The Lichenologist **49**(5): 431–455 (2017)
doi:10.1017/S002428291700038X

Corticolous sorediate *Lecanora* species (*Lecanoraceae*, Ascomycota) containing atranorin in Europe

Jiří MALÍČEK, Franz BERGER, Zdeněk PALICE and Jan VONDRÁK

Abstract: Sixteen sorediate epiphytic species of *Lecanora* with atranorin from Europe are reported here. *Lecanora substerilis* is described as a new species from Carpathian beech forests in the Czech Republic, Slovakia, Romania and Ukraine; it belongs to the *L. subfusca* group in its strict sense and is characterized by its usually verrucose thallus, sorediate apothecial margin, epihymenium with coarse granules at paraphyses tips, amphithecium with large crystals and it produces atranorin and fatty acid(s). A new, yellow chemotype of *L. barkmaniana* containing pulvinic acid derivatives is recognized from Austria. Morphological, ecological and chemical variation in *L. exspersa, L. farinaria* and *L. variolascens* is discussed in detail, and brief comments on the remaining 11 species are provided. Evaluation of the type material and molecular data indicate that the predominantly saxicolous *L. caesiosora* is a sorediate form of *L. cenisia*. Molecular data confirmed the identities of the sorediate forms of *L. albella* and *L. allophana* that are conspecific with their fertile counterparts. New Central European localities are listed for the rare species, *L. barkmaniana*, *L. exspersa*, *L. mughosphagneti*, *L. norvegica* and *L. variolascens*. Positions in ITS and mtSSU phylogenies are outlined for most species. Identification keys to fertile as well as sterile populations are provided.

Key words: epiphytic lichens, *Lecanora subfusca* group, *Lecanora substerilis*, old-growth beech forests, pulvinic acid

Accepted for publication 12 *March* 2017

Introduction

Members of the genus *Lecanora*, as currently recognized, are mainly characterized by their lecanorine apothecia and a crustose or rarely placodioid thallus. Sexual reproduction predominates but vegetative reproduction by soredia is also quite common. Sorediate European species usually have a crustose thallus; leprose (e.g. *L. expallens*, *L. rouxii*) and placodioid (only in saxicolous *L. lisbonensis* and *L. lojkaeana*) growth forms are rare. Soralia vary from small delimited ones (e.g. *L. exspersa*, *L. impudens*) to those covering almost the entire thallus (e.g. *L. barkmaniana*, *L. thysanophora*). It is difficult to identify many predominantly sterile species and thus chemotaxonomic methods, mainly spot tests or thin-layer chromatography, are necessary for their correct identification (e.g. Brodo *et al.* 1994; Malíček 2014; Zduńczyk & Kukwa 2014).

This study focuses on sorediate taxa occurring on tree bark or wood which contain atranorin and/or chloratranorin as a major secondary metabolite. Some sterile specimens cannot be unambiguously identified without DNA sequence data due to the large within-species variabilities and a limited number of phenotypic characters. In contrast, our sequence data of mtSSU and ITS loci did not distinguish some closely related species that we still regard as 'good species' with respect to their differences in anatomical, chemical and ecological characters.

During our research on forest lichen diversity in Central Europe in recent years, several unidentified sorediate crusts have

J. Malíček and Z. Palice: Institute of Botany, Academy of Sciences of the Czech Republic, Zámek 1, 252 43 Průhonice, Czech Republic; and Department of Botany, Faculty of Sciences, Charles University in Prague, Benátská 2, CZ-128 01, Prague 2. Email: jmalicek@seznam.cz
F. Berger: Raiffeisenweg 130, A 4794 Kopfing, Austria.
J. Vondrák: Institute of Botany, Academy of Sciences of the Czech Republic, Zámek 1, 252 43 Průhonice; and Department of Botany, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic.

been collected, some of which could belong to new taxa of *Lecanora* or to new chemotypes (e.g. with gangaleoidin) of already known species. One crust collected at several localities, which was proved by DNA sequence data to be *Lecanora*, was distinctive and is described here as new. Five other taxa are treated in detail, the others are briefly commented upon. Identification keys (for specimens with apothecia and for sterile specimens) to all 16 species known from Europe are provided. Generally, this group of lichens is taxonomically very difficult, and detailed TLC and DNA analyses are recommended for correct identifications.

Material and Methods

This study is based on material collected by the authors and deposited either in private or public herbaria (FB: hb. F. Berger, JM: hb. J. Malíček, PRA). In addition, other specimens, including type material, were studied in B, BG, BM, BRA, E (collections of B. J. Coppins), GZU, H, L, M, PRA (collections of Z. Palice and J. Vondrák), PRA-V, S, SZU and UPS. Type material of *Lecanora farinaria* and *L. inversa* was examined only via JStor Global Plants.

Anatomical and chemical examination

Microscopic descriptions are based on hand-cut sections mounted in water. The solubility of epihymenial crystals was studied in 50% HNO_3. The amphithecium and apothecial cortex were observed in KOH. Crystals and granules in apothecia were observed in polarized light (POL). For the terminology of anatomical characters, the work of Brodo (1984) was followed. Thin-layer chromatography (TLC), with a few minor modifications, followed the methods of Orange *et al.* (2010). Lichen compounds were applied on a set of three glass plates and placed into A, B' and C solvents. The distance between starting and finishing lines was *c.* 100 mm. Two or three drops (according to the quantity of tested material) of acetone were added to each test tube. Fatty acids were detected by dipping each of these plates into water tanks. Chloratranorin was not distinguished from atranorin by TLC; their mutual presence is constant in all involved species but this is not repeated in species descriptions. Five samples extracted in methanol were analyzed by LC-MS (liquid chromatography and mass spectrometry), following the methods of Valný *et al.* (2016) with a few modifications: the analyses were performed under a linear gradient program (min/%B) 0/5, 1·5/5, 12·5/58 followed by a 1·5-min column clean-up (100% B) and 1·5 min equilibration (5% B). The total analysis time was 20 min.

DNA extraction, amplification and sequencing

Initially, simple NaOH extraction (Werner *et al.* 2002) was used for DNA isolations. This is recommended for quick isolations of non-problematic loci, for example nrITS and mtSSU regions in some richly fertile taxa (*L. argentata*, *L. chlarotera*) or very fresh material. Thereafter, Invisorb Spin Plant Mini Kit (Invitek) and CTAB protocol (Cubero *et al.* 1999) were used with better results. The fungal nuclear ITS region and mitochondrial SSU were amplified with the following primers: ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990), mrSSU1, mrSSU2 and mrSSU3R (Zoller *et al.* 1999). We also tested nuclear IGS, *Mcm7*, LSU, SSU and protein-coding β-tubulin, *RPB2* and TEF; these were used mainly in problematic sterile samples where no or only one-locus data were available. However, the amplification was unsuccessful in almost all cases.

PCR reactions of nrITS and mtSSU were prepared for a 20 µl final volume containing 14 µl of double-distilled water, 4 µl MyTaq polymerase reaction buffer, 0·2 µl MyTaq DNA polymerase, 0·4 µl of each of the 25 mM primers and 1 µl of the sample. Amplifications of both loci consisted of an initial 1 min denaturation at 95 °C, followed by 35 cycles of 1 min at 95 °C, 1 min at 55–56 °C, 1 min at 72 °C, and a final extension of 7 min at 72 °C. The PCR products were quantified on a 0·8% agarose gel stained with ethidium bromide and cleaned with GenElute PCR Clean-Up Kit (Sigma), according to the manufacturer's protocols, or with the sodium acetate/ethanol purification method. In total, 30 new nuclear ITS and 60 mtSSU sequences were generated (Table 1).

Unfortunately, we were unable to obtain sequences from five species due to the lack of fresh material (*L. viridissima*, epiphytic *L. cenisia* f. *soredians*) and difficulties with gene amplification (*L. jamesii*, *L. mughosphagneti*, *L. norvegica*). Acquiring sequences of many sterile species was very problematic and often had limited success. For example, the ITS region from *L. impudens*, *L. thysanophora* and *L. allophana* f. *sorediata* was unsuccessfully amplified in all attempts, despite employing various troubleshooting methods (touchdown PCR, nested PCR, tuning PCR settings, application of specific primers etc.). It was also necessary to use only a short mtSSU region (SSU2 × SSU3R) of *c.* 400 BP in many cases because it had higher efficiency than a long one (SSU1 × SSU3R) of *c.* 700 BP. Some species (*L. allophana* f. *sorediata*, *L. farinaria*) are represented only by one or two sequences due to a limited amount of fresh material and the amplification problems discussed above.

Alignment and phylogenetic analysis

Sequences were edited in BioEdit 7.2.5 free software (Hall 1999) and then aligned by the online application MAFFT version 7 (Katoh & Standley 2013) with L-INS-i method (Katoh *et al.* 2005). The alignments were manually revised. The final ITS alignment contained 613 positions and 48 sequences; the mtSSU alignment had 895 positions and 70 sequences. Gaps were coded in SeqState by simple coding (Simmons & Ochoterena 2000). Molecular phylogenies were reconstructed by Bayesian inference as incorporated in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001;

TABLE 1. *GenBank Accession numbers and voucher information for sequenced specimens used in this paper. Sequences in bold are newly produced.*

Taxon	Source - Specimen	ITS	mtSSU
Lecanora albella	Austria, Niederösterreich, *J. Malíček* 5855 (hb. JM)	**KY548049**	n/a
L. albella	Austria, Styria, *J. Hafellner* 51518 (GZU)	AY541241	n/a
L. albella	Czech Republic, Šumava Mts, *J. Malíček* 7336 (hb. JM)	**KY548048**	**KY502423**
L. albella f. *sorediata*	Austria, Salzburg, *F. Berger* 29362 (hb. FB)	**KY548044**	**KY502430**
L. alboflavida 1	Great Britain, Scotland, *B. J. Coppins* s. n. (E)	**KY548045**	**KY502427**
L. alboflavida 2	Great Britain, Scotland, *B. J. Coppins* s. n. (E)	n/a	**KY502428**
L. alboflavida 3	Great Britain, Scotland, *B. J. Coppins* s. n. (E)	n/a	**KY502429**
L. allophana	Albania, Valbona, *J. Malíček* 4226 (hb. JM)	n/a	**KY502455**
L. allophana	Austria, Styria, *U. Arup* L98005 (hb. Arup)	AF159939	n/a
L. allophana	Finland, Kimito, *J. Malíček* 9491 (hb. JM)	**KY548051**	**KY502416**
L. allophana	France, Massif Central Mts, *I. Frolov & J. Vondrák* (PRA)	**KY548055**	**KY502418**
L. allophana	Germany, Oberammergau, *J. Malíček* 7009 (hb. JM)	**KT630248**	**KT630256**
L. allophana	Russia, Caucasus Mts, *J. Malíček* 9626 (hb. JM)	**KY548050**	**KY502421**
L. allophana	Slovakia, Muránska Planina, *J. Malíček* 3775 (hb. JM)	n/a	**KY502456**
L. allophana f. *sorediata*	Albania, Drenovë, *J. Malíček* 4198 (hb. JM)	n/a	**KY502459**
L. allophana f. *sorediata*	Germany, Saldenburg, *R. Cezanne & M. Eichler* 8311 (M)	n/a	**KY502431**
L. allophana f. *sorediata*	Serbia, Suva Planina Mts, *J. Malíček* 7757 (hb. JM)	n/a	**KY502451**
L. argentata	Czech Republic, Pohorská Ves, *J. Malíček* 1963 (hb. JM)	**KT630245**	**KT630264**
L. argopholis	Austria, *U. Arup* L97504 (LD)	n/a	DQ787358
L. barkmaniana	Czech Republic, Třeboň, *Z. Palice* 17448 (PRA)	n/a	**KY502438**
L. barkmaniana	Germany, Bodensee, *R. Cezanne & M. Eichler* 7806 (M)	n/a	**KY502432**
L. barkmaniana	Great Britain, Cambridgeshire, *M. Powell* (hb. JM)	n/a	**KY502439**
L. barkmaniana	The Netherlands, Nieuweroord, *J. Malíček* 6960 & *L. Syrovátková* (hb. JM)	n/a	**KT630259**
L. barkmaniana 1	Austria, Niederranna, *F. Berger & J. Malíček* 7352 (hb. JM)	**KT630247**	**KT630257**
L. barkmaniana 2	Austria, Niederranna, *F. Berger & J. Malíček* 7353 (hb. JM)	**KT630246**	**KT630258**
L. bicincta	Australia, Australian Capital Territory, *U. Trinkaus* 109 (GZU)	AY541263	n/a
L. campestris	Sweden, *U. Arup* (hb. Arup) [Arup & Grube 2000, *Can. J. Bot.* **78:** 318–327]	AF159930	n/a
L. campestris	Sweden, *U. Arup* L97370 (hb. Arup)	n/a	DQ787362
L. carpinea	Slovenia, Vojsko, *J. Prügger* 62808 (GZU)	AY398710	n/a
L. carpinea	Sweden, *U. Arup* L03192 (hb. Arup)	n/a	DQ787364
L. cateilea	Canada, British Columbia, *T. Goward & J. Poelt* (GZU)	AY541250	n/a
L. cenisia	Austria, Steiermark, *J. Malíček* 5869 (hb. JM)	**KY548047**	**KY502425**
L. cenisia	Germany, Schwarzwald Mts, *J. Malíček* 5903 (hb. JM)	n/a	**KY502424**
L. cenisia	Romania, Cindrel Mts, *J. Malíček* 6714 (hb. JM)	**KY548046**	**KY502426**
L. cenisia 1	Czech Republic, Český les Mts, *J. Malíček* 5953 (hb. JM)	n/a	**KY502437**
L. cenisia 2	Czech Republic, Hrubý Jeseník Mts, *J. Malíček* 8702 (hb. JM)	**KY548041**	**KY502435**
L. cenisia f. *soredians*	Czech Republic, Hrubý Jeseník Mts (type locality), *J. Malíček* 8703 (hb. JM)	n/a	**KY502436**
L. chlarotera	Czech Republic, Sedlec-Prčice, *J. Malíček* 2699 (hb. JM)	n/a	**KY502422**
L. chlarotera	Germany, Hinterzarten, *J. Malíček* 5890 (hb. JM)	n/a	**KT630263**
L. chlarotera	UK, Scotland, *C. J. Ellis & B. J. Coppins* L642: 25 (E)	FR799206	n/a
L. cinereofusca	USA, North Carolina, Dare Co., *J. Lendemer* 34415 (NY)	KP224470	KP224465
L. exspersa	Austria, Gerlos, *J. Malíček* 5391 (hb. JM)	**KT630244**	**KT630255**
L. exspersa	France, Briançon, *I. Frolov* & *J. Vondrák* 16585 (PRA)	**KY548056**	**KY502417**
L. exspersa	Slovakia, Nová Sedlica, *J. Šoun* & *J. Vondrák* 12339 (PRA)	**KY548035**	**KY502452**
L. exspersa 1	Russia, Caucasus Mts, *J. Malíček* 9624 (hb. JM)	**KY548053**	**KY502420**
L. exspersa 1	Ukraine, Ugolka, *J. Malíček* 8235 (hb. JM)	**KY548036**	**KY502450**
L. exspersa 2	Russia, Caucasus Mts, *J. Malíček* 9625 (hb. JM)	**KY548054**	**KY502419**
L. exspersa 2	Ukraine, Uholka, *J. Vondrák* 14118 (PRA)	**KY548058**	n/a
L. exspersa 3	Russia, Caucasus Mts, *J. Malíček* 9629 (hb. JM)	**KY548057**	**KY502415**
L. farinaria	Scotland, Islay, *M. Powell* 1777 (hb. JM)	n/a	**KT630261**
L. farinaria 1	Norway, Sogn og Fjordane, Selje, *T. Tønsberg & Z. Palice* 20106 (PRA)	**KY548042**	n/a
L. farinaria 2	Norway, Sogn og Fjordane, Selje, *T. Tønsberg* 46170 & *Z. Palice* (BG)	**KY548043**	**KY502433**

TABLE 1 (*continued*).

