










Standard Paper

New phylogenetic insights into the lichen genus *Lecanora* s. lat. (*Lecanoraceae*, *Ascomycota*): resurrection of the genera *Glaucomaria*, *Straminella* and *Zeora*

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Abstract

A new phylogenetic analysis of *Lecanora* s. lat. is presented based on a dataset of seven loci, including recently published mitochondrial markers. In this analysis, comprising 136 specimens and 572 sequences, several clades that can be circumscribed taxonomically are recovered as monophyletic with strong support. *Lecanora* divides into two large monophyletic subclades. The well-supported MPRPS clade *sensu* Medeiros *et al.* (2021) combines the genera *Lecanoropsis*, *Myriolecis*, *Protoparmeliopsis*, *Rhizoplaca* and the *Lecanora polytropa*- and *L. varia*-groups. The second unsupported clade contains the genera *Bryonora*, *Palicella*, *Pulvinora* and *Vainionora*, plus the *Lecanora albella/subcarnea*-, *L. carpinea/rupicola*-, *L. intumescens*-, *L. subfusca*- and *L. symmicta*-groups. *Japewia*, *Lecidella*, *Miriquidica*, *Ramboldia* and members of the *Lecanora fuscescens*-group are placed outside these two clades. Phylogenetic, morphological and chemical evidence supports the resurrection of three genera: *Glaucomaria* (for the *Lecanora carpinea/rupicola*-group), *Straminella* (for the *L. varia*-group), and *Zeora* (for the *L. symmicta*-group). Descriptions for each of the resurrected genera are provided, including new taxonomic combinations and lists of additional *Lecanora* species likely to be transferred to the proposed new genera pending further studies. Comments on the nomenclature of the new genera, as well as for *Lecanoropsis* and *Myriolecis*, are provided.

Keywords: generic circumscription; *Lecanoropsis*; *Myriolecis*; mitochondrial loci; nomenclature; systematics

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Introduction

The crustose lichen genus *Lecanora* Ach. in Luyken, was created by Acharius as a segregate of the genus *Lichen* L. Shortly afterwards, Acharius (1810) considerably expanded *Lecanora*, which included three subdivisions (*Rinodina*, *Psoroma* and *Placodium*), 132 species and 166 forms (as α , β , γ , etc.). Currently, the exact number of species reported to belong to *Lecanora* is unknown but is probably in the range of 600 (Lumbsch & Elix 2004). Since the advent of molecular sequence data and its use in taxonomy, new species have continually been discovered and added to the genus (e.g. Lendemer & Tripp 2015; Malíček *et al.* 2017; Printzen *et al.* 2017; Yakovchenko *et al.* 2019; Ivanovich *et al.* 2025).

When Acharius created the genus (Acharius, in Luyken 1809), he provided a general description, ‘*Apoth. orbiculatum crassum sessile; lamina prolifera colorata immarginata discum plano convexum formante margineque thallose tumido elevato sublibero cincta, intus cellulifera striataque. Thallus crustaceus uniformis vel effiguratus*’ [‘Apothecium circular, thick, sessile; bright coloured lamina forming a flat-convex disc, surrounded by a ring of semi-free raised swollen thalline margin, cellular and striated inside. Thallus crustose, uniform or effigurate’]. The first genus to be segregated from *Lecanora* was *Zeora* Fr. in his ‘*Systema Orbis Vegetabilis*’. Later, Massalongo (1852, 1853, 1855) proposed the segregation of multiple genera from *Lecanora*, for example *Acarospora* A. Massal., *Aspicilia* A. Massal., *Gyalolechia* A. Massal., *Haematomma* A. Massal., *Lecania* A. Massal., *Mischoblastia* A. Massal., *Ochrolechia* A. Massal., *Pachyospora* A. Massal., *Polyozosia* A. Massal. and *Thalloidima* A. Massal. This led to a circumscription of the genus roughly equivalent to the family *Lecanoraceae* as currently understood. Regarding this large split, Massalongo (1852) wrote:

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'Coming now to the details of each genus, it should be noted that the genus *Lecanora* was reduced by me to the species with a crustose thallus and very small homogeneous spores, thus preserving for the most part the limits set by its author. The genus *Rinodina*, used by Acharius to indicate a section of his *Lecanora*, as well as the name *Catillaria* of the [genus] *Lecidea*, are here used in the opposite sense, so that they can be considered as new genera. The former, I hope, will be preserved, but the latter will perhaps be considered by some as a spurious genus, if it proves that the spores which I knew to be bilocular constantly insensibly change to monolocular, and that the excipulum is also subject to change. The genera *Gyalolechia*, *Thalloidima*, *Acarospora*, *Ochrolechia*, *Haematomma*, *Pachyospora*, *Mischoblastia*, which I propose for the first time, if not now, then later, will certainly be accepted, so natural and distinct are they!¹

With Massalongo's (1852) proposal to place multiple groups with different morphology outside *Lecanora*, he understood the heterogeneity of the genus in its old circumscription and the need to divide it into 'natural and distinct' groups.

Further attempts to split *Lecanora* into more natural or practical groups included the separation of, for example, *Myriolecis* Clem., *Rhizoplaca* Zopf, and the creation of new subgeneric groups for morphologically similar species (Fries 1871–74; Smith 1921; Zahlbruckner 1926). Most authors in the early and mid-20th century largely maintained the circumscription of *Lecanora* used by Zahlbruckner (1926) in his catalogue and some of its subgroups introduced by Smith (1921), such as the *Lecanora subfusca*-, *L. symmicta*- and *L. varia*-groups. One exception was Choisy (1929, 1949) who, acknowledging the diversity of *Lecanora*, proposed several new genera combining species with a small number of shared characters. These included *Glaucumaria* M. Choisy, *Lecanoropsis* M. Choisy ex Ivanovich and *Straminella* M. Choisy, all treated in this paper, as well as *Protoparmeliopsis* M. Choisy. Further attempts to split *Lecanora* into more natural units were made by Poelt (1958), Eigler & Poelt (1965) and Eigler (1969), who among others introduced *Squamarina* Poelt, and recognized *Aspicilia* as well as *Glaucumaria* and *Straminella* as separate genera. Genera segregated more recently from *Lecanora* include *Bryonora* Poelt, *Miriquidica* Hertel & Rambold, and the resurrected *Protoparmeliopsis* (Hafellner & Türk 2001).

DNA-based phylogenetic approaches provide a better taxonomic understanding of *Lecanora* s. lat., from species to subgeneric groups and their evolutionary relationships (e.g. Grube *et al.* 2004; Pérez-Ortega *et al.* 2010; Zhao *et al.* 2015; Kondratyuk *et al.* 2019; Yakovchenko *et al.* 2019; Ivanovich *et al.* 2021, 2025; Medeiros *et al.* 2021). Zhao *et al.* (2015) have provided the most comprehensive phylogenetic overview and classification of *Lecanora* s. lat. based on molecular data to date. In their study, *Protoparmeliopsis* and *Rhizoplaca* were confirmed to be monophyletic and their segregation from *Lecanora* s. str. is now generally accepted. The *Lecanora dispersa*-group was also confirmed to be monophyletic and the generic name *Myriolecis* was suggested for it. Although the *Lecanora carpinea/rupicola*-, *L. polytropa*- and *L. varia*-groups appeared phylogenetically distinct and received strong statistical support, they were not segregated (Zhao *et al.* 2015). Other groups treated in this latter publication, such as the *Lecanora saligna*- and *L. subcarnea*-groups, were not strongly supported. The *L. saligna*-group was finally raised to genus level by Ivanovich *et al.* (2025), who resurrected and validated the invalidly published name *Lecanoropsis* M. Choisy (1949) for this group of species.

As a consequence of some other studies, further genera have recently been segregated from *Lecanora*, such as *Palicella* Rodr. Flakus & Printzen (Rodríguez Flakus & Printzen 2014) and *Pulvinora* Davydov *et al.* (Davydov *et al.* 2021). These genera were segregated

on the basis of their supported monophyly (in addition to other evidence), but appeared nested within *Lecanora* s. lat. On the other hand, several morphologically circumscribed groups have been retained in *Lecanora* and not segregated into new genera because researchers hesitated to separate them based on equivocal or sparse morphological and/or chemical data (Lumbsch *et al.* (1997), with the *Lecanora carpinea*-group; Grube *et al.* (2004), with the *L. rupicola*-group; Printzen (2001), with the *L. saligna*-group; Śliwa & Wetmore (2000), with the *L. varia*-group). This currently leaves the genus *Lecanora* still polyphyletic and morphologically heterogeneous.

Our study seeks to further clarify the taxonomic structure and generic circumscriptions within *Lecanora* s. lat. By including more mitochondrial regions in the phylogenetic analysis, a small number of additional lineages were recovered as monophyletic and statistically well supported (the *Lecanora carpinea/rupicola*-, *L. symmicta*- and *L. varia*-groups). Based on morphological and chemical characters, and phylogenetic support, we propose the segregation of these groups into the genera *Glaucumaria*, *Zeora* and *Straminella*, respectively. We include descriptions for the newly established genera, comment on their nomenclature and propose new taxonomic combinations. Finally, we include a list of taxa that we suspect may belong to the newly segregated genera, but for which no DNA sequences are available for confirmation.

Materials and Methods

Taxa selection

Specimens of *Lecanora* s. lat. were collected by the authors or obtained on loan from the following herbaria: ASU, BRY–C, FR, GLM, H, HBG, ICH, MIN, NY, PRA, S, UCR, UPS, and the private collections of Rainer Cezanne and Marion Eichler (Darmstadt, Germany), Bruce McCune (Corvallis, USA), Toby Spribille (Edmonton, Canada), and Christian Dolnik (Kiel, Germany).

Morphological and chemical analyses on selected specimens were performed as described in Ivanovich *et al.* (2021). Photographs of specimens shown in Figs 3–7 were obtained using a Zeiss Axio Zoom V16 stereomicroscope. Chemical analyses (spot tests KOH 10% (K), Sodium hypochlorite (C), Paraphenylenediamine (Pd) (Orange *et al.* 2001) and amphithecial granule solubility (KOH/HNO₃) were performed on hand-cut sections of apothecia of selected specimens.

Multiple GenBank (Clark *et al.* 2016) sequences were added to the dataset based on the similarity of the selected species to *Glaucumaria*, *Straminella* and *Zeora*. Additional sequences from GenBank were included to represent in a comprehensive way the different genera segregated from *Lecanora* s. lat. and morphological groups distinguished within the genus. Preferably (but not exclusively) species were chosen for which ITS, mtSSU and nuLSU amplified from the same voucher were available. *Pseudophebe minuscula* (Nyl. ex Arnold) Brodo & D. Hawksw., *Usnea antarctica* Du Rietz and *Usnea aurantiacoatra* (Jacq.) Bory were included as outgroup. The selected outgroup taxa belong to the family *Parmeliaceae*, which is relatively closely related to *Lecanoraceae* (both belonging to *Lecanorales*; Miadlikowska *et al.* 2014), and was the chosen outgroup family in Zhao *et al.* (2015).

DNA extraction, amplification and sequencing

DNA was extracted from apothecia using the DNeasy Plant Mini Kit (Qiagen) or the GF-1 Plant DNA Extraction Kit (GeneOn),

¹Translated from Italian

Table 1. Summary of primers and PCR programs used in the phylogenetic analyses.

Locus	Primer name	Direction	Sequence (5' → 3')	Citation
<i>atp6</i>	<i>atp6F2</i>	forward	ACTAACATAGGACTTTACTTAAC	Ivanovich <i>et al.</i> 2025
	<i>atp6R2</i>	reverse	ACCTGAAAATGCTATAATAAAAGC	Ivanovich <i>et al.</i> 2025
<i>cob</i>	<i>cobF2</i>	forward	AGTCATCCTTTGCTAAAATTGG	Ivanovich <i>et al.</i> 2025
	<i>cobR2</i>	reverse	TGTTCTAGGAGCTTTATATG	Ivanovich <i>et al.</i> 2025
<i>cox3</i>	<i>cox3F2</i>	forward	CAGGTGTTTTAAACATGC	Ivanovich <i>et al.</i> 2025
	<i>cox3R2</i>	reverse	TAAAAACAAGAACCATATGTAC	Ivanovich <i>et al.</i> 2025
<i>nad1</i>	<i>nad1F1</i>	forward	TGCAAGAAGATTAGGTCC	Ivanovich <i>et al.</i> 2025
	<i>nad1R1</i>	reverse	CAAATAAGAACAATGCTAGC	Ivanovich <i>et al.</i> 2025
mtSSU	<i>mrssu1</i>	forward	AGCAGTGAGGAATATTGGTC	Zoller <i>et al.</i> 1999
	<i>mrssu3r</i>	reverse	ATGTGGCACGTCTATAGCCC	Zoller <i>et al.</i> 1999
nuLSU	AL2R	forward	GCGAGTGAAGCGGCAACAGCTC	Mangold <i>et al.</i> 2008
	LR6	reverse	CGCCAGTTCTGCTTACC	Vilgalys & Hester 1990
ITS	ITS1F	forward	CTTGTTTCATTTAGAGGAAGTAA	Gardes & Bruns 1993
	ITS4	reverse	CGCCGTTACTGGGGCAATCCCTG	White <i>et al.</i> 1990

Cycler program for ITS, mtSSU, nuLSU				Cycler program for <i>atp6</i> , <i>cob</i> , <i>cox3</i> , <i>nad1</i>			
	Temp (°C)	Time (s)	Cycles		Temp (°C)	Time (s)	Cycles
Denaturation	94	300	×1	Denaturation	94	300	×1
Phase 1	94	30	×4	Phase 1	94	30	×10
	54	30			55 to 46	30	
Phase 2	72	60	×32	Phase 2	72	60	×30
	94	30			94	30	
Final extension	48	30	×1	Final extension	45	30	×1
	72	60			72	60	
	72	600			72	600	

following the manufacturers' protocols. Remnants of the substratum were cleaned from apothecia under a dissecting microscope prior to DNA extraction. PCR was performed on seven loci: ITS, nuLSU, mtSSU, *atp6*, *cob*, *cox3* and *nad1*. A summary of primers and cycler programs used to amplify the different loci can be found in Table 1. Amplification of the selected regions was performed using PCR Ready-To-Go beads (GE Healthcare) in 25 µl reactions containing 5 µl DNA, 18 µl of double-distilled H₂O and 1 µl of each primer. PCR products were checked on 1% agarose gels using electrophoresis. Successful PCR amplicons were Sanger-sequenced by MacroGen Europe (Amsterdam, the Netherlands). Forward and reverse sequences were assembled in Geneious Prime 2019.2.1 (<https://www.geneious.com>) and manually edited. DNA sequences were submitted to GenBank (Table 2).

Phylogenetic reconstruction

Alignments. Locus-specific alignments of consensus sequences were created through GUIDANCE2 (Landan & Graur 2008; Penn *et al.* 2010; Sela *et al.* 2015). For ITS, nuLSU and mtSSU, aligned positions with a score below 0.93 were removed. For the coding regions *atp6*, *cob*, *cox3* and *nad1*, columns with low scores were

not removed from the alignments. Instead, sequences with indels were compared to their original chromatograms, and singleton columns were subsequently removed after checking for codon frame shifts and translational coherency (no stop codons within the sequence) in the sequences and the alignments. Additionally, both ends of all the datasets were trimmed. Single-locus trees, concatenated nuclear loci (ITS and nuLSU) trees, and concatenated mitochondrial loci trees were then inferred from alignments using the IQ-TREE web server (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016). The resulting topologies were visually compared to each other to check for statistically supported incongruencies (Som 2015).

