



# *Gilbertaria*, a first crustose genus in the *Sphaerophoraceae* (*Lecanoromycetes*, *Ascomycota*) for *Catillaria contristans*, *Toninia squalescens* and related species

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## Abstract

Lecideoid lichen-forming fungi are a large, heterogeneous group that includes many species described during the nineteenth century that are of unclear taxonomic status. We revise such a group, the species of which have previously been treated under the much-misunderstood names *Catillaria contristans* or *Toninia squalescens*, and use a seven-locus phylogeny to determine its phylogenetic position. We found strong support for a previously unrecognized monophyletic lineage within the *Sphaerophoraceae*, comprising five phylogenetic species, and describe the new genus *Gilbertaria* to accommodate them. The new genus is characterized by a crustose growth form, 1-septate ascospores, thick ((1.5–)2–3(–4) µm wide) paraphyses and asci of the *Biatora*-type. We revise the nomenclature and give new delimitations and descriptions of the Northern Hemisphere species *Gilbertaria contristans* comb. nov., *G. holomeloides* comb. nov., *G. squalescens* comb. nov. and describe the new species *G. astrapeana* from the Falkland Islands.

**Keywords** *Catillaria* · Five new taxa · *Lecidea* · Phylogeny · Three new typifications · Taxonomy

## Introduction

Lecideoid lichen-forming fungi are a large and heterogeneous group of crustose lichens that is characterized by apothecia without symbiotic algal cells in the apothecial margin. In the early days of lichenological research, the majority of the then known lecideoid species (about a hundred) were referred to the genus *Lecidea* Ach. (Acharius 1803). Subsequent work by nineteenth century lichenologists added several hundred lecideoid species, many also described in the genus *Lecidea*, while at the same time other lichenologists were developing a more fine-grained classification that led to the introduction of numerous new genera, such as *Bacidia* De Not., *Biatora* Fr.,

*Buellia* De Not., *Catillaria* A.Massal., *Lecidella* Körb., *Micarea* Fr. and *Rhizocarpon* Ramond ex DC.

At the beginning of the twentieth century, the Austrian lichenologist Alexander Zahlbruckner set out to catalogue all the lichens described at that time (Zahlbruckner 1921–1940). His aim was not just to list described names but to also express his taxonomic opinion and to list all published literature treating each taxon. Such a gigantic project necessitated some simplifying shortcuts, one of which was to mechanically refer crustose lichens with hyaline ascospores, a green, non-*Trentepohlia* algal symbiont and lacking algal cells in the apothecial margin to either the genus *Lecidea* if ascospores were 1-celled, to *Catillaria* if ascospores were 2-celled, to *Bacidia* if ascospores had 3 or more transverse septa and to *Rhizocarpon* if they were muriform. In addition, because of the disproportionate importance placed on thalline morphology, species with a squamulose thallus were placed in *Lecidea* sect. *Psora* Schaer. if the ascospores were one-celled and in *Toninia* A.Massal. if they were septate. This led to species with similar apothecial characteristics being placed in different genera and, subsequently, different families. Zahlbruckner's taxonomic system came to dominate taxonomical thinking about lichens for decades at the expense of a more natural taxonomy based on a wider suite of apothecial characters.

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Beginning in the 1960s and 70s, the search for a more natural classification of lecideoid lichens was revitalized. This included revisions at the species level, requiring the revival of previously described genera as well as the description of numerous new ones (e.g. Hertel 1967; Coppins 1983; Hertel 1984; Hertel and Rambold 1987; Timdal 1991; Printzen 1995; Schmuil et al. 2011; Kistenich et al. 2018). However, many species and species groups have not been revised since Zahlbruckner's time and are still classified following his artificial taxonomy. One example of this concerns the group of small crustose species with 1-septate ascospores that are currently treated under the names *Catillaria contristans* (Nyl.) Zahlbr. and *Toninia squalezens* (Nyl.) Th.Fr. During the nineteenth century, several new species were described in this group: *Catillaria sphaeralis* Körb., *Lecidea contristans* Nyl., *Lecidea dufourii* Nyl., *Lecidea holomeloides* Nyl., *Lecidea hypocyanea* Stirt., *Lecidea squalezens* Nyl. and *Thalloidima rimulosum* Th.Fr. A first recognition that these names denoted very similar entities was made by Fries (1874), who included *Catillaria sphaeralis*, *Lecidea dufourii* and his own *Thalloidima rimulosum* as synonyms of *Toninia* (= *Lecidea*) *squalezens*. Zahlbruckner (1921–1940) accepted four species in this group in three different genera: *Catillaria contristans* (including *Lecidea holomeloides*), *C. sphaeralis* (including *L. dufourii*), *Toninia squalezens* (including *Thalloidima rimulosum*) and *Lecidea hypocyanea*, which was retained in *Lecidea* because, according to its protologue, it had simple ascospores. Vainio (1934) implicitly used Zahlbruckner's taxonomic generic scheme for these species, and accepted *Toninia squalezens* (including *Thalloidima rimulosum*) and *Catillaria dufourii* (including *C. sphaeralis*), but he also described the new species *Catillaria kivakkensis* Vain., which he considered close to *C. dufourii* (Nyl.) Vain. (Vainio 1934). A further addition to this group was made from North America by Lowe (1939), who described *Lecidea subramosa* J. Lowe, although he did not compare his new species to other names described in this group. After the 1930's, it seems that no further species have been added.

Although it has long been acknowledged that these species are not congeneric with the type species of the genus in which they are placed (e.g. Timdal 1991; Coppins 1992), in the absence of a modern revision of this group, modern floras (e.g. Foucard 2001; Hitch et al. 2009; Wirth et al. 2013) essentially retain Zahlbruckner's generic classification, the only difference being a further reduction in the number of species, with only two species being currently accepted: *Catillaria contristans* and *Toninia squalezens*. The taxonomic status of these names as well as their many suggested synonyms is, however, unclear and typifications are often lacking. For example, several checklists (e.g. Hafellner and Türk 2016; Nimis 2016) list *Catillaria sphaeralis* as a synonym of *C. contristans*, although neither name has been lectotyped

and *C. sphaeralis* is, in fact, the older name. In addition, as a consequence of the lingering Zahlbrucknerian classification, the similarity of *C. contristans* and *T. squalezens* has largely been forgotten and these species are generally not compared to each other, in spite of their many anatomical similarities (cfr. Foucard 2001; Fletcher and Coppins 2009; Hitch et al. 2009).

The confusion surrounding the names *Catillaria contristans* and *Toninia squalezens* has also had implications for molecular phylogenies. The first researchers to include *C. contristans* in a phylogenetic analysis were Andersen and Ekman (2005), who recovered the species in a paraphyletic *Micarea*, close to the *Micarea peliocarpa* group. However, the specimen from which the sequences were obtained was actually a species of *Micarea*, *M. oreina* Kantvilas & Coppins (Kantvilas and Coppins 2019). Next, in a phylogeny including many different families, Ekman et al. (2008) recovered a specimen identified as *Protomicarea limosa* (Ach.) Hafellner on a highly supported branch together with *Sphaerophorus globosus* (Huds.) Vain. Sequences from this specimen were subsequently used for further phylogenetic work but the specimen was redetermined first as *Catillaria contristans* (Ekman and Blaaid 2011) and then as *Toninia squalezens* (Kistenich et al. 2018). As these examples illustrate, the unclear species boundaries of *C. contristans* and *T. squalezens* mean, not only that it is difficult to distinguish these species from each other, but also that there is a clear risk that they are confused with other crustose lichens that occur in the same habitat, such as species of *Micarea* or *Protomicarea* Hafellner. Hence, there is a great need for a modern revision of this group. Our aim with this study was to perform such a revision of *Catillaria contristans*, *Toninia squalezens* and their suggested synonyms, as well as to determine their phylogenetic position.

## Material and methods

### Morphology and anatomy

Measurements were made under a light microscope on material mounted in water, using an oil-immersion, objective lens, with a precision of 0.5 µm for measurements of finer anatomical structures (e.g. ascospores and paraphyses). Only well-developed ascospores lying outside the asci were measured. Ascospore dimensions and length/breadth ratios are presented in the format: (minimum value observed–) mean value ± standard deviation (–maximum value observed) with n being the number of measurements. To examine colour reactions of pigments and solubility of crystals, we used a 10% solution of KOH (abbreviated K), a 4–5% solution of common commercial bleach (abbreviated C) and a 50% solution of HNO<sub>3</sub> (abbreviated N). Anatomical features (especially paraphyses) were sometimes examined after staining of tissues with

Floxine B. Apical structures of asci were examined in an iodine solution (0.3–0.4% I, abbreviated I) after pretreatment with K (abbreviated KI). We checked thallus reactions with K, C and, in addition, an ethanolic solution of paraphenylenediamine (abbreviated Pd). We performed HPTLC (following the method described by Arup et al. 1993) using solvent system C (Orange et al. 2010). Material from the following herbaria was included in the study: ASU, BM, E, H, L, MICH, MSC, O, QFA, S, TUR and UPS.