Taxon	Source - Specimen	ITS	mtSSU
Lecanora glabrata	Sweden, Skåne, *U. Arup* L011003 (LD)	n/a	DQ787360
L. hybocarpa	Spain, Guadalajara, *H. T. Lumbsch* s. n. (F)	EF105412	n/a
L. hybocarpa	USA, Tennessee, *F. Lutzoni et al.* 03.07.04-2 (DUKE)	n/a	DQ912273
L. impudens	Czech Republic, Šumava Mts, *J. Malíček* 5071 (hb. JM)	n/a	**KY502458**
L. impudens	Romania, Fagaras Mts, *J. Malíček* 6618 (hb. JM)	n/a	**KY502460**
L. impudens	Slovakia, Muránska Planina, *J. Malíček* 2413 (hb. JM)	n/a	**KY502457**
L. impudens 1	Austria, Steiermark, *J. Hafellner* 76555 (GZU)	n/a	**KY502454**
L. impudens 2	Austria, Tirol, *J. Malíček* 7005 (hb. JM)	n/a	**KY502453**
L. intumescens	Austria, Styria, *J. Hafellner* 51153 (GZU)	AY541254	n/a
L. intumescens	Czech Republic, Hrubý Jeseník Mts, *J. Malíček* 8480 (hb. JM)	**KY548040**	**KY502441**
L. intumescens	Norway, Hordaland, *S. Ekman* 3162 (BG)	n/a	AY300892
L. intumescens	Ukraine, Ugolka, *J. Malíček* 8203 (hb. JM)	**KY548039**	**KY502443**
L. leptyrodes	Slovenia, Trnovski gozd, *J. Prügger* 65224 (GZU)	AY541255	n/a
L. paramerae	Spain, Guadalajara, *H.T. Lumbsch* s. n. (F)	EF105413	n/a
L. pulicaris	Finland, Kimito, *J. Malíček* 9484 (hb. JM)	**KY548052**	n/a
L. pulicaris	Slovakia, Nová Sedlica, *J. Malíček & J. Vondrák* 6486 (hb. JM)	n/a	**KT630262**
L. pulicaris	Ukraine, Uholka, *J. Vondrák* s. n. (PRA)	n/a	**KY502434**
L. rupicola subsp. *sulphurata*	Turkey, Prov. Izmir, *H.T. Lumbsch* s. n. (GZU)	AY541260	n/a
L. sorediomarginata	Portugal	GU480121	n/a
L. sorediomarginata	Portugal	GU480122	n/a
L. subcarnea	Sweden, Västergötland, *U. Arup* L97580 (hb. Arup)	AY541267	n/a
L. substerilis	Romania, Paring Mts, *J. Malíček* 6690 (hb. JM)	n/a	**KT630252**
L. substerilis 1	Slovakia, Stužica, *J. Vondrák* 12294 (CBFS)	**KT630243**	**KT630254**
L. substerilis 1	Ukraine, Ugolka, *J. Malíček* 8111 (hb. JM)	n/a	**KY502448**
L. substerilis 2	Slovakia, Stužica, *J. Vondrák* 12387 (CBFS)	n/a	**KT630253**
L. substerilis 2	Ukraine, Ugolka, *J. Malíček* 8162 (hb. JM)	n/a	**KY502447**
L. substerilis 3	Ukraine, Ugolka, *J. Malíček* 8209 (hb. JM)	**KY548037**	**KY502449**
L. thysanophora	Czech Republic, Šumava Mts, *J. Malíček* 8656 (hb. JM)	n/a	**KY502440**
L. thysanophora	Germany, Bayern, *J. Malíček* 7020 (hb. JM)	n/a	**KY502444**
L. thysanophora	USA, Pennsylvania, *J. Lendemer* 16933 (NY)	n/a	KC184024
L. thysanophora	Ukraine, Ugolka, *J. Malíček* 8272 (hb. JM)	n/a	**KY502442**
L. variolascens	Austria, Ybbstaler Alpen Mts, *J. Malíček* 8422 (hb. JM)	**KY548038**	**KY502445**
L. variolascens 1	Slovakia, Muránska Planina, *J. Malíček* 3100 (hb. JM)	n/a	**KY502446**
L. variolascens 2	Slovakia, Muránska Planina, *A. Guttová, J. Halda & Z. Palice* 11380 (PRA)	n/a	**KT630260**
Protoparmelia badia	Spain, Guadalajara, *H.T. Lumbsch* s. n. (F)	n/a	EF105420
P. badia	USA, Montana, *T. Spribille* s. n. (GZU)	JN009728	n/a
P. ochrococca	USA, Oregon, *B. McCune* 31673 (OSU)	KP822293	KP822489

n/a = data not available

Ronquist & Huelsenbeck 2003). The Kimura 2-parameter model using a gamma shaped distribution and proportion of invariant sites (K2P+G+I) was suggested as the best DNA substitution model for ITS, and the Hasegawa-Kishino-Yano model using a gamma shaped distribution and proportion of invariant sites (HKY+G+I) for mtSSU. This was evaluated with the help of the program Modeltest (Posada & Crandall 1998). Each analysis was performed using a run with four MCMC chains. Trees were sampled after every 500th generation. Analyses were stopped when the average standard deviation of split frequencies between the simultaneous chains was <0·01. To eliminate trees sampled before reaching apparent stationarity, the first 25% of entries was discarded as burn-in and the rest were used to compute majority-rule consensus, where the relative occurrences of nodes are identified with Bayesian posterior probabilities (Figs 1 & 2). Final trees were modified in Adobe Illustrator CS3.

Results and Discussion

Phylogeny

Nuclear ITS and mitochondrial SSU trees are presented separately because of the gapped sequence dataset (see Table 1). As expected,

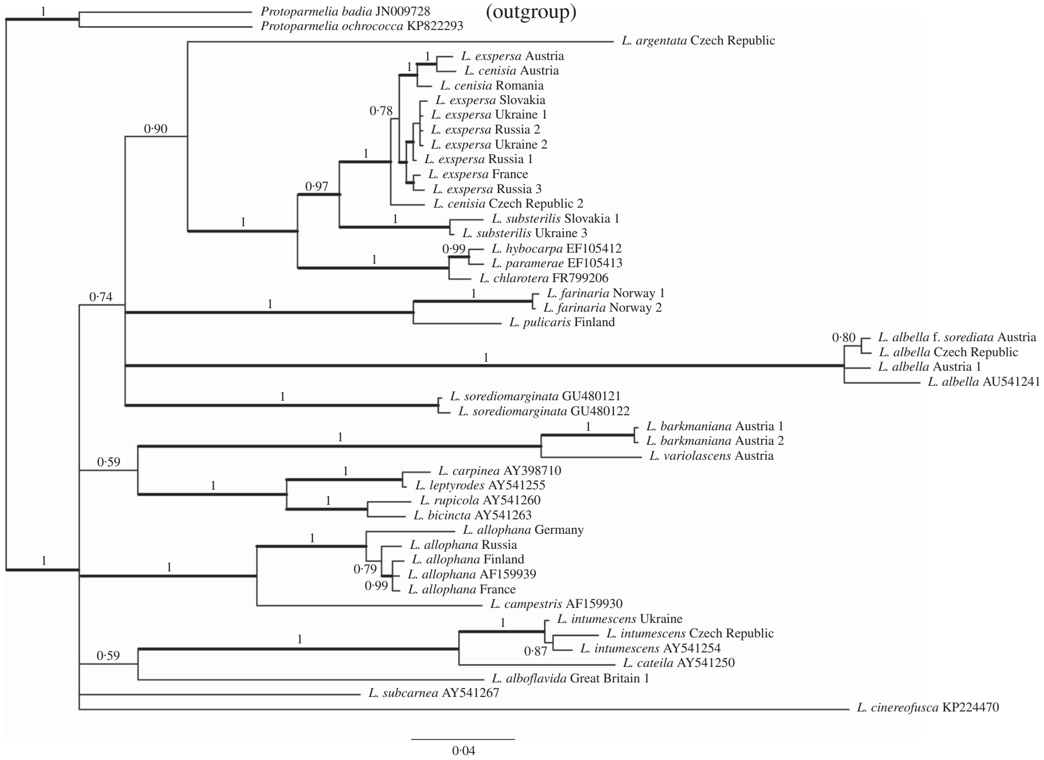

FIG. 1. Bayesian phylogenetic reconstruction (75% majority-rule consensus) of the nrITS showing positions of sorediate epiphytic *Lecanora* specimens containing atranorin. Branches with >0·95 Bayesian posterior probability values are indicated by thicker lines.

the ITS region was more variable than the mtSSU. Almost all species were represented by highly supported clades but phylogeny at higher taxonomic levels remained unresolved in both loci.

According to ITS, members of the *Lecanora subfusca* group in its strict sense (Brodo 1984) were placed into four clades: 1) with small amphithecial crystals and terpenoids represented by *L. allophana* and *L. campestris*; 2) with large amphithecial crystals and fatty acids or gangaleoidin chemosyndrome; 3) the clade of *L. farinaria* and *L. pulicaris*; and 4) the clade of *L. cinereofusca* (Fig. 1).

MtSSU phylogeny indicated a monophyly of the *L. subfusca* group, except for an unrelated species, *L. cinerefusca* (Fig. 2). Species with small and large amphithecial crystals were again distinguished; consequently *L. farinaria* and *L. pulicaris* formed isolated clades. Due to a lower variability of this region, some closely related species were not separated from each other (e.g. *L. cenisia* and *L. exspersa*) although they differ markedly in many characters.

Species

Lecanora albella f. sorediata (Schaer.) H. Olivier

Expo. Syst. Descr. Lich. Ouest Fr. **1:** 277 (1897)—*Lecanora pallida* f. *sorediata* Schaer., *Enum. critic. lich. europ. (Bern)*: 78 (1850); type: not seen.

Lecanora albella is characterized by strongly pruinose apothecia and the presence of protocetraric acid in the apothecia giving a distinct Pd+ red reaction. The sorediate form is characterized by greenish, rounded, flat to convex, well-delimited soralia of

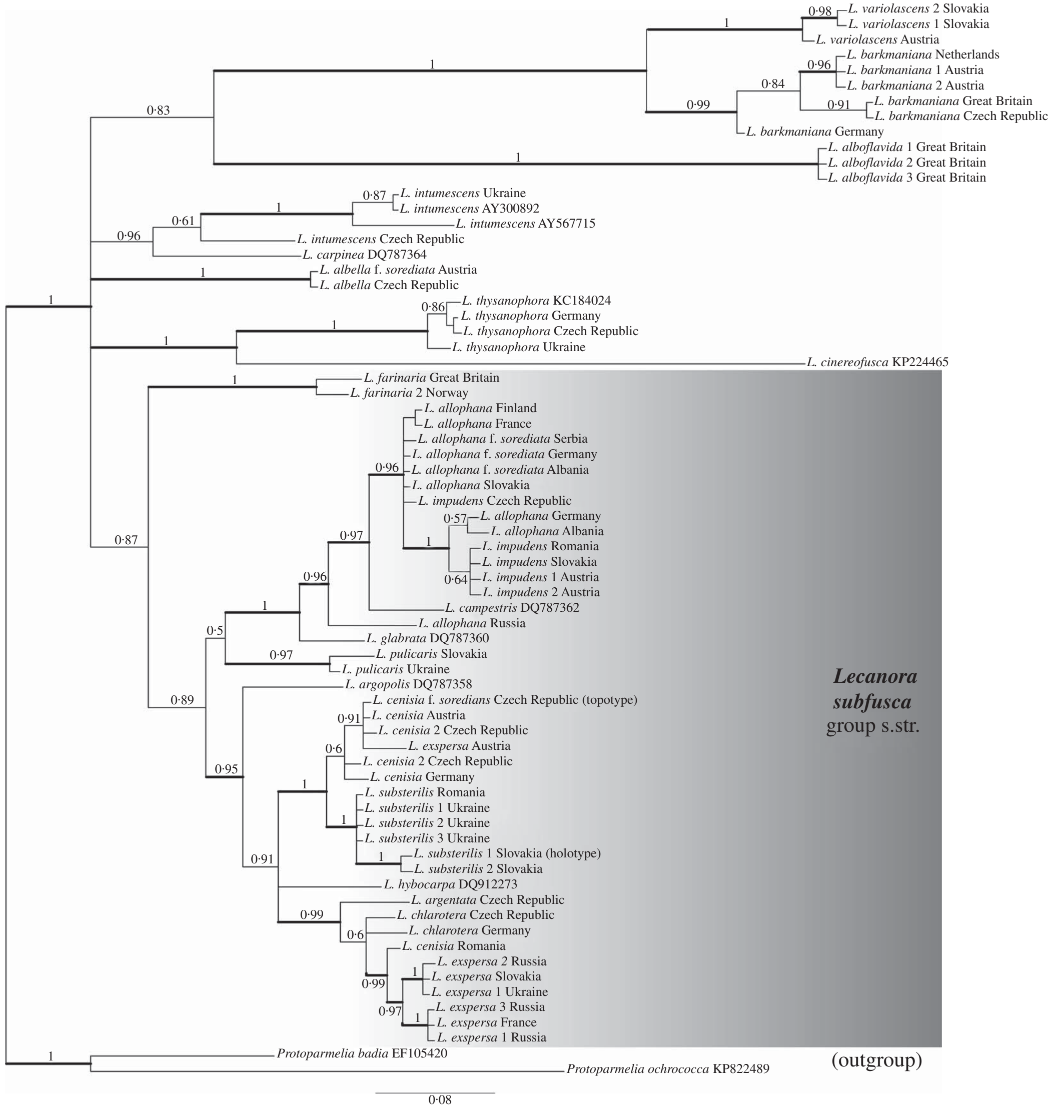

FIG. 2. Bayesian phylogenetic reconstruction (75% majority-rule consensus) of the mitochondrial SSU showing positions of sorediate epiphytic *Lecanora* specimens containing atranorin. Branches with >0·95 Bayesian posterior probability values are indicated by thicker lines.

c. 0·5–2·0 mm diam. and a smooth and thin thallus. Soralia and thallus contain roccellic acid. In the ITS and mtSSU phylogenetic reconstructions, sorediate and non-sorediate populations are closely related and collectively form supported clades distant from all other species included (Figs 1 & 2). The species prefers old-growth beech forests but it is occasionally found on other phorophytes and in other forest types.