Phylogenetic analysis. All single-locus datasets were merged into a concatenated alignment and a partitioning scheme was suggested, considering each codon position of the coding regions of the mitochondrial loci, the regions ITS1, 5.8S and ITS2 for the ITS region, and mtSSU and nuLSU as a single partition. A maximum likelihood (ML) tree and the optimal partition scheme were inferred with IQ-TREE using the default settings of an Ultrafast Bootstrap (Minh *et al.* 2013; Hoang *et al.* 2017), 3000 bootstrap repetitions, and automatic substitution model selection with

Table 2. Specimen voucher information and GenBank Accession numbers for the *Lecanoraceae* sequences used in the phylogenetic analyses. Lecanomics ID refers to the online database <https://lecanomics.org>.

Taxa	Lecanomics code/GenBank	Country	Voucher	ITS	mtSSU	nuLSU	atp6	cob	cox3	nad1
<i>Bryonora castanea</i>	GenBank			OM423658	OM417201	OM423613	—	—	—	—
<i>B. septentrionalis</i>	GenBank			OM423667	OM417209	OM423617	—	—	—	—
<i>Glaucomaria bicincta</i>	1198	China	FR-0175453	PV928816	PV928852	—	—	PV955783	PV955815	—
<i>G. bicinctoidea</i>	1772	Germany	FR-0175438	PV928817	PV928853	PV943335	—	—	—	PV955844
<i>G. carpinea</i>	512	Germany	FR-0183027	PQ099893	PQ214793	PQ100509	—	PQ284158	PQ301001	PQ300972
<i>G. flavescens</i>	GenBank			AF517889	—	—	—	—	—	—
<i>G. leptyroides</i>	GenBank			MK778610	MK778538	—	—	—	—	—
<i>G. cf. leptyroides</i>	197	Iran	FR-0175447	PV928818	PV928854	PV943336	—	PV955784	PV955816	PV955845
<i>G. lajkaeana</i>	GenBank			AY398709	PQ483942	—	—	—	—	—
<i>G. rupicola</i>	384	Spain	FR-0264951	PV928819	PV928855	—	ON101753	ON101753	ON101753	ON101753
<i>G. subcarpinea</i>	GenBank			DQ451657	OQ683007	—	—	—	—	—
<i>G. swartzii</i>	GenBank			DQ451656	—	—	—	—	—	—
<i>Japevia aliphatica</i>	GenBank			NRL73885	MN547347	—	—	—	—	—
<i>J. taroensis</i>	GenBank			HQ650656	HQ660559	DQ899300	—	—	—	—
<i>Lecanora albella</i>	GenBank			KY548048	KY502423	—	—	—	—	—
<i>L. alboflavida</i>	GenBank			OL604044	OL604124	OL663903	—	—	—	—
<i>L. allophana</i>	853	Austria	FR-0265834	—	PV928856	—	PV955759	PV955785	PV955817	PV955846
<i>L. argopholis</i>	587	Kyrgyzstan	FR-0175455	PV928820	PV928857	PV943337	PV955760	PV955786	PV955818	PV955847
<i>L. barkmaniana</i>	GenBank			OQ717893	OQ646269	—	—	—	—	—
<i>L. bermudensis</i>	9	Bermuda	FR-0264718	PQ099891	PQ214791	PQ100507	PQ139248	PQ284156	PQ300999	PQ300970
<i>L. cadubriae</i>	255	Czech Republic	FR-0279001	PQ099892	PQ214792	PQ100508	PQ139249	PQ284157	PQ301000	PQ300971
<i>L. caesiortubella</i>	GenBank			JN943722	JQ782666	JN939506	—	—	—	—
<i>L. caledonica</i>	GenBank			OQ945707	OQ945756	OQ946444	—	—	—	—
<i>L. campestris</i>	844	Germany	FR-0175454	PV928821	PV928858	PV943338	PV955761	PV955787	PV955819	PV955848
<i>L. cateilea</i>	GenBank			OQ945708	—	—	—	—	—	—
<i>L. caucasica</i>	1676	Russia	FR-0175450	PV928822	PV928859	—	—	PV955788	PV955820	—
<i>L. chlorotera</i>	1159	Austria	FR-0175445	PV928826	—	—	—	PV955792	PV955824	PV955852
<i>L. chlorophaeodes</i>	GenBank			AY398704	—	—	—	—	—	—
<i>L. circumborealis</i>	556	Germany	FR-0183023	PQ099894	PQ214794	PV943342	PQ139250	PQ284159	PQ301002	PQ300973
<i>L. crystalliniformis</i>	GenBank			MW832796	MW832802	MW832821	—	—	—	—
<i>L. epiphyron</i>	707	Russia	FR-0175457	PV928827	PV928863	—	PV955765	PV955793	PV955825	PV955853

(Continued)

Table 2. (Continued)

Taxa	Lecanomics code/GenBank	Country	Voucher	ITS	mtSSU	nuLSU	atp6	cob	cox3	nad1
<i>L. excludens</i>	GenBank			OQ945710	OQ945758	OQ946446	—	—	—	—
<i>L. farinacea</i>	GenBank			JN943725	JQ782672	JN939513	—	—	—	—
<i>L. flavidomarginata</i>	GenBank			OL604056	OL604135	OL663915	—	—	—	—
<i>L. formosa</i>	GenBank			OL604027	OL604109	OL663887	—	—	—	—
<i>L. fulvastra</i>	GenBank			LC269720	OL604089	—	—	—	—	—
<i>L. fuscobrunnea</i>	GenBank			OL331409	OM103928	OL331783	—	—	—	—
<i>L. glabrata</i>	182	Iran	FR-0175446	PV928828	PV928864	PV943343	PV955766	PV955794	PV955826	PV955854
<i>L. horiza</i>	562	Greece	FR-0175443	PV928829	PV928865	PV943344	PV955767	PV955795	PV955827	PV955855
<i>L. hybocarpa</i>	GenBank			EF105412	EF105417	EF105421	—	—	—	—
<i>L. intricata</i>	GenBank			OL603995	OL604076	OL663863	—	—	—	—
<i>L. intumescens</i>	388	France	FR-0279044	PQ099895	PQ214795	—	PQ139252	PQ284161	PQ301004	PQ300974
<i>L. cf. intumescens</i>	689	Russia		PV928823	PV928860	PV943338	PV955762	PV955789	PV955821	PV955849
<i>L. kohu</i>	GenBank			MF115999	MF116001	MF116000	—	—	—	—
<i>L. laxa</i>	GenBank			PQ228282	—	—	—	—	—	—
<i>L. cf. laxa</i>	328	Chile	FR-0175439	PV928824	PV928861	PV943340	PV955763	PV955790	PV955822	PV955850
<i>L. marjohnstonii</i>	GenBank			—	MH221526	MH887500	MH221526	MH221526	MH221526	MH221526
<i>L. mughicola</i>	503	Austria	FR-0183024	MT938983	MT939210	PQ100510	PQ139253	PQ284162	PQ301005	PQ300975
<i>L. orientoafriicana</i>	GenBank			NR120113	JQ900617	—	—	—	—	—
<i>L. paramerae</i>	GenBank			EF105413	EF105418	EF105422	—	—	—	—
<i>L. physciella</i>	374	Falkland Is.	MSC 10790	PV928830	—	—	—	—	—	—
<i>L. polytropa</i>	1020	Switzerland	FR-0183025	PQ099896	PQ214796	—	PQ139254	PQ284163	PQ301006	PQ300976
<i>L. cf. polytropa</i>	sl16512a	USA		PV928825	PV928862	PV943341	PV955764	PV955791	PV955823	PV955851
<i>L. prolificans</i>	400	USA	FR-0183035	MT938974	MT939201	PV943345	PQ139255	PQ284165	PQ301008	PQ300977
<i>L. pseudargentata</i>	238	Bermuda	FR-0264719	PV928831	PV928866	PV943346	ON101752	ON101752	ON101752	ON101752
<i>L. pulicaris</i>	554	Germany	FR-0175449	PV928832	PV928867	PV943347	—	—	—	—
<i>L. solaris</i>	GenBank			MW257119	MH520107	MW257119	—	—	—	—
<i>L. somervellii</i>	GenBank			ON180228	ON180461	ON180354	—	—	—	—
<i>Lecanora</i> sp.	675	Russia	FR-0175452	PV928833	PV928868	—	PV955768	PV955796	PV955828	—
<i>Lecanora</i> sp.	1183	China	FR-0175448	PV928834	PV928869	PV943348	PV955769	PV955797	PV955829	PV955856
<i>L. subcarnea</i>	389	Germany	FR-0279045	—	PV928870	—	ON101763	ON101763	ON101763	ON101763
<i>L. subcavicola</i>	610	USA	FR-0265494	PV928835	PV928871	PV943349	PV955770	PV955798	PV955830	PV955857

(Continued)

Table 2. (Continued)

Taxa	Lecanomics code/GenBank	Country	Voucher	ITS	mtSSU	nuLSU	atp6	cob	cox3	nad1
<i>L. utahensis</i>	393	USA	UCR-264945	—	—	—	PV955771	PV955799	PV955831	PV955858
<i>L. variolascens</i>	GenBank			KY548038	KY502445	—	—	—	—	—
<i>Lecanoropsis albicollis</i>	555	Germany	FR-0183021	MT938990	MT939219	—	PQ139258	PQ284168	—	PQ300980
<i>L. anopta</i>	168	Iran	FR-0362758	MT938926	MT939156	—	PQ139259	PV955800	PV955832	PV955859
<i>L. cf. anopta</i>	1679	Austria	FR-0175456	PV928837	PV928873	—	PV955772	PV955801	—	PV955860
<i>L. anoptizodes</i>	1678	Czech Republic	FR-0362765	PV928836	PV928872	PV943350	—	—	—	—
<i>L. austrocascadensis</i>	985	USA	FR-0183030	—	—	—	PQ139260	PQ284169	—	—
<i>L. conferrarum</i>	992	USA	FR-0362766	PV928839	PV928875	—	PV955774	PV955803	PV955833	PV955862
<i>L. coracina</i>	1136	USA	FR-0183036	PV928840	—	PV943352	PQ139262	PQ284171	PQ301012	PQ300982
<i>L. iapyx</i>	267	USA	FR-0183034	PV928841	PV928876	PV943353	PV955775	PV955804	—	PV955863
<i>L. micans</i>	265	USA	FR-0183033	MT938953	MT939183	—	PQ139264	PQ284173	PQ301013	PQ300984
<i>L. omisssa</i>	245	Russia	FR-0183020	MT938948	MT939178	—	—	PQ284174	—	PQ300985
<i>L. saligna</i>	203	Germany	FR-0183022	MT938930	MT939160	PV943354	PQ139265	PQ284175	PQ301014	PQ300986
<i>L. sarcopoidoides</i>	573	Slovakia	FR-0183018	MT938997	MT939226	PV943355	PQ139266	PQ284176	PQ301015	PQ300987
<i>L. subininctula</i>	595	Japan	FR-0267107	MT939007	MT939236	—	PQ139267	PQ284177	PQ301016	PQ300988
<i>L. subintricata</i>	11	Czech Republic	FR-0261122	MT938923	MT939153	PQ100512	PQ139268	PQ284178	PQ301017	PQ300989
<i>L. cf. subintricata</i>	600	Japan	FR-0267112	PV928838	PV928874	PV943351	PV955773	PV955802	—	PV955861
<i>L. subbravida</i>	291	Russia	GLM-54344	MT938968	MT939194	PQ100513	PQ139269	PQ284179	PQ301018	PQ300990
<i>L. subsaligna</i>	251	Czech Republic	FR-0279046	MT938950	MT939180	PQ100514	PQ139270	PQ284180	PQ301019	PQ300991
<i>Lecidella elaeochroma</i>	391	Germany	FR-0261123	PQ099899	PQ214799	PQ100515	PQ139271	PQ284181	PQ301020	PQ300992
<i>L. enteroleucella</i>	GenBank			KT453757	KT453838	KT453792	—	—	—	—
<i>L. stigmatea</i>	GenBank			KT453760	KT453852	KT453802	—	—	—	—
<i>Miriquidica complanata</i>	GenBank			KF562187	SUKP940385	KF562179	—	—	—	—
<i>M. garovaglii</i>	GenBank			KF562188	AV567711	AY756357	—	—	—	—
<i>M. gyrizans</i>	GenBank			NR171243	MN508282	MN460217	—	—	—	—
<i>M. leucophaea</i>	GenBank			KP822311	KP822516	KP796396	—	—	—	—
<i>Myriolecis dispersa</i>	377	Czech Republic	FR-0264963	PQ099900	PQ214800	PQ100516	PQ139272	PQ284182	PQ301021	PQ300993
<i>M. expectans</i>	882	Antarctica	FR-0175444	PV928842	PV928877	PV943356	PV955776	PV955805	PV955834	PV955864
<i>Palicella filamentosa</i>	646	Germany	HBG-24718	PQ099901	PQ214801	PV943357	PQ139273	PQ284183	PQ301022	PQ300994
<i>P. schizochromatica</i>	GenBank			HQ650652	HQ660555	HQ660532	—	—	—	—
<i>Protoparmeliopsis garovaglii</i>	43	Iran	FR-0261137	PV928843	PV928878	PV943358	PV955777	PV955806	PV955835	—

(Continued)

Table 2. (Continued)

Taxa	Lecanomics code/GenBank	Country	Voucher	ITS	mtSSU	nuLSU	atp6	cob	cox3	rad1
<i>P. muralis</i>	380	Czech Republic	FR-0264962	PQ099902	PQ214802	PQ100517	PQ139274	PQ284184	PQ301023	PQ300995
<i>P. peltata</i>	44	Iran	FR-0261138	PV928844	PV928879	PV943359	PV955778	PV955807	PV955836	—
<i>Pseudephebe minuscula</i>		Antarctica	FR-0279003	PQ099903	PQ214803	PQ100518	PQ139275	PQ284185	PQ301024	PQ300996
<i>Pulvinora pringlei</i>	GenBank			MW257114	MW257153	MW257114	—	—	—	—
<i>P. stereothallina</i>	GenBank			MW257112	MW257152	MW257112	—	—	—	—
<i>Ramboldia brunneocarpa</i>	GenBank			EU075542	EU075528	EU075520	—	—	—	—
<i>R. elabens</i>	GenBank			MK811668	KJ766482	KJ766648	—	—	—	—
<i>R. laeta</i>	GenBank			EU075544	EU075530	DQ431920	—	—	—	—
<i>R. sanguinolenta</i>	GenBank			EU075548	EU075534	EU075523	—	—	—	—
<i>R. stuartii</i>	GenBank			EU075549	EU075535	EU075522	—	—	—	—
<i>Rhizoplaca mcleanii</i>	GenBank			MK970664	MN023038	—	—	—	—	—
<i>R. melanophthalma</i>	45	Iran	FR-0261139	PV928845	PV928880	—	PV955779	PV955808	PV955837	—
<i>R. novomexicana</i>	GenBank			MN756822	KT453824	MN756822	—	—	—	—
<i>R. parilis</i>	GenBank			MN756808	KT453859	MN756808	—	—	—	—
<i>R. porterii</i>	GenBank			NR119883	KT453861	KT453816	—	—	—	—
<i>R. shushanii</i>		USA		MN756828	PV928881	MN756828	PV955780	PV955809	PV955838	PV955865
<i>Straminella burgaziae</i>	GenBank			GU480117	—	—	—	—	—	—
<i>S. conizaoides</i>	244	Czech Republic	FR-0183019	MT938947	MT939177	—	PQ139251	PQ284160	PQ301003	—
<i>S. densa</i>	GenBank			GU480094	—	—	—	—	—	—
<i>S. printzenii</i>	233	Spain	FR-0183026	PQ099897	PQ214797	—	PV955781	PQ284164	PQ301007	—
<i>S. varia</i>	239	Czech Republic	FR-0261120	PQ099898	PQ214798	PQ100511	PQ139257	PQ284167	PQ301010	PQ300979
<i>Usnea antarctica</i>		Antarctica	FR-0264581	PV928846	PV928882	—	ON101761	ON101761	ON101761	ON101761
<i>U. aurantiacoatra</i>		Antarctica	FR-0264585	PQ099904	PQ214804	PQ100519	PQ139276	PQ284186	PQ301025	PQ300997
<i>Vainionora</i> sp.	1539	Rwanda	FR-0175442	PV928847	PV928883	PV943360	PV955782	—	PV955839	PV955866
<i>Vainionora</i> sp.	1544	Rwanda	FR-0175437	PV928848	PV928884	PV943361	—	PV955810	—	—
<i>Zeora aitema</i>	607	Japan	FR-0267119	PQ099890	PQ214790	PV943362	PQ139247	PQ284155	PQ300998	—
<i>Z. atrosulphurea</i>	GenBank			KV266931	—	—	—	—	—	—
<i>Z. austrocalifornica</i>	GenBank			GU480103	—	—	—	—	—	—
<i>Z. compallens</i>	GenBank			MT803546	OQ683010	—	—	—	—	—
<i>Z. confusa</i>	GenBank			GU480120	—	—	—	—	—	—
<i>Z. expallens</i>	GenBank			OQ717896	OQ682991	—	—	—	—	—