### DNA extraction, amplification and sequencing

We extracted total DNA using a QIAGEN Plant DNA Mini Kit following the manufacturer's instructions or, alternatively, with Chelex 100 (Bio-Rad, Hercules, CA, USA) following the procedure described by Ferencova et al. (2017). To achieve a 10% solution of Chelex, we used 0.1 g of Chelex per ml extract. For amplification and sequencing, we used the primers MS1, MSU7 as well as mrSSU1, mrSSU2 and mrSSU3R (used as nested primers for *Austropeltum glareosum* Henssen, H.Döring & Kantvilas and on their own in all other cases) for the mitochondrial ribosomal small subunit 12S, hereafter mtSSU (White et al. 1990; Zhou and Stanosz 2001; Zoller et al. 1999); NSSU97A, NSSU1088, NS8 and SR11R for nuclear ribosomal small subunit 18S, hereafter nSSU (Kauff and Lutzoni 2002; Spatafora et al. 1995; White et al. 1990); LRlecF and LRlecR for nuclear ribosomal large subunit 28S, hereafter LSU (Schneider et al. 2015); ITS1F and ITS4 for nuclear ribosomal DNA ITS1-5.8-ITS2, hereafter ITS (Gardes and Bruns 1993; White et al. 1990); the newly designed MCM7-580for (5' ATG CCN AVR GAR CAN ADG-3') and MCM7-1560rev (5'-GCR ACW CCD GGR TCR CCC AT-3') as well as MCM7-709for and MCM7-1348rev (either as nested primers or on their own) for the Mini-chromosome Maintenance Complex 7 (Schmitt et al. 2009), hereafter *MCM7*; and fRPB2-5F and fRPB2-7cR with the nested primers RPB2-980F and RPB2-1554R for the RNA polymerase II complex subunit, hereafter *RPB2* (Liu et al. 1999; Reeb et al. 2004). For the amplification of mtSSU and nSSU, we used the Phusion Green Hot Start II High-Fidelity DNA Polymerase Master Mix. For mtSSU, we used the following PCR thermal profile: an initial hold at 98 °C for 30 s followed by 35 cycles of denaturation at 98 °C for 10 s, annealing 30 s at 60.1 °C (for the primer pair MS1 + MSU7) or 60.3 °C (for the primer pair mrSSU1 + mrSSU3R) or 64.2 °C (for the primer pair mrSSU2 + mrSSU3R) and polymerization at 72 °C for 30 s, and finally a hold at 72 °C for 10 min. For nSSU, we used the following thermal profile when using the primer pair NSSU97A + NS8: an initial hold at 98 °C for 30 s followed by 35 cycles of denaturation at 98 °C for 10 s, annealing at 66.2 °C for 30 s and polymerization at 72 °C for 50 s, and finally a hold at 72 °C for 10 min. When running a nested PCR for nSSU with the primer pair SR11R +

NSSU1088, the same program was used, but the annealing temperature was set to 63.1 °C and the time for polymerization to 50 s.

For ITS, LSU, *MCM7* and *RPB2*, we used VWR Red Taq DNA Polymerase Master Mix following the manufacturer's protocols. For the amplification of ITS, we used this PCR thermal profile: an initial hold at 94 °C for 3 min followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 45 s and polymerization at 72 °C for 1 min., and finally a hold at 72 °C for 10 min. For LSU, we used the following PCR thermal profile: an initial hold at 94 °C for 3 min followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 57 °C for 45 s and polymerization at 72 °C for 1 min 45 s; and finally, a hold at 72 °C for 10 min. For *MCM7*, we used the following PCR thermal profile both for the primer pair MCM7-580for + MCM7-1560rev and for MCM7-709for + MCM7-1348rev: an initial hold at 94 °C for 3 min followed by 3 cycles of denaturation at 94 °C for 45 s, annealing at 57 °C for 45 s and polymerization at 72 °C for 1 min 45 s; then, 4 cycles of 94 °C for 40 s, 54 °C for 40 s, 72 °C for 45 s; 4 cycles of 94 °C for 40 s, 51 °C for 40 s, 72 °C for 45 s; 30 cycles of 94 °C for 30 s, 48 °C for 30 s, 72 °C for 45 s; and finally, a hold at 72 °C for 10 min. When running nested PCR for *MCM7*, the same thermal profile was used for the second as for the first PCR. We used a two-step nested PCR for *RPB2*. For the first step, using the primer pair fRPB2-5F and fRPB2-7cR, we used the following PCR thermal profile: an initial hold at 94 °C for 3 min followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 53 °C for 45 s, polymerization at 72 °C for 1 min 45 s and finally a hold at 72 °C for 10 min. For the second step, using the primer pair RPB2-980F and RPB2-1554R, we used this PCR thermal profile: an initial hold at 94 °C for 3 min followed by 15 cycles of denaturation at 94 °C for 30 s, annealing at 65 °C for 45 s (decreasing 1° each cycle), and polymerization at 72 °C for 1 min 20 s; then, 28 cycles of 94 °C for 30 s, 50 °C for 45 s, 72 °C for 1 min 20 s, and finally a hold at 72 °C for 10 min. PCR products were subsequently purified with Exo-sap-IT (USB Corporation) and sent for sequencing to Macrogen Europe Inc.

### Taxon sampling

To determine the phylogenetic position of *Gilbertaria*, we assembled a sequence data set with a selection of species and genera from families considered to belong to the *Sphaerophorineae*: the *Pilocarpaceae* (the genera *Byssoloma* Trevis., *Calopadia* Vězda, *Fellhanera* Vězda and *Micarea*), the *Psoraceae* (*Brianaria* S.Ekman & M.Svensson, *Protoblastenia* (Zahlbr.) J.Steiner, *Psora* Hoffm.), the *Ramalinaceae* (*Bacidia*, *Biatora*, *Bilimbia* De Not., *Lecania* A.Massal. and *Ramalina* Ach.) and the *Sphaerophoraceae* (Miadlikowska et al. 2014; Wijayawardene et al. 2018). As

BLAST-searches, and earlier phylogenies (Ekman et al. 2008; Ekman and Blaaliid 2011) indicated that *Gilbertaria* could belong to the latter family, we included all genera considered to belong to the *Sphaerophoraceae*: *Austropeltum* Henssen, H. Döring & Kantvilas, *Bunodophoron* A. Massal., *Calycidium* Stirt., *Leifidium* Wedin, *Neophyllis* F. Wilson, and *Sphaerophorus* Pers. (Prieto et al. 2013; Wedin and Döring 1999; Wedin et al. 2000; Wedin 2002; Wijayawardene et al. 2018). We found it difficult to get amplifications from the sole member of the genus *Austropeltum*, *A. glareosum*, and failed to get any other marker than mtSSU from this species. The *A. glareosum* terminal in our analysis, therefore, contains sequences from two different specimens: nSSU from GenBank and mtSSU from our sequenced specimen (see Table 1). Further, we included two genera from the monogeneric families *Psilolechiaceae* (*Psilolechia* A. Massal.) and *Scoliciosporaceae* (*Scoliciosporum* A. Massal.), because these have usually emerged close to the *Sphaerophorineae* in earlier studies (e.g. Kraichak et al. 2018; Miadlikowska et al. 2014). In a recent phylogeny (Kraichak et al. 2018), the *Scoliciosporaceae* appeared paraphyletic because the two representatives of the family (*Scoliciosporum intrusum* (Th. Fr.) Hafellner and *S. umbrinum* (Ach.) Lojka) ended up on different branches, with *S. umbrinum* seemingly belonging to the *Sphaerophoraceae*. The cause of this result seems to be the *RPB1* sequence for *S. umbrinum* used in that analysis (GenBank ID AY756397). This sequence blasts with species of *Bunodophoron* and is, in fact, almost identical to a sequence from *B. australe* (Laurer) A. Massal. (MF954576). Other loci from *S. umbrinum*, nominally from the same voucher, are not close to *Bunodophoron*. We thus consider the *RPB1* sequence in question as erroneous and have not used it for our analysis. Two sequences of *Protomicarea limosa* available in Genbank (HQ660558, HQ650655) were included in test analyses, but were found to be distant to anything else included and were thus removed from the final analysis. As an outgroup, we selected species from two genera of the *Lecanoraceae* (*Lecanora* (Ach.) and *Lecidella*) because this family appears on a sister branch to the *Sphaerophorineae* (e.g. Miadlikowska et al. 2014). For the selected genera and species, we downloaded sequences of mtSSU, nSSU, LSU, ITS, *MCM7*, *RPB1* and *RPB2* from GenBank (Table 1).

## Sequence alignment

For the non-protein-coding markers (ITS, mtSSU, nSSU and LSU), we used two different alignment strategies. The first was to estimate the alignment using an iterative method (PASTA) that optimizes the alignment using maximum likelihood, which in principle implies no subsequent removal of ambiguous positions or anything else from the resulting alignments. The second strategy was to align using MAFFT and then filter out positions that contribute to guide-tree

uncertainty using GUIDANCE2. This potentially means removing large parts of the alignment that have been assessed as ambiguous from the subsequent analysis.

For the first strategy, we estimated separate alignments for ITS, mtSSU, nSSU and LSU using PASTA (Mirarab et al. 2015), with the mask option activated, MAFFT (algorithm L-INS-i) as the aligner, OPAL for the pairwise merging and FastTree as the tree estimator, with GTR +  $\Gamma$  as the model for molecular evolution. Inspection of the alignment of mtSSU revealed problems due to the presence of a long intron. We therefore estimated the mtSSU dataset using MAFFT with the algorithm E-INS-i, which is designed to handle sequence data sets with multiple conserved domains divided by long gaps (Katoh et al. 2019). From the MAFFT alignment of mtSSU, we removed one intron of 923 bp from *G. squalescens*. We then estimated the mtSSU alignment using PASTA, as described above. To minimize potential problems with missing data, the ends of all the PASTA alignments were trimmed. For the second alignment strategy, we first estimated alignments for the same four non-protein coding markers with MAFFT, using the algorithm E-INS-i (Katoh et al. 2019) and then performed filtering of ambiguous positions using GUIDANCE2 (Sela et al. 2015), running 100 bootstrap-replicates. Alignment positions that fell below the default confidence score of 0.93 were removed, which meant removing 43.9% of the ITS, 8.8% of the mtSSU, 14.4% of the LSU and 2% of the nSSU alignment, respectively. As for the PASTA alignments, the ends of the GUIDANCE2 alignments were trimmed.

For the protein-coding genes (*MCM7*, *RPB1* and *RPB2*), we estimated alignments with MAFFT using the algorithm E-INS-i (Katoh et al. 2019). After aligning the sequences, we identified several non-coding introns in the *RPB1* and *RPB2* alignments. These were very variable and not possible to unambiguously align, so we removed them before any further analysis was performed. No such introns were detected in the alignment of *MCM7*. A subsequent filtering with GUIDANCE2 of the alignments of the protein-coding genes did not indicate any positions falling below the confidence score of 0.93. The alignments of the three protein-coding genes are thus the same in both the PASTA alignment set and in the GUIDANCE2 alignment set.