Specimens examined. **Austria:** *Salzburg*: Obersulzbachtal, 47°11'41"N, 12°15'43"E, alt. 1300 m, *Alnus*, 2015, *F. Berger* 29362 (hb. Berger).

Lecanora alboflavida Taylor

Fl. Hibern. **2:** 260 (1836); type: not seen.

Lecanora inversa Nyl., *Flora, Regensburg* **62:** 361 (1879)—*Ochrolechia inversa* (Nyl.) J. R. Laundon, *Lichenologist* **2:** 130 (1963); type: [Ireland], on furze [*Ulex europaeus*], Finnihy River, Co. Kerry, [*Taylor*], (BM975547—lectotype?).

The species is characterized by the thick, smooth to more often pustulate thallus and rounded soralia which tend to be confluent later. Apothecia are rare and ascospores unknown. Based on anastomosing paraphyses, Laundon (1963) transferred the species into the genus *Ochrolechia*. It produces xanthones (arthothelin, thiophaninic acid and sometimes others). *Lecanora alboflavida* has an isolated position among *Lecanora* species included in both trees (Figs 1 & 2). It is a very distinct taxon among the other sorediate *Lecanora* species containing atranorin due to its yellowish thallus and soralia that are UV+ as well as C+ orange. The thallus colour reflects the xanthone concentration and may vary from grey to yellow. It can be misidentified as saxicolous *Pertusaria flavicans*, which lacks atranorin, and *Lecidella subviridis*, which has a very similar chemistry but a much thinner thallus with usually confluent and never rounded soralia.

Lecanora alboflavida is a poorly known and very rare oceanic species. It occurs on acidic bark of old trees, rarely on slate and sandstone rocks. Most of its localities are known from the British Isles. It has also been reported from Norway, France and Macaronesia (Edwards *et al.* 2009) but the material has not been examined. Nevertheless, the Norwegian record is absent from the checklist of Fennoscandian lichens (http://130.238.83.220/santesson/home).

The species was described from transition rocks (Taylor 1836). According to Laundon (1963), Taylor's only saxicolous specimen (i.e. the type) is in fact *L. epanora*. Therefore, the correct name should be *Lecanora inversa*, which was described by Nylander (1879) based on Taylor's epiphytic material. However, we follow the concept of British authors (Edwards *et al.* 2009) because we haven't yet studied Taylor's collections.

Specimens examined. **Great Britain:** *Scotland*: **V. C. 73,** Kirkudbrightshire: Glen Trool, Caldons Wood, 55°4'36–39"N, 4°30'40–51"E, alt. 80 m, *Betula* and *Quercus*, 2016, *B. J. Coppins* (E, dupl. hb. JM).—**Ireland:** *North Kerry*: Cahnicaun Wood, Killarney Lakes, *Quercus*, 1982, *P. W. James* (BM); Derrycunihy, woods above Galway's Bridge, 1982, *P. W. James* (BM).

Lecanora allophana f. sorediata Vain.

Medd. Soc. Fauna Flora Fenn. **3:** 103 (1878); type: not seen.

The sorediate morphotype of *L. allophana* produces delimited, white to yellowish soralia but apothecia are frequently present as well. The sorediate form frequently accompanies non-sorediate populations. The presence of terpenoids *allophana*-unknowns distinguishes this species from all other European corticolous *Lecanora*. For a detailed description of the taxon and its chemical substances, see Tønsberg (1992) and Malíček (2014).

The taxon strongly resembles *L. impudens*, which nests within the *L. allophana* clade in the mtSSU phylogeny (Fig. 2); an amplification of nrITS for the sorediate form was unsuccessful. However, the taxa differ in secondary metabolites and ascospore size, and we have tentatively kept them at the species level.

Selected specimens examined. **Austria:** *Tirol*: Heiterwang, 47°27'18"N, 10°45'32"E, alt. 980 m, 2014, *Fraxinus excelsior*, *J. Malíček* 7005 & 7006 (hb. JM).—**Albania:** *Korcë County*: Drenovë National Park, Korča [Korcë], 40°35'02"N, 20°50'43"E, alt. 1400 m, *Populus tremula*, 2011, *J. Malíček* 4198 & *F. Bouda* (hb. JM).—**Germany:** *Bayern*: Allgäu, am Bannwaldsee nördl. Füssen, 800 m, *Fraxinus excelsior*, 1956, *An. & Ad. Schröppel & J. Poelt* (PRA-V 14603). *Niederbayern*: Burganlage oberhalb von Saldenburg, alt. 560 m, Esche, 2011, *R. Cezanne* & *M. Eichler* 8311 (M).—**Macedonia:** *Galichica National Park*: Stenje, Mt. Magaro, 40°56'46"N, 20°52'16"E, alt. 1150 m, old *Quercus cerris*, 2014, *J. Malíček* 7964 (hb. JM).—**Serbia:** *Suva Planina Mts*: Sopotnica, 43°10'00"N, 22°08'59"E, alt. 690 m, old *Quercus cerris*, 2014, *J. Malíček* 7757 (hb. JM).—**Slovakia:** Muránska planina National Park, Cigánka Reserve, 48°45'34·8"N, 20°03'37·8"E, alt. 920–925 m, *Acer pseudoplatanus*, 2010, *J. Malíček* 3081 & *Z. Palice* 13483 *et al.* (hb. JM, PRA).

Lecanora barkmaniana Aptroot & Herk

As *L. barkmaneana* in *Lichenologist* **31:** 3 (1999) [see orthographic correction in *Lichenologist* **31:** 553 (1999)]; type: Netherlands, Prov. Friesland, De Blesse, 7 km

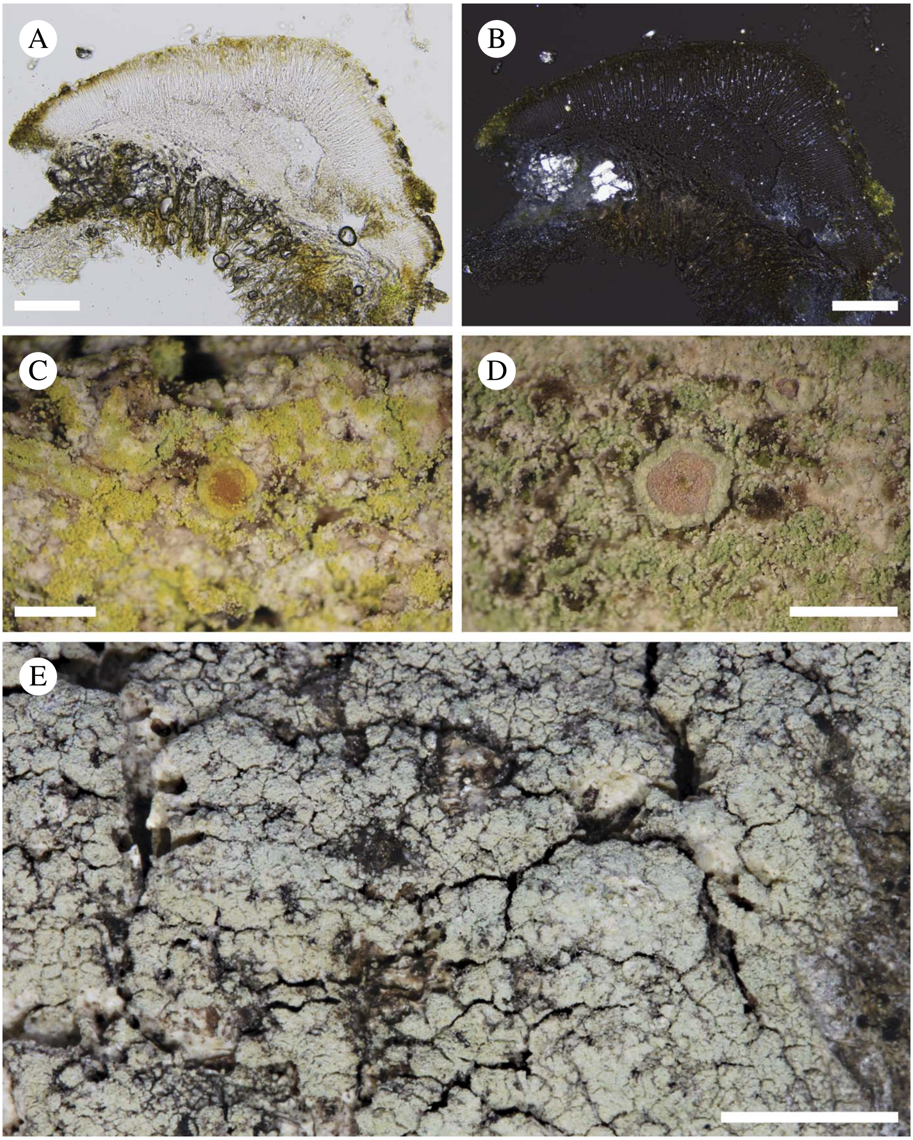

FIG. 3. Habitus of *Lecanora barkmaniana*. A, apothecial section of the chemotype with pulvinic acid derivatives; B, the same in polarized light; C, apothecium with high concentration of pulvinic acid derivatives; D, Austrian collection without the yellow pigment; E, isotype of *L. barkmaniana* (L64338). Scales: A & B = 100 µm; C & D = 1 mm; E = 1 cm. In colour online.

south of Wolvega, 6°05'E, 52°50'N, young wayside *Quercus robur*, at the base of the trunk, *C. M. van Herk* 1996 (B—holotype; L 0064338—isotype!).

(Fig. 3A–E)

Thallus white to pale grey, matt, up to 8 cm diam. or exceptionally covering large areas, thin to rarely strongly verrucose or pustulose (up to 0·25 mm thick), pustules frequently fissured, filled by large calcium oxalate crystals (POL+); *prothallus* absent or indistinct, whitish grey, visible in some collections, especially from smooth bark; *photobiont* trebouxioud, cells globose to subglobose, 7–13 µm diam.; *soralia* more or less delimited when young, later confluent or forming a continuous leprose crust covering the whole thallus, but esorediate parts of the thallus remain visible at least in the marginal zone; *soredia* whitish grey with a yellow tinge, rarely greenish yellow to golden yellow, farinose, 25–35(–40) µm diam.

Apothecia rare, lecanorine, sessile, 0·5–0·9 mm diam.; *margin* slightly to strongly crenulate or flexuose, medium thick (*c.* 0·1 mm), grey to rarely yellow, often partly sorediate; *discs* yellow to pale brown, matt, usually with very small and scattered pruina-like granules.

Thalline exciple with numerous photobiont cells; *amphithecium* ±paraplectenchymatous, with large crystals, often forming clusters; *cortex* indistinct; *hypothecium* colourless, yellowish in K; *hymenium* colourless, 50–75 µm high, composed of unbranched paraphyses 1·5–2·0 µm thick, conglutinated, very slightly swollen at tips, K/I −; *epihymenium* with pale brownish granules (POL−), rarely with golden orange pigment and granules, granules at paraphyses tips, soluble or partly insoluble in K; *asci Lecanora*-type, 35–50 × 9–15 µm, 8-spored but usually fewer spores observed; *ascospores* simple, colourless, broadly ellipsoid to rarely subglobose, 12–15 × 8·5–10·0 µm.

Conidiomata unknown.

Chemistry. Atranorin, chloratranorin and zeorin as major substances (nine specimens including the isotype analyzed by TLC, two by LC). According to Aptroot & van Herk (1999), atranorin was only a minor compound in their HPLC analysis; however, we detected comparable amounts of both substances. A new yellow chemotype with pulvinic acid complex is reported here from Austria (specimens marked by ⋆). An unidentified yellow pigment (visible by TLC in solvents A, B' and C) is produced as a major compound, and a trace of calycin is visible in solvent C. Probably the pigment is closely related to pulvinic acid due to the presence of the two together in tested material of *Candelariella* species. This pulvinic acid derivative is characterized as a yellow spot (UV+ orange before heating) on TLC plates. In the B' solvent, the spot is below the level of pulvinic acid and in the same position as norstictic acid. The common chemotype of *L. barkmaniana* sometimes accompanies the yellow form in Austria. The pulvinic acid derivatives are often unevenly distributed on the thallus and apothecia: some parts are vivid lemon yellow, others have the normal tinge. Spot reactions of thallus and soralia: Pd− or Pd+ yellow (in the yellow chemotype), K+ yellow, C−, KC−, UV−.

Phylogeny. Based on ITS and mtSSU sequences, *L. barkmaniana* does not belong to the *L. subfusca* group in a narrow sense as suggested by Aptroot & van Herk (1999), but forms an isolated clade with *L. variolascens* (Figs 1 & 2).

Ecology. In Western Europe, *L. barkmaniana* occurs mainly on wayside deciduous trees (e.g. *Quercus robur*), usually at eutrophicated sites (Aptroot & van Herk 1999). Central European localities are characterized by natural deciduous woodlands with, for example, *Quercus robur*, *Alnus glutinosa* and *Fraxinus excelsior*. The Austrian populations are concentrated mainly at the bottom of wind- and sun-protected river gorges; this area has *c.* 1000 mm of precipitation a year and an average annual temperature of *c.* 9 °C. These sites are interesting due to the occurrence of several species with suboceanic distributions (e.g. *Coniocarpon cinnabarinum* and *Micarea coppinsii*).

Distribution. The species has a subatlantic distribution, occurring mainly in Western Europe (Great Britain, Netherlands, Germany, France etc.). Scattered localities are reported here from Central Europe: Austria, the Czech Republic and Slovenia (see below). Surprisingly it does not occur in Scandinavia. A dubious record has been published from Korea (Kondratyuk *et al.* 2013). The yellow chemotype is known only from the Danube Valley and some of its tributaries in Upper Austria, very close to the north-western border with Germany in the Bayerischer Wald Foothills region.

Remarks. Despite resembling several other sorediate crusts (e.g. *Lecanora compallens*, *Lecidella elaeochroma* f. *sorediata*, *L. subviridis*), *L. barkmaniana* is well characterized by the grey-white thallus, ±continuously covered by yellowish confluent soralia, and its chemistry. The ascospore size of 7–12 × 3–4 µm reported by Aptroot & van Herk (1999) in its original description is probably based on immature or poorly developed ascospores. Our measurements of the well-developed, fertile material from Austria indicated larger dimensions. The yellow variety of *L. barkmaniana* is one of a small number of species in the genus producing pulvinic acid derivatives (see Lumbsch 1994; Morse & Ladd 2016). The morph with golden yellow soralia resembles *Chrysothrix candelaris* or *Candelariella efflorescens* agg.