(Continued)

Table 2. (Continued)

Taxa	Lecanomics code/GenBank	Country	Voucher	ITS	mtSSU	nuLSU	atp6	cob	cox3	nad1
<i>Z. flavoleprosa</i>	GenBank			MW979431	MW979426	—	—	—	—	—
<i>Z. helmutii</i>	GenBank			NR_161059	—	—	—	—	—	—
<i>Z. orosthea</i>	428	Scotland	FR-0175440	PV928850	PV928886	PV943363	—	PV955812	PV955841	—
<i>Z. parasymmicta</i>	GenBank			MW832793	MW832799	—	—	—	—	—
<i>Z. pulverulenta</i>	GenBank			LC669639	—	—	—	—	—	—
<i>Z. stanislai</i>	GenBank			MN387010	MT784070	—	—	—	—	—
<i>Z. straminea</i>	655	Germany		PV928851	PV928887	PV943364	—	PV955813	PV955842	PV955868
<i>Z. strobilina</i>	GenBank			OQ717459	KU308740	KJ766583	KU308740	KU308740	KU308740	KU308740
<i>Z. cf. strobilina</i>	1540	Rwanda	FR-0175429	PV928849	PV928885	—	—	PV955811	PV955840	PV955867
<i>Z. strobilinoidea</i>	GenBank			MG973238	—	—	—	—	—	—
<i>Z. sulphurea</i>	GenBank			AF070030	EF105423	EF105419	—	—	—	—
<i>Z. symmetrica</i>	1266	Japan	FR-0265888	—	PV928888	—	—	PV955814	PV955843	—

ModelFinder (Kalyaanamoorthy *et al.* 2017). For the Bayesian Inference analysis (BI), the same partition scheme was applied, and substitution models obtained in ModelFinder were translated into models supported by MrBayes (Table 3). *Pseudephebe minuscula* was selected as outgroup. Substitution model parameters were unlinked between data partitions. The branch length prior was set after calculating the average branch length of the ML tree, following the method outlined by Ekman & Blaaid (2011). The BI was executed through MrBayes v. 3.2 (Ronquist *et al.* 2012) as implemented on the CIPRES platform (Miller *et al.* 2010), where three independent runs starting from random trees and six Markov chains incrementally heated by a factor of 0.15 were set to run for 40 000 000 generations. Trees were sampled every 200 generations and the first 50% of the sampled trees was discarded as burn-in. The analysis was set to stop when the standard deviation between split frequencies dropped below 0.01, considering only those bipartitions with a frequency of at least 30% in the tree sample. The resulting ML and BI trees were visualized and graphically improved using iTOL (Interactive Tree of Life webpage; Letunic & Bork 2021), where the best-fit ML tree was chosen for display (Figs 1 & 2), and posterior probabilities obtained from the BI were mapped onto the tree nodes (Fig. 2). Clades with $\geq 95\%$ ML bootstrap (% UFBoot; as BS) and ≥ 0.95 posterior probability (PP) are considered well supported.

Results

In total, 408 single-locus DNA sequences were generated for 70 specimens: 65 for ITS, 65 for mtSSU, 45 for nuLSU, 55 for atp6, 65 for cob, 59 for cox3, and 54 for nad1. Additionally, 164 sequences obtained from GenBank were added to the dataset. A total of 136 specimens and 572 sequences were included in this analysis. All sequences generated in this work were deposited in GenBank (Table 2). The concatenated alignment matrix spanned 3201 aligned nucleotide positions, with 1138 parsimony-informative positions, 402 sites with a single substitution, and 1661 constant sites. Substitution models applied to each partition are listed in Table 3.

The phylogeny shows that multiple morphologically and chemically circumscribed groups and genera were recovered as monophyletic with statistical support (Figs 1 & 2). However, internal nodes that would help to elucidate relationships between these genera and groups were usually unsupported.

The phylogeny presented in Figs. 1 and 2 shows that almost all taxa included in the analysis are assigned to genus-level clades with high support. This encompasses the genera *Japewia* Tønsberg (BS = 100%/PP = 1), *Ramboldia* Kantvilas & Elix (100/1), *Miriquidica* (100/1), *Pulvinora* (98/1), *Palicella* (100/1), *Glaucosmaria* (100/1), *Bryonora* (97/1), *Vainionora* Kalb (100/1), *Zeora* (95/0.93), *Lecidella* Körb. (96/0.99), *Rhizoplaca* (100/1), *Protoparmeliopsis* (100/1), *Myriolecis* (100/1), *Straminella* (100/1) and *Lecanoropsis* (98/1), as well as the *Lecanora albella/subcarnea*-group (98/1), and the *L. intumescens*-group (100/1). Species from the *L. subfusca*-group are paraphyletic and distributed across three clades, here called *L. subfusca*-group clade 1 (96/1), clade 2 (99/1) and clade 3 (100/1). In addition, there are two yet unnamed species groups: a clade (99/1) containing the saxicolous *Rhizoplaca mcleanii* (C. W. Dodge) Castello along with four species similar to *Lecanoropsis* (relationship unsupported), and one containing *Lecanora cadubrianae* (A. Massal.) Hedl. and *L. physciella* (Darb.) Hertel (98/0.93) in a highly supported (100/1) relationship with

Table 3. Substitution models and parameters chosen for each partition set of the concatenated data matrix for ML and BI approaches.

Charset	Regions	Positions	Model translation into MrBayes	Best model according to ModelFinder	Rates	Ngammacat	Nst	Statefreq
1	atp6pos1	1–369\3	GTR+F+G4	TIM3+F+G4	gamma	4	6	empirical
	atp6pos2	2–369\3	GTR+F+G4	TIM3+F+G4	gamma	4	6	empirical
	cox3pos1	659–1117\3	GTR+F+G4	GTR+F+G4	gamma	4	6	empirical
	cox3pos2	660–1117\3	GTR+F+G4	TVM+F+G4	gamma	4	6	empirical
	nad1pos2	1119–1626\3	GTR+F+G4	TPM3+F+G4	gamma	4	6	empirical
	ITS1	2193–2255	GTR+F+G4	TIM2+F+G4	gamma	4	6	empirical
2	cobpos2	371–658\3	GTR+G4	TIM2e+G4	gamma	4	6	equal
	nad1pos3	1120–1626\3	GTR+G4	TIM2e+G4	gamma	4	6	equal
	ITS2	2413–2489	GTR+G4	TIMe+G4	gamma	4	6	equal
3	atp6pos3	3–369\3	GTR+F+I+G4	TPM2u+F+I+G4	invgamma	4	6	empirical
	cox3pos3	661–1117\3	GTR+F+I+G4	TPM3u+F+I+G4	invgamma	4	6	empirical
4	nad1pos1	1118–1626\3	F81+F+G4	F81+F+G4	equal	4	1	empirical
5	mtSSU	1627–2192	HKY+F+I+G4	HKY+F+I+G4	invgamma	4	2	empirical
6	28S	2490–3201	HKY+I+G4	TNe+I+G4	invgamma	4	2	equal
7	cobpos1	370–658\3	HKY+F+G4	TN+F+G4	gamma	4	2	empirical
8	cobpos3	372–658\3	HKY+G4	TNe+G4	gamma	4	2	equal
9	5_8S	2256–2412	GTR+I+G4	TIM3e+I+G4	invgamma	4	6	equal

Miriquidica. A small number of orphaned species appear among these clades: *Lecanora formosa* (Bagl. & Carestia) Knoph & Leuckert and *L. subcavicola* B. D. Ryan appear paraphyletic at the base of *Palicella*; *Lecanora argopholis* (Ach.) Ach. is basal to the *L. subfusca*-group clade 2, clade 1 and *Zeora*; and *Lecanora kohu* Printzen *et al.* is sister to the *L. subfusca*-group clade 1.

Japewia, *Ramboldia* and the *Miriquidica/L. cadubriae/L. physiciella* clade appear in this order at the base of *Lecanoraceae*. The remainder of the genera and groups fall into two major clades. One of these comprises the well-supported (100/1) MPRPS clade *sensu* Medeiros *et al.* (2021) (Fig. 1) and *Lecidella*, the other an unsupported clade comprising most of the other species included in this analysis plus a small number of genera outside *Lecanora s. lat.*

Discussion

We used four recently published mitochondrial loci (Ivanovich *et al.* 2025) that proved to be useful for providing critical insight into phylogenetic relationships within *Lecanoraceae*. The success rates of DNA amplification and the high levels of variability of the regions *atp6*, *cob*, *cox3*, and *nad1*, indicate their suitability for the delimitation of genera in difficult systematic groups such as *Lecanoraceae*. The combination of these new markers with those more conserved such as nuclear LSU and mitochondrial SSU provided enough phylogenetic signal to support the monophyletic nature of some of the morphologically and chemically circumscribed groups within *Lecanora s. lat.*

The effectiveness of the new markers in also inferring relationships at subgeneric level is illustrated by the fact that within *Lecanoropsis*, where most taxa are represented by a complete 7-loci dataset, internal nodes are mostly well resolved, while within *Zeora*, where for the majority of the taxa only ITS, mtSSU and/or nuLSU

were available, internal nodes are unsupported or supported in only one of the analyses. Comparison with previously published phylogenetic analyses also points to the effectiveness of these mitochondrial loci for phylogenetic resolution of previously unsolved lineages. For example, in the analysis of Zhao *et al.* (2015), *Lecanoropsis* (the *Lecanora saligna*-group) appears unsupported in their 2-loci analysis. In Kondratyuk *et al.* (2019), the multiple clades formed by the genera *Glaucomaria*, *Miriquidica*, *Ramboldia* and *Straminella* also appear unsupported.

The 7-loci dataset resulted in a phylogenetic reconstruction (Figs 1 & 2) in which the monophyly of several previously distinguished morphological groups within *Lecanora*, including the *Lecanora carpinea/rupicola*- (= *Glaucomaria*), the *L. symmetrica*- (= *Zeora*) and the *L. varia*-groups (= *Straminella*), was confirmed. This result aligns with other phylogenies published previously (Pérez-Ortega *et al.* 2010; Zhao *et al.* 2015; Ivanovich *et al.* 2021, 2025; Zhang *et al.* 2022; Weber *et al.* 2023), indicating that there is sufficient evidence to support the generic segregation of these groups.

Other groups that appear to be monophyletic and received good support are the *Lecanora albella/subcarnea*-, the *L. intumescens*-, and the *L. polytropa*-groups. For the time being, we have chosen not to segregate these groups due to their unclear morphological circumscriptions which make it difficult to assess which *Lecanora* species could belong to them.

Interestingly, specimens belonging to the *Lecanora subfusca*-group formed three separate supported clades. Unexpectedly, *L. argopholis*, a species so far included in the *L. subfusca*-group, appeared outside of all three *L. subfusca* clades in an unresolved position. The *L. subfusca*-group clades are not discussed further in this paper since an in-depth analysis of this group is in progress (L. Li *et al.*, unpublished data).

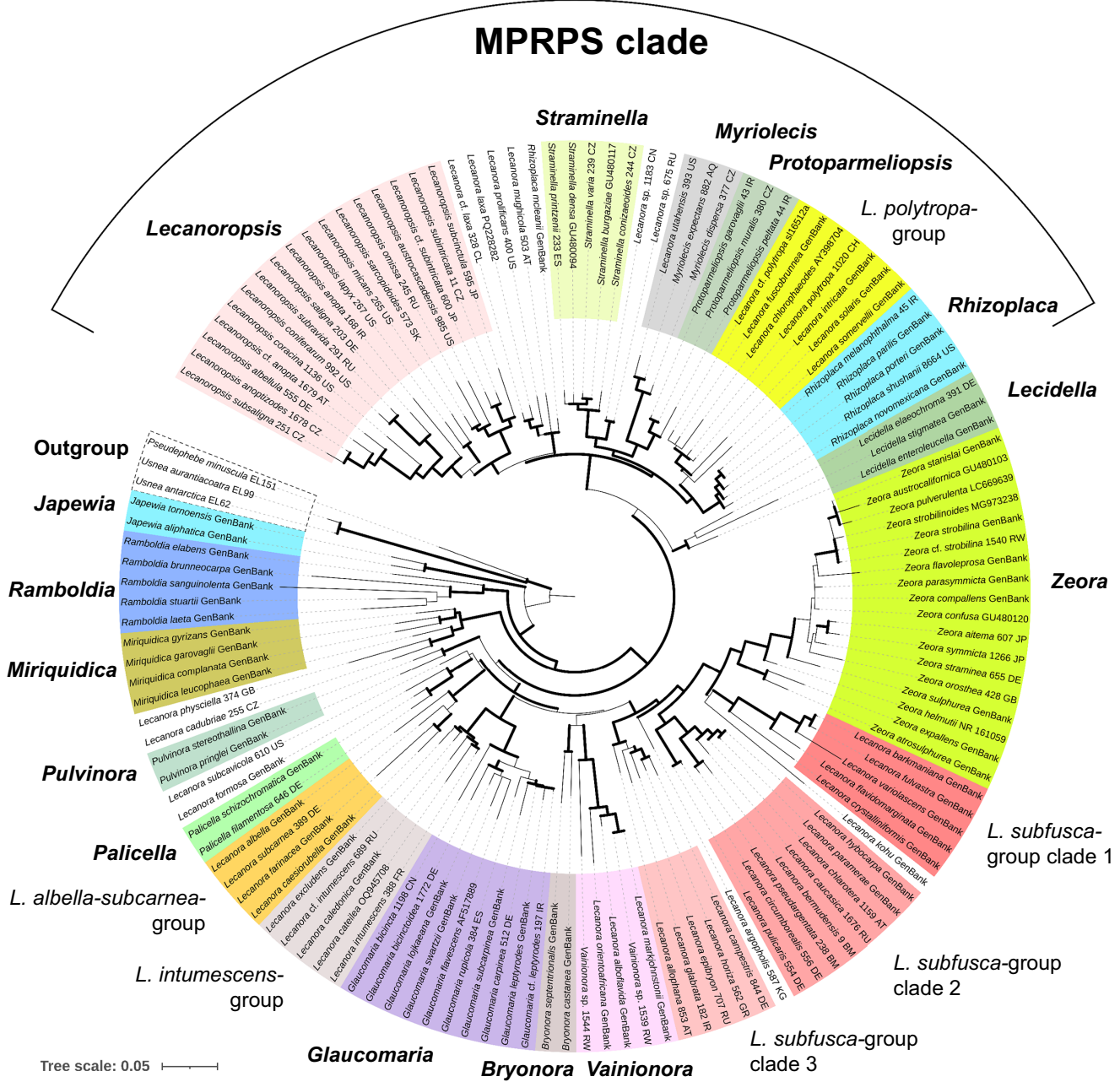


Figure 1. Maximum likelihood overview topology of *Lecanora* s. lat. based on a 7-loci concatenated dataset. Supported nodes (bootstrap support values $\geq 95\%$; Bayesian posterior probability ≥ 0.95) are shown in bold.

