very rarely granular (pol+), granules between paraphyses tips, coarse (soluble in K and insoluble in N), epipsamma absent or present, undefined (insoluble in K and soluble in N); hypothecium hyaline, 40–60 μm high; subhymenium distinct, granular; hypothecium hyaline or almost so, 45–90(–120) μm high, composed of prosoplectenchyma, darkened by granules. Paraphyses thick (averaging more than 2 μm wide), simple, slightly expanded and usually pigmented, ± free in K. Ascii clavate, 8-spored; ascospores hyaline, simple, narrowly ellipsoid (broadly ellipsoid to narrowly ellipsoid), 9–12.0–15(–18) × 4–4.7–6 μm, Q = 1.8–2.6–3.3. Pycnidia not seen.

CHEMISTRY. Apothecial margin K–, C– or C+ yellow, KC– or KC+ yellowish, PD–; disc K–, C– or C+ yellow, KC– or KC+ yellowish, PD–; apothecia UV-negative or ± pale yellow. Lichen products: ± lichenxanthones; or no lichen products detected by TLC.

HABITAT. Growing directly on calcareous rock but preferentially on bones and caribou antlers.

DISTRIBUTION. The taxon occurs predominantly in the Arctic zone of North America but also in the alpine belt in the mountains. It is known also from Europe and represents an arctic-alpine element.

DISCUSSION. Lecanora beringii appeared to be conspecific with L. zosterae in many respects, and especially its apothecial anatomy. Morphologically the two taxa differ in some details, above all the raised apothecia of L. beringii which are often surrounded at the base by small areoles of thallus. Therefore, variety is considered the most appropriate taxonomic status for it.

NOMENCLATURAL NOTES. The lecotype of L. beringii was selected by I. M. Brodo in 1993 (according to the label information) but this lecotypification was never published.

Lecanora turbinata was described by Poelt et al. (1995). The author was hesitant to use a new name as marked on the label. At first he considered applying the name ‘beringii’ for his original specimen. Finally he decided to use the new name for his collection. The species is very distinctive but perfectly matches the present understanding of L. beringii, and that name will have to replace L. turbinata along with its taxonomic rank.

REMARKS. In 2002 during revision of the herbarium material I labeled all these specimens ‘L. turbinata Poelt & Leuckert’.

SPECIMENS SEEN. CANADA. BRITISH COLUMBIA. Near Napier Lake on Rt. no. 5, 20.5 mi. S of junction of Rts. 1 & 5, 30 May 1966, Brodo 7755 (CANL). NORTH-

Specimens have also been seen from Austria (GZU), Greenland (CANL, MIN, S) and Russia (CANL, S: Novaya Zemlya; S: Siberia).

*Lecanora zosterae* var. *palanderi* (Vain.) Śliwa, comb. nov.

**Lecanora zosterae** var. *palanderi* (Vain.) Śliwa, comb. nov.


Thallus within the substratum, immersed and not apparent, or thin, continuous, whithis or grey. Apothecia scattered to clustered, evenly distributed (not crowded), constricted at the base, 0.6–1.6(–3.5) mm diam.; disc plane, smooth, reddish brown, lead brown or brown to almost black, slightly to moderately pruinose; margin prominent, or level with the disc, rarely becoming excluded, relatively thin, smooth, entire, even or flexuose, uniform, concolorous with thallus or distinctly white, pruinose. Amphithecium 60–140 μm thick, corticate, algae not abundant in the area below the cortex, algal layer continuous below hypothecium; cortex distinctly delimited, differentiated, indistinct or thin (30–40 μm) laterally and clearly expanded at the base (up to 40–80 μm), composed of adglutinated hyphae to apparently paraplectenchymatous, or gelatinous, cortical granules absent or sparse (pol+, insoluble in K, soluble in K, soluble in N); paraplectenchymatous and between paraphyses tips (soluble in K and insoluble in N), epipsamma present (insoluble in K and soluble in N); hymenium hyaline, 45–60 μm high; subhymenium hyaline, indistinct; hypothecium hyaline or almost so, 60–65 μm high, composed of adglutinated hyphae, clear, without granules; paraphyses slender (1–1.5 μm wide), simple to sparsely branched, with clavate or slightly expanded to capitate (up to 3 μm) and usually pigmented tips, compact, coherent or free in K; ascospores, 8-spored; ascospores hyaline, simple, ellipsoid (ellipsoid to narrowly ellipsoid), 9–11.0(–13) × 4–4.8(–6) μm, Q = 2.1–2.3–2.7. Pycnidia not seen.

**CHEMISTRY.** Apothecial margin K–, C–, KC–, PD–; disc K–, C–, KC–, PD–; ascospores hyaline, simple, ellipsoid (ellipsoid to narrowly ellipsoid), 9–11.0(–13) × 4–4.8(–6) μm, Q = 2.1–2.3–2.7. Pycnidia not seen.

**Fig. 70. Lecanora zosterae** var. *palanderi* (Vain.) Śliwa (Scotter 20242, CANL). Scale bar = 1 mm.
HABITAT. Predominantly on bryophytes and other organic substrata.

DISTRIBUTION. The taxon is known from the northern parts of Europe and North America. In North America it occurs also in the alpine belt in the mountains. It perhaps represents an arctic-alpine element.