Specimens examined. **Austria:** *Upper Austria*: Schärding, Waldkirchen, Kleiner Keßlbach, 290 m, *Fraxinus*, 2004, *F. Berger* *19451 (hb. Berger); *ibid*., 48°27'51"N, 13°47'20"E, 2014, *J. Maliček* *7352 & *F. Berger* (hb. JM); Rohrbach, Neustift, valley of the River Ranna, alt. 340 m, 48°29'28"N, 13°46'52"E, *Alnus glutinosa*, 2004, *F. Berger* *19437 (hb. Berger, BG); *ibid*.:, 48°28'46"N, 13°46'37"E, alt. 300 m, *J. Maliček* *7353 & *F. Berger* (hb. JM); Braunau, Salzachtal, Auwald W St. Radegund, 365 m, *Alnus glutinosa*, 2004, *F. Berger* *19718 (hb. Berger); Engelhartszell, Kronschlag, 48°28'42"N, 13°45'43"E, alt. 340 m, *Juglans regia*, 2014, *J. Maliček* 6981, 7350, 7351 & *F. Berger* (hb. JM).—**Czech Republic:** *S Bohemia*: Třeboň, nature reserve Stará řeka, alluvial oak forest, 48°59'00"N, 14°50'39"E, alt. 435 m, *Quercus robur*, 2014, *Z. Palice* 17448 (PRA).—**Germany:** *Bayern*: Bodensee, Weißenberg, alt. 530 m, Linde, *R. Cezanne & M. Eichler* 7806 (M).—**Great Britain:** *England*: **V.C. 29,** Cambridgeshire: Gamlingay Wood, *Populus tremula*, 2013, *M. Powell* (hb. JM).—**The Netherlands:** *Drente*: 7 km W of Diever, Vledder, *Quercus robur*, 1993, *P. v.d. Boom* 15075 (PRA-V); Hoogeveen, Nieuweroord, 52°43'28"N, 6°34'30"E, alt. 0–50 m, *Quercus robur*, 2014, *J. Maliček* 6960 & *L. Syrovátková* (hb. JM).—**Slovenia:** *Dinaric Alps Mts*: Postojna, 45°49'14"N, 14°14'46"E, alt. 460 m, *Acer campestre*, 2016, *J. Maliček* 9463 (hb. JM).

Lecanora cenisia f. soredians (Suza) Malíček comb. nov.

MycoBank No.: MB 822389

Lecanora cenisia var. *soredians* Suza, *Sb. Klubu Přírodovědeckého v Brně* **11:** 152 (1929); type: [Czech Republic], Moravia, Sudeti or., Jeseníky, in monte Vozka (Fuhrmannstein), ad saxa schistosa in fissis subumbrosis, 1370 m, 1928, *J. Suza* (PRM 639535!—holotype).

Lecanora caesiosora Poelt, *Denkschr. Regensb. Bot. Ges.* **26:** 82 (1966); nom. nov. – *Lecanora soralifera* H. Magn., *Bot. Notiser* **1937:** 135 (1937); type: Magnusson: *Lich. sel. Scand. exs.* 270b, Sweden, Västergötland: Partille, northwest of Tultered, on stone fence, open situation, 1936, *A. H. Magnusson* (UPS—holotype; B!, BRA!—isotypes).

(Fig. 4A)

The sorediate form of *L. cenisia* is characterized by a thick verrucose thallus and large, flat to convex, rounded soralia. It produces roccellic acid, rarely replaced by nephrosteranic acid. For a detailed description see Brodo *et al.* (1994) and Malíček (2014). *Lecanora cenisia* is predominantly a saxicolous species occurring on exposed as well as sheltered siliceous rocks in montane areas. The sorediate form prefers overhanging rocks. Epiphytic growth is rare and most records are from twigs of *Rhododendron* in the subalpine zone (Hinteregger 1994), where it can be easily misidentified as *L. exspersa*.

In contrast to Brodo *et al.* (1994) and Malíček (2014), we prefer to regard *L. caesiosora* as a sorediate form of *L. cenisia*. Both taxa are morphologically and chemically identical, they also share ecological preferences (although *L. caesiosora* prefers vertical and overhanging rocks) and apothecial anatomy, and often grow together. Synonymization of *L. caesiosora* with *L. cenisia* is supported by the mtSSU data (Fig. 2); the sorediate form shares the same sequence as the typical *L. cenisia* and co-occurs at the type locality of f. *soredians*. Nevertheless, the taxonomy of *L. caesiosora sensu* Brodo *et al.* (1994) still remains partially unclear because of its wide variation. The rare chemotype with nephrosteranic acid might potentially represent a saxicolous form of *L. exspersa*, but molecular data are not available.

Epiphytic specimens examined. **Austria:** *Tirol*: Ötztaler Alpen, S von Obergurgl, Gurgler-Heide, Gaisberglift, 1950 m, *Rhododendron ferrugineum*, 1986, *E. Hinterreger* (GZU).—**Czech Republic:** *Šumava Mts*: cirque of the Černé jezero lake, 49°10'35"N, 13°11'10"E, 1150 m, *Sorbus aucuparia*, 1995, *Z. Palice* 232 (PRA).

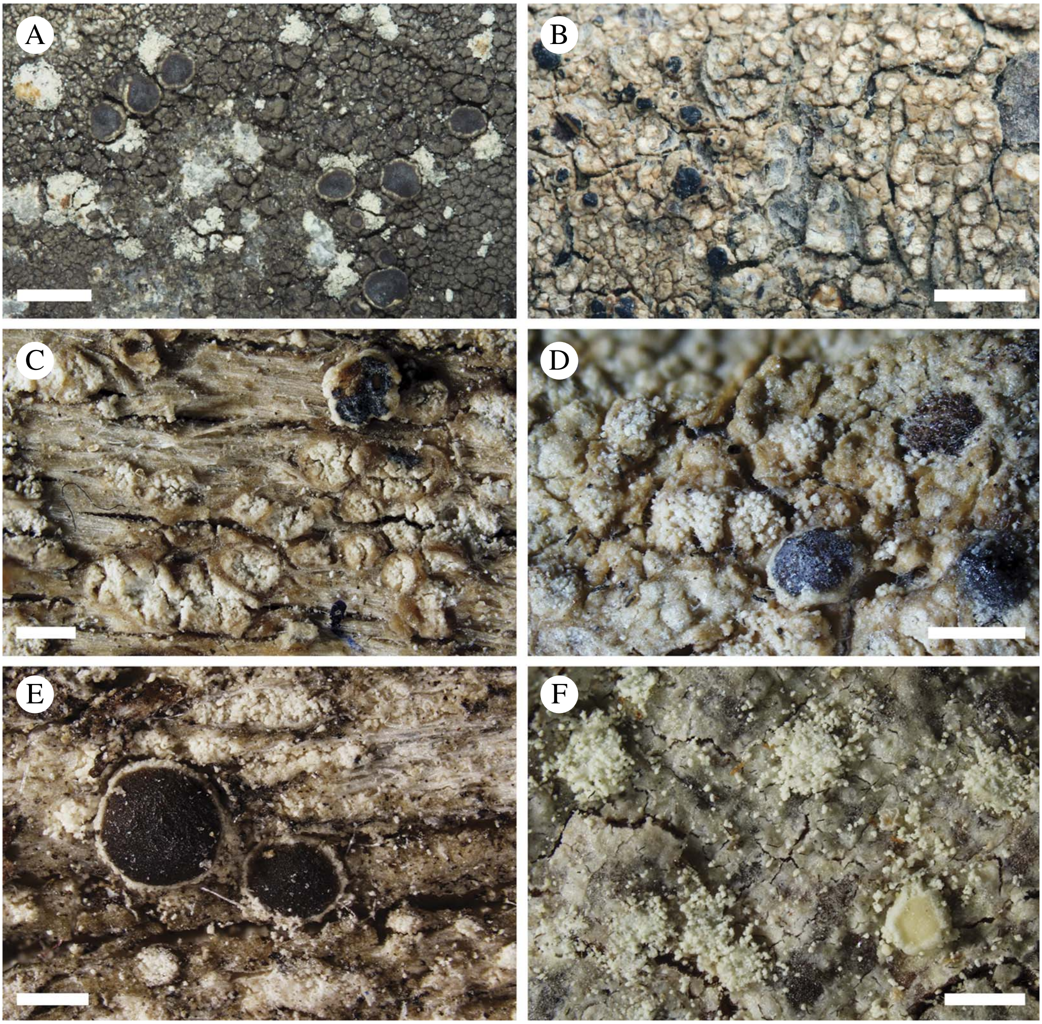

FIG. 4. A, holotype of *Lecanora cenisia* f. *soredians* (PRM); B & C, type collection of *L. elisa* (= *L. exspersa*) (H-NYL 27609 & M); D, type material of *L. exspersa* (M); E, habitus of *L. farinaria* (B); F, fertile specimen of *L. jamesii* (JM 9007). Scales: A & B = 2 mm; C–F = 0·5 mm. In colour online.

Lecanora exspersa Nyl.

Flora, Regensburg **58:** 443 (1875); type: [Romania], ad ramulos abietum in regione "Aragyes" infra alpem Retyezát, com. Hunyad in Transsylvania, 1873, *Lojka* (H-NYL 27610!—holotype; M 207003!—isotype).

Lecanora raesaenenii Gyeln. [as 'räsänenii'], *Acta Faun. Fl. Univers., Ser. 2, Bot.* **1** (no. 5–6)**:** 10 (1933); nom. nov. for *Lecanora coilocarpa* var. *sorediata* Räsänen, *Medd. Soc. Fauna Flora Fenn.* **43:** 118 (1917); type: [Finland] Ob. Simo. Pahnila, huoneen semalla, [on wood], 1913 & 1915, *V. Räsänen* (H!—lectotype).

Lecanora elisa Nyl., *Flora, Regensburg* **64:** 178 (1881); type: [Romania], ad ramulos Pini cembrae in regione "Arágyes" infra alpem Retyezát, com. Hunyad in Transsylvania, 1874, *Lojka* (H-NYL 27609!—holotype; M 207005!—isotype).

(Fig. 4B–D)

Thallus whitish grey, thin, usually slightly pustulate to areolate-cracked, rarely ± smooth; *prothallus* absent or black when adjacent to other lichens; *photobiont* trebouxioid, cells globose, 7–12(–15) µm diam.; *soralia* whitish, distinctly paler than the esorediate part of the thallus, rarely yellowish (in populations from beech forests), flat or concave when young, 0·2–0·8 mm diam., rounded, delimited by a thalline rim that can be missing in large or old soralia, only occasionally confluent; *soredia* farinose, 20–50 µm diam.

Apothecia usually absent or poorly developed, sessile or immersed when young, up to 0·5 mm diam.; *margin* flexuose, uneven, later disappearing or discontinuous; *discs* brown to brownish black, sometimes slightly pruinose, flat to convex. *Amphithecium* with large crystals (*pulicaris*-type), but these are usually absent; *cortex* indistinct or if present up to 40 µm at base; *hypothecium* colourless; *hymenium* 40–100 µm high; *epihymenium* reddish brown to brown, granules usually sparse to rarely almost absent, coarse, at paraphyses tips (*chlarotera*-type), soluble in HNO_3; *asci* and *ascospores* not developed in the material studied but according to Hinteregger (1994), asci 8-spored and ascospores 7–11 × 4–6 um.

Pycnidia brown to brown-grey according to Hinteregger (1994); *conidia* filiform, straight to curved, 15–25 × 1·0–1·2 µm.

Chemistry. Nephrosteranic acid as a major secondary compound; a trace amount of 1–2 unknown fatty acids (under nephrosteranic a.) found in 11 samples (n = 32). In one collection (GZU/*Poelt* 11706), roccellic acid instead of nephrosteranic acid was detected. Hinteregger (1994) reported roccellic acid from several specimens but, according to our data, nephrosteranic acid is the prevailing substance and roccellic acid is more typical for some similar species, such as *L. cenisia* f. *soredians*, *L. farinaria* and *L. substerilis*. The bark of *Rhododendron*, the most common substratum of this species, is rich in various terpenoids that form very distinct spots on TLC plates.

Etymology. The species was described by Nylander (1875) as *L. exspersa*, but Zahlbruckner (1928) treated it as *L. expersa* without any orthographical comments and most subsequent authors apparently followed his concept. We use Nylander's original spelling which means 'poured out' (ex-spersum).

Ecology. It is quite common on *Rhododendron ferrugineum*, especially on old twigs and stems in the subalpine belt, up to 2500 m (Hinteregger 1994). It also occurs on the acidic bark of a range of other phorophytes (see the specimens examined) as well as hard coniferous wood and decorticated twigs. Some populations are reported here from old-growth beech forests, on trunks of beeches and a few other trees close to the tree line at elevations above 1150 m. Generally, *L. exspersa* prefers microhabitats directly influenced by a long snow lie, such as tree bases and low shrubs.

Distribution. To date, the species has been reported only from Eurasia, mainly the Alps, Finland (Santesson *et al.* 2004) and the boreal-Arctic zone of Russia (Urbanavichus 2010). Single records are from Romania (Nylander 1875), Montenegro (Vězda 2000) and the Bavarian Forest (Printzen *et al.* 2002). It is reported here for the first time from the Czech Republic, France, Slovakia, Ukraine and the Caucasus. The previous record from Slovakia (Palice *et al.* 2006) is erroneous, being based on stunted specimens of *L. pulicaris* with partly eroding, 'sorediate' thalli. The Slovakian and Ukrainian localities are situated in old-growth forests of Stužica and Uholka-Shyrokyi Luh in the Carpathians.

Phylogeny. ITS and mtSSU phylogenies are not congruent in the relationships between *L. cenisia*, *L. exspersa* and some other species in the *Lecanora subfusca* group. In the ITS phylogeny, *Lecanora exspersa* is not distinguished from *L. cenisia* but they form a well-supported clade distinct from other taxa. In the mtSSU, a single sequence of *L. exspersa* from the Austrian Alps is in a clade with *L. substerilis* and most of the *L. cenisia* sequences, whereas other sequences of *L. exspersa* form a supported clade together with *L. argentata*, *L. chlarotera* and one *L. cenisia* specimen from Romania. We decided to maintain the 'classical' phenotypic delimitation of *L. exspersa*, although it does not correspond with mtSSU (and partly with ITS); this decision might be temporary but establishing any other taxonomic alternative needs stronger support.

Remarks. *Lecanora exspersa* growing on wood can easily be misidentified as *Ochrolechia microstictoides* or *O. alboflavescens* in the field, but both species differ chemically. Very similar morphotypes can be sometimes formed by *L. farinaria*, but the overall distribution and ecology of these species are different. The predominantly saxicolous *L. cenisia* f. *soredians* sometimes occurs on *Rhododendron ferrugineum* (Hinteregger 1994) but its thallus is thicker and verrucose, the soralia are large (up to 1 mm diam.), usually convex, delimited for a long time, and roccellic acid is produced as the major secondary compound. The beech forest populations occur together with *L. substerilis* which has greyish white soralia without a thalline rim and produces roccellic acid.