We checked for incongruence among markers by performing a separate maximum likelihood analysis of each of the eleven alignments (four PASTA alignments, four filtered with GUIDANCE2 and three for the protein-coding genes) using IQTree with 500 non-parametric bootstrap replicates (Nguyen et al. 2015). The single marker trees from these analyses were then compared to identify any conflicting results, defined as conflicting clades with > 75% bootstrap support. We found no such conflicts and, therefore, decided to concatenate the eleven alignments into two sets of seven markers each: (I) the four PASTA alignments + the three protein coding gene

Taxon	Voucher/source	nrSSU	ITS	LSU	nSSU	MCM7	RPBI	RPB2
<i>Austrorpetium glareosum</i>	New Zealand, Wedin 4944 (BM), Wedin and Döring 1999; Tasmania, Kantvilas 337/07 (HO)	<b>OPI161937</b>			AF117982			
<i>Bacidia arceutina</i>	Sweden, Ekman 3110 (BG), Kistenich et al. 2018	MG925846	AF282083	MG926041			MG926140	MG926230
<i>Bacidia schweinitzii</i>	U.S.A., Lutzoni et al. 03.07.04-03 (DUKE), Miadlikowska et al. 2006	DQ972998	DQ782850				DQ782830	DQ782872
<i>Biatora chrysanthoides</i>	Sweden, Svensson 3208 (UPS)	<b>OPI161938</b>		<b>OPI161930</b>		<b>OPI198704</b>		
<i>Bilimbia sabuletorum</i> 1	North America, Björk 11302 (UBC), Miadlikowska et al. 2014	KJ766361		KJ766534	KJ766694		KJ766839	
<i>Bilimbia sabuletorum</i> 2	Norway, Ekman 3091 (BG), Andersen and Ekman 2005	AY567721	AM292670	AY756346			AY756413	AM292761
<i>Brianaria sylvicola</i>	Sweden, Ekman 3629 (BG), Andersen and Ekman 2005	AY567769		AY756331			AY756392	
<i>Bunodophoron melanocarpum</i>	Colombia, Soto 26 (?), Soto et al. 2018					MF954551	MF954593	
<i>Byssoloma leucoblepharum</i>	Portugal, Ekman 3502 (BG), Andersen and Ekman 2005	AY567778	AY756459	AY756317	AF455135		AY756380	
<i>Catopadina foliicola</i>	Costa Rica, Lücking 16011 (BG), Andersen and Ekman 2005	AY567782	AY756462	AY756318			AY756381	
<i>Calycidium cuneatum</i>	[?], J. Wedin 8034 (S), Prieto et al. 2013	JX000117	JX000114	JX000083		JX000154		
<i>Fellhanera bouteillei</i>	Sweden, Ekman 3417 (BG), Andersen and Ekman 2005	AY567787	AY756463	AY756348			AY756382	
<i>Fellhanera subtilis</i>	Sweden, Westberg ULR040 (UPS)	<b>OPI161958</b>						<b>OPI198715</b>
<i>Gilbertaria astrapeana</i>	Falkland Islands, Fryday 10915 (holotype, MSC)	<b>OPI161939</b>	<b>OPI161959</b>					<b>OPI198712</b>
<i>Gilbertaria contristans</i> 1	Sweden, Nordin 7877 (UPS)	<b>OPI161940</b>	<b>OPI161960</b>					
<i>Gilbertaria contristans</i> 2	Sweden, Nordin 7573 (UPS)	<b>OPI161941</b>	<b>OPI161961</b>					
<i>Gilbertaria contristans</i> 3	Iceland, Nordin 6821 (UPS)	<b>OPI161942</b>	<b>OPI161962</b>					
<i>Gilbertaria contristans</i> 4	Sweden, Westberg UCCLR102 (UPS)	<b>OPI161963</b>						
<i>Gilbertaria holomeloides</i> 1	Sweden, Svensson 3264 (UPS)	<b>OPI161943</b>	<b>OPI161964</b>	<b>OPI161931</b>				
<i>Gilbertaria holomeloides</i> 2	Sweden, Svensson 3493 (UPS)	<b>OPI161944</b>	<b>OPI161965</b>	<b>OPI161933</b>				
<i>Gilbertaria holomeloides</i> 3	Sweden, Westberg et al. PL336 (UPS)	<b>OPI161946</b>	<b>OPI161966</b>	<b>OPI161932</b>				<b>OPI198711</b>
<i>Gilbertaria holomeloides</i> 4	Sweden, Westberg PAD024 (UPS)	<b>OPI161947</b>	<b>OPI161967</b>					
<i>Gilbertaria holomeloides</i> 5	Sweden, Westberg PAD324b (UPS)	<b>OPI161945</b>	<b>OPI161968</b>					
<i>Gilbertaria holomeloides</i> 6	Sweden, Svensson 3513 (UPS)	<b>OPI161945</b>		<b>OPI161934</b>				
<i>Gilbertaria</i> sp.	Norway, Timdal 11347 (O), Kistenich et al. 2018	MG925863	MG925962	MG926063			MG926162	
<i>Gilbertaria squalescens</i> 1	Sweden, Nordin 7451 (UPS)	<b>OPI161969</b>						
<i>Gilbertaria squalescens</i> 2	U.S.A., Fryday 9172 (MSC)	<b>OPI161971</b>						
<i>Gilbertaria squalescens</i> 3	Sweden, Svensson 3442 (UPS)	<b>OPI161952</b>	<b>OPI161973</b>	<b>OPI161936</b>	<b>OPI161929</b>	<b>OPI198700</b>		<b>OPI198710</b>
<i>Gilbertaria squalescens</i> 4	Sweden, Westberg UCCLR149 (UPS)	<b>OPI161955</b>	<b>OPI161976</b>					<b>OPI198709</b>
<i>Gilbertaria squalescens</i> 5	Norway, Andersen 92 (BG), Andersen and Ekman 2005	AY567733		AY756332			AY756394	
<i>Gilbertaria squalescens</i> 6	Sweden, Svensson 3633 (UPS)	<b>OPI161954</b>	<b>OPI161975</b>			<b>OPI198699</b>		<b>OPI198708</b>
<i>Gilbertaria squalescens</i> 7	Sweden, Svensson 3581 (UPS)	<b>OPI161950</b>	<b>OPI161970</b>			<b>OPI198701</b>		
<i>Gilbertaria squalescens</i> 8	Sweden, Westberg PAD318 (UPS)	<b>OPI161953</b>				<b>OPI198697</b>		
<i>Gilbertaria squalescens</i> 9	Sweden, Svensson 3440 (UPS)		<b>OPI161972</b>					<b>OPI198707</b>
<i>Gilbertaria squalescens</i> 10	Sweden, Svensson 3443 (UPS)		<b>OPI161974</b>					

(continued)	Taxon	Voucher/source	nrSSU	ITS	LSU	nSSU	MCM7	RPBI	RPB2
	<i>Gilbertaria squalescens</i> 11	Sweden, Westberg JMT131 (UPS)	<b>OPI161948</b>				<b>OPI198698</b>		<b>OPI198705</b>
	<i>Gilbertaria squalescens</i> 12	Sweden, Svensson 3272 (UPS)	<b>OPI161949</b>				<b>OPI198703</b>		<b>OPI198706</b>
	<i>Gilbertaria squalescens</i> 13	Sweden, Westberg ULR128 (UPS)	<b>OPI161951</b>		<b>OPI161935</b>		<b>OPI198702</b>		
	<i>Gilbertaria squalescens</i> 14	Canada, Gagnon 142.2f (QFA)	AY567720	AF282067	AY300840	AF091589		MG926175	AM292767
	<i>Lecania cyrtella</i>	Sweden, Ekman 3017 (BG)	AM292735	AM292685					
	<i>Lecania fuscilla</i>	Sweden, Arup L03046 (LD)							
	<i>Lecanora caesiortubella</i>	Australia, Lumbsch 19974k (F), Schoch et al. 2012	JN943728	JN939508			JN992711	JN987920	
	<i>Lecanora formosa</i>	China, ZX YN0188, Zhao et al. 2016	KT453820	KT453769	KT453774		KT453877		KT453979
	<i>Lecanora intumescens</i>	Norway, Ekman 3162 (BG), Andersen and Ekman 2005	AY300892		AY300841	AF091586		AY756386	
	<i>Lecidella elaeochroma</i>	Belgium, Ertz 7605 (BR), Miadlikowska et al. 2006		HQ650605	DQ986747			DQ986818	
	<i>Leifidium tenerum</i>	New Zealand, Tibell 16587 (UPS), Wedin et al. 1998		AF117998	AY453643	U70959			
	<i>Micarea adnata</i>	Norway, Andersen 48 (BG), Andersen and Ekman 2005	AY567751	AY756468	AY756326	AF455134		AY756388	
	<i>Micarea alabastrites</i>	Norway, Andersen 17 (BG), Andersen and Ekman 2005	AY567764	AY756469	AY756327			AY756389	
	<i>Micarea laeta</i>	Finland, Launis 1010135 (H), Launis et al. 2019	MG707781	MG521570			MG692541		<b>OPI198714</b>
	<i>Micarea lignaria</i>	Sweden, Svensson 3818 (UPS)	<b>OPI161956</b>						
	<i>Neophyllis melacarpa</i>	[no voucher info.] Wedin et al. 2000	AY340511		AY340556	AF117981			
	<i>Protoblastenia calva</i>	Croatia, Guedian CG659 (DUKE), Miadlikowska et al. 2006	DQ986904	HQ650618	JQ301601	JQ301653		DQ986830	DQ992446
	<i>Psitolechia leprosa</i> 1	Norway, Tonsberg and Bottnen 27362 (BG), Andersen and Ekman 2005	AY567730		AY756333			AY756395	
	<i>Psitolechia leprosa</i> 2	Sweden, Svensson 3408 (UPS)	<b>OPI161957</b>				<b>OPI198696</b>		<b>OPI198713</b>
	<i>Psitolechia lucida</i>	Norway, Andersen 8 (BG), Andersen and Ekman 2005	AY567729	AY756497	AY756334	AF455132			
	<i>Psora californica</i>	U.S.A., Timdal SON139/04 (O, Leavitt et al. 2018	EF524292	EF524322	EF521302			EF524334	
	<i>Psora decipiens</i>	U.S.A., Rui & Timdal US259/01, Leavitt et al. 2018					MG783717	MG783845	
	<i>Ramalina almqvistii</i>	U.S.A., Talbot AML008-X-01A (GZU), Spribille et al. 2020	MT039418	MT041620	MT039416		MT041632		
	<i>Ramalina complanata</i>	U.S.A., Hillis 2002.06.02 (DUKE), Miadlikowska et al. 2006						DQ883782	
	<i>Ramalina dilacerata</i>	U.S.A., Wetmore 83868 in Wetmore, Lich. Exs. 99 (BG), Kistenich et al. 2018	MG925917	MG926013	MG926104			MG926203	
	<i>Scoliosporium intrusum</i>	Norway, Ekman s.n. (BG), Andersen and Ekman 2005	AY567767		AY756329			AY756391	
	<i>Scoliosporium umbrinum</i>	Norway, Ekman 3005 (BG), Andersen and Ekman 2005	AY567719		AY300861	AF091587			
	<i>Sphaerophorus fragilis</i>	Canada, Lutzoni and Miadlikowska 07.13.03-17 (DUKE), Miadlikowska et al. 2006	DQ986789	HQ650600	DQ986805	DQ983487			
	<i>Sphaerophorus globosus</i> 1	Canada, Scheidegger s.n. (DUKE 47680), Miadlikowska et al. 2006	DQ986866	HQ650622	DQ986767	DQ986712		DQ986836	DQ992453
	<i>Sphaerophorus globosus</i> 2	Norway, Spribille 41201 and Holten (GZU), Spribille et al. 2020	MN508300	MN483149	MN460232		MN437626		

alignments, and (II) the four GUIDANCE2 alignments + the three protein coding gene alignments. The final alignments are included in Supplemental Material 1.