DISCUSSION. Lecanora palanderi is anatomically conspecific with L. zosterae. However, the two taxa differ in some morphological details, above all by the moderately to heavily pruinose apothecial disc of L. palanderi which is also predominantly dark coloured. Therefore, variety is proposed as its taxonomic rank.


Specimen has also been seen from Russia (S).

EXCLUDED OR UNTREATED TAXA

Listed below are species not considered for one of the following reasons: (i) although preliminarily considered members, excluded from the L. dispersa complex based on the present study (L. elen- kini, L. flotiviana, L. thalophila, L. utahensis); (ii) they show some affinities to the complex but not enough material was examined to include them in the treatment (L. actophila, L. populicola); (iii) they belong to the L. dispersa complex but were not determined in North American material (L. conferta).

**Lecanora actophila** Wedd.


This is a saxicolous species with unclear affinities. It has not traditionally been treated as related with L. dispersa complex, however, the species chemistry (the lichen xanthones produced) suggests that the relation of L. actophila to the former group of taxa requires further consideration.

SPECIMENS EXAMINED. CANADA. BRITISH CO- LUMBIA. Queen Charlotte Islands, Moresby Island, Takakia Lake, 6 July 1967, Brodo & Shchepanek 11017 (MIN).

Specimens have also been seen from Finland (MIN) and Sweden (MIN).

**Lecanora conferta** (Fr.) Grognot

The species is similar to *L. fugiens* in its spot test reactions, pruinose apothecial disc and epithelial granule properties, but has much more abundant apothecia which often become angular by compression. *Lecanora conferta* also occupies a different habitat; it occurs on hard limestone. The species is reported from several European countries and it is likely to be found in North America.

Specimens have also been seen from Sweden (WIS) and Portugal (WIS).

*Lecanora elenkinii* Mereschk.  


This is a mysterious saxicolous species. It superficially resembles *L. crenulata* due to considerably thick and distinctly crenate apothecial margin, however, the species produces isouinic acid and unknown pigment. *Lecanora elenkinii* is hitherto known exclusively from its locus classicus.

*Lecanora flotoviana* Spreng.  

*Fig. 72. Lecanora flotoviana* Spreng. (Sprengel, B – topotype). Scale bar = 1 mm.

This saxicolous lichen is excluded from *L. dispersa* complex on account of its chemistry: usnic and ± psoromic acids were detected in original collection of the species (Śliwa 2007).

**REMARKS.** The species quotation in the Sonoran desert treatment (Ryan *et al.* 2004) as well as all specimens labeled by me as ‘*L. flotoviana* Spreng.’ in 2002 refer to *L. semipallida* [= *L. flotoviana* auct. non Spreng.] (Śliwa 2007).

Specimens have been seen from Germany (B, GOET, L).

*Lecanora populicola* (DC.) Duby  

*Fig. 72. Lecanora flotoviana* Spreng. (Sprengel, B – topotype). Scale bar = 1 mm.

This corticolous lichen has not traditionally been treated as related with *L. dispersa* complex; however, the species chemistry (the lichen xanthones produced) indicate its affinity to this group of taxa. The inclusion if *L. populicola* into the latter is still an open question.


Specimen has also been seen from Poland (KRAM).
**Lecanora thallophila** H. Magn.


This interesting lichenicolous species is characterized by yellowish, considerably large apothecia (up to 2.7 mm in diam.). Although considered as related with *L. dispersa* group, *L. thallophila* was found to produce isousnic acid and therefore was excluded from the complex. For detailed characteristics see Ryan *et al.* (2004).


**Lecanora utahensis** H. Magn.


This long forgotten saxicolous taxon was regarded as a member of the *L. dispersa* group in Ryan *et al.* (2004). However, the recent chemical study of the type material indicated that the species produces isousnic acid and therefore the appropriate usage of the name is in urgent need of reconsideration. Full account of the status and application of the name is being published separately.


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REFERENCES


SYNOPSIS OF EXSICCATES EXAMINED

Listed by author, exsiccate name, number, original name and herbarium, and followed by accepted name in bold.


ARNOLD, Lich. Exsicc.: 93. Lecanora agardhianoides (M), L. agardhiana; 300d. Lecanora sambuci (KRAM, M, MIN, types), L. sambuci; 931a. Lecanora crenulata (M), L. crenulata 931b. Lecanora crenulata (M; types), L. crenulata; 996b. Lecanora hagenii f. umbrina (M, MIN), L. hagenii; 1225. Lecanora agardhiana var. ciliophthalma (GZU, KRAM, M, MIN), L. agardhiana; 1377c. Lecanora hagenii (KRAM, UPS), L. hagenii; 1703. Lecanora alberscens, lichicolous (M, MIN), L. dispersa; 1808. Lecanora crenulata (M, MIN), L. crenulata.


FLÖRKE, Deutsche Lich.: 89. Lecanora angulosa var. galactina (M), L. alberscens.


MALME, Lich. Suecici Exsicc.: 434. Lecanora hagenii (MIN, UPS, WIS), L. hagenii; 496. Lecanora hagenii (MIN, WIS), L. dispersa; 544. Lecanora


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