Selected specimens examined. **Austria:** *Salzburg*: Hohe Tauern, Krimml, 47°12'33"N, 12°10'21"E, alt. 1080 m, *Alnus incana*, 2012, *J. Malíček* 5417, 5551 (hb. JM); *ibid*., Gerlos, 47°10'57"N, 12°06'45"E, alt. 1740 m, *Rhododendron ferrugineum*, 2012, *J. Malíček* 5391 (hb. JM); *ibid*., Mt. Hoher Sonnblick, 47°03'41·2"N, 12° 59'26·0"E, alt. 1875 m, *Pinus mugo*, 2014, *F. Bouda*, *Z. Palice* 18558 & *O. Peksa* (PRA).—**Czech Republic:** *S. Bohemia*: Šumava Mts, Nová Pec: glacial cirque of the lake Plešné jezero, alt. 1250 m, *Acer pseudoplatanus*, 48° 46'27"N, 13°51'26·5"E, 2016, *Z. Palice* 22028 (PRA). *Hrubý Jeseník Mts*: Mt. Praděd, 50·07723°N, 17·25190° E, alt. 1190 m, *Sorbus aucuparia*, 2015, *J. Vondrák* 16550 (PRA).—**France:** *Provence-Alpes-Côte d'Azur*: Briançon, Montgenèvre, 44·929099°N, 6·719706°E, alt. 1840 m, *Larix decidua*, 2016, *I. Frolov & J. Vondrák* 16585 (PRA).—**Montenegro:** Montes Durmitor, silva virginea supra lacum 'Zminje jezero', loco Surdup dicto, alt. 1500–1700 m, 1984, *A. Vězda* (GZU).—**Russia:** *Republic of Bashkortostan*: Yuryuzan', vill. Tyulyuk, alt. 1200–1300 m, 54°33'51"N, 58°50'37"E, wood of *Picea obovata*, 2011, *J. Vondrák* 13214 (PRA); Yuzhnouralskiy zapovednik, Katav-Ivanovsk, 54° 30'47"N, 58°18'36"E, alt. 1100–1200 m, wood of *Picea*, 2011, *J. Vondrák* 13391 (PRA). *Caucasus Mts*: Caucasian Biosphere Reserve, primeval forests in the surroundings of Guzeripl, alt. 1460–1900 m, *Abies nordmanniana*, *Betula* sp., *Fagus orientalis*, 2016, *J. Malíček*, *Z. Palice* & *J. Vondrák* (many specimens in hb. JM, PRA).—**Slovakia:** *Poloniny Mts*: Nová Sedlica, Stužica, 49°5'24"N, 22°32'57"E, alt. 1150 m, *Acer pseudoplatanus*, 2014, *J. Šoun & J. Vondrák* 12339 (PRA).—**Slovenia:** *Julian Alps*: Triglav National Park, 46°26'32"N, 13°43'37"E, alt. 1800 m, *Larix decidua*, 2016, *J. Malíček* 9446 (hb. JM).—**Ukraine:** *Zakarpattia Oblast*: Velyka Uhol'ka, Mt. Menchul, 48°17'52"N, 23° 39'59"E, alt. 1200 m, *Fagus sylvatica*, 2015, *F. Berger*, *J. Malíček* 8235, *Z. Palice* 19165, 19235 & *J. Vondrák* 14117, 14118 (hb. Berger, JM, PRA).

Lecanora farinaria Borrer

Suppl. Engl. Bot. **2:** tab. 2727 (1834); type: England, Sussex, Hurstpierpoint, Danny sandfields, on wood, *Borrer* (BM—holotype & possible isotype 1089246!).

(Fig. 4E)

Thallus immersed to thin (up to 0·1 mm thick), grey-white, smooth; *prothallus* indistinct or black; *photobiont* trebouxioid, 6–11 µm diam.; *soralia* white, greenish or yellowish white, delimited to confluent, rounded to ellipsoid, 0·2–1·0 mm, sometimes covering the whole thallus surface (e.g. as in the holotype), flat to more rarely convex, often bordered by a thin thalline rim; *soredia* farinose, 20–50 µm diam.

Apothecia rare, sessile or with constricted bases, 0·4–1·0(–1·5) mm; *margin* sorediate, up to 0·1 mm thick, often becoming excluded, white, regular to more often flexuose; *discs* brown to black, matt, epruinose, flat to slightly convex. *Amphithecium* with large crystals (*pulicaris*-type) or crystals absent, with abundant algal cells; *cortex* absent; *hypothecium* colourless; *hymenium* 50–80(–100) µm; *epihymenium* pale brown to reddish brown, rarely with green pigment, K+ olive, HNO_3 + brownish red to red, interspersed with fine granules (POL+) soluble in K, insoluble in N (*pulicaris*-type); *paraphyses* 1·5–2·0 µm, up to 3·0 µm at apices; *asci* 8-spored; *ascospores* broadly ellipsoid to subglobose, 14–18(–20) × (9–)10–13(–15) µm, thick-walled (1·0–1·5 µm).

Conidiomata unknown.

Chemistry. Roccellic acid (major) with traces of 1–2 additional fatty acids.

Ecology. *Lecanora farinaria* prefers humid forests at lower elevations, especially close to the coast. The most common substrata are *Alnus incana*, *Sorbus aucuparia* (Tønsberg 1992) and timber.

Distribution. *Lecanora farinaria* has been reported from many European countries, North America and Asia (see Kukwa & Kubiak 2007) but some of these records could be based on misidentifications. It is an oceanic species known mainly from Great Britain (Edwards *et al*. 2009) and Norway (Tønsberg 1992). It very probably occurs in other Western European and Scandinavian countries (material not seen). A record from Ukraine by Kondratyuk & Coppins (1999) belongs to *L. substerilis* and the specimen from Sardinia by Zedda (2002) is *L. impudens*. In Central Europe, the species has been reported from humid parts of the Austrian Alps (Tønsberg *et al*. 2001) and Poland (Kukwa & Kubiak 2007).

Phylogeny. The Bayesian analysis of the mtSSU region demonstrated a quite isolated position within the *L. subfusca* group (Fig. 2), but the ITS region placed the species together with *L. pulicaris* in an isolated clade (Fig. 1).

Remarks. *Lecanora farinaria* is a very variable species, especially in terms of the soralia and thallus. Tønsberg (1992) mentioned morphotypes with an areolate or tuberculate thallus containing calcium oxalate crystals. This is a fairly common feature in several other sorediate *Lecanora* species but probably very rare in *L. farinaria*. Sterile material can be easily confused with several similar taxa (*L. exspersa*, *L. impudens*, *L. substerilis* etc.) but its ecology and/or distribution differ. Apothecial anatomy is very similar to *L. pulicaris*, a closely related species according to the ITS phylogeny (Fig. 1).

Selected specimens examined. **Austria:** Hohe Tauern, Krimml, 47°12'44"N, 12°10'09"E, alt. 1050 m, *Alnus incana*, 2012, *J. Malíček* 5417 (hb. JM). *Tirol*: Brandenberg, Kaiserklamm, 47°33'N, 11°54'E, alt. 730–760 m, *Salix*, *T. Tønsberg* 24270 (BG).—**Great Britain:** *Scotland*: **V.C. 96,** East Inverness: Glen Affric, SW shore of Loch Beinn a Mhea, 57°15·99'N, W004°57·77', *Vaccinium*, alt. 235 m, 2004, *Z. Palice* 9831 (PRA). **V.C. 102,** South Ebudes: Island of Islay, on fence post, 2011, *M. Powell* 1777 (hb. JM).—**Norway:** *Nordland*: Vefsn, W of Lake Fustvatnet, alt. 40–60 m, *Alnus incana*, 1982, *T. Tønsberg* 7615a (GZU). *Møre og Romsdal*: Rauma, W of Innfjorden, 40 m, *Corylus avellana*, 1979, *T. Tønsberg* 3817 (GZU). *Sogn og Fjordane*: Selje, 62·0562°N, 5·3912°E, alt. 270–280 m, *Sorbus aucuparia*, 2015, *T. Tønsberg* 46170 & *Z. Palice* 20106 (BG, PRA).

Lecanora impudens Degel.

Svensk Bot. Tidskr. **38:** 50 (1944); nom. nov. for *Pertusaria farinacea* H. Magn., *Bot. Not.* **1942:** 15 (1942); type: Sweden, Södermanland, Botkyrka, Tullinge gård, on *Ulmus* in an avenue, 1938, *A. H. Magnusson* 16125 (UPS 65900!—holotype).

Lecanora maculata (Erichsen) Almb. [nom. illeg.], *Bot. Not.* **1952:** 251 (1952); *Pertusaria maculata* Erichsen, *Rabenh. Kryptog. Flora Deutsch.* **5:** 646 (1936).

Lecanora impudens is morphologically identical to *L. allophana* f. *sorediata* but they are separated by chemistry and ascospore size (up to 14 µm in *L. impudens*). *Lecanora impudens* produces an unknown fatty acid and the terpenoid *impudens*-unknown or atranorin alone. For a detailed description of the species and chemical substances, see Tønsberg (1992) and Malíček (2014).

Lecanora impudens prefers trees with a higher bark pH (e.g. *Fraxinus excelsior*) in open landscape. It has a mostly continental distribution in Europe, being completely absent from Western Europe; however, it does occur in the more continental part of Norway (Tønsberg 1992). The record from Sardinia is phytogeographically interesting. Generally, it is not a very common lichen but it can be locally widespread, as in some regions of Scandinavia, the Alps and the Carpathians.

Some authors (e.g. Poelt & Vězda 1981; Clauzade & Roux 1985; Schreiner & Hafellner 1992; Wirth 1995) have regarded *L. impudens* and *L. allophana* f. *sorediata* as conspecific. Both taxa are very similar and share almost the same habitat; their status has not been resolved by mtSSU phylogeny (Fig. 2). We have separated them at the species level on the basis of their different chemistry and ascospore size.

Selected specimens examined. **Austria:** *Steiermark*: Grazer Bergland, Straßegg Sattel *c.* 8 km E von St. Jakob-Breitenau, 47°23'20"N, 15°31'50"E, 1180 m, *Fraxinus*, 1999, *J. Hafellner* 49623 (GZU).—**Italy:** [*Sardinia*:] Illorai, Monte Artu, alt. 900 m, old *Quercus pubescens*, 1996, *L. Zedda* (B).—**Romania:** *Fagaras Mts*: Sibiu, Mt. Moldoveanu, 45°34'22"N, 24°42'04"E, alt. 1380 m, *Acer pseudoplatanus*, 2013, *J. Malíček* 6618, *F. Bouda* & *L. Syrovátková* (hb. JM).—**Russia:** *Orenburg Region*: Maloe Churaevo, 51°40'09"N, 57°27'14"E, alt. 250–500 m, *Ulmus laevis*, 2011, *J. Vondrák* 13073, 13080 (PRA).—**Slovakia:** *Strážovské vrchy*: prope pg. Briestenné, 500 m, ad cort. Juglandis, 1976, *I. Pišút* (BRA).

Lecanora jamesii J. R. Laundon

Lichenologist **2:** 122 (1963); type: UK, Pembroke, near Pontfaen, Afon Gwaun, V.C. 45, on rotting branches of *Salix* over stream, 350 ft., 1958, *P. W. James* (BM—holotype).

(Fig. 4F)

This species is well characterized by its yellow delimited soralia containing usnic acid and the production of 2-O-methylsulphurellin as a diagnostic substance. Apothecia are rare, containing large crystals in the amphithecium and with a granular, pale yellowish brown epihymenium (Laundon 1963). In Europe, the species is reported from oceanic parts of Western Europe and humid regions of the Austrian Alps (e.g. Brodo & Elix 1993; Tønsberg *et al.* 2001). For a detailed description, see Laundon (1963) and Edwards *et al.* (2009).

Selected specimens examined. **Austria:** Wildnisgebiet Dürrenstein, Lunz am See, primeval beech-silver fir forest "Grosser Urwald", 47°46'56"N, 15°05'02"E, alt. 1200 m, *Fagus sylvatica*, 2015, *J. Maliček* 8471, *F. Berger*, *O. Breuss* & *R. Türk* (hb. JM); *ibid.*, See bei Oisklause, 47°46'33"N, 15°08'54"E, alt. 1010–1020 m, Holz von *Picea abies*, *F. Berger*, *O. Breuss*, *J. Maliček* & *R. Türk* 56240 (SZU).—**Canada:** *British Columbia*: Hyphocus Island, 48°55·808'N, 125°31·679'W, alt. 2–10 m, *Alnus rubra*, 2011, *T. Tønsberg* 41348 (BG).—**France:** *Bretagne*: Monts d'Arrée, St. Herbot, alt. 250 m, *Salix atrocinerea*, 1984, *P. Clerc* 6298 (S).—**Great Britain:** *England*: **V.C. 3,** South Devon: Slapton bei Start, *Salix*, 1971, *J. Poelt* 10545 (GZU). *Scotland*: **V.C. 101,** Lochgilphead, Kilmartin, 56°08'43"N, 5°32'04"W, alt. 50 m, *Salix aurita*, 2014, *J. Maliček* 9005, *B. J. Coppins* & *J. Vondrák* (hb. JM). **V.C. 103,** Argyllshire, Mull, Salen, *Salix aurita*, 1968, *P. W. James* (S – Vězda: *Lich. Sel. Exs.* 789).—**USA:** *Washington*: Olympic National Park, Ozette Lake, 48°07·2'N, 124°36·1'W, alt. 10 m, *Salix*, 1999, *T. Tønsberg* 28040 *&* *C. Printzen* (M).

Lecanora mughosphagneti Poelt & Vězda

Biblioth. Lichenol. **16:** 364 (1981); type: [Germany], Bavaria, Allmannshauser Filz, *Arnold* in *Lich. exs.* 1832 (M!—holotype).

A thin, whitish to pale grey thallus and early coalescent soralia with fine, whitish soredia covering almost the whole thallus are typical for this species. In well-developed specimens, the thallus can be quite thick with a cotton-like or arachnoid prothallus. Whitish pruinose apothecia of the *L. albella* type are known only from the type material (Poelt & Vězda 1981). The species produces caperatic and roccellic acids. Protocetraric acid was detected in apothecia only (Lumbsch *et al.* 1997). For a detailed description, see Poelt & Vězda (1981) and Lumbsch *et al.* (1997).

To date, *L. mughosphagneti* has been recorded only from Germany, Austria (Lumbsch *et al.* 1997) and Switzerland (Bürgi-Meyer *et al.* 2014). It is reported here as new for the Czech Republic. The species grows mainly on trunks of *Pinus* spp. in boggy pine forests. It can be found at the same sites as the very similar *L. norvegica* which differs in the Pd+ red reaction of its soralia (protocetraric acid). A detailed study of both species will be published elsewhere (Z. Palice & T. Tønsberg, unpublished data).

Selected specimens examined. **Czech Republic:** *Southern Bohemia*: Šumava Mts, Smolná Pec: waterlogged spruce forest with *Pinus rotundata*, 48°51'03"N, 13°53'05"E, alt. 815 m, *Pinus rotundata*, 2010, *J. Maliček* 2736 & *Z. Palice* (hb. JM); Třeboň region, Suchdol nad Lužnicí, Červené blato, alt. 470 m, *Pinus rotundata*, 2010, *J. Maliček* 2953 (hb. JM).—**Germany:** *Bayern*: Föhrenrinden in der Pupplinger Au im Isarthale bei Wolfratshausen, 1893, *Arnold* (M – *Lich. Monac. Exs.* 297); Spirkenfilz zw. Bernried u. Bern. Filz, Spirke, 1955, *J. Poelt* (M); Spirkenfilz südlich Rohrmoos, Gemeinde Forst, *Pinus uncinata*, 1964, *J. Poelt* (M).