Taxonomy

The genus Glaucumaria M. Choisy

Glaucumaria was one of several new genera created by Choisy (1929) to subdivide the large genera *Lecanora* and *Lecidea* Ach., since he understood that many species that probably belonged in *Lecanora* were wrongly placed in the genus *Lecidea*. Choisy (1929) decided to elevate some of the more characteristic groups within *Lecanora* to generic level. Regarding *L. glaucoma* (= *L. rupicola* (L.) Zahlbr.), *L. angulosa* (= *L. carpinea* (L.) Vain.) and *L. albella* (= *L. pallida* Rabenh.), he wrote:

‘... distinct by a commonly colourless or very pale epithecium, characteristic of apothecia covered with a thick white pruina (rarely attenuated, the disc being then more or less dark and the epithecium olive or more rarely

yellow). This group can form a particular genus that I will name *Glaucumaria* nov. gen. Choisy.’²

Eigler (1969) later accepted the generic segregation of *Glaucumaria* by Choisy and recognized within it the *G. carpinea*- and *G. pallida*-groups. Later, Santesson (1993) found that *Lecanora pallida* (Schreb.) Rabenh. was an illegitimate younger homonym of *L. pallida* Chevall., and introduced the name *Lecanora albella* (Pers.) Ach., based on *Lichen albellus* Pers. (= *Lecanora albella* (Pers.) Ach.) as the oldest available name for the species. Brodo *et al.* (2019) accordingly changed the name of the *Lecanora pallida*-group to the *L. albella*-group. Following Brodo *et al.* (2019), the *Lecanora albella*-group is

²Translated from French

MPRPS clade

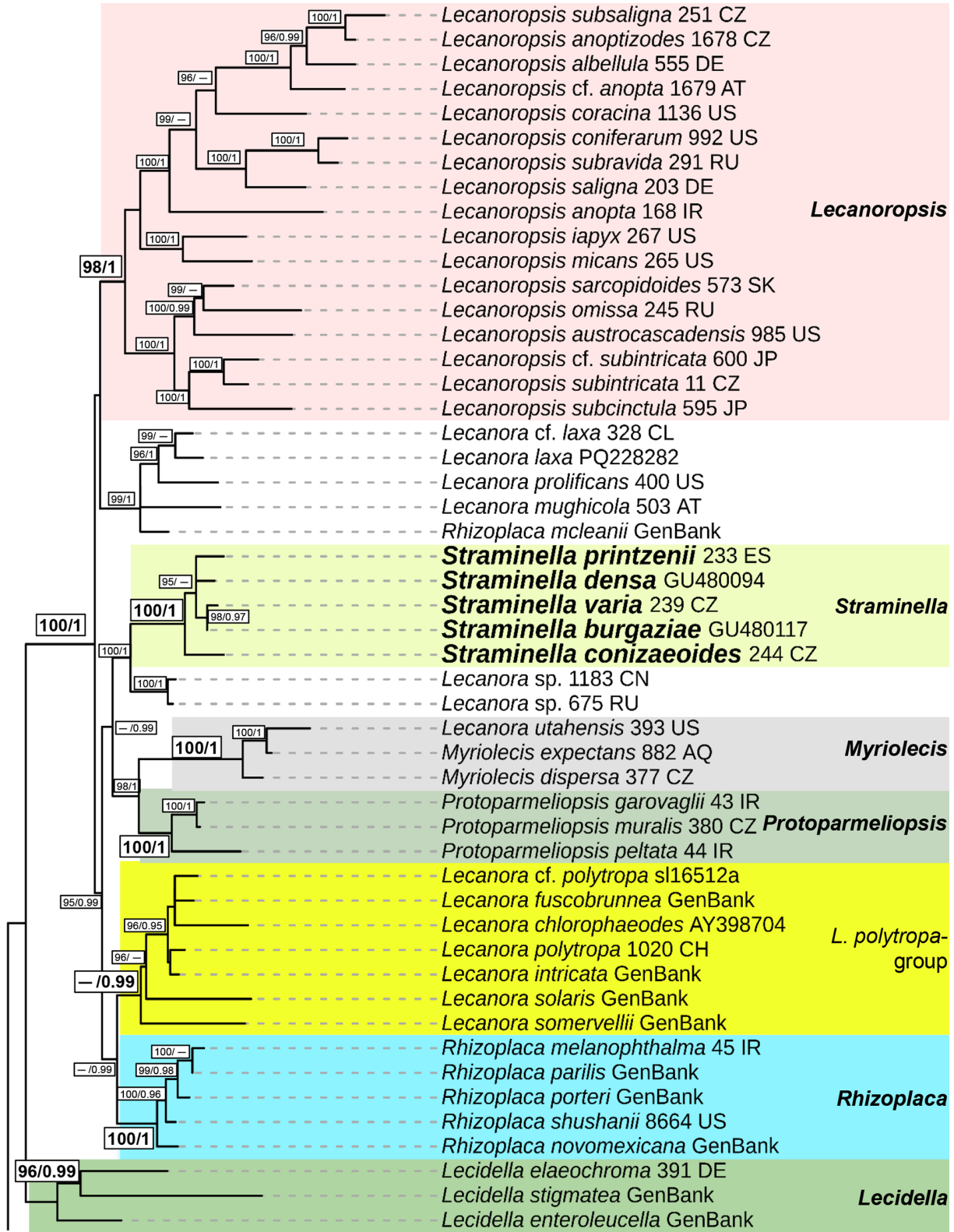
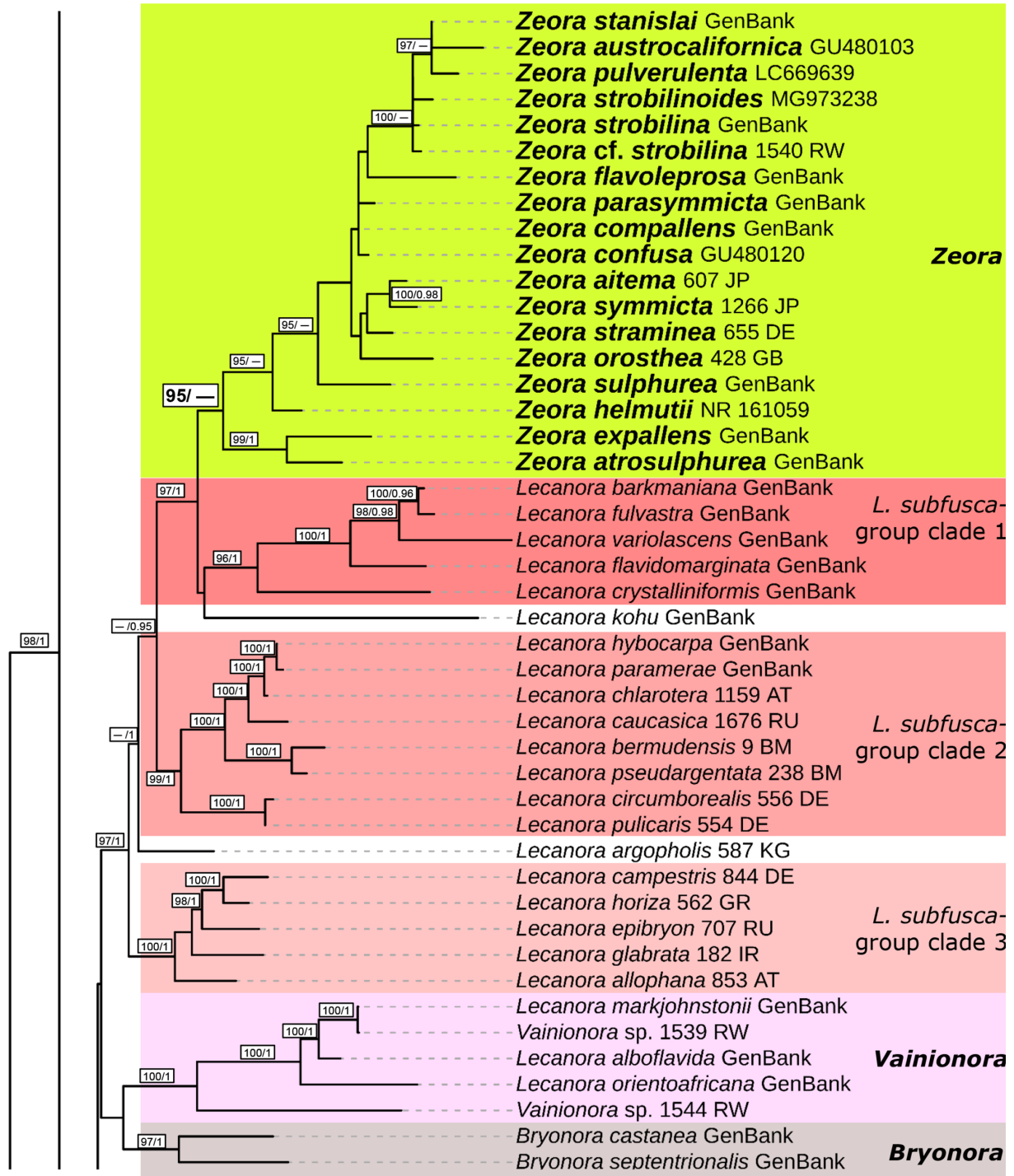


Figure 2. Maximum likelihood detailed topology of *Lecanora* s. lat. based on a 7-loci concatenated dataset. Bootstrap support values (BS) $\geq 95\%$ and Bayesian posterior probability (PP) ≥ 0.95 are depicted on the nodes as follows: BS/PP. Lower bootstrap values on nodes with high posterior probability and vice versa are not shown. Newly resurrected genera are shown in bold: *Glaucomaria* (for the *Lecanora carpinea/rupicola*-group), *Straminella* (for the *L. varia*-group), and *Zeora* (for the *L. symmicta*-group).

Lecanora s. lat. clade



Tree scale: 0.05

Figure 2. (Continued)

Lecanora s. lat. clade (cont.)

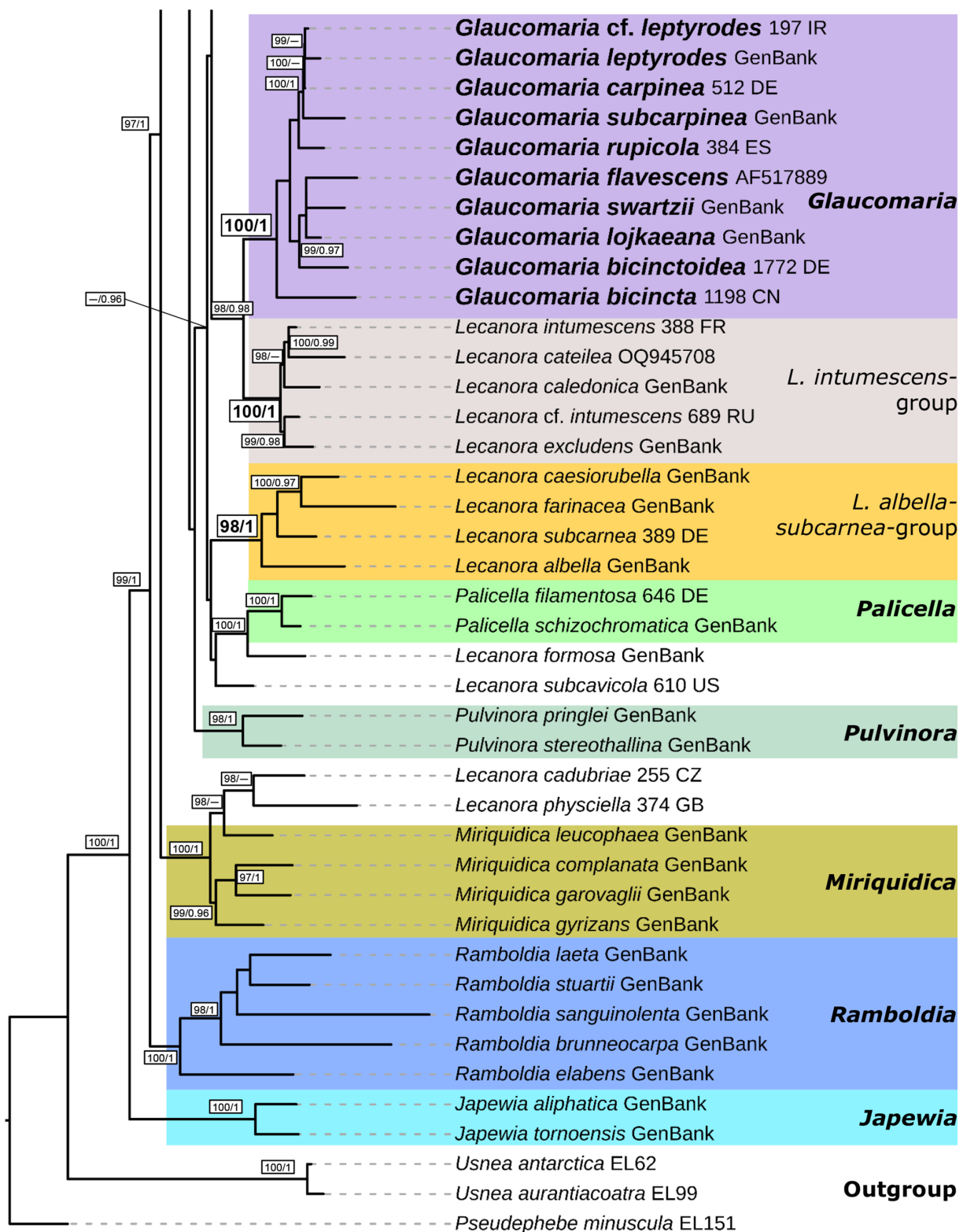


Figure 2. (Continued)

characterized by pruinose apothecial discs, a Pd+ red or yellow reaction, a lack of large oxalate crystals in the amphithecium, and a poorly developed or absent amphithecial cortex. Our phylogenetic results provide no evidence of a close relationship between the *Lecanora albella*- and the *L. carpinea/rupicola*-groups. Thus, for now, we do not include the *L. albella*-group in *Glaucomarina*.