### Partitioning schemes

We made two analyses of each of the two alignment sets, one Bayesian analysis using MrBayes and one maximum likelihood analysis using IQTree. We estimated a separate partitioning scheme for each of these four analyses. For the Bayesian analysis, we assessed the division of the two concatenated alignment sets into partitions using PartitionFinder 2.1.1. (Lanfear et al. 2017), which also allows for simultaneous estimation of models of molecular evolution for the partitions. We restricted the estimation to models implemented in MrBayes 3.2.6., used BIC for model selection, assumed linked branched lengths (= edge-proportional model) and used the ‘greedy’ algorithm (Lanfear et al. 2012). For the PASTA alignments set, we assessed the division of the concatenated alignment into 15 partitions: mtSSU, nSSU, LSU, ITS1, 5.8S, ITS2 and independent 1st, 2nd, and 3rd codon positions for each of the three protein-coding genes *MCM7*, *RPB1* and *RPB2*. For the GUIDANCE2 alignment set, we assessed the division of the concatenated alignment into 13 partitions: mtSSU, nSSU, LSU, ITS (including 5.8S) and independent 1st, 2nd, and 3rd codon positions for *MCM7*, *RPB1* and *RPB2*. The best model fit for the PASTA alignment set was achieved when eleven of the partitions were merged into four: (1) ITS1 + ITS2; (2) the 1st codon positions of *MCM7*, *RPB1* and *RPB2*; (3) the 2nd codon positions of *MCM7*, *RPB1* and *RPB2*; and (4) the 3rd codon positions of *MCM7*, *RPB1* and *RPB2*. For the resulting eight partitions, GTR +  $\Gamma$  was selected as the best model for *MCM7* 1st + *RPB1* 1st + *RPB2* 1st and mtSSU; *RPB2* 2nd; GTR +  $\Gamma$  + I for ITS1 + ITS2 and *MCM7* 2nd + *RPB1* 2nd + *RPB2* 2nd; SYM +  $\Gamma$  + I for LSU; K80 +  $\Gamma$  + I for nSSU and *MCM7* 3rd + *RPB1* 3rd + *RPB2* 3rd; and K80 for 5.8S. The best model fit for the GUIDANCE2 alignment set was achieved when nine of the partitions were merged into three: (1) the 1st codon positions of *MCM7*, *RPB1* and *RPB2*; (2) the 2nd codon positions of *MCM7*, *RPB1* and *RPB2*; and (3) the 3rd codon positions of *MCM7*, *RPB1* and *RPB2*. For the resulting seven partitions, GTR +  $\Gamma$  was selected as the best model for *MCM7* 1st + *RPB1* 1st + *RPB2* 1st and mtSSU; GTR +  $\Gamma$  + I for *MCM7* 2nd + *RPB1* 2nd + *RPB2* 2nd; SYM +  $\Gamma$  + I for LSU; and K80 +  $\Gamma$  + I for ITS, nSSU and *MCM7* 3rd + *RPB1* 3rd + *RPB2* 3rd.

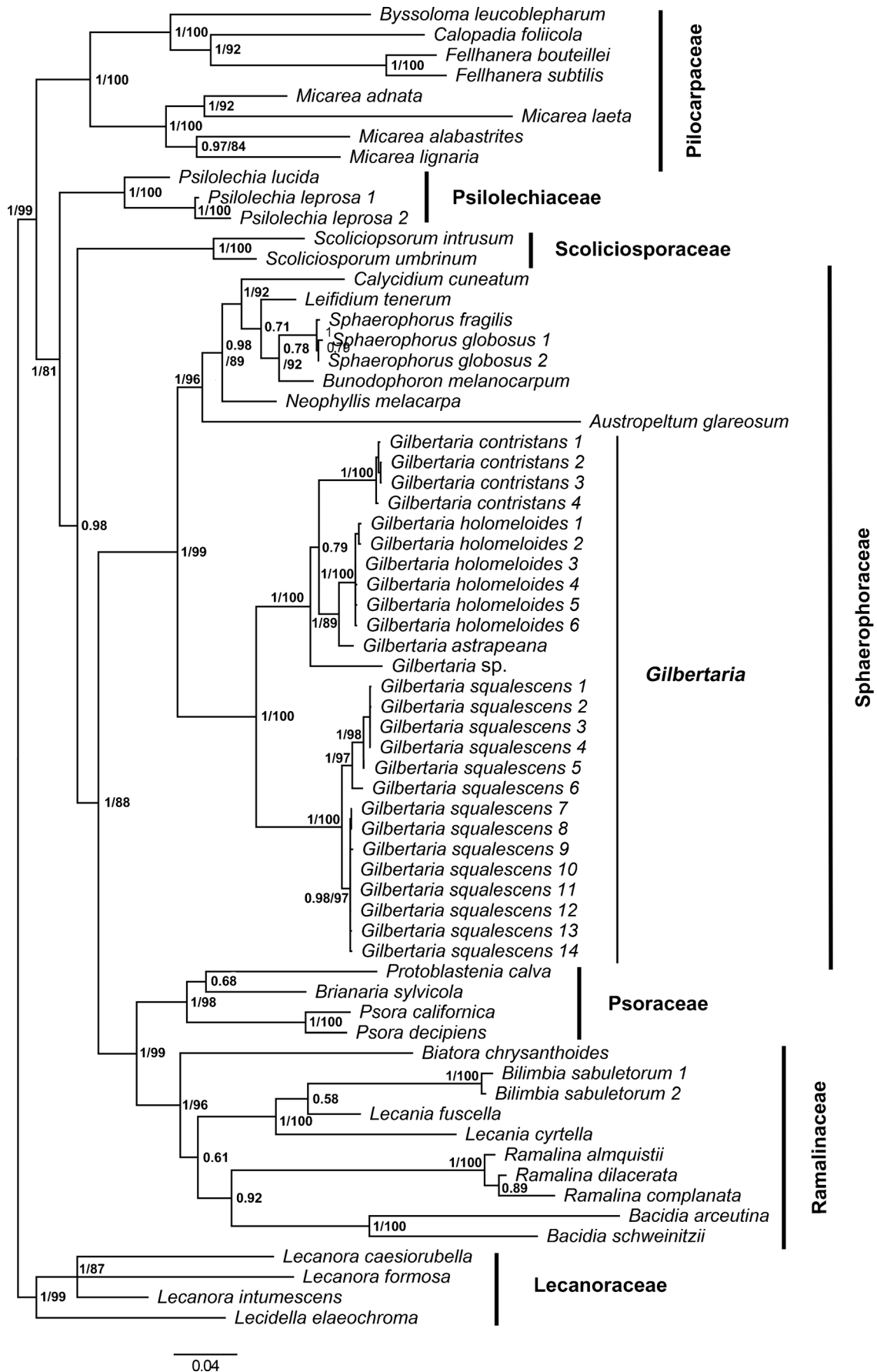
For the maximum likelihood analyses, we assessed partitioning schemes and their models of molecular evolution with ModelFinder as implemented in IQTree (Kalyaanamoorthy et al. 2017). For each of the two alignment sets, we assessed the same 15 and 13 partitions as for the Bayesian analysis. The best model fit for the PASTA

alignment set was achieved when ten of the partitions were merged into three: (1) 5.8S + *RPB1* 2nd + *RPB2* 2nd + *MCM7* 2nd; (2) *RPB1* 1st + *RPB2* 1st + *MCM7* 1st; and (3) *RPB1* 3rd + *RPB2* 3rd + *MCM7* 3rd. For the resulting eight partitions, TIM2e+I+G4 was selected as the best model for ITS1 and *RPB1* 3rd + *RPB2* 3rd + *MCM7* 3rd; TPM3u+F+I+G4 for 5.8S + *RPB1* 2nd + *RPB2* 2nd + *MCM7* 2nd; TNe+G4 for ITS2; TIM2+F+G4 for *RPB1* 1st + *RPB2* 1st + *MCM7* 1st; TVM+F+G4 for mtSSU; TIM3e+I+G4 for LSU; and K2P+I+G4 for nSSU. The best model fit for the GUIDANCE2 alignment set was achieved when eleven of the partitions were merged into four: (1) the 1st codon positions of *MCM7*, *RPB1* and *RPB2*; (2) the 2nd codon positions of *MCM7*, *RPB1* and *RPB2*; (3) the 3rd codon positions of *MCM7*, *RPB1* and *RPB2*; and (4) LSU + nSSU. For the resulting six partitions, TNe+I+G4 was selected as the best model for ITS; TIM2+F+G4 for *RPB1* 1st + *RPB2* 1st + *MCM7* 1st; TPM3+F+I+G4 for *RPB1* 2nd + *RPB2* 2nd + *MCM7* 2nd; TIM2e+I+G4 for *RPB1* 3rd + *RPB2* 3rd + *MCM7* 3rd; TVM+F+G4 for mtSSU; and TNe+I+G4 for LSU + nSSU.