Lecanora norvegica Tønsberg

Sommerfeltia **14:** 165 (1992); type: Norway, Oppland, Sel, Sjoa, UTM grid ref.: 32V, NP 2839, alt. 280–300 m, on *Pinus sylvestris*, 1990, *T. Tønsberg* 13145 (BG—holotype; E—isotype).

This species is very similar to *L. mughosphagneti*, from which it differs in its Pd+ red soralia due to the presence of protocetraric acid. Roccellic acid was detected as a minor compound. According to Tønsberg (1992), soralia are green to grey-green and discrete at first, but these characters are probably not reliable for a differentiation of these species. For a detailed description see Tønsberg (1992).

It has been reported from Norway (Tønsberg 1992), Sweden (Santesson *et al.* 2004), Switzerland (Dietrich & Scheidegger 1996), Estonia (Jüriado 2000), Lithuania

(Motiejūnaitė *et al.* 2007) and European Russia (Stepanchikova *et al.* 2010). *Lecanora norvegica* is recorded here as new for the Czech Republic. The species prefers humid mire pine forests. *Cliostomum leprosum*, *Loxospora elatina* and *Ochrolechia microstictoides* are other sorediate species with a similar ecology; therefore TLC is necessary for correct identification.

Selected specimens examined. **Czech Republic:** *Northern Moravia*: Jeseníky Mts, Rejvíz, 50°13'13"N, 17°17'13"E, alt. 760 m, *Pinus rotundata*, 2012, *J. Malíček* 5131 & *L. Syrovátková* (hb. JM). *Southern Bohemia*: Novohradské hory Mts, Pohoří na Šumavě, Stodůlecký vrch, 48°35'09"N, 14°42'20"E, alt. 955 m, *Pinus sylvestris*, 2012, *J. Malíček* 5707, *J. Kocourková, Z. Palice & J. Vondrák* (hb. JM).—**Norway:** *Oppland*: Sel, Sjoa, 61°41'N, 9°33"E, alt. 300 m, *Pinus sylvestris*, 1992, *T. Tønsberg* 17746 (M).

Lecanora sorediomarginata S. A. Rodrigues, A. Terrón & Elix

Lichenologist **43:** 102 (2011); type: Portugal, Beira Litoral, Figueira da Foz, Dunas de Quiaios, alt. 49 m, *Pinus pinaster* in a pine forest on sand dunes, 2006, *S. A. Rodrigues* (AVE-L—holotype; LEB-Lichenes 7581—isotype).

This recently described species (Rodrigues *et al.* 2011) is characterized by the endosubstratal or very thin thallus, coalescent soredia, sorediate apothecial margin and C+ red reaction due to the presence of 3,5-dichloro-2'-O-methylnorstenosporic acid as a major compound. Atranorin and chloratranorin are present only as minor substances. To date it has been reported only from the bark of pines in coastal regions of Portugal. *Lecanora sorediomarginata* is distinguished by its chemistry and specific ecology. For a detailed description see Rodrigues *et al.* (2011).

Lecanora substerilis Malíček & Vondrák sp. nov.

MycoBank No.: MB 813677

A member of the *L. subfusca* group in a strict sense, macroscopically similar to *L. farinaria* but the thallus often thick and verrucose; thalline apothecial margin sorediate; epihymenium with coarse granules at paraphyses tips; amphithecium with large crystals; roccellic acid alone or together with an unidentified fatty acid as major secondary metabolites; on bark of beeches in old-growth beech forests.

Type: Slovakia, Poloniny Mts, Nová Sedlica, protected area Stužica, in a valley, alt. 600–800 m, 49°04'24"N, 22°32'35"E, *Fagus sylvatica*, 2014, *J. Šoun & J. Vondrák* (PRA JV12294—holotype; 12303—isotype). Sequences of the holotype: KT630243 (ITS) and KT630254 (mtSSU).

(Fig. 5A–E)

Thallus crustose, grey, matt, forming patches up to 5 cm diam., sterile specimens usually with a thin thallus up to 0·1 mm thick, in fertile material thallus well developed and strongly pustulose (>0·5 mm thick); *pustules* low and almost indistinct to strongly developed and globose to clavate with constricted bases, filled with large calcium oxalate crystals (POL+); *prothallus* indistinct or whitish grey; *photobiont* trebouxioid; *soralia* pale grey to grey-green, punctiform to rarely confluent, flat, 0·2–0·6 mm diam.; *soredia* farinose to granulose, simple or in consoredia, 25–75 μm diam., coarser in fertile collections.

Apothecia lecanorine, known only from the holotype, *c.* 1 mm diam., with a constricted base, probably arising from pustules; *margin* 0·2 mm thick, uneven and slightly pustulate when young, later sorediate; *discs* brown, matt, pruina absent. *Amphithecium* with abundant large crystals (*pulicaris*-type), filled with numerous trebouxioid photobiont cells (5–14 μm diam.) surrounded by 2·5–3·5 μm thick and branched hyphae, lower part without algal cells and crystals ±paraplectenchymatous; *cortex* not observed; *hypothecium* colourless, prosoplectenchymatous; *hymenium* colourless, 60–80 μm high; *paraphyses* 1·5–2·0 μm thick, not or very slightly broadening at tips; *epihymenium chlarotera*-type, red-brown (K+ pale brown), with coarse, brown, irregular granules (POL+) abundant at paraphyses tips, 1–2(–5) μm diam., soluble in KOH; *asci* 8-spored, *Lecanora*-type, *c.* 45–55 × 12 μm; *ascospores* well developed, simple, colourless, broadly ellipsoid to subglobose, 10–14 × 7–11(–12) μm.

Conidiomata unknown.

Chemistry. Atranorin, roccellic acid alone or together with an unidentified fatty acid. In four of 12 specimens examined, traces of several terpenoids (probably from bark) detected by TLC. Soralia: K+ yellow, Pd−, C−, UV−.

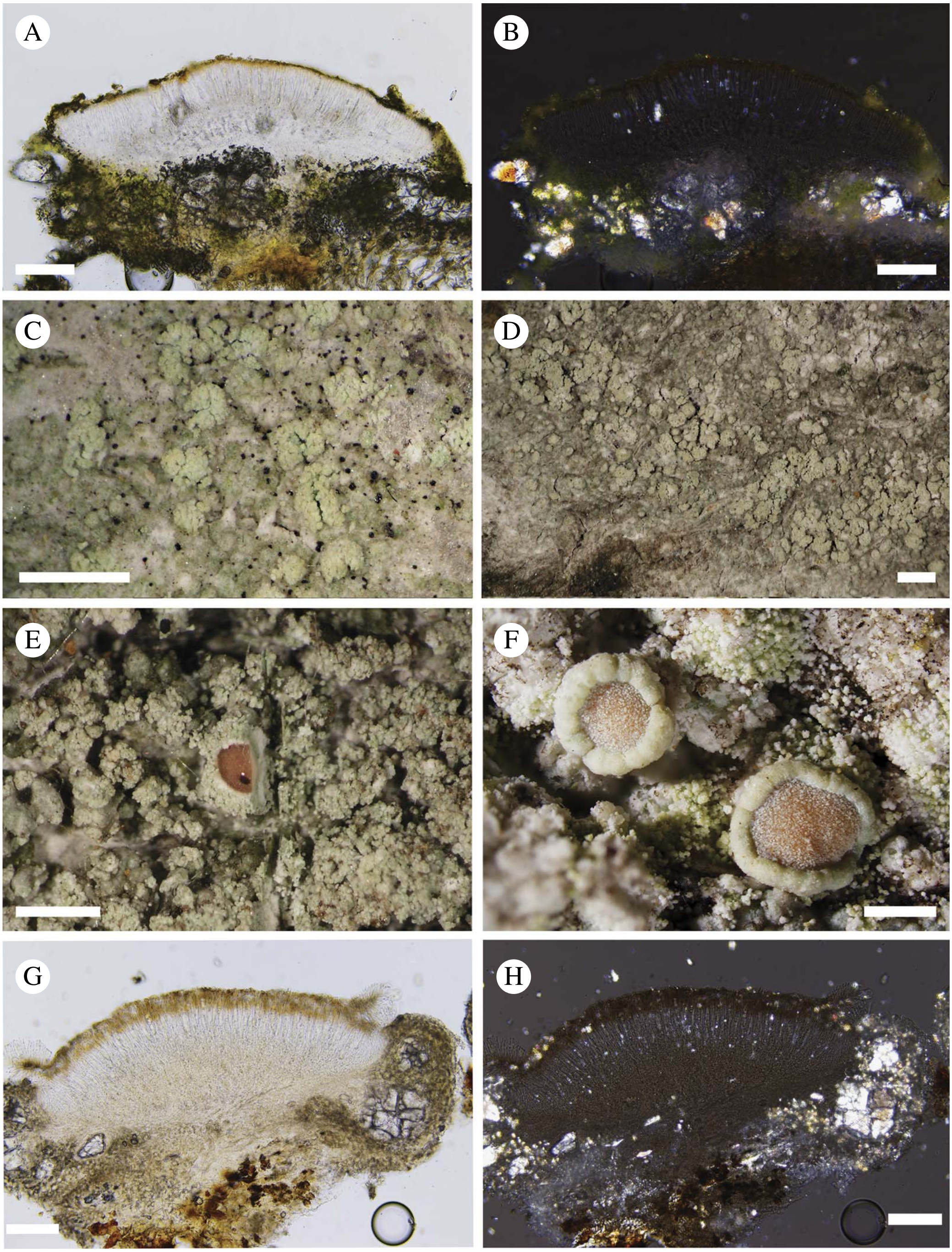

FIG. 5. A & B, apothecial sections of the holotype of *Lecanora substerilis* using brightfield and polarized light microscopy respectively; C & D, sorediate thallus of *L. substerilis*; E, apothecium of the holotype specimen (PRA JV12294); F, habitus of *L. variolascens* (JM 8422); G & H, apothecial sections of *L. variolascens* using brightfield and polarized light microscopy respectively. Scales: A, B, G & H = 100 µm; C–E = 1 mm; F = 0·5 mm. In colour online.

Etymology. This species is mostly collected sterile; fertile material is very rare.

Phylogeny. *Lecanora substerilis* belongs to the *L. subfusca* group. In the nrITS phylogeny, it forms a supported clade that is well resolved from the closest outgroup including *L. cenisia* and *L. exspersa* (Fig. 1). It also forms a supported clade in the mtSSU that is in polytomy with the latter taxa.

Ecology and distribution. This new species is so far known only from Carpathian beech forests, especially from old-growth woodlands at elevations of 450–1235 m. It has been published from Stužica beech-silver fir forest in Slovakia as *Lecanora* cf. *farinaria* (Vondrák *et al.* 2015). It is fairly common on *Fagus sylvatica* in this reserve and one collection is also from *Abies alba*. The most frequently associated species are *Lecanora argentata*, *Candelariella xanthostigma*, *Hypogymnia physodes*, *Lecanora pulicaris*, *Porina aenea* and *Scoliciosporum umbrinum*. The second site from Slovakia is situated in the Muránska planina National Park. *Lecanora substerilis* is a common species in the Ukrainian virgin beech forest Uholka-Shyrokyi Luh where it is associated with, for example, *Buellia griseovirens* and *Rinodina efflorescens*. It is also known from a humid beech forest (1050 m a.s.l.) in the Paring Mountains (Muntii Parâng) in Romania and a mountain old-growth beech forest (1235 m a.s.l.) in the Beskydy Mountains in the Czech Republic.

Remarks. *Lecanora substerilis* strongly resembles the western *L. farinaria* but the latter differs in its smooth, immersed to thin thallus and the *pulicaris*-type of epihymenium (with fine granules). Sterile specimens are hardly distinguishable from, for example, *L. allophana* f. *sorediata*, *L. impudens*, *L. exspersa*, *L. variolascens* and *L. cenisia* f. *soredians*. These taxa are absent or very rare in beech forests. The first three species do not contain roccellic acid in the thallus. *Lecanora exspersa* usually occurs at higher elevations and its soralia have a distinct thalline rim; *L. cenisia* f. *soredians* has larger (at least 0·5–1·0 mm diam.) and convex soralia.

Additional specimens examined. **Czech Republic:** *Moravskoslezské Beskydy Mts*: Mt. Kněhyně, 49°29'41·9"N, 18°18'44·3"E, *Fagus sylvatica*, alt. 1235 m, 2016, *J. Maliček & Z. Palice* 21699 (PRA).—**Romania:** *Paring Mts*: Petrosani, 100 m E of Cabana Mija, 45°24'24"N, 23°30'22"E, 1050 m, *Fagus sylvatica*, 2013, *J. Maliček* 6690 & *F. Bouda* (hb. Malíček).—**Slovakia:** *Bukovské vrchy Mts*: Nová Sedlica, Stužica, S-facing slopes between Mt. Kamenná lúka (1201 m) and Mt. Kremenec (1221 m), 49°05'10"N, 22°33'09"E, 1050 m, *Fagus sylvatica*, 2013, *J. Maliček* 6541 & *J. Vondrák* (hb. JM); *ibid.*, 800 m, 49°04'20"N, 22°32'06"E, *Fagus sylvatica*, 2014, *J. Šoun* & *J. Vondrák* (CBFS JV12387); *ibid.*, in valley, 600–800 m, 49°04'24"N, 22°32'35"E, *Abies alba*, 2014, *J. Šoun* & *J. Vondrák* (CBFS JV12293). *Muránska planina National Park*: Čertova dolina protected area, 48°44'22"N, 19°52'00"E, alt. 950 m, *Fagus sylvatica*, 2012, *J. Maliček* 5269, *A. Guttová* & *Z. Palice* (hb. JM).—**Ukraine:** *Zakarpattia Oblast Region*: Khust, Velyka Uhol'ka, at many sites in the Uholka old-growth forest, 48°14–15'N, 23°39–41'E, alt. 460–820 m, *Fagus sylvatica* and *Acer pseudoplatanus*, 2015, *F. Berger* 29182, 29183, *J. Maliček* 8111, 8162, 8209, 8294, *Z. Palice* 19223, 19611 & *J. Vondrák* (hb. FB, JM, PRA).

Lecanora thysanophora R. C. Harris

Bryologist **103:** 790 (2000); type: USA, New York, Clinton Co., Town of Mooers, trail to The Gulf Unique Area, 1·5 mi (2·4 km) NW of Cannon Corners Road (Co. Rd. 10) on Rock Road, 1 mi (1·6 km) N of Davison Road at Cannon Corners, 44°59'N, 73°46·5'W, conifer-red maple woods, 1996, *Buck* 30804 (NY—holotype).