Hafellner (1984) lectotypified *Glaucomarina* on *Lecanora rupicola* (L.) Zahlbr. without providing any comment. Leuckert & Poelt (1989) analyzed the *L. rupicola*-group in depth, focusing mainly on the diversity of secondary metabolites, finding that all taxa accepted by them produced the chromone sordidone (or its derivative eugenitol) in the hymenium and/or thallus. Similarly, Lumbsch *et al.* (1997) found the presence of chromones in several corticolous, pruinose taxa of *Lecanora*. Some of the species studied by Lumbsch *et al.* (1997) had already been suggested as belonging to the *L. carpinea*-group by Eigler (1969). Grube *et al.* (2004) pointed out that all species within this group have apothecia with a conspicuous whitish to yellowish pruina made of sordidone. However, they did not accept the generic status of *Glaucomarina* without clarification of the phylogenetic relationships of the species within *Lecanora* s. lat. Later, phylogenetic analyses unveiled the monophyly of the sordidone-producing taxa of *Lecanora* (Blaha & Grube 2007; Zhao *et al.* 2015; Malíček *et al.* 2017; Kondratyuk *et al.* 2019). Cannon *et al.* (2022) recognized the genus *Glaucomarina* for the *Lecanora rupicola*-group and included the species occurring in the British Isles. Our phylogeny also supports the segregation of the *Lecanora carpinea/rupicola*-group characterized by the production of the chromones sordidone and eugenitol under *Glaucomarina*.

Glaucomarina sulphurea (Hoffm.) S. Y. Kondr. *et al.* is a combination based on one ITS sequence (AY541260; Grube *et al.* 2004) of *Lecanora rupicola* subsp. *sulphurata* (Ach. ex Nyl.) Leuckert & Poelt that was placed in the *Glaucomarina* clade in the analysis of Kondratyuk *et al.* (2019). However, when creating the new combination, Kondratyuk *et al.* (2019) incorrectly indicated *Verrucaria sulphurea* Hoffm. as the basionym. The correct basionym of *Lecanora rupicola* subsp. *sulphurata* (Ach. ex Nyl.) Leuckert & Poelt (the name of the specimen used in their analysis) is *Lecanora glaucoma* var. *sulphurata* Ach., as pointed out by Leuckert & Poelt (1989). *Lecanora sulphurea* (Hoffm.) Ach., the currently accepted name of *Verrucaria sulphurea* Hoffm., is a member of the *Lecanora symmicta*-group (treated here as *Zeora sulphurea* (Hoffm.) Flot., see below). Kondratyuk *et al.* (2019) did include one specimen of *L. sulphurea* in their analysis. This specimen appears in the *Lecanora symmicta*-group, which is concordant with our analysis. The failure to include a 'full and direct reference' to the basionym makes the combination *Glaucomarina sulphurea* (Hoffm.) S. Y. Kondr. *et al.* invalid according to Art. 41.5 (Turland *et al.* 2025).

The correct new combination for *Lecanora rupicola* subsp. *sulphurata* should have been either *Glaucomarina rupicola* subsp. *sulphurata* or *G. sulphurata* if treated at species rank. We refrain from suggesting any of these combinations because current evidence from molecular studies indicates that *Glaucomarina rupicola* subsp. *sulphurata* is conspecific with *Glaucomarina rupicola* subsp. *rupicola* (Grube *et al.* 2004).

Lumbsch *et al.* (1997) studied *Lecanora subpallens* Zahlbr., a later synonym of *Lecanora protervula* Stirton, and reported the presence of sordidone in this species. Brodo *et al.* (2019), who showed the name *Lecanora protervula* to be the oldest name available for *L. subpallens*, provided a detailed description of the species, fitting into the concept of *Glaucomarina*. Unfortunately, no molecular data are available for *L. protervula* to confirm this assumption.

Glaucomarina M. Choisy

Bull. Soc. bot. Fr. **76**, 522 (1929); type: *Lecanora rupicola* (L.) Zahlbr., designated by Hafellner (1984).

(Figs 3 & 4)

Thallus crustose, epibsubstratal, usually whitish to pale grey, yellowish with a tint of green, grey or orange, greenish grey to greyish brown, continuous, smooth to rimose or verrucose-areolate, most species esorediate, sorediate in *G. flavescens*, *G. lojkaeana*, and in the varieties *G. bicincta* var. *sorediata* and *G. rupicola* ssp. *rupicola* var. *efflorens* (Leuckert & Poelt 1989); isidia absent, generally without true cortex or/and hypothallus. *Prothallus* white, whitish grey or beige, bluish brown to blackish or absent.

Apothecia lecanorine, adpressed to sessile, single to crowded; discs flat to convex, yellowish to pinkish and carneous to brown and dark brown, typically covered by conspicuous whitish, yellowish or bluish grey pruina, rarely nearly epruinose. *Glaucomarina flavescens* and *G. lojkaeana* are typically sterile taxa and can be found very rarely with apothecia. Margin concolorous with thallus, mainly prominent and persistent, entire to flexuose. *Margin* lecanorine, variable, commonly interspersed with small granules dissolving in KOH, POL+, sometimes underdeveloped or absent in specimens where apothecia are immersed or weakly erumpent from the substratum. *Glaucomarina carpinea* shows a thick, strongly gelatinized cortex, whereas the *G. rupicola/bicincta* complex is characterized by an amphithecial 'phenocortex' *sensu* Poelt (1989), of dead hyphal and algal cells (Blaha & Grube 2007). *Glaucomarina swartzii*-subgroup develops an 'eucortex' which corresponds to a typical amphithecial cortex in lecanorine margins. *Epithymenium* hyaline or yellowish brown, greyish brown to brown and dark brown, also greenish to dark olivaceous brown; granular. *Hymenium* hyaline. *Subhymenial layers* hyaline to pale yellow. *Parathecium* hyaline (except in *G. bicincta* which has an apically pigmented parathecium that can be seen as an inner black ring around the apothecial disc). *Asci* *Lecanora*-type, clavate, with 8 spores. *Ascospores* ellipsoid, simple.

Conidia as leptoconidia *sensu* van den Boom & Brand (2008), filamentous, curved.

Chemistry. K+ pale yellow to yellow (K– in *G. bicincta*; K± yellow in *G. bicinctoidea*); C+ yellow, orange to orange-red; Pd± pale yellow to yellow (orange-red in the thallus of *G. lojkaeana*). All *Glaucomarina* species produce sordidone and atranorin as major metabolites, with chloroatranorin and/or eugenitol as minors. Most saxicolous species also produce roccellic acid, and some taxa may produce psoromic acid and xanthonones (arthothelin, thiophanic acid, and their derivatives). A rare compound 3a-hydroxy-4-O-demethylbarbatate, was reported from *G. bicinctoidea* (Blaha & Grube 2007).

Substratum. Corticolous (*L. carpinea*-subgroup; Grube *et al.* 2004); saxicolous (*G. rupicola*- and *G. swartzii*-subgroups; Grube *et al.* 2004).

Distribution. Subcosmopolitan; species from this genus are present on almost all continents, except for Antarctica.

List of species

Glaucomarina bicincta (Ramond) S. Y. Kondr., Lőkös & Farkas

In Kondratyuk *et al.*, *Acta Bot. Hung.* **61**(1–2), 153 (2019).—*Lecanora bicincta* Ramond, *Mém. Acad. Sci. Inst. France* **6**, 132 (1823 [1827]).

(Fig. 4A)

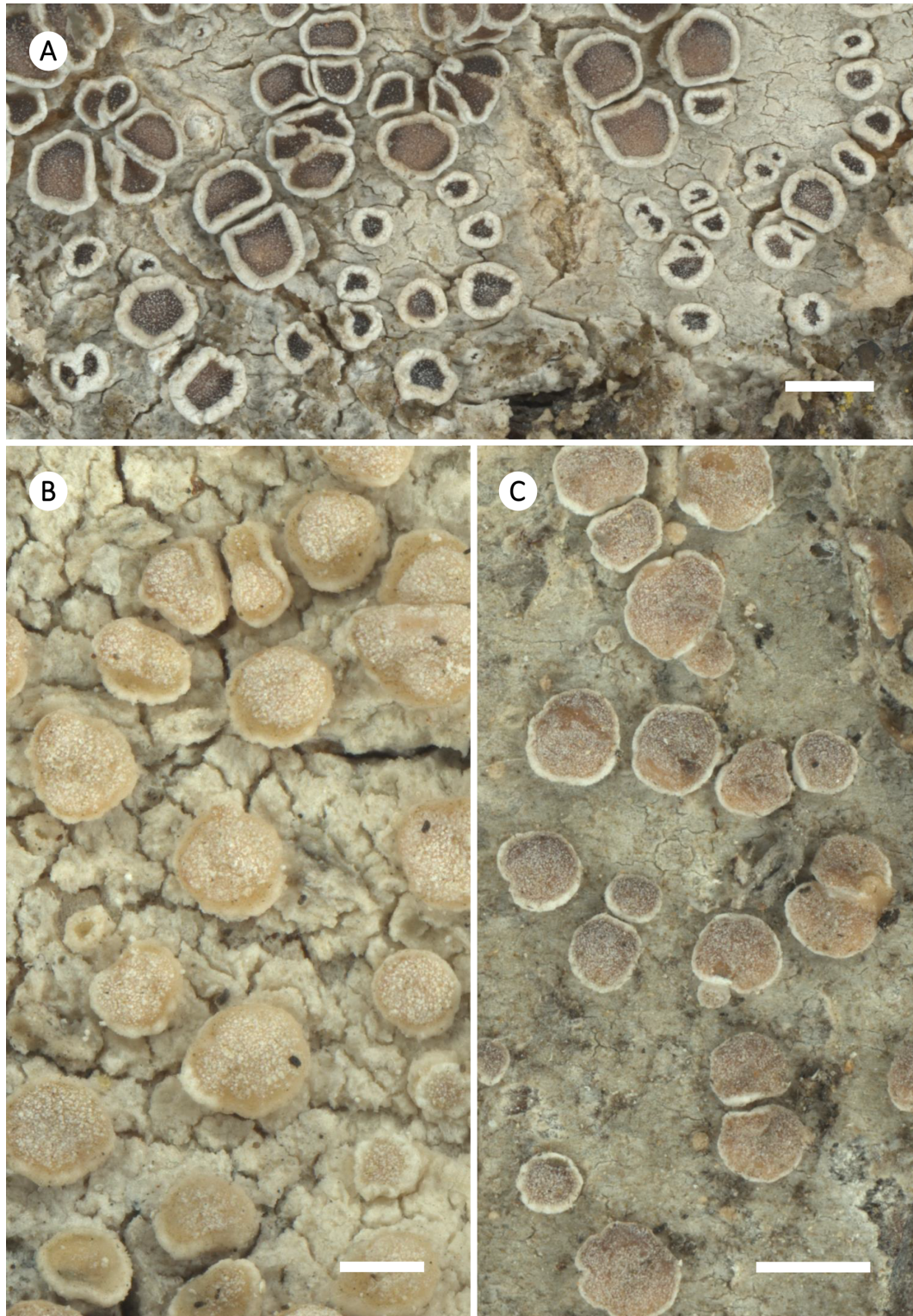


Figure 3. Habitus of selected corticolous species of *Glaucomaria*. A, *G. carpinea*; Germany, Thüringen, R. Cezanne & M. Eichler 11561 (FR-0183027; L512). B, *G. leptyroides*; Sweden, Värmland, U. de Bruyn 4862 (FR-0261657). C, *G. subcarpinea*; Russia, Altaysky Kray, C. Printzen 8574 (FR-0045453). Scales: A & C = 1 mm; B = 0.5 mm.

Glaucomaria bicinctoidea (Blaha & Grube) Ivanovich-Hichins
comb. nov

Mycobank No.: MB 858687

Lecanora bicinctoidea Blaha & Grube, *Mycologia* **99**(1), 53 (2007).

(Fig. 4B)

Glaucomaria carpinea (L.) S. Y. Kondr., Lökös & Farkas

In Kondratyuk *et al*, *Acta Bot. Hung.* 61(1–2), 153 (2019).—*Lichen carpineus* L., *Sp. pl.* **2**, 1141 (1753).—*Lecanora carpinea* (L.) Vainio, *Meddn Soc. Fauna Flora Fenn.* **14**, 23 (1888).

(Fig. 3A)

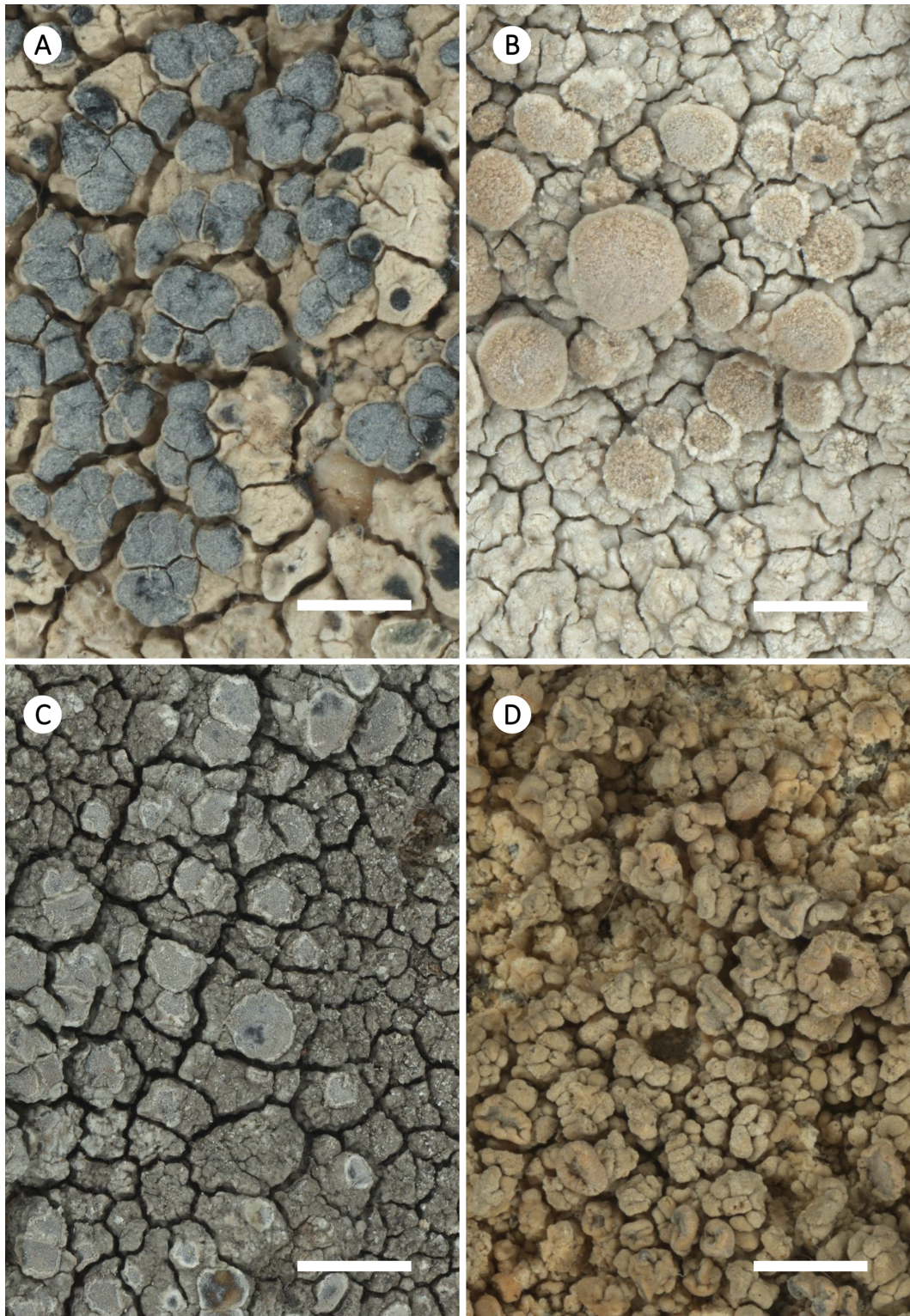


Figure 4. Habitus of selected saxicolous species of *Glaucomaria*. A, *G. bicincta*; China, Changdu, L. S. Wang 18-60827 (FR-0175453). B, *G. bicinctoidea*; Germany, Hessen, R. Cezanne & M. Eichler 12338 (FR-0175438). C, *G. rupicola*; Czech Republic, Prague, Z. Palice 21087 (FR-0264960). D, *G. swartzii*; Slovakia, Prešov, H. Lojka 25 (FR-0080158). Scales: A & B = 1 mm; C & D = 2 mm.