### Phylogenetic analysis

We performed phylogenetic analyses of the two concatenated, partitioned alignment sets, implementing the models of molecular evolution from PartitionFinder using MrBayes 3.2.6. (Ronquist et al. 2012). We used flat Dirichlet priors for the substitution rates and state frequencies, an exponential (1) distribution for the gamma shape parameter and uniform distributions for invariant sites and topology. In test runs using maximum likelihood analysis, the total tree length for the PASTA alignment set was found to be  $\approx 3.5$ . We therefore adjusted the branch length prior to a compound Dirichlet prior with  $\alpha = 1$  and  $\beta = 0.29$ . Likewise, the total tree length for the GUIDANCE2 alignment set was  $\approx 4$ , and the branch length prior for that analysis thus set to  $\alpha = 1$  and  $\beta = 0.25$ . We performed two runs of four MCMC chains each, three heated and one cold. For initial test runs, we set the temperature of the heated chains to 0.20 but reduced this to 0.10 to improve swapping rates. The sample frequency was set to every 100th generation and the fraction of trees discarded as burn-in was set to 25%. We ran the analysis for a fixed number of generations and convergence was then assessed using the *convenience* package in R vers. 4.2.1., both in terms of checking whether enough samples had been obtained and whether these represent the true posterior distribution (Guimarães Fabreti and Höhna 2022). If any parameter has been sampled less than 625 times, *convenience* will assess convergence as having failed. We considered a posterior probability (PP) of 0.95 or higher as high support.

In addition to the Bayesian analysis, we also performed maximum likelihood analyses of the concatenated alignment with IQTree vers. 1.6.12 (Chernomor et al. 2016; Nguyen

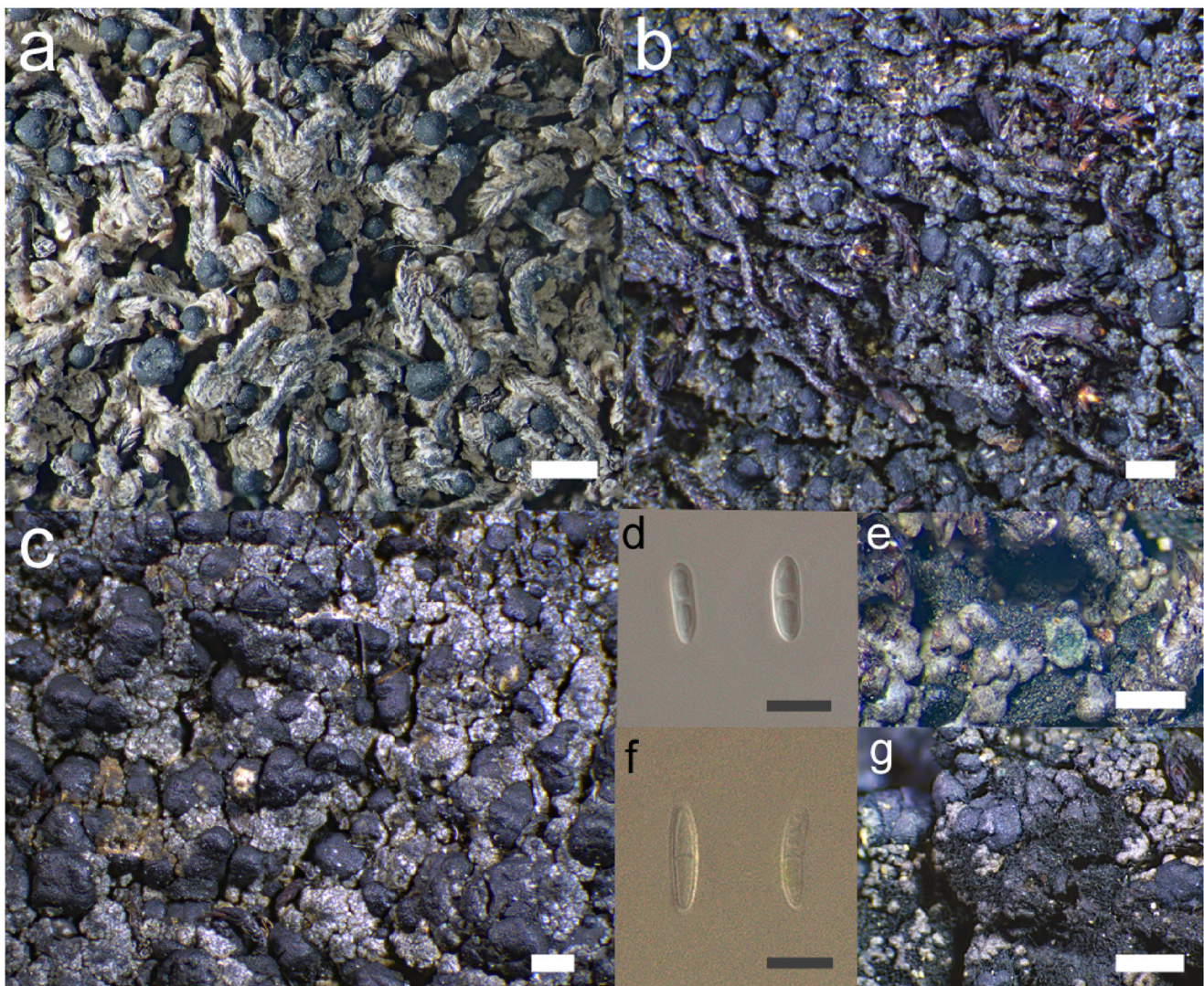


**Fig. 1** Majority-rule consensus tree based on a Bayesian MCMC analysis of PASTA alignment set of mrSSU, nSSU, LSU, ITS, *MCM7*, *RPB1* and *RPB2*, showing the phylogenetic position of *Gilbertaria* in the *Sphaerophoraceae*. Branch support is given as posterior probability (PP)/bootstrap support (BS). Bootstrap support values are from a corresponding maximum likelihood analysis. Only BS values > 70% are shown

et al. 2015), using the partitioning scheme and models of molecular evolution from ModelFinder. As in the Bayesian analysis, we used edge-proportional partition models. We assessed branch support by running 500 non-parametric bootstrap replicates. We considered a bootstrap support (BS) of 75 or higher as high support.

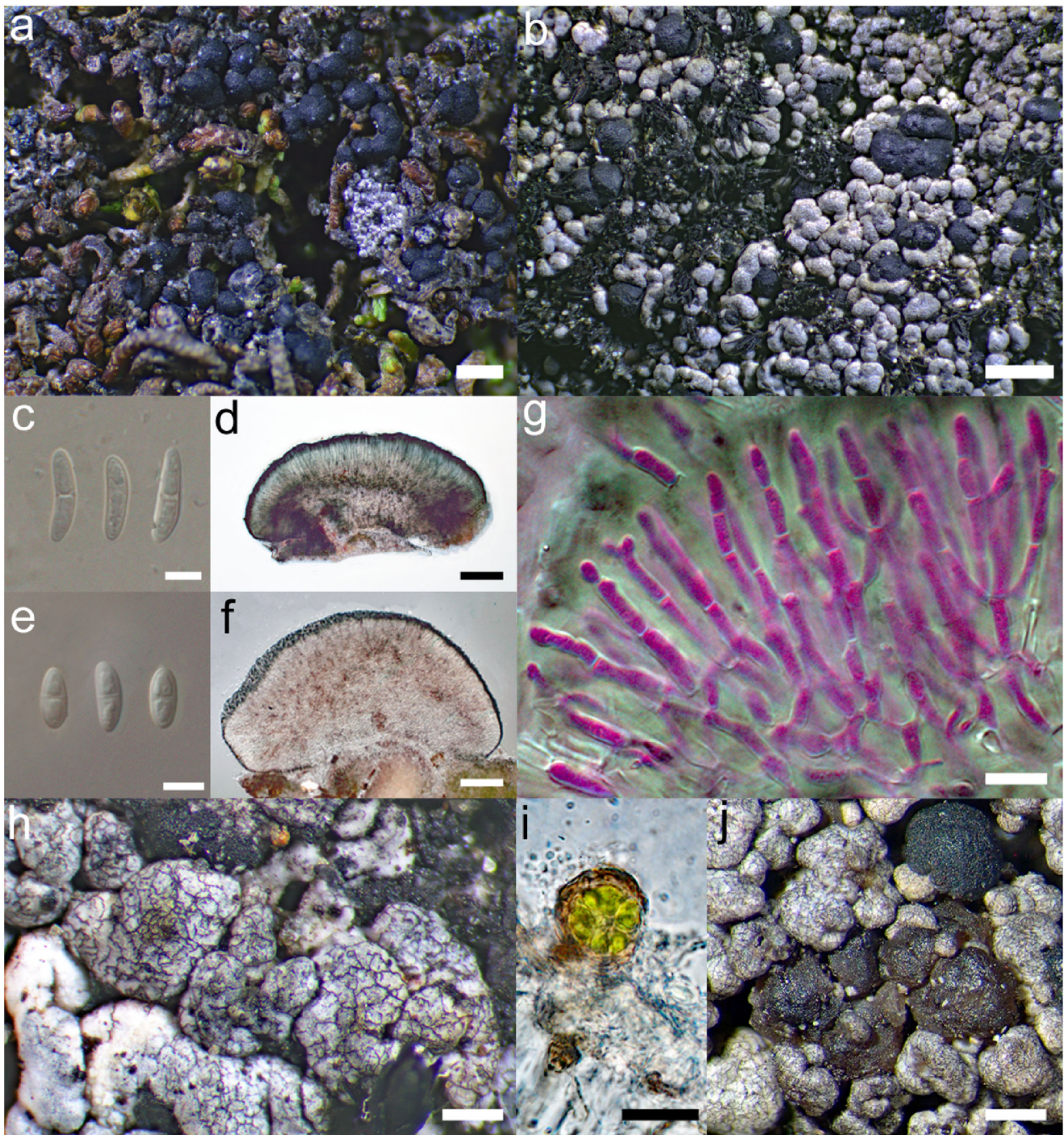
## Results

We generated 68 new sequences (Table 1). The final PASTA alignment set included 65 terminals, 208 sequences and had 9228 characters, 1778 of which were parsimony-informative. The final GUIDANCE2 alignment set had 8731 characters, 1511 of which were parsimony-informative. The Bayesian analysis of the PASTA alignment set was halted after running for 25 million generations, resulting in a posterior of 375,002 samples. Assessment of convergence using the *convenience* package indicated that convergence had been achieved. The Bayesian analysis of the GUIDANCE2 alignment set was likewise halted after 25 million generations, but the convergence assessment indicated that convergence had failed. The