Lecanora thysanophora differs from all species included in this paper by its continuously sorediate, yellow to bluish yellow thallus and the arachnoid prothallus which can be absent or poorly developed in young thalli. Apothecia are unknown in European populations. In addition to atranorin, it produces usnic acid, zeorin and specific terpenoid(s) of *thysanophora*-unknowns visible only as UV+ blue spots after sulphuric acid spraying and heating. It belongs to a more or less isolated lineage according to mtSSU (Fig. 2).

In Europe, the species is quite common in beech forests in some parts of the Alps and Carpathians, and scattered in some other mountains in Central Europe (e.g. Šumava/ Bavarian Forest Mts). Surprisingly, it is widely distributed in northern Poland, commonly found also on *Carpinus betulus* and *Quercus* (Zduńczyk & Kukwa 2014), and in some surrounding countries (Golubkov & Kukwa 2006; Motiejūnaitė *et al.* 2006). For a detailed description see Harris *et al.* (2000).

It can be confused with *Haematomma ochroleucum* which, however, contains porphyrilic acid (see Zduńczyk & Kukwa (2014) for details). Both can occur on bark and rock but *H. ochrolecum* is mainly saxicolous and *L. thysanophora* is mainly corticolous.

Selected specimens examined. **Austria:** *Tirol*: Brandenberg, NW of Kaiserklamm, 47°32'48"N, 11°54'39"E, alt. 750 m, *Salix elaeagnos*, 2012, *J. Malíček* 5538 (hb. JM).—**Czech Republic:** *Šumava Mts*: Mt. Smrčina, 48°43'59"N, 13°56'17"E, alt. 1105 m, *Fagus*, 2015, *J. Malíček* 8656 & *J. Vondrák* (hb. JM).—**Germany:** *Bayern*: Oberammergau, Graswang, 47°33'44"N, 11°02'15"E, alt. 920 m, *Fagus*, 2014, *J. Malíček* 7020 (hb. JM).—**Ukraine:** *Zakarpattia Oblast Province*: Kvasovo, flood-plain forest Otok, 48° 12'35"N, 22°46'08"E, alt. 120 m, *Populus nigra*, 2013, *J. Malíček* 6445 & *J. Vondrák* (hb. JM).

Lecanora variolascens Nyl.

Flora, Regensburg **64:** 183 (1881); type: [Germany, Baden-Württemberg], Heidelberg, an *Carp.* et *Sorbus* rar., *v. Zwackh* 252 (H-NYL 27851!—holotype).

Lecanora bavarica Poelt, *Ber. Bayer. Bot. Ges.* **29:** 68 (1952); type: [Germany], Oberbayern, Ldks. Starnberg u. Bernried, Obere Hochebene, Ulme an der Straße nach Unterzeismering, ziemlich am Grunde des Stammes, 1951, *J. Poelt* (M!—holotype).

(Fig. 5F–H)

Thallus quite variable, smooth to rough, often verrucose especially in the centre, greyish, thin to medium thick (up to 0·2 mm), filled by large calcium oxalate crystals; *photobiont* trebouxioid; *soralia* flat to slightly convex, concolorous with the thallus, at first delimited (0·3–1·0 mm diam.), later more or less confluent and rarely forming a sorediate crust covering the thallus; *soredia* farinose.

Apothecia frequently present, 0·5–1·0(–1·5) mm diam., sessile or rarely with constricted bases, plane; *discs* reddish brown to dark brown, medium to strongly whitish to bluish pruinose, rarely non-pruinose; *margin* smooth to coarse, matt, thick, partly flexuose, elevated, sometimes slightly crenulate. *Epihymenium* reddish brown, in K± colourless to pale orange-brown, pigment more or less intensifying in HNO_3, with coarse brown granules 3–5(–8) μm diam. on the surface of paraphyses tips, soluble in K, very slowly soluble in HNO_3, POL−; *amphithecium* of *pulicaris*-type, with very large crystals of calcium oxalate (up to 100 μm diam.), soluble in HNO_3; *true cortex* absent; *hypothecium* colourless to yellowish; *hymenium* 60–80 μm high; *paraphyses* (1·0–)1·5–2·0 μm thick, at tips slightly swollen (up to 3·0 μm); *asci* 8-spored; *ascospores* broadly ellipsoid, (9·0–) 10·0–12·5 × 6–8(–9) μm.

Conidiomata unknown.

Chemistry. Atranorin, chloratranorin and zeorin detected by TLC and LC as major compounds. In two specimens (of 14 analyzed by TLC) including the holotype, a trace of an unknown colourless spot (C4, UV−) with a fatty character was recorded. Disc C−; soralia K+ yellow, Pd+ yellow, C−. Crystals of terpenoids are usually visible on old collections.

Phylogeny. The species is not closely related to the morphologically similar *L. intumescens* but it forms an isolated clade with *L. barkmaniana* (Figs. 1 & 2).

Ecology. *Lecanora variolascens* occurs on ±acidic bark (mainly of oaks and pines) but usually in slightly eutrophicated places, as noted by Lumbsch *et al.* (1997). It is closely associated with *Candelariella efflorescens* agg., *C. reflexa* s. str., *C. xanthostigma*, *Catillaria nigroclavata*, *Opegrapha rufescens*, *Phlyctis argena*, *Physcia adscendens*, *Physconia distorta* and *Lecidella albida*. It prefers well-lit forests at medium elevations.

Distribution. The species is rare and known only from several European countries: Austria, France, Germany, Italy, Poland and Switzerland (Lumbsch *et al.* 1997; Nimis & Martellos 2003; Roux 2015). It is reported here as new for Slovakia.

Remarks. *Lecanora variolascens* is a distinctive species but it has been rarely reported. Many specimens have been found in herbaria by chance as unidentified or incorrectly identified specimens. This confusion might have arisen as a result of a vague and ambiguous description of the taxon by earlier authors. Apothecia of some morphotypes (e.g. the holotype) can resemble *L. intumescens* which differs mainly in the apothecial anatomy (e.g. tiny crystals in the amphithecium). Indeed, Nylander (1881) and Brodo (1984) suggested that this sorediate taxon is closely related to *L. intumescens*, if not conspecific. Lumbsch *et al.* (1997) distinguished it from *L. intumescens*, included the Central European *L. bavarica* Poelt as its synonym, and provided a more detailed description. Unfortunately, the authors characterized *L. variolascens* as a species with psoromic acid and relatively small crystals in the amphithecium (nevertheless of the *pulicaris*-type according to the mentioned size). The Pd+ yellow reaction of the soralia, suggesting the presence of psoromic acid, could be caused by a high concentration of atranorin; no psoromic or 2'-O-demethylpsoromic acids were detected by TLC ($n = 14$), liquid chromatography or mass spectrometry ($n = 3$) in the material examined, which included two specimens studied by Lumbsch *et al.* (1997).

The sorediate thallus strongly resembles *L. impudens*, *L. allophana* f. *sorediata*, *L. farinaria* and several *Ochrolechia* species. In such cases, TLC or spot reactions are necessary for certain identification. *Lecanora variolascens* is chemically identical to *L. barkmaniana*, which is usually sterile with yellowish soralia that soon become confluent. When apothecia are present, ascospores of *L. barkmaniana* are distinctly larger than in *L. variolascens*. *Lecanora carneolutescens* Nyl., regarded as endemic to south-western North America, shares chemical and anatomical characters with *L. variolascens*. It differs in its non-pruinose apothecia and larger ascospores, 12·5–16·0 × 8·5–10·5 μm (Ryan *et al.* 2004).

Specimens examined. **Austria:** *Steiermark*: Kalvarienberg SW oberhalb vom Landeskrankenhaus Feldbach, Umgebung eines alten Lehmabbaus, 340 m, *Malus domestica*, 1993, *B. Wieser* 642 (GZU). *Oberösterreich*: Rading (nw. Windischgarsten), an Föhrenstämmen im Radinger Moor, 600 m, 1986, *S. Wagner* (GZU, dupl. ex SZU 10491); Haiden bei Ischl, 1867, *H. Lojka* (GZU). *Lower Austria*: Ybbstaler Alpen Mts, Langau, Maierhöfen, 47°51'36·9"N, 15°06'46·2"E, alt. 680 m, *Pyrus communis*, 2015, *J. Malíček* 8422 (hb. JM).—**France:** *Aquitaine*: Pyrénées Atlantiques, St. Engrâce, 47°46·83'N, 3°29·67'W, 600 m, *Acacia*, 1992, *J. L. Spier* 4898 (L).—**Germany:** *Oberbayern*: Starnberg, Moorsinger Schlucht, *Quercus*, 1952, *A. Schreppel* (GZU). *Bayern*: Allgäu, an *Acer* am Forggensee nördlich Füssen, 785 m, 1956, *J. Poelt* (B, S, *Lich. Alp.* 4).—**Slovakia:** *Muránska planina plateau*: Poludnica Nature Reserve, well-lit oak forest, 48°45·44'N, 20°01·72'E, alt. 660 m, *Quercus*, 2007, *A. Guttová, J. Halda & Z. Palice* 11380 (PRA, BG); *ibid.*, *c.* 48°45'33"N, 20°02'01"E, alt. 700–750 m, *Quercus petraea* agg., 2010, *J. Malíček* 3100, *A. Guttová & Z. Palice* (hb. JM); *ibid.*, 48°45'19"N, 20°01'46"E, alt. 565 m, 2014, *A. Guttová, Z. Fačkovcová & Z. Palice* 18379 (PRA); *ibid.*, Šiance Nature Reserve, 48°45'55"N, 20°03'55"E, alt. 886 m, *Quercus*, 2012, *A. Guttová & Z. Palice* 17959 (PRA).

Lecanora viridissima A. Nordin, Sundin & G. Thor

Nordic Journal of Botany **15:** 555 (1995); type: Sweden, Gotland, Lummelunda Parish, Ellstädaränget wooded meadow, *c.* 1 km NW Bunge and *c.* 1 km E of Lummelunda church, 57°46'N, 18°28'E, *Quercus robur*, 1990, *A. Nordin, R. Sundin & G. Thor* 1300 (S!—holotype).

This species is characterized by a yellow to green sorediate thallus forming small patches up to 1 cm; apothecia are unknown. This small lichen can be very easily overlooked in a mosaic with other species. It resembles, for example, young *L. expallens*. Based on herbarium material from S, it often occurs together with morphologically very similar *Lecidella subviridis* and *Pyrrhospora quernea*. Some specimens identified as *Lecanora viridissima* are indeed these taxa, including the holotype which is a mixture of *Lecidella subviridis* and *L. viridissima*. All these lichens differ chemically, so careful TLC/LC analysis is necessary for correct identifications. *Lecanora viridissima* produces, in addition to atranorin, an unknown substance in position B'5 and C5. This compound is recognized in TLC after charring as a yellow spot with a large pale halo and fatty character; it is pale yellow-green to brown in long-wave UV light (not observed in low concentrations). It is very probably related to 2-O-methylsulphurellin and some planaic acid derivatives due to the very characteristic spots on TLC plates. It differs from the 2-O-methylsulphurellin in the lower position on TLC plates and typical double yellow spot in solvent B'.

Lecanora viridissima is a poorly known species reported only from Gotland in Sweden. It occurs on the bark of *Quercus robur* and *Fraxinus excelsior* mainly in wooded meadows (Nordin *et al.* 1995). *Lecanora argentata* and *Phlyctis* *argena* were the most common closely associated species in the material studied.

Selected specimens examined. **Sweden:** *Gotland*: Träkumla, Tjängdarve, 59°33'N, 18°19'E, *Fraxinus*, 1989, *A. Nordin, R. Sundin & G. Thor* 49 (S); Rone, Oggesänget, 57°12'N, 18°25'E, *Quercus*, 1990, *A. Nordin, R. Sundin & G. Thor* 1186 (S); Lojsta, 57°18'N, 18°23'E, *Quercus*, 1989, *A. Nordin, R. Sundin & G. Thor* 353 (S); Atlingbo, 57°28'N, 18°22'E, *Fraxinus*, 1989, *A. Nordin, R. Sundin & G. Thor* 207 (S); Hemse, 57°13'N, 18°22'E, *Quercus*, 1990, *A. Nordin, R. Sundin & G. Thor* 999 (S).

Key to European corticolous sorediate *Lecanora* species containing atranorin

With well-developed apothecia . . . . Key A
Without apothecia. . . . . Key B

Key A

1 Apothecia distinctly pruinose 2
Apothecia slightly pruinose or pruina absent. 5

2(1) Usnic acid present; soralia yellowish to bluish green, prothallus arachnoid . . . . **L. thysanophora**
Usnic acid absent; soralia white to white-grey; prothallus not distinctly arachnoid 3

3(2) Apothecia Pd+ yellow or Pd−; amphithecium with large crystals . . . . **L. variolascens**
Apothecia Pd+ red; amphithecium with small crystals 4

4(3) Soralia coalescent; on bark of *Pinus* . . . .**L. mughosphagneti**
Soralia delimited, rounded; on deciduous trees . . . . **L. albella f. sorediata**

5(1) Soralia C+ red, on bark of *Pinus* in coastal regions . . . .**L. sorediomarginata**
Soralia C− 6

6(5) Thallus and soralia yellowish; containing xanthones . . . . **L. alboflavida**
Thallus white-grey, soralia whitish to yellowish; without xanthones 7

7(6) Amphithecium with small crystals (*allophana*-type). 8
Amphithecium with large crystals (*pulicaris*-type) 9

8(7) Ascospores 14–20 × 8–11 µm; terpenoids *allophana*-unknown present. . . . . **L. allophana f. sorediata**
Ascospores 10–14 × 5·5–8·0 µm; terpenoid *impudens*-unknown present or containing atranorin alone . . . . **L. impudens**

9(7) Soralia yellow or greenish yellow; containing usnic acid 10
Soralia white, grey-white to yellowish; usnic acid absent. 11

10(9) Prothallus arachnoid, thallus leprose; *thysanophora*-unknown(s) present . . . . **L. thysanophora**
Prothallus never arachnoid, soralia well delimited; 2-O-methylsulphurellin present . . . .**L. jamesii**

11(9) Ascospores broadly ellipsoid to subglobose, 14–17(–20) × 10–13 µm; epihymenium with fine granules (*pulicaris*-type) . . . . **L. farinaria**
Ascospores ellipsoid to broadly ellipsoid, up to 15 × 10 µm; epihymenium with coarse granules (*chlarotera*-type) 12

12(11) Soralia confluent; zeorin present. . . . . **L. barkmaniana**
Soralia delimited at least when young; zeorin absent. 13

13(12) Apothecial margin sorediate (at least when mature); roccellic acid present . . . . . .
. . . . **L. substerilis**
Apothecial margin without soredia; roccellic or nephrosteranic acid present . . . 14

14(13) Apothecia <1·0 mm diam., thallus thin, soralia with a distinct thalline rim, concave to flat . . . . **L. exspersa**
Apothecia usually >1·0 mm diam., thallus thick, coarse, soralia large (at least 0·5–1·0 mm), convex, delimited to locally confluent . . . . . . **L. cenisia f. soredians**