***Glaucomaria flavescens* (Cl. Roux & Tønsberg) Ivanovich-Hichins comb. nov.**

Mycobank No.: MB 858688

Lepraria flavescens Cl. Roux & Tønsberg, in Tønsberg, *Graphis Scripta* **13**(2), 48 (2002).—*Lecanora rouxii* S. Ekman & Tønsberg, in Grube *et al.*, *Mycol. Res.* **108**(5), 512 (2004).

Notes. When transferring *G. flavescens* from *Lepraria* to *Lecanora*, Ekman & Tønsberg (in Grube *et al.* 2004) proposed the new epithet ‘rouxii’ because the name *Lecanora flavescens* (Bagl.) Bagl. already existed. In the genus *Glaucomaria*, the older epithet has priority. The basionym *Lepraria flavescens* Cl. Roux & Tønsberg was previously published by Clauzade & Roux (1977), but it lacked proper reference to the type specimen

(‘Holotypus in herbario Cl. Roux’), making it invalid according to Art. 40 (Turland *et al.* 2025). A later attempt to validate this name in Clauzade & Roux (1980) failed by not correctly citing the exact page of the protologue, but rather a general reference to the publication itself (Arts 38.14 and 41.5). Later, Tønsberg (2002), in his work on *Lepraria* from Norway, provided a direct reference to the original diagnosis and a full citation of the type, thereby validating the name. However, he mistakenly indicated ‘*Lepraria flavescens* Cl. Roux & Tønsberg’ as a replacement name (‘nom. nov.’) and not a new species ‘sp. nov.’. This can, however, be treated as a ‘correctable error’ according to Art. 6.14, and thus the publication of *Lepraria flavescens* Cl. Roux & Tønsberg by Tønsberg (2002) counts as validly published.

***Glaucomarina leptyroides* (Nyl.) Ivanovich-Hichins & Printzen comb. nov.**

Mycobank No.: MB 859412

Lecanora angulosa (Schreb.) Ach. var. *leptyroides* Nyl., *Lich. Env. Paris*: 59 (1896: 59).—*Lecanora leptyroides* (Nyl.) G. B. F. Nilsson, *Ark. Bot.* 24A(no. 3), 82 (1931).

(Fig. 3B)

Notes. This taxon was first mentioned by Nylander (1874) as *L. angulosa* var. *leptyroides*, but a valid description was first published later (Nylander 1896). This variety was then elevated to species rank by Nilsson (1931) as *L. leptyroides* (Nyl.) G. B. F. Nilsson. Nilsson cited the correct basionym without providing a direct citation for it, which could have been either Nylander (1874) or Nylander (1896). Nevertheless, this combination fulfils Art. 41.1 and Art. 41.3 and is therefore valid. Lumbsch *et al.* (1997) published a description and lectotypified the name *L. leptyroides*. Kondratyuk *et al.* (2019), when transferring the species from *Lecanora* to *Glaucomarina*, cited the incorrect basionym, referring to ‘*Lecanora leptyroides* G. B. F. Nilsson’ and not *Lecanora angulosa* (Schreb.) Ach. var. *leptyroides* Nyl. Additionally, they cited the incorrect authorship for the name, citing *Lecanora leptyroides* G. B. F. Nilsson and not *Lecanora leptyroides* (Nyl.) G. B. F. Nilsson, thus rendering *Glaucomarina leptyroides* (G. B. F. Nilsson) S. Y. Kondr. *et al.* an invalid combination.

***Glaucomarina lojkaeana* (Szatala) S. Y. Kondr., Lőkös & Farkas**

In Kondratyuk *et al.*, *Acta Bot. Hung.* 61(1–2), 154 (2019).—*Lecanora lojkaeana* Szatala, *Annl. hist.-nat. Mus. natn. hung.* 46 (n.s. 5), 135 (1954).

***Glaucomarina rupicola* (L.) P. F. Cannon**

In Cannon *et al.*, *Revisions of British and Irish Lichens* 25, 75 (2022).—*Lichen rupicola* L., *Mant. Pl.* 1, 132 (1767).—*Lecanora rupicola* (L.) Zahlbr., *Cat. Lich. Univers.* 5, 525 (1928).

(Fig. 4C)

Notes. The combination *Glaucomarina rupicola* (L.) S.Y. Kondr. *et al.* in Kondratyuk *et al.* (2019) was invalidly published by the authors according to Art. 41.1, because no basionym was cited and no statement of ‘comb. nov.’ was included.

***Glaucomarina subcarpineae* (Szatala) S. Y. Kondr., Lőkös & Farkas**

In Kondratyuk *et al.*, *Acta Bot. Hung.* 61(1–2), 154 (2019).—*Lecanora subcarpineae* Szatala, *Annl. hist.-nat. Mus. natn. hung.* 46(n.s. 5), 136 (1954).

(Fig. 3C)

***Glaucomarina swartzii* (Ach.) S. Y. Kondr., Lőkös & Farkas**

In Kondratyuk *et al.*, *Acta Bot. Hung.* 61(1–2), 154 (2019).—*Lichen swartzii* Ach., *K. Vetensk-Acad. Nya Handl.* 15(3), 185 (1794).—*Lecanora swartzii* (Ach.) Ach., *Lich. Univ.*, 363 (1810).

(Fig. 4D)

The genus *Straminella* M. Choisy

Straminella was introduced by Choisy (1929), with *Lecanora varia* (Hoffm.) Ach. (as *Lecanora varia* ‘Ach.’) as the type species. The genus was characterised as having a yellow thallus, claviform asci, conglutinate and partially branching paraphyses, as well as filiform, curved conidia (Choisy 1929). Eigler (1969) and Hafellner (1984) list *Straminella* as a genus in *Lecanoraceae*, while Motyka (1995–1996) assigned some species of the group to different sections (*L. varia* to sect. *Chlaronae* or *L. conizaeoides* Nyl. ex Croub. to sect. *Conizaeae*) but chose to maintain *Lecanora* as the generic name.

Kondratyuk *et al.* (2019) accepted the name *Straminella* for what was elsewhere known as the *Lecanora varia*-group (e.g. Smith 1918, 1921; McCune 2017) and based this decision on molecular data without providing any further descriptions. They incorporated six species into *Straminella*, including *Straminella bullata* (Follmann & A. Crespo) S.Y. Kondr. *et al.* and *S. maheui* (Hue) S.Y. Kondr. *et al.* as separate species. However, Gómez-Bolea & Barbero Castro (2009) showed that *Rhizoplaca bullata* (Follmann & A. Crespo) Leuckert & Poelt is conspecific with *Polycauliona maheui* Hue, which they recombined into *Rhizoplaca maheui* (Hue) Gómez-Bolea & M. Barbero. In the phylogeny provided by Kondratyuk *et al.* (2019), *S. bullata* is not included, and *S. maheui* is in a sister relationship with all other *Straminella* species. Due to its fruticose growth form and apothecial characters that set it clearly apart from the other species in *Straminella*, we suggest retaining the name *Rhizoplaca maheui* (Hue) Gómez-Bolea & M. Barbero and excluding it from *Straminella* until further studies have been conducted. We provide here a description of the genus and a provisional list of taxa belonging to it.

***Straminella* M. Choisy**

Bull. Soc. Bot. Fr. 76, 522 (1929); type: *Lecanora varia* (Hoffm.) Ach. (1810), designated by Choisy (1929).

(Fig. 5)

Thallus mainly epibsubstratal, greenish yellow, greenish, greyish yellow to beige, typically esorediate (except *S. conizaeoides* which can produce soredia). **Prothallus** not apparent.

Apothecia lecanorine, single to crowded and very numerous, slightly immersed to adpressed to sessile, rounded to flexuose, moderately concave to flat to weakly convex; disc pale yellow to brownish or yellowish green to greenish or greyish brown (becoming blackish in both *S. printzenii* and *S. varia*), apothecial discs epruinose to pruinose. Margin typically prominent and

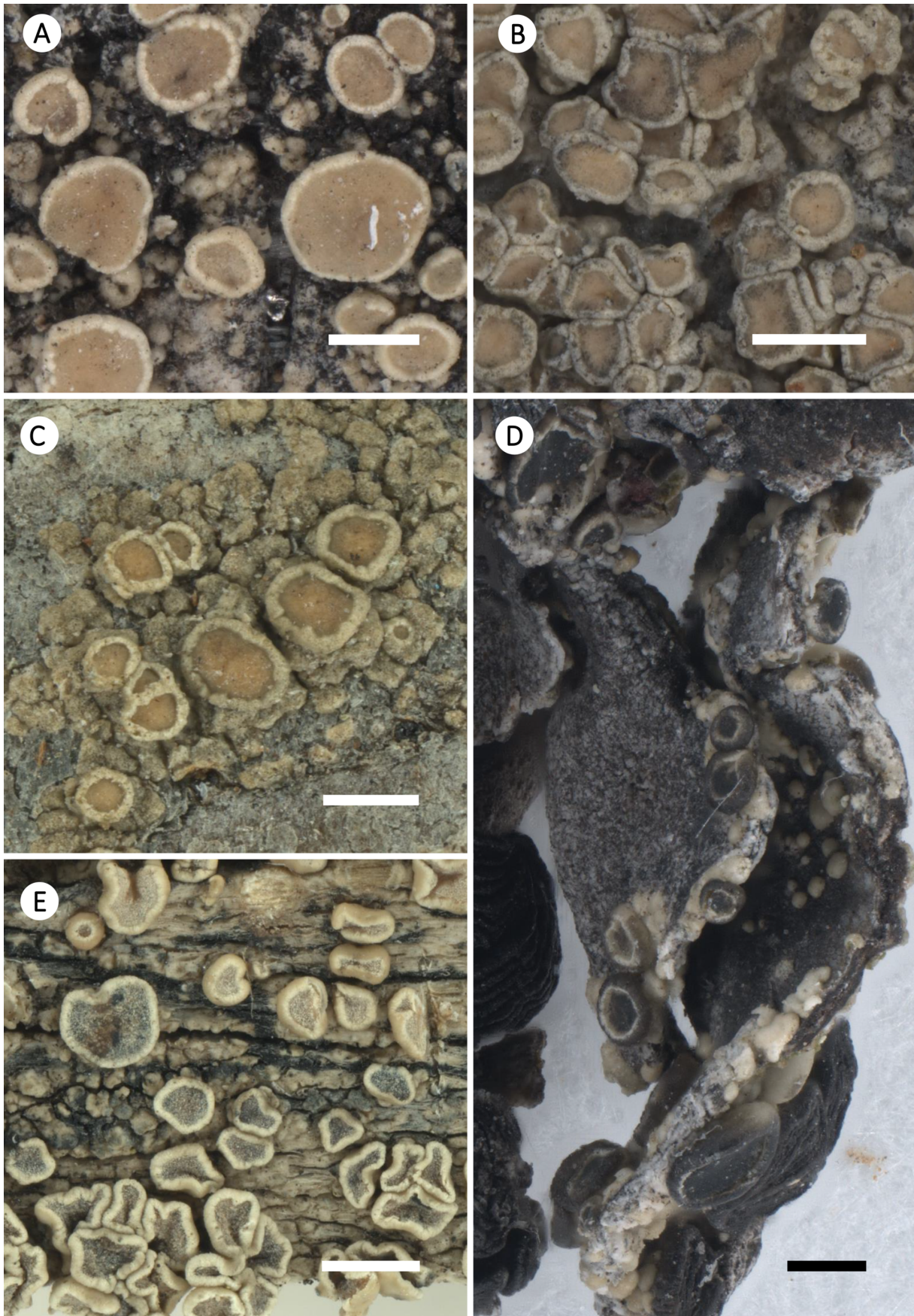


Figure 5. Habitus of selected species of *Straminella*. A, *S. burgaziae*; Spain, Zamora, S. Pérez-Ortega & A. Álvarez (FR-0212659). B, *S. conizaeoides*; Germany, Hessen, J. H. Reimer (FR-0055139). C, *S. densa*; USA, Arizona, S. Pérez-Ortega (FR-0212649). D, *S. printzenii*; Spain, Castilla y León, S. Pérez-Ortega & M. Arróniz-Crespo (FR-0183026; L233; isotype; growing on *Umbilicaria* sp.). E, *S. varia*; Austria, Tirol, S. Pérez-Ortega & C. Printzen (FR-0212999). Scales: A–D = 0.5 mm; E = 1 mm.

persistent in old apothecia. *Margin* lecanorine, basally distinctly thickened, hyaline to brown (blackened in *S. printzenii*), with POL+, KOH-soluble granules. *Epihymenium* brown or greenish brown to greenish black, with POL+, KOH-soluble granules. *Hymenium* hyaline to pale yellow. *Paraphyses* simple to weakly branched, 1–2 µm wide, anastomosing below, not or slightly widened at the apex. *Subhymenial layers* distinct, sometimes very short in height in relation to the hymenium, subhymenium hyaline or pale yellow. *Asci* *Lecanora*-type (*sensu* Honegger 1978), 8-spored, cylindrical-clavate. *Ascospores* hyaline, non-septate, ellipsoid to broadly ellipsoid, length to width ratio 1.73–2.3.

Conidia filiform, curved.

Chemistry. C–, K± yellow, Pd+ yellow (orange to red in *S. conizaeoides*). Usnic acid is the main substance; additionally, psoromic acid and 2'-*O*-demethylpsoromic acid can be found in the majority of the *Straminella* taxa, with the exception of *S. conizaeoides* which produces fumarprotocetraric acid instead.

Substratum. Frequently on bark or wood. *Straminella conizaeoides* can be found on a wide range of low pH substrata. *Straminella printzenii* is lichenicolous, reported to inhabit *Umbilicaria* Hoffm. and *Psorinia* Gotth. Schneid. (Flakus & Śliwa 2012).

Distribution. Currently known from North America, North Africa, Europe, East Asia and Australia.

Notes. Eigler (1969) kept all species with a yellow-green thallus under *Straminella* M. Choisy em. Eigler, including taxa belonging to *Zeora* (the *Lecanora symmicta*-group, see below under the *Zeora* section) and *Lecanoropsis*. Following the circumscription by Eigler (1969), the general characters of the group would be the presence of usnic acid and the absence of large calcium oxalate crystals in the amphithecium (Brodo & Elix 1993). Our own results and the molecular studies of *Lecanoraceae* by other authors (Pérez-Ortega *et al.* 2010; Zhao *et al.* 2015; Kondratyuk *et al.* 2019; Lee & Hur 2021; Weber *et al.* 2023; Ivanovich *et al.* 2025) clearly show that species with these traits are found in separate clades. *Straminella* (as the '*Lecanora varia*-group') has received attention from several authors (Śliwa & Wetmore 2000; Printzen 2001; Laundon 2003; Martínez & Aragón 2004; Pérez-Ortega *et al.* 2010; de la Rosa *et al.* 2010; Flakus & Śliwa 2012), and descriptions of particular species of the genus, as well as their heterotypic synonyms, can be found in the cited references.