**Fig. 2** *Gilbertaria astrapeana* and *G. contristans*. **a** *Gilbertaria astrapeana*, (Fryday 10914, holotype, MSC). **b** Smaller (younger) form of *G. contristans* with sessile apothecia (Malme s.n., S F332038). **c** Mature form of *Gilbertaria contristans* with large and flat apothecia (Malme s.n., S F331995). **d** *G. contristans*, ascospores (Malme s.n., S

F331975). **e** *G. contristans*, thallus with soralium (Westberg UCCLR102, MSC). **f** *G. astrapeana*, ascospores (Fryday 10914, isotype, E). **g** *G. contristans*, thallus and apothecia associated with filamentous cyanobacteria (Nordin 7451, UPS). Scale bars: **a, b, c, g** 1 mm; **e** 0.4 mm; **d, f** 10  $\mu$ m



**Fig. 3** *Gilbertaria holomeloides*, *G. squalezens* and *Moriola* sp. **a** *Gilbertaria holomeloides* (Svensson 3264, UPS). **b** *Gilbertaria squalezens* (Svensson 3443, UPS). **c** *Gilbertaria holomeloides*, ascospores (Westberg PAD024, UPS). **d** *G. holomeloides*, section through apothecium (Westberg PAD324b, UPS). **e** *G. squalezens*, ascospores (Svensson 3443, UPS). **f** *G. squalezens*, section through apothecium (Nordin 7451, UPS). **g** *G. squalezens*, paraphyses after

treatment with K and staining in Floxine B (Westberg PAD318, UPS). **h** Thallus squamules of *G. squalezens* covered in black hyphal net of *Moriola* sp. (Nordin 7561, UPS). **i** Section of goniocysts of *Moriola* sp. growing on apothecium of *G. squalezens* (Fryday 9175, MSC). **j** Degenerated apothecia of *G. squalezens* infected by *Moriola* sp. (Fryday 9175, MSC). Scale bars: **a**, **j** 0.5 mm; **b** 1.0 mm; **c**, **e** 5  $\mu$ m; **d** 70  $\mu$ m; **f** 100  $\mu$ m; **g** 7.5  $\mu$ m; **h** 0.25 mm; **i** 10  $\mu$ m

analysis was therefore continued for an additional 15 million generations, after which convergence had been achieved and the resulting posterior consisted of 600,002 samples.

We found high support for a monophyletic new genus within the *Sphaerophoraceae* and describe this as the new genus *Gilbertaria* below. Comparisons of analysis results for

the two different alignment sets showed no important differences, with the support for the node uniting the *Sphaerophoraceae* being high across all four analyses (PASTA alignment set: PP = 1, BS = 99; GUIDANCE2 alignment set: PP = 1, BS = 100), as was the support for the node uniting *Gilbertaria* (PASTA alignment set: PP = 1, BS = 100; GUIDANCE2 alignment set: PP = 1, BS = 100). Because of the similar results, only the results from the analyses of the PASTA alignment set are presented in Fig. 1.

Within the genus *Gilbertaria*, we found high support for the existence of at least five distinct species (Fig. 1). Four of these correspond to entities possible to delimit anatomically, and we revise three of these species and describe one as new below. A fifth terminal (*Gilbertaria* sp. in Fig. 1) could represent an additional, undescribed species.

## Taxonomy

***Gilbertaria* M. Svensson & Fryday, gen. nov.** Figs. 2a–g, 3a–j

MB845153

Distinguished from other genera of the *Sphaerophoraceae* by the crustose habit and 1-septate ascospores formed in asci of the *Biatora*-type.

Type species: *Gilbertaria contristans* (Nyl.) M. Svensson & Fryday

*Thallus* granular-areolate, grey or very thin, gelatinous; rarely with solitary soralia, K–, C–, UV– or UV+ faintly grey. *Photobiont* chlorococcoid, 6–15 µm. All species are frequently associated with tufts of filamentous cyanobacteria (*Stigonema* sp.) that occur between areoles or in the vicinity of apothecia. *Apothecia* black, lecideine, more or less flat to strongly convex, usually without any discernible margin, without pruina, without crystals refracting polarized light, without any discernible boundary tissue (sensu Döring and Wedin 2000) between vegetative and regenerative tissue. *Proper exciple* absent or composed of sparsely branched, radiating hyphae. *Hymenium* 50–70 µm tall; *paraphyses* comparatively broad, (1.5–)2–3(–4) µm, septate, not or only slightly thickened apically, without pigmented cap, slightly branched above, sometimes anastomosing, conglutinate in a hymenial gel. *Hypothecium* colourless or dilute brown, rarely darker brown, massively developed (250–350 µm deep). *Asci* 8-spored, cylindrical to clavate, 10–45 × 4–20 µm; *tholus* KI+ blue with a narrow conical masse axiale, the border of the surrounding tholus KI+ darker blue (*Biatora*-type; cf. Hafellner 1984, 266 for illustration). *Ascospores* (0–)1(–3) septate, 5–18 × 2–6 µm. *Conidiomata* not observed by us.

*Chemistry*: Standard spot tests all negative and no secondary metabolites detected by HPTLC. However, the one species with a well-developed thallus (*G. squalescens*) is sometimes UV+ faintly grey to white. Traces of unidentified

compounds were detected in some specimens, especially of *G. contristans*. However, these likely emanate from the substrate, as similar compounds were detected in the same specimens when only the bryophyte substrate was analyzed by HPTLC. Two pigments occur in the apothecia of *Gilbertaria*: one blue, K+ brighter greenish blue, N+ magenta (Cinereorufa-green sensu Meyer and Printzen 2000) and one brown, K–, N+ magenta or N+ golden-brown.

*Etymology*: The genus commemorates the British lichenologist Dr Oliver Gilbert (1936–2005), with the suffix ‘-aria’ from *Catillaria*, the genus where the generitype species was previously placed. In a series of papers between 1982 and 1995, Dr Gilbert led the effort to rediscover and document the lichen biota of the mountainous areas of the British Isles. These included an account of the outstandingly rich lichen biota of the Ben Lawers National Nature Reserve (Gilbert et al. 1988), from where the type specimen of the generitype of the new genus was collected more than a century previously.

*Ecology*: All *Gilbertaria* species are primarily alpine and grow on dead or dying bryophytes on rock-walls or in areas of late snowlie.

*Notes*: Within the *Sphaerophoraceae*, *Gilbertaria* is the only known genus consisting of species with a crustose growth form. The genera *Bunodophoron*, *Calycidium*, *Leifidium* and *Sphaerophorus* all further differ from *Gilbertaria* by forming mazaedia, in which non-septate, often pigmented ascospores are formed in prototunicate asci without any apical structures (Wedin 1993; Wedin et al. 1998). The two remaining genera of the family both have lecideine apothecia with Lecanoralean asci but are clearly different from any species of *Gilbertaria*. The two known species of *Neophyllis* both have squamulose thalli containing lichen substances, form up to 2 mm broad apothecia on top of podetia and have broad (5–13 × 4–7 µm) unicellular ascospores (Wei and Ahti 2002; Kantvilas 2022). The sole species of the genus *Austropeltum*, *A. glareosum*, has a squamulose to foliose thallus, forms large (up to 5 mm diam.), stalked apothecia on the lobe margins, and has fusiform, unicellular ascospores (Henssen et al. 1992). Both genera also have asci with an amyloid tholus penetrated by a darker-staining tube-structure (Henssen et al. 1992; Kantvilas 2022), which is different to that found in *Gilbertaria*.

*Gilbertaria* species have sometimes been confused with the type species of the genus *Protomicarea*, *P. limosa*. However, *Protomicarea limosa* differs from *Gilbertaria* by having reddish brown pigments in the apothecia, an ascus of the *Psora*-type with unicellular ascospores and a white thallus usually containing pannarin (Hafellner and Türk 2001; Coppins 2009). The recently described genus *Micareopsis* R.C. Harris & Lendemer, with the single species *M. irriguata* R.C. Harris & Lendemer, is somewhat similar to *Gilbertaria*, but differs by having an ascus of

the *Lecanora*-type, a reddish-brown K+ purple pigment in the hypothecium and by having a thallus containing sphaerophorin (Lendemer et al. 2013).

We have not observed pycnidia on any collection of *Gilbertaria* but Cannon et al. (2022) described them for '*Catillaria*' *contristans* as 'black, ± immersed, the wall dark green; conidiogenous cells in chains; conidia 3.5–4 × 0.7–1 µm, bacillar'. However, one collection of *G. squalescens* (Fryday 9175) supported several conidiomata resembling acervuli up to 0.2 mm across with a thick roughened, ± carbonaceous upper surface, and with bacilliform conidia, 4–6 × 1 µm. These conidiomata were concentrated in a small area of the thallus and, because we have not seen them on any other collection and acervuli are not usually produced by lichenized fungi, we suspect that they may belong to a lichenicolous fungus.

***Gilbertaria astrapeana* Fryday & M. Svensson, sp. nov.**

Fig. 2a, f

MB845154

Distinguished from *G. contristans* and *G. squalescens* by the lack of a visible thallus and from *G. holomeloides* by the longer ascospores. Further distinguished from all three species by its DNA sequence data.

Type: Falkland Islands, West Falkland, Port Howard, Mt Maria, Lightning Rocks, 51.619028°S, 59.601849°W, 575 m, over bryophytes on S-facing rocks, 26 January 2015, A.M. Fryday 10914 (holotype: MSC [TLC: negative]; isotype: E).

*Thallus* effuse, covering several cm<sup>2</sup>, at most a thin, pale brown gelatinous film may be present; apothecia arising directly from the *Gymnomitrium* substrate. *Photobiont* chlorococcoid, a few cells c. 10–15 µm diam. with a thick hyaline wall 1–2 µm wide, but not definitely associated with the fungus.