Key B

1 Soralia Pd+ red (protocetraric acid); on *Pinus* bark . . . .**L. norvegica**
Soralia Pd+ yellow or negative 2

2(1) Soralia C+ red; on *Pinus* bark in coastal regions . . . . **L. sorediomarginata**
Soralia C− ; usually on broadleaved trees 3

3(2) Thallus with fatty acid(s) 4
Thallus with other secondary metabolites 9

4(3) Caperatic acid present; soralia coalescent . . . .**L. mughosphagneti**
Caperatic acid absent; soralia delimited to confluent 5

5(4) Nephrosteranic acid present; soralia delimited by a distinct thalline rim . . . .
. . . . **L. exspersa**
Note: Rarely, roccellic acid is present instead of nephrosteranic acid; saxicolous ecotypes of *L. cenisia* rarely produce nephrosteranic acid as well.
Roccellic acid present; soralia rarely with a distinct thalline rim 6

6(5) Thallus immersed to thin, never pustulate 7
Thallus thick, coarse, areolate to pustulate or thin, but at least locally pustulate . . . 8

7(6) Thallus immersed to very thin; soralia often with a yellowish tint, delimited (up to 1 mm diam.) to confluent; oceanic species . . . . **L. farinaria**
Thallus thin and smooth; soralia whitish, delimited, rounded, *c.* 0·5–2·0 mm diam.; in beech forests. . . . . **L. albella f. sorediata**

8(6) Thallus thick, coarse, areolate to pustulate; soralia large (at least 0·5–1·0 mm), convex, delimited to locally confluent; mountain taxon . . . .
. . . . **L. cenisia var. soredians**
Thallus thinner, at least locally pustulate; soralia mostly punctiform; on smooth bark of deciduous trees (mainly beech) in forests; continental species . . . .
. . . . **L. substerilis**

9(3) Usnic acid present 10
Usnic acid absent 11

10(9) Arachnoid prothallus absent, thallus white-grey; soralia delimited; 2-O-methylsulphurellin as a major compound . . . . **L. jamesii**
Arachnoid prothallus present; soralia coalescent, covering most of the thallus; with zeorin and *thysanophora*-unknowns . . . . **L. thysanophora**

11(9) Thallus and soralia yellow; xanthones present; oceanic species . . . **L. alboflavida**
Thallus grey; soralia whitish to yellow; xanthones absent 12

12(11) Zeorin present 13
Zeorin absent 14

13(12) Soralia with yellow tinge, covering almost whole thallus . . . . . . **L. barkmaniana**
Soralia white, delimited . . . . **L. variolascens**

14(12) Soralia coalescent, yellow-green; *viridissima*-unknown present . . . **L. viridissima**
Soralia ±delimited, white or yellowish; terpenoids or atranorin alone present 15

15(14) *Impudens*-unknown and/or a fatty acid or atranorin alone produced. . . . **L. impudens**
Allophana-unknowns as major secondary metabolites . . . . **L. allophana f. sorediata**

We are grateful to the curators of B, BG, BM, BRA, GZU, H, L, M, PRA, S, SZU and UPS for the loan of selected material. Mark R. D. Seaward provided useful criticism and kindly revised the manuscript. Brian J. Coppins, Mark Powell and Tor Tønsberg provided material for DNA studies. Zdeněk Kameník kindly helped with the methods of liquid chromatography and mass spectrometry. Two anonymous reviewers helped to improve the manuscript. The study was supported by grant nos. 647412 and 1074416 from the Charles University Grant Agency.

References

Aptroot, A. & van Herk, C. M. (1999) *Lecanora barkmaneana*, a new nitrophilous sorediate corticolous lichen from the Netherlands. *Lichenologist* **31:** 3–8.

Brodo, I. M. (1984) The North American species of the *Lecanora subfusca* group. *Beiheft zur Nova Hedwigia* **79:** 63–185.

Brodo, I. M. & Elix, J. A. (1993) *Lecanora jamesii* and the relationship between *Lecanora* s. str. and *Straminella*. *Bibliotheca Lichenologica* **53:** 19–25.

Brodo, I. M., Owe-Larsson, B. & Lumbsch, H. T. (1994) The sorediate, saxicolous species of the *Lecanora subfusca* group in Europe. *Nordic Journal of Botany* **14:** 451–461.

Bürgi-Meyer, K., Dietrich, M. & Martig, B. (2014) Bemerkenswerte Flechtenfunde in Luzerner- und Obwaldner Hochmoor - Bergföhrenwäldern. *Meylania* **52:** 18–25.

Clauzade, G. & Roux, C. (1985) Likenoj de Okcidenta Europo. Ilustrita Determinlibro. *Bulletin de la Société Botanique du Centre-Ouest, Nouvelle Série. Numéro spécial* **7:** 1–891.

Cubero, O. F., Crespo, A., Fatehi, J. & Bridge, P. D. (1999) DNA extraction and PCR amplification method suitable for fresh, herbarium-stored, lichenized, and other fungi. *Plant Systematics and Evolution* **216:** 243–249.

Dietrich, M. & Scheidegger, C. (1996) The importance of sorediate crustose lichens in the epiphytic lichen flora of the Swiss plateau and the Pre-Alps. *Lichenologist* **28:** 245–256.

Edwards, B., Aptroot, A., Hawksworth, D. L. & James, P. W. (2009) *Lecanora* Ach. in Luyken (1809). In *The Lichens of Great Britain and Ireland* (C. W. Smith, A. Aptroot, B. J. Coppins, A. Fletcher, O. L. Gilbert, P. W. James & P. A. Wolseley, eds): 465–502. London: British Lichen Society.

Gardes, M. & Bruns, T. D. (1993) ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2:** 113–118.

Golubkov, V. V. & Kukwa, M. (2006) A contribution to the lichen biota of Belarus. *Acta Mycologica* **42:** 155–164.

Hall, T. A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41:** 95–98.

Harris, R. C., Brodo, I. M. & Tønsberg, T. (2000) *Lecanora thysanophora*, a common leprose lichen in North America. *Bryologist* **103:** 790–793.

Hinteregger, E. (1994) Krustenflechten auf den *Rhododendron*-Arten (*Rh. ferrugineum* und *Rh. hirsutum*) der Ostalpen unter besonderer Berücksichtigung einiger Arten der Gattung *Biatora*. *Bibliotheca Lichenologica* **55:** 1–346.

Huelsenbeck, J. P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* **17:** 754–755.

Jüriado, I., Lõhmus, P. & Saag, L. (2000) Supplement to the second checklist of lichenized, lichenicolous and allied fungi of Estonia. *Folia Cryptogamica Estonica* **37:** 21–26.

Katoh, K. & Standley, D. M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30:** 772–780.

Katoh, K., Kuma, K., Toh, H. & Miyata, T. (2005) MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* **33:** 511–518.

Kondratyuk, S. Y. & Coppins, B. J. (1999) Basement for the lichen monitoring in Uzhansky National Nature Park, Ukrainian part of the Biosphere Reserve 'Eastern Carpathians'. *Roczniki Bieszczadzkie* **8:** 149–192.

Kondratyuk, S., Lökös, L., Tschabanenko, S., Haji-Moniri, M., Farkas, E., Wang, X., Oh, S. O. & Hur, J. S. (2013) New and noteworthy lichen-forming and lichenicolous fungi. *Acta Botanica Hungarica* **55:** 275–349.

Kukwa, M. & Kubiak, D. (2007) Six sorediate crustose lichens new to Poland. *Mycotaxon* **102:** 155–164.

Laundon, J. R. (1963) The taxonomy of sterile crustaceous lichens in the British Isles 2. Corticolous and lignicolous species. *Lichenologist* **2:** 101–151.

Lumbsch, H. T. (1994) Calycin in *Lecanora fulvastra*. *Lichenologist* **26:** 94–96.

Lumbsch, H. T., Plümper, M., Guderley, R. & Feige, G. B. (1997) The corticolous species of *Lecanora sensu stricto* with pruinose apothecial discs. *Symbolae Botanicae Upsalienses* **32:** 131–162.

Malíček, J. (2014) A revision of the epiphytic species of the *Lecanora subfusca* group (*Lecanoraceae*, Ascomycota) in the Czech Republic. *Lichenologist* **46:** 489–513.

Morse, C. A. & Ladd, D. (2016) *Lecanora inaurata*, a new member of the *L. subfusca* group from central North America. *Lichenologist* **48:** 377–385.

Motiejūnaitė, J., Suija, A., Lõhmus, P., Kuznetsova, E., Tõrra, T., Prigodina-Lukošienė, I. & Piterāns, A. (2006) New or noteworthy lichens, lichenicolous and allied fungi found during the 16th Symposium of Mycologists and Lichenologists in Latvia. *Botanica Lithuanica* **12:** 113–119.

Motiejūnaitė, J., Stončius, D., Dolnik, C., Tõrra, T. & Uselienė, A. (2007) New and noteworthy for Lithuania lichens and lichenicolous fungi. *Botanica Lithuanica* **13:** 19–25.

Nimis, P. L. & Martellos, S. (2003) *A Second Checklist of the Lichens of Italy with a Thesaurus of Synonyms*. Saint-Pierre, Valle d'Aosta: Museo Regionale di Scienze Naturali.

Nordin, A., Sundin, R. & Thor, G. (1995) Two sorediate crustose lichens assigned to *Lecanora*. *Nordic Journal of Botany* **15:** 553–556.

Nylander, W. (1875) Addenda nova ad Lichenographiam Europaeam. Continuatio tertia et vicesima. *Flora* (*Regensburg*) **58:** 440–448.

Nylander, W. (1879) Addenda nova ad Lichenographiam Europaeam. Continuatio secunda et tricesima. *Flora* (*Regensburg*) **62:** 353–362.

Nylander, W. (1881) Addenda nova ad Lichenographiam Europaeam. Continuatio sexta et tricesima. *Flora* (*Regensburg*) **64:** 177–189.

Orange, A., James, P. W. & White, F. J. (2010) *Microchemical Methods for the Identification of Lichens*. London: British Lichen Society.

Palice, Z., Guttová, A. & Halda, J. P. (2006) Lichens new for Slovakia collected in the National Park Muránska planina (W Carpathians). In *Central European Lichens – Diversity and Threat* (A. Lackovičová, A. Guttová, E. Lisická & P. Lizoň, eds): 179–192. Ithaca: Mycotaxon Ltd.

Poelt, J. & Vězda, A. (1981) Bestimmungsschlüssel europäischer Flechten. Ergänzungsheft II. *Bibliotheca Lichenologica* **16:** 1–390.

Posada, D. & Crandall, K. A. (1998) MODELTEST: testing the model of DNA substitution. *Bioinformatics* **14:** 817–818.

Printzen, C., Halda, J., Palice, Z. & Tønsberg, T. (2002) New and interesting lichen records from old-growth forest stands in the German National Park Bayerischer Wald. *Nova Hedwigia* **74:** 25–49.

Rodrigues, S. A., Terrón-Alfonso, A., Elix, J. A., Pérez-Ortega, S., Tønsberg, T., Fernández-Salegui, A. B. & Soares, A. M. V. M. (2011) *Lecanora sorediomarginata*, a new epiphytic lichen species discovered along the Portuguese coast. *Lichenologist* **43:** 99–111.

Ronquist, F. & Huelsenbeck, J. P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19:** 1572–1574.

Roux, C. (ed.) (2015) *Liste des lichens et champignons lichénicoles de France métropolitaine* (mise à jour 2015/01/03). Available at: http://lichenologue.org/fr/.

Ryan, B. D., Lumbsch, H. T., Messuti, M. I., Printzen, C., Sliwa, L. & Nash, T. H., III (2004) *Lecanora*. In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 2* (T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries & F. Bungartz, eds): 176–286. Tempe, Arizona: Lichens Unlimited, Arizona State University.

Santesson, R., Moberg, R., Nordin, A., Tønsberg, T. & Vitikainen, O. (2004) *Lichen-forming and Lichenicolous Fungi of Fennoscandia*. Uppsala: Museum of Evolution, Uppsala University.

Schreiner, E. & Hafellner, J. (1992) Sorediöse, corticole Krustenflechten im Ostalpenraum. I. Die Flechtenstoffe und die gesicherte Verbreitung der besser bekannten Arten. *Bibliotheca Lichenologica* **45:** 1–291.

Simmons, M. P. & Ochoterena, H. (2000) Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* **49:** 369–381.

Stepanchikova, I. S., Kukwa, M., Kuznetsova, E. S., Motiejūnaitė, J. & Himelbrant, D. E. (2010) New records of lichens and allied fungi from the Leningrad Region, Russia. *Folia Cryptogamica Estonica* **47:** 77–84.

Taylor, T. (1836) *L. albo-flavida*. In *Flora Hibernica. Part the Second. Comprising the Musci, Hepaticae and Lichenes* (J. T. Mackay, ed.): 260. Dublin: W. Curry, Jnr.

Tønsberg T. (1992) The sorediate and isidiate, corticolous, crustose lichens in Norway. *Sommerfeltia* **14:** 1–331.

Tønsberg, T., Türk, R. & Hofmann, P. (2001) Notes on the lichen flora of Tyrol (Austria). *Nova Hedwigia* **72:** 487–497.

Urbanavichus, G. (2010) *A Checklist of the Lichen Flora of Russia*. St. Petersburg: Nauka.

Valný, M., Honsa, P., Kirdajová, D., Kameník, Z. & Anděrová, M. (2016) Tamoxifen in the mouse brain: implications for fate-mapping studies using the tamoxifen-inducible Cre-loxP system. *Frontiers in Cellular Neuroscience* **10:** 243.

Vězda, A. (2000) *Lichenes Rariores Exsiccati. Fasc. 45* (*numeris 441–450*). Brno: published by the author.

Vondrák, J., Malíček, J., Šoun, J. & Pouska, V. (2015) Epiphytic lichens of Stužica (E Slovakia) in the context of Central European old-growth forests. *Herzogia* **28:** 108–130.

Werner, O., Ros, R. M. & Guerra, J. (2002) Direct amplification and NaOH extraction: two rapid and simple methods for preparing bryophyte DNA for polymerase chain reaction (PCR). *Journal of Bryology* **24:** 127–131.

White, T. J., Bruns, T. D., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR Protocols: a Guide to Methods and Applications* (M. A. Innis, D. H. Gelfand, J. J. Sninsky & T. J. White, eds): 315–322. San Diego: Academic Press.

Wirth, V. (1995) *Die Flechten Baden-Württembergs*. Teil 1. Stuttgart: Ulmer.

Zahlbruckner, A. (1928) *Catalogus Lichenum Universalis. 5*. Leipzig: Gebrüder Borntraeger.

Zduńczyk, A. & Kukwa, M. (2014) A revision of sorediate crustose lichens containing usnic acid and chlorinated xanthones in Poland. *Herzogia* **27:** 13–40.

Zedda, L. (2002) The epiphytic lichens on *Quercus* in Sardinia (Italy) and their value as ecological indicators. *Englera* **24:** 1–457.

Zoller, S., Scheidegger, C. & Sperisen, C. (1999) PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. *Lichenologist* **31:** 511–516.