List of species

Straminella burgaziae (I. Martínez & Aragón) S. Y. Kondr., Lőkös & Farkas

In Kondratyuk *et al.*, *Acta Bot. Hung.* **61**(1–2), 158 (2019).—*Lecanora burgaziae* I. Martínez & Aragón, *Bryologist* **107**(2), 223 (2004).

(Fig. 5A)

Straminella conizaeoides (Nyl. ex Cromb.) S. Y. Kondr., Lőkös & Farkas

In Kondratyuk *et al.*, *Acta Bot. Hung.* **61**(1–2), 158 (2019).—*Lecanora conizaeoides* Nyl. ex Cromb., *J. Bot., Lond.* **23**, 195 (1885).

(Fig. 5B)

Straminella densa (Śliwa & Wetmore) S. Y. Kondr., Lőkös & Farkas

In Kondratyuk *et al.*, *Acta Bot. Hung.* **61**(1–2), 158 (2019).—*Lecanora varia* subsp. *densa* Śliwa & Wetmore, *Bryologist* **103**(3), 486 (2000).—*Lecanora densa* (Śliwa & Wetmore) Printzen, *Bryologist* **104**(3), 394 (2001).

(Fig. 5C)

Straminella printzenii (Pérez-Ort., M. Vivas & Hafellner) Pérez-Ort. & Ivanovich-Hichins comb. nov.

Mycobank No.: MB 858686

Lecanora printzenii Pérez-Ort. *et al.*, in Lumbsch *et al.*, *Phytotaxa* **18**, 76 (2011).

(Fig. 5D)

Straminella varia (Hoffm.) S. Y. Kondr., Lőkös & Farkas

In Kondratyuk *et al.*, *Acta Bot. Hung.* **61**(1–2), 158 (2019).—*Patellaria varia* Hoffm., *Descr. Adumb. Plant. Lich.* **1**(4), 102 (1790).—*Lecanora varia* (Hoffm.) Ach., *Lich. Univ.*, 377 (1810).

(Fig. 5E)

Notes. There are some species, such as *Lecanora subviridis* de la Rosa & Messuti and *L. vinetorum* Poelt & Huneck, that have been suggested to belong to the *Lecanora varia*-group, but we hesitate to assign them to *Straminella* due to a lack of molecular data.

Lecanora laxa (Śliwa & Wetmore) Printzen was assigned to the *Lecanora varia*-group by Śliwa & Wetmore (2000), Laundon (2003) and Pérez-Ortega *et al.* (2010). In contrast, Printzen (2001) stated that *L. laxa* is morphologically and chemically more similar to *Lecanoropsis coniferarum* (Printzen) Ivanovich & Printzen and *L. saligna* (Schrad.) Ivanovich & Printzen than to *Straminella densa* and *S. varia*. Our phylogenetic analysis places *Lecanora laxa* in neither the *Lecanoropsis* nor the *Straminella* clade, but rather in a third, well-supported clade together with *Lecanora mughicola* Nyl. and *L. prolificans* Ivanovich *et al.* Due to its placement outside of both clades, we refrain from recombining *Lecanora laxa* into either *Lecanoropsis* or *Straminella*.

The genus *Zeora* Fr.

Zeora was first introduced by E. Fries (1825), who characterized it as having waxy apothecia with a disappearing, pulverulent thalline margin. Furthermore, the author noted that many species are sterile with a leprose thallus, and listed several species. Flotow (1850) used the name *Zeora* very broadly for crustose lichens with a lecanorine margin and made the combination *Zeora orosthea* (Ach.) Flot. Also focusing on the excipulum, Körber (1855) and Leunis (1886) considered *Zeora* to be similar to *Lecanora*, but with species usually having a margin composed of a dark proper excipulum within the thalline margin. The term for this, a zeorine margin, is mainly used when the proper exciple can be recognized as a parathecial crown, as is the case, for example, in many species of *Acarospora* or in *Glaucomaria bicincta*, but not in any of the taxa understood here as *Zeora*. Choisy (1929) used the name *Zeora* Fr. for *Lecanora* species with a more or less dark greenish epihymenium and a well-developed proper margin, and included *Lecanora cenisia* Ach. and *L. sulphurea* (Hoffm.) Ach. (as *L. sulphurea* Ach. in Choisy (1929)) within it. Hafellner (1984) designated *Lecanora orosthea* (Ach.) Ach. as the type species of *Zeora*.

For the combination *Glaucomaria sulphurea* (Hoffm.) S. Y. Kondr. *et al.* (Kondratyuk *et al.* 2019), see above.

In the circumscription suggested by our phylogeny, *Zeora* comprises species with a typically yellowish-greenish, sometimes sorediate thallus, a disc margin often becoming excluded, and the amphithecial margin appearing ecorticated and lacking large crystals. Most species are corticolous or lignicolous, although saxicolous species do occur in the group (e.g. *Z. atosulphurea* and *Z. orosthea*). They typically produce usnic acid and zeorin, but no atranorin (except for *Z. sulphurea*). *Zeora* differs from *Straminella* by the thallus appearance (granular, farinose and/or sorediate in *Zeora* vs esorediate and warted in *Straminella*), the disc margins (usually becoming excluded in *Zeora*, persistent in *Straminella*) and the amphithecial margin being corticated in *Straminella*. Additionally, species of *Zeora* produce zeorin but no psoromic acid, whereas those of *Straminella* typically produce psoromic acid (except *S. conizaeoides*) but not zeorin.

In our phylogenetic analysis, *Zeora* clustered closely with clade 1 of the *Lecanora subfusca*-group, represented here by *Lecanora barkmaniana* Aptroot & Herk (as '*barkmaneana*'), *L. crystalliniformis* (B. G. Lee & Hur) Li J. Li & Printzen, *L. flavidomarginata* B. de Lesd., *L. fulvastra* Kremp. and *L. variolascens* Nyl. Species in this clade share more morphological and chemical similarities with *Lecanora subfusca* s. str. and the taxa included in *Lecanora subfusca* clades 2 and 3 than with *Zeora*, such as a persistent apothecial margin, large KOH-insoluble crystals in the amphithecium, and the production of atranorin. Phylogenetically, however, the *Lecanora subfusca* clade 1 appears to be more closely related to *Zeora* than to the other *L. subfusca* clades present in our analysis.

Taxa assigned here to *Zeora* were previously assigned to the informal *Lecanora symmicta*-group (e.g. Smith 1921; Printzen & May 2002) or *sulphurea*-group (Smith 1921) but also the *Lecanora varia*-group (Śliwa & Wetmore 2000). Based on margin anatomy, Printzen (2001) assigned some species to his group 1 (*Lecanora confusa* and *L. strobilina*) and others to group 2 (*L. symmicta*). The heterogenous classification of species from the *L. symmicta*-group carried out by different authors shows the difficulty in discriminating species of *Zeora* from taxa belonging to other groups within *Lecanora* s. lat. that also produce usnic acid.

Zeora Fr.

Syst. orb. veg. **1**, 244 (1825); type: *Lecanora orosthea* (Ach.) Ach. (1810), designated by Hafellner (1984).

(Figs 6 & 7)

Thallus thin and partially endophloedal to thick, episubstratal, with a granular, farinose to entirely sorediate surface and with a pale yellow, yellow-green to mint green, bluish/greyish yellow or yellowish brown thallus surface, rarely whitish, sometimes with a black hypothallus. *Photobiont* chlorococcoid algae.

Apothecia rarely lacking, flat to convex, some with white pruina on yellow to brown discs, sometimes darkening with age. *Zeora compallens* and *Z. stanislai* have so far only been found sterile. *Margin* biatorine or lecanorine, typically excluded, with granules typically dissolving in KOH (except *Z. strobilina*, with granules insoluble in KOH but soluble in HNO₃), without large oxalate crystals. *Epihymenium* with a large variety of pigmentation or hyaline, with crystals dissolving in KOH. *Hymenium* hyaline to pale yellow to yellowish brown. *Subhymenial layers* hyaline (except *Z. expallens* and *Z. strobilina* that can have subhymenial layers pigmented pale yellow). *Paraphyses* simple to sparsely branching and anastomosing, without

swollen apices or weakly capitate. *Asci* *Lecanora*-type (*sensu* Honegger 1978), 8 spores per ascus (except *Z. strobilinoidea* with (12–)16(–32) spores). *Ascospores* hyaline, simple, narrowly ellipsoid to broadly ellipsoid, occasionally 1-septate.

Conidia as leptoconidia *sensu* van den Boom & Brand (2008), filamentous, frequently curved, simple 12–25 × 0.5–1 μm.

Chemistry. C± yellow to orange; K± faint yellow to yellow-brown; KC± faint yellow to yellow-brown; Pd± orange-red. Usnic acid and zeorin are the usual major substances; atranorin, arthothelin, α-collatolic acid, decarboxysquamatic acid, fumarprotocetraric acid, gangaleoidin, norstictic acid, placodiolic acid, skyrin or thiophanic acid are present in some species, sometimes only in trace amounts. Additionally, a range of unknown substances has been reported for several species, such as 'expallens-unknown' or 'flavoleprosa-unknown', compounds detected in *Z. expallens* (Tønsberg 1992) and *Z. flavoleprosa* (Tønsberg 1992; Czarnota *et al.* 2009) respectively. Printzen (2001) also reported an unidentified xanthone for *Z. confusa*.

Substratum. Most species grow on bark or wood, some are saxicolous on siliceous rocks.

Distribution. Subcosmopolitan; species of this genus are present on almost all continents, except for Antarctica.

List of species

Zeora aitema (Ach.) L. M. Weber & Ivanovich-Hichins comb. nov.

Mycobank No.: MB 858689

Lecidea aitema Ach., *K. Vetensk-Acad. Nya Handl.* **29**, 261 (1808).—*Lecanora aitema* (Ach.) Hepp, *Flecht. Europ.*, no. 69 (1853).

(Fig. 6A)

Zeora atosulphurea (Wahlenb.) L. M. Weber & Ivanovich-Hichins comb. nov.

Mycobank No.: MB 858690

Lichen atosulphureus Wahlenb., *Fl. Lapp.*, 411 (1812).—*Lecanora atosulphurea* (Wahlenb.) Ach., *Syn. Meth. Lich.* (Lund), 149 (1814); as '*atro-sulphurea*'.

(Fig. 6B)

Zeora austrocalifornica (Lendemer & K. Knudsen) L. M. Weber & Ivanovich-Hichins comb. nov.

Mycobank No.: MB 858691

Lecanora austrocalifornica Lendemer & K. Knudsen, *Opuscula Philolichenum* **6**, 73 (2009).

Zeora compallens (Herk & Aptroot) L. M. Weber & Ivanovich-Hichins comb. nov.

Mycobank No.: MB 858692

Lecanora compallens Herk & Aptroot, *Lichenologist* **31**(6), 544 (1999).

(Fig. 6C)

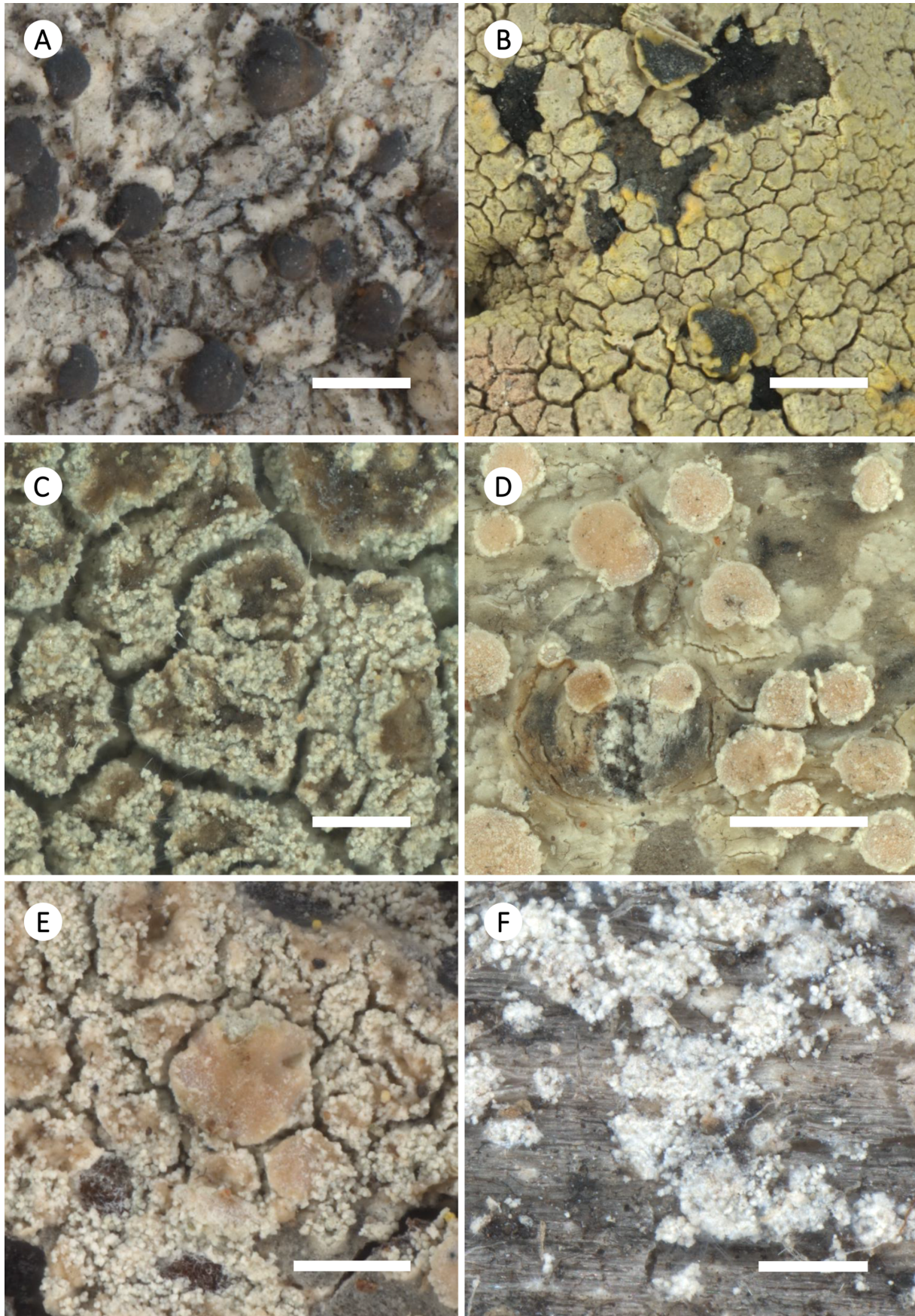


Figure 6. Habitus of selected species of *Zeora*. A, *Z. aitema*; Norway, Hordaland, C. Printzen, T. Tønsberg & S. Ekman s. n. (FR-0211866). B, *Z. atrosulphurea*; Portugal, Madeira, H. J. Reimer (FR-0057516). C, *Z. compallens*; Germany, Niedersachsen, U. de Bruyn 1693 (FR-026141). D, *Z. confusa*; Great Britain, Scotland, B. Coppins s. n. (FR-0068184). E, *Z. expallens*; USA, Alaska, C. Printzen 5078 (FR-0259478). F, *Z. flavoleprosa*; Russia, Altayski krai, E. Davydov 6792 (FR-0089689). Scales: A, B & D = 1 mm; C, E & F = 0.5 mm.