*Apothecia* black, lecideine, strongly convex even when immature, proper margin not apparent, 0.2–0.5 mm diam; usually ± orbicular but larger apothecia becoming irregular or even slightly lobed. *In section, proper exciple* not apparent. *Hymenium* 50–70 µm tall; *paraphyses* 1.5–2(–2.5) µm wide, septate, cells 15–20(–25) µm long, not constricted at the septum, slightly branched especially towards the apices, which are not swollen and are immersed in a hymenial gel; upper 5–10 µm (*epihymenium*) patchily dark blue- (K+ greenish-blue, N+ magenta), overlaid by a few minute granules that are POL–, K–, N+ blue, lower 30–70 µm dilute grey (K+ dilute purple-brown, N+ orange-red) with dark streaks and spots (K+ blue-black, N+ magenta); lower part (*subhymenium*) merging imperceptibly into the hypothecium. *Hypothecium* massively developed (–350 µm deep), composed of randomly organized, hyaline hyphae, c. 3 µm wide with numerous dark blue streaks and spots (K+ greenish-blue, N+ magenta). All pigments ultimately N+ magenta. Asci *Biatora*-type, cylindrical c. 30 × 10 µm, becoming clavate and c. 15 µm wide;

*ascospores* hyaline, 1-septate, (14–)15.4 ± 0.9(–17) × (3–)3.3 ± 0.3(–4) µm; l/b ratio (4.3–)4.7 ± 0.3(–5.1), *n* = 20, narrow ellipsoid with rounded, pointed attenuated apices, but with one end more rounded and the other tapering to a more pointed apex. *Conidiomata* not observed.

*Etymology*: The epithet is derived from *Astrape* (ἄστραπή), the Greek goddess of lightning and the type locality 'Lightning Rocks'.

*Ecology and distribution*: Known only from the type collection, which occurred on a bryophyte (*Gymnomitrium* sp.) mat on a siliceous rock outcrop in wind-swept, alpine tundra. Associated species: *Coccotrema corallinum* Messuti and *Lepra argentea* Fryday.

*Notes*: The type collection was originally determined as *Catillaria contristans* (Fryday et al. 2019), but the lack of a visible thallus suggested it may represent a distinct taxon. This was confirmed by DNA sequence data, which showed that it was closer to *G. holomeloides*, which also lacks a visible thallus but has shorter ascospores. This is the only confirmed record of a species of *Gilbertaria* from the Southern Hemisphere (see below under *G. contristans* for further discussion).

***Gilbertaria contristans* (Nyl.) M. Svensson & Fryday, comb. nov.** Fig. 2b–e, g

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≡ *Lecidea contristans* Nyl., Flora 48: 354 (1865). *Biatorina contristans* (Nyl.) Arnold, Flora 53: 473 (1870). *Catillaria contristans* (Nyl.) Zahlbr., Catalog. Lich. Univ. 4: 35 (1926).—Type: [Scotland,] Ben Lawers' top, 1864–07, I. Carroll 136 (lectotype: H-Nyl 18859 = H9510370!, designated here, MBT10008586; isolectotype: BM000974769!).

= *Lecidea sabuletorum* f. *simplicior* Nyl., Lich. Scand.: 206 (1861). *Lecidea dufourii* Ach. ex Nyl. [as 'duforei'], Flora (Regensburg) 50: 373 (1867). *Lecidea simplicior* (Ach. ex Nyl.) Lindsay, J. Linn. Soc. 9: 372 (1867) [ICN 41.3]. *Lecidea sabuletorum* var. *dufourii* (Ach. ex Nyl.) Leight., Lich.-Flor. Great Brit.: 338 (1871). *Bilimbia sabuletorum* f. *simplicior* (Ach. ex Nyl.) Branth, Meddel. Grönland 3: 494. (1892). *Bilimbia sphaeroides* subsp. *muscorum* f. *dufourii* (Ach. ex Nyl.) Boist., Nouv. Flore. Lich. (2): 190 (1903). *Bacidia dufourii* (Ach. ex Nyl.) Lettau, Hedwigia 52: 133 (1912). *Bilimbia trisepta* f. *simplicior* (Ach. ex Nyl.) Vain., Acta. Soc. Faun. et Flor. Fennic. 53: 258 (1922). *Catillaria dufourii* (Ach. ex Nyl.) Vain. Acta. Soc. Faun. et Flor. Fennic. 53: 140 (1922). *Thalloidima dufourii* (Ach. ex Nyl.) Hav., Bergens Mus. Årbok, Naturv. Raekke 2: 41 (1936).—Type: [Sweden, Härjedalen,] Funnesdalsberget [= Funäsdalsberget], [no date,] Thedenius (lectotype: H-Nyl 18849 = H9510371!, designated here, MBT10008587).

= *Lecidea hypocyanea* Stirt., Scot. Natural. 5: 218 (1879), non *Lecidea hypocyanea* Vain. nom. illeg. [ICN Art. 53.1],

Lichenogr. Fenn. 4: 300 (1934).—Type: Scotland, East Clough[?], Ben Lawers, 1874-08, [J. Stirton] (holotype: BM 000974761!).

*Thallus* rarely more than 1–2 cm across, light grey to lead grey, often discoloured light yellowish to light yellowish brown in old herbarium material, composed of smooth shiny granules 0.2–0.3 mm across, sometimes becoming proliferate and forming shortly branched areoles to 0.8 mm that may form a confluent crust to 1.5 mm across, K–, C–, Pd–, UV–. *Cortex* up to 20 µm thick, composed of hyaline, horizontally arranged cells c. 10 × 4 µm. Areoles rarely bursting open to form blue-green *soralia* 0.2–0.3 mm across. *Photobiont* chlorococcoid, cells 7–12(–14) µm diam.

*Apothecia* black, shiny, convex and marginless when young, becoming flatter when mature, immersed between areoles or sessile, (0.4–)0.7–0.9 mm diam, often with an irregular outline and/or appearing to be formed from several confluent apothecia, 1.2–1.5 mm across. *In section, proper exciple* not clearly differentiated from the hymenium, ± hyaline or pale blue internally becoming increasingly blue pigmented outwards with the outer 5–10 µm often strongly blue pigmented; composed of radiating, sparsely branched and anastomosing hyphae 1.5–2.5 µm wide laterally, becoming less well organized below the hypothecium with hyphae up to 4 µm wide. *Hymenium* 60–70 µm tall, ± hyaline or pale blue with the upper 5–10 µm (*epihymenium*) strongly blue pigmented (K+ brighter greenish blue, N+ magenta), often with a thin (< 5 µm) *epipsamma*; *paraphyses* conglutinated even in K, ± simple, sometimes branched near the apex, septate with cells 15–20 µm long, only slightly (or not at all) constricted at the septum, 1.5–3.0 µm wide, not or only slightly widened at the apex. *Hypothecium* hyaline to dilute brown (K–), c. 250 µm deep, composed of randomly arranged hyphae c. 3 µm wide. *Asci* *Biatora*-type, cylindrical, c. 30 × 10 µm; *ascospores* hyaline, (0–)1(–3)-septate, irregularly biseriolate in ascus, (9.5–)13.3 ± 2.0(–18) × (2.5–)4.1 ± 0.8(–6) µm; l/b ratio (1.7–)3.41 ± 0.9(–6), *n* = 75, ellipsoid, often ± dacryoid with one end rounded and the other tapering to a narrow, rounded point. *Conidiomata* not observed.

*Ecology and distribution:* *Gilbertaria contristans* is an alpine species that grows on tufts of dead bryophytes (e.g. *Andreaea* Hedw., *Racomitrium* Brid.) on acid rocks, including seepages. Associated species include *Buellia chionea* (Th.Fr.) Sheard, *Frutidella caesioatra* (Schaer.) Kalb, and *Stereocaulon* spp.

*Gilbertaria contristans* is known from Northern and Central Europe as well as Greenland, but its status in North America is uncertain. It was first reported for the continent by Miller et al. (2005) and confirmed by Hinds et al. (2009) but we re-examined the specimens upon which those reports were based and they do not appear to represent a species of *Gilbertaria*. It was also reported from Alaska by Dillman

et al. (2012) but the specimen upon which this report is based (Thor 8863, in S) was not available for study. Other collections from the USA (Alaska) and Canada identified as this species are included in the Consortium of North American Lichen Herbaria database (<https://lichenportal.org/cnalh/>). One of these collections (from Québec) is a misidentification of *G. holomeloides* (see below), and another from Alaska (in ASU) is *Micarea turfosa* (A.Massal.) Du Rietz and it is probable that *G. contristans* has not been correctly reported from the continent. Although *Gilbertaria contristans* has been reported from Australia (Tasmania) that report is based on a misidentification (see below). It has been reported from New Zealand (Galloway 2007) and although we have not seen this collection, Galloway's description of the habitat as 'on soil in snowbanks' and apothecia as 'convex to subglobose' suggests it is more likely to be *G. astrapeana* or *G. holomeloides*. However, the description of the thallus as 'warty granular' excludes both of these species. It was also reported from the South Shetland Islands by Søchting et al. (2004) and, although we have not examined the specimens, macrophotographs of these collections likely represent a *Micarea* sp.

*Notes:* We located two syntypes of *Lecidea contristans*. The collection BM00974769 is very small and contains only 2–3 apothecia. As the collection H-Nyl 18859 is somewhat larger, we designate this collection as the lectotype.

When describing *Lecidea sabuletorum* f. *simplicior*, Nylander (1861) referred to material from at least three localities: 'supra muscos ad Helsingfors [ipse] et in Sueciae montibus [Thedenius] atque supra terram in Lapponia'. We found two collections that are likely part of the original material under the name *Lecidea sabuletorum* f. *simplicior* in H-Nyl, namely a Thedenius collection (H-Nyl 18849) and a collection from 'Rossia Lapponia' made by G. Selin in 1861 (H-Nyl 18841). The material collected in Helsinki cited by Nylander (1861) was not found in H-Nyl. However, this collection was apparently examined by Fries (1874), who, based on this, reduced *L. sabuletorum* f. *simplicior* to synonymy with *Lecidea verrucula* Norman (= *Micarea turfosa*). We located a collection with the label 'Helsingfors prope rivum Tali, W. Nylander 1851' in UPS (L-774560!), which likely is the same collection as the one cited in the protologue of Nylander (1861). This collection indeed represents *Micarea turfosa*, whereas the collections H-Nyl 18849 and H-Nyl 18841 are both referable to *G. contristans* (see also Coppins 1983: 200). We view a lectotypification on one of the latter two collections as preferable, as that would be more in line with how the name has been used. As the Thedenius collection is the larger of the two, we designate this as the lectotype of *L. sabuletorum* f. *simplicior*.

*Lecidea sabuletorum* f. *simplicior* was subsequently raised to the level of species by Nylander (1867, as *Lecidea dufourei*) and possibly also by Lindsay (1867, as *Lecidea*

*simplicior*). In the latter case, Lindsay did not directly cite the basionym, but the name could still be legitimate because he gave the authority of his name as ‘Nyl. MS’ and also mentioned that it could be a mere variety of *Lecidea sabuletorum*, which could be considered an indirect reference to the basionym thus validating the name (ICN Art 41.3). Anyway, Lindsay’s *L. simplicior* has, as far as we know, never been in use.

When raising *Lecidea sabuletorum* f. *simplicior* to the level of species, Nylander (1867) chose the new epithet ‘*dufourii*’, an unpublished name that he ascribed to Acharius (various spellings of this epithet occur in the literature; both above and in the following we have chosen to correct the spelling to ‘*dufourii*’ following ICN Art. 60.8). The status of *Lecidea dufourii* is that of a replacement name for *L. sabuletorum* f. *simplicior*, both because the wording in the protologue suggests that this was Nylander’s intention (ICN Art. 6.11), but also because *L. dufourii* was validated only by reference to the earlier description of *L. sabuletorum* f. *simplicior* (ICN Art. 6.12). Consequently, the designated lectotype of *L. sabuletorum* f. *simplicior* is also the lectotype of *L. dufourii* (ICN Art. 7.4). The material cited by Nylander (1867) when introducing the name *L. dufourii* (likely corresponding to H-ACH 442, its smaller duplicate UPS-ACH L-00423, and H-Nyl 18848a, b and c) is therefore not part of the original material of *L. dufourii*. Although it does not matter for the typification, we note that the poorly developed material in H-ACH and UPS-ACH represents a species with a dark thallus growing on calcareous rock, which is not conspecific with (or even closely related to) H-Nyl 18848a, b or c, which all are *G. contristans*.

In the past, there has been much confusion regarding the delimitation of *Gilbertaria contristans* and *G. squalescens*, with old herbarium collections of these two species seemingly randomly assigned to either of these two epithets (or their synonyms). We have found several examples of collections where the species occur in mixtures or are glued next to each other, apparently because the collector considered them to be of the same species. Several taxonomists have also treated them as one species, for example Fries (1874, as *Toninia squalescens*) and Körber (Koerber 1861, as *Catillaria sphaeralis*, where the original material includes both species). In contrast, modern floras (e.g. Foucard 2001; Fletcher and Coppins 2009; Hitch et al. 2009) tend to accept both species, but without pointing out that they are similar to each other. As we show here, *G. contristans* and *G. squalescens* are well separated both morphologically and genetically. *Gilbertaria contristans* differs from *G. squalescens* in having a thallus composed of smaller areoles that often forms a confluent crust, as opposed to a thallus of larger, bullate areoles in *G. squalescens*. *Gilbertaria contristans* may, unlike *G. squalescens*, also form soralia, a feature which we report for the first time here. However, these are too rare to

be of much use for species determinations. The apothecia in *G. contristans* tend to be rather flat and are immersed between areoles or sessile, whereas the apothecia in *G. squalescens* are mostly strongly convex with a ± constricted base. Finally, the ascospores in *G. contristans* are on average longer (usually > 10 µm; < 10 µm in *G. squalescens*) and have a higher length/breadth ratio (c. 3.5; 2.5 in *G. squalescens*).

*Gilbertaria contristans* may also be confused with other crustose lichens with 1-septate ascospores and similar pigmentation. Material from Tasmania reported as *Catillaria contristans*, and from which sequences were used in the phylogenetic analysis of Andersen and Ekman (2005), actually represents *Micarea oreina* (Kantvilas and Coppins 2019). This species differs from *G. contristans* by, for example, having thin, anastomosing paraphyses 1–1.7(–2) µm wide, broader ascospores (–8 µm wide) and aascus of the *Micarea*-type (Kantvilas and Coppins 2019). Other species of *Micarea*, for example *M. lignaria* (Ach.) Hedl. and *M. viridiatra* Coppins, may occur in the same habitat as *G. contristans*, but can also be distinguished by having thin, anastomosing paraphyses and a ‘micareoid’ (4–8 µm in diam.) photobiont. A further species with 1-septate ascospores and pigmentation similar to *G. contristans* is *Megalania jemtlandica* (Th.Fr. & Almq.) Fryday, which differs by having larger ascospores (16–26 × 7–10 µm; Fryday 2004a).

According to Cannon et al. (2022), *G. contristans* may have immersed pycnidia, containing conidia 3.5–4 × 0.7–1 µm.

**Selected additional specimens examined: Finland.** *Inari Lapland*: Inari par., Pitkävuo, 1870-09, F. Silén 300 (H9221063). Utsjoki par., Kevo Subarctic Research Station c. 3 km SW, cliff Kotkapahta in Kevojoki valley, on *Andreaea* in seepage, 1965-08-20, T. Ahti 20913 (H 9221061). *Lapponia Enontekiensis*: Enontekiö par., Enontekis, Pietsovara, 1867, J.P. Norrlin (H 9221063, UPS L-707497). Enontekiö par., SW-Saena, ad rupem subcalcar. muscorum, 1949-07-21, A.J. Huuskonen (H 9221060). **France.** Vosgesis [= in the Vosges mountains], 1840, M. Blind (H-Nyl 18848a); Vosgesis, [no date, no collector] in herb. Lenormand (H-Nyl. 18848b). **Greenland.** *Disko*: Mellanfjorden, 1871-08-07, T.M. Fries (S F331952 [TLC: negative]). Nepisat [= Nipisat], 1871-06-21, T.M. Fries (S F331953). **Iceland.** *Borgarfjarðarsýsla*: Akrafjallet [= Akrafjall], 1937-07-28, B. Lyng (S F331958 [TLC: negative]; UPS L-797513). *Vesturland*: Hvammur, 1876-08-13, C. Grönlund (UPS L-797517). *Snæfellsnessýsla*: Fróðárheiði pass, Miðfjell and Knarrarfjall Mts, elev. 360 m, 64.50470N 23.28388W, over mosses on basaltic rock, 2009-07-22, A. Nordin 6821 (UPS L-204756). **Norway.** *Finnmark*: Werrethamn, 1802-06-18, G. Wahlenberg (UPS L-797514 [TLC: negative]). Sør-Varanger, slope E of lake Båtvatnet, elev., 120 m, UTM: NS8075 (2333 II), mossy rock in pine forest, 1986-07-22, E. Timdal 4639 (O L101196). *Hordaland*:

Ulvik, Finse, Jomfrunut, 1916-07-19, G.E. Du Rietz (UPS L-604110). *Nordland*: Nordal hd, Geiranger, elev. 100 m, on moss, 1947-07-10, A.H. Magnusson 20807 (UPS L-145351). Vega par., Vega Island, Eidem, hill S of the old farm, exposed rock, 1976-06-15, G. Degelius V-1568 (UPS L-72595). *Sogn og Fjordane*: Flora, Levrasundet, on mosses, 1977-06-29, S.W. Sundell 11817 (UPS L-710818). *Sør-Trøndelag*: Oppdal, Dovre, Jerkind, Geteryggen, 1863, T.M. Fries (with *G. squalescens*, UPS L-797509). Ørland, Vardeheia, elev. 80-150 m, UTM (WGS84): NR 368-372 662-663 (map: 1522 II), on *Andreaea* sp., 1997-07-15, R. Haugan 7443 (O-L119417). **Russia**. *Laponia Orientalis*: 1861, G. Selin (H-Nyl 18841). **Sweden**. *Härjedalen*: Ljusnedal par., Anåfjället (Ånnfjället), klipphylla nära krönet 1301, 1950-08-09, S.W. Sundell 123-50 (UPS L-709450). Tännäs par., Funnäsdalsberget, 1866, S. Almquist (with *G. squalescens*, S F332018). *Jämtland*: Åre par., Handöl, 1873, S. Almquist & E. Almquist (S F332032 [TLC: negative]); Handölsfällan, 1913-08-31, G.E. Du Rietz (UPS L-167818 [TLC: negative]); Täljstensberget, 1913-07-29, G.E. Du Rietz (UPS L-167819 [TLC: negative]). Åre par., Snasahögen, blockhav i övre regio alpina, 1913-07-12, G.E. Du Rietz (S F332036; UPS L-167817 [TLC: negative]); 1910-07-23, G.O. Malme (S F331975); 1913-06, G.O. Malme (S F332038); 1914-06-14, G.O. Malme (S F331993 [TLC: negative]); Skurdalsporten, 1914-06-25, G.O. Malme (S F331995 [TLC: negative]). Undersåker par., Vällista [= Mt. Välliste], 1913-06-15, G.O. Malme (S F331990 [TLC: negative]); 1914-06, E.P. Vrang (with *G. squalescens*, UPS L-797489 [TLC: negative]). Undersåker par., Mt. Middagsvalen, ca 2 km SE of Vallbo, ca 200 m S of the highest part, elev. 860 m, 63°14090N, 13°04617E, on flat, mossy rock, 2013-08-16, A. Nordin 7573 (UPS L-632796). Undersåker par., Gåsäliden, close to the path from Edsåsen, c. 7.5 km SW of Undersåker, elev. 850, 63°27854N, 13°12772E, on bryophytes on horizontal rock, 2015-08-24, A. Nordin 7877 (UPS L-722977). Åre par., Mt. Täljstensvalen, at the summit, 63°2427N, 12°4604E, on mosses on rock, 2018-07-24, M. Westberg, UCCLR102 (UPS L-931311, MSC). *Lule Lappmark*: Gällivare par., Dundret, elev. 800 m, 1921-08-11, A.H. Magnusson 6318 (UPS L-797498). Kvikkjokk par., in saxi muscosi infra Skärfi [= Skierfe], 1871, P.J. Hellbom & E.V.M. Hellbom (with *G. squalescens*, S F332030). *Torne Lappmark*: Jukkasjärvi par., Abiskosuolo, on irrigated rocks on an islet, 1921-07-08, A.H. Magnusson 5578 (S F332028; S F332022 [TLC: negative]; UPS L-797494); on steep rock, to the north (UPS L-71954). **United Kingdom**. [Wales:] Cader [= Cadair] Idris, [no date, W.A. Leighton?] no. 115 (H-Nyl 18848c).

**Exsiccata: Iceland**. *Arnesýsla*: valley of the Sauoá river, N of the Gafudalur farmstead 2 km N of the village of Hveragerdi, lat/long 64°01N, 21°12E, grid: RN 7016800 154230, alt. 80 m, growing on cushions of *Andreaea* on steep faces of big boulders situated at the edge of the stream, 1979-

06-28, H. Hertel 21165 (Hertel, Lecid