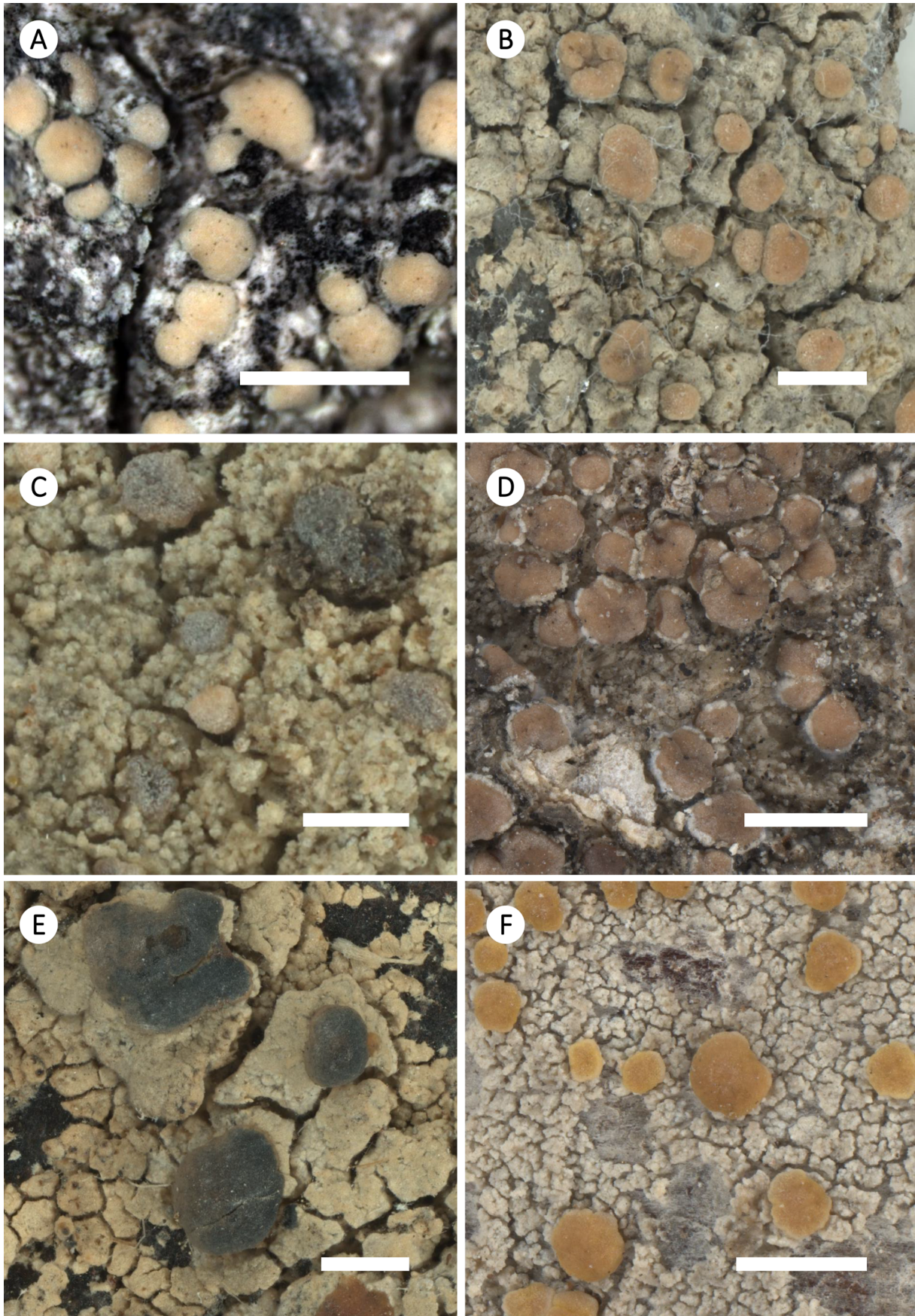


Figure 7. Habitus of selected species of *Zeora* (cont.). A, *Z. helmutii*; Australia, Tasmania, *Kantvilas* 460/11 (HO-563771; type). B, *Z. orosthea*; Great Britain, Scotland, *B. Coppins* 25566 (FR-0175440; L428). C, *Z. straminea*; Germany, Nordrhein-Westfalen, *J. Lahm* 1829 (FR-0050171). D, *Z. strobilina*; Ecuador, Galápagos Isl., *W. Weber* Exs. 138 (FR-0059930). E, *Z. sulphurea*; Greece, South Aegean, *K. Fritsch* 12242 (FR-0080152). F, *Z. symmicta*; Russia, Altayski krai, *C. Printzen* 8334 (FR-0068138). Scales: A & B, D–F = 1 mm; C = 0.5 mm.

***Zeora confusa* (Almb.) L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 858693

Lecanora confusa Almb., *Kungl. Svenska Vetenskapsakad. Avhandl. Natursk.* **11**, 72 (1955).

(Fig. 6D)

***Zeora expallens* (Ach.) L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 858694

Lecanora expallens Ach., *Lich. Univ.*, 374 (1810).

(Fig. 6E)

***Zeora flavoleprosa* (Tønsberg) L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 858695

Lecanora flavoleprosa Tønsberg, *Sommerfeltia* **14**, 161 (1992).

(Fig. 6F)

***Zeora helmutii* (Pérez-Ort. & Kantvilas) Pérez-Ort., L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 858696

Lecanora helmutii Pérez-Ort. & Kantvilas, *Herzogia* **31**(1), 643 (2018).

(Fig. 7A)

Zeora orosthea* (Ach.) Flot.Lichen orostheus* Ach., *Lich. suec. prodr.* (Linköping), 38 (1799 [1798]).—*Lecanora orosthea* (Ach.) Ach., *Lich. Univ.*, 400 (1810).

(Fig. 7B)

***Zeora parasymmicta* (B. G. Lee & Hur) L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 858697

Lecanora parasymmicta B. G. Lee & Hur, *MycKeys* **84**, 172 (2021).***Zeora pulverulenta* (Müll. Arg.) L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 859417

Lecanora pulverulenta Müll. Arg., *Nuovo G. Bot. Ital.* **23**(1), 124 (1891).***Zeora stanislai* (Guzow-Krzem., Łubek, Malíček & Kukwa) L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 858700

Lecanora stanislai Guzow-Krzem. *et al.*, in Guzow-Krzemińska *et al.*, *Phytotaxa* **329**(3), 205 (2017).***Zeora straminea* (Stenh.) L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 858701

Biatora straminea Stenh. *K. svenska Vetensk-Akad. Handl., ser. 3* **34**, 196 (1846).—*Lecanora sublivescens* (Nyl.) Arnold, *Flora* **67**, 336 (1884).

(Fig. 7C)

Notes. As stated in Weber *et al.* (2023), *Biatora straminea* is effectively the oldest valid name for *Lecanora sublivescens* (Nyl.) Arnold but, at species level and within *Lecanora*, the epithet ‘*straminea*’ was blocked by the older *Lecanora straminea* Ach. Within *Zeora*, however, this combination is available.

***Zeora strobilina* (Spreng.) L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 858698

Parmelia strobilina Spreng., *Syst. veg., Ed. 16* **4**(1), 300 (1827).—*Lecanora strobilina* (Spreng.) Kieff., *Bull. Soc. Hist. Nat. Metz* **19**, 74 (1895).

(Fig. 7D)

***Zeora strobilinoidea* (Giralt & Gómez-Bolea) L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 858699

Lecanora strobilinoidea Giralt & Gómez-Bolea, *Lichenologist* **23**(2), 107 (1991).***Zeora sulphurea* (Hoffm.) Flot.***Verrucaria sulphurea* Hoffm., *Descr. Adumb. Plant. Lich.* **1**(2), 56 (1790).—*Lecanora sulphurea* (Hoffm.) Ach., *Lich. Univ.*, 339 (1810).

(Fig. 7E)

***Zeora symmicta* (Ach.) L. M. Weber & Ivanovich-Hichins comb. nov.**

MycoBank No.: MB 858702

Lecanora varia var. *symmicta* Ach., *Lich. Univ.*, 379 (1810; as *L. varia* θ *L. symmicta*).—*Lecanora symmicta* (Ach.) Ach., *Syn. Meth. Lich.* (Lund), 340 (1814).

(Fig. 7F)

Notes. Discussions by Kantvilas & LaGreca (2008), LaGreca & Lumbsch (2013) and Weber *et al.* (2023) indicate that *Zeora symmicta* might constitute an aggregate of various species or a ‘species complex’. It may therefore be helpful in a future taxonomic revision of *Zeora* to circumscribe this species based on molecular genetic analyses and to epitypify *Zeora symmicta* s. str. to a specimen with DNA sequences.

There are some additional species that most likely belong to *Zeora* but we hesitate to assign them to this genus due to a lack of molecular data: *Lecanora americana* (B. de Lesd.) Printzen (nom.

illeg., non *Lecanora americana* (B. de Lesd.) Zahlbr.; if this taxon were eventually moved into *Zeora*, the epithet *americana* would be available), *Lecanora brucei* Printzen, *L. confusoides* Bungartz & Printzen, *Lecanora conizella* Nyl., *L. cupressi* Tuck. ex Nyl., *L. fluoroxylina* Aptroot & M. F. Souza, *L. orae-frigidae* R. Sant., *L. perconfusa* Printzen, *L. sabinae* Hern.-Padr. & Vänskä, *L. simeonensis* K. Knudsen & Lendemer, *L. subaureoides* Aptroot & Bungartz, *L. substrobilina* Printzen, *L. subtectata* (Stirt.) Kantvilas & LaGreca, and *L. terpenoidea* Bungartz & Elix.

For more detailed descriptions of all species in the List of Species, see Giralt & Gómez-Bolea (1991), Tønsberg (1992), van Herk & Aptroot (1999), Printzen (2001), Kantvilas & LaGreca (2008), LaGreca & Lumbsch (2013), Guzow-Krzemińska *et al.* (2017), Pérez-Ortega & Kantvilas (2018), Lee & Hur (2021) and Weber *et al.* (2023).

The genus *Lecanoropsis* M. Choisy ex Ivanovich and associated taxa

In our phylogenetic analysis, the monophyly of *Lecanoropsis* confirms the results published by Ivanovich *et al.* (2025). *Lecanoropsis* can then be circumscribed as corticolous and lignicolous crustose lichens with an endosubstratal to poorly developed episubstratal (except *L. coracina* Ivanovich *et al.*), esorediate thallus, lecanorine apothecia (except for *L. anopta* (Nyl.) Ivanovich & Printzen, which forms more or less biatorine mature apothecia), a corticate thalline margin without large KOH-insoluble crystals, several types of conidia (the most conspicuous are called macroconidia), and containing dibenzofuran-derivatives such as isousnic and usnic acid, but without atranorin or psoromic acid.

Taxa with morphological and chemical similarities such as *Lecanora mughicola* and *L. prolificans* (clade between *Lecanoropsis* and *Straminella*, see Figs 1 & 2), previously thought to belong in the *Lecanora saligna*-group, cluster in another well-supported monophyletic clade together with *Lecanora laxa* and *Rhizoplaca mcleanii*. They produce isousnic and usnic acid but lack macroconidia.

Rhizoplaca mcleanii is a saxicolous Antarctic species that develops a dark brown-grey or black squamulose, peltate to foliose umbilicate thallus, with numerous lecanorine apothecia that are typically marginal, immersed at first and becoming sessile later, producing broad ellipsoid spores with thick walls (Castello 2010). *Rhizoplaca mcleanii* was first transferred from *Lecanora* into *Rhizoplaca* by Castello (2010), and later to *Lecanoropsis* by Kondratyuk *et al.* (2019) on the basis of a single locus (ITS) in their ML analysis. The thallus morphology in *R. mcleanii* matches the circumscription of *Rhizoplaca* (Arup & Grube 2000), which makes its placement in *Lecanoropsis* dubious. Additionally, in Kondratyuk *et al.* (2019), the transfer of *R. mcleanii* into *Lecanoropsis* receives no statistical support. According to their results (see Kondratyuk *et al.* 2019: fig. 2), *Lecanoropsis* forms a non-supported clade separated from *Rhizoplaca mcleanii*. Since the morphology of *R. mcleanii* does not match that of *Lecanoropsis*, and in our analysis the specimen of *R. mcleanii* appeared outside of *Lecanoropsis*, we have no reason to support the transfer of *Rhizoplaca mcleanii* into *Lecanoropsis*. Therefore, for now we suggest retaining the name *Rhizoplaca mcleanii* (C. W. Dodge) Castello.

The genus *Myriolecis* Clem., *Lecanora utahensis* H. Magn., and a brief commentary on the genus name *Polyozosia* A. Massal.

Myriolecis (= *Polyozosia* A. Massal., formerly the *Lecanora dispersa*-group) forms a well-supported clade close to *Protoparmeliopsis* in

our analysis. These results are consistent with phylogenies published by Śliwa *et al.* (2012, 2023) and Zhao *et al.* (2015). The *Lecanora dispersa*-group was treated in detail by Śliwa (2007). According to these authors, the genus comprises corticolous or saxicolous crustose lichens, with a typically endosubstratal, more rarely well-developed thallus and lecanorine apothecia (except for *M. persimilis* (Th. Fr.) Śliwa *et al.*, which appears to have biatorine-like apothecia) with a thick persistent margin and becoming conspicuously crenulate with time. Species of *Myriolecis* produce a wide range of xanthenes, with some also producing gyrophoric acid (e.g. *M. salina* (H. Magn.) Śliwa *et al.*) or pannarin (e.g. *M. dispersa* (Pers.) Śliwa *et al.*) as minors. Several taxa do not produce any compound detectable by TLC (e.g. *Myriolecis sambuci* (Pers.) Clem.).

Lecanora utahensis H. Magn. is a saxicolous species often found on sandstone rocks and soil in the Sonoran Desert (Ryan *et al.* 2004). It shares the majority of characters that circumscribe *Myriolecis*, except that it does not produce xanthenes but rather isousnic acid. Ryan *et al.* (2004) placed *L. utahensis* in the *L. dispersa*-group, whereas Śliwa (2007) indicated that it does not belong there due to its chemistry. Later, however, Śliwa *et al.* (2023: 378) described *Myriolecis suevica* V. Wirth *et al.*, which produces isousnic acid like *Lecanora utahensis*, thereby expanding the concept of *Myriolecis*. Our results show a close phylogenetic relationship between *L. utahensis* and the species of *Myriolecis* included in our dataset. As pointed out by Śliwa *et al.* (2023), this genus comprises several subclades, one of which conforms to *Polyozosia*, a name resurrected only recently by Kondratyuk *et al.* (2019) as the older and valid name for *Myriolecis*. According to Massalongo (1855) *Polyozosia* originally comprised *Polyozosia* ?? *aipospila* (Wahlenb.) A. Massal., *P. poliophaea* (Wahlenb.) A. Massal. and *P. spodophaea* (Wahlenb. ex Ach.) A. Massal. (as '*spadophaea*'), and was typified by Hafellner (1984) based on *Polyozosia poliophaea*. We refrain from recombining *Lecanora utahensis* into *Myriolecis* because it is currently unclear to which of these subclades *L. utahensis* belongs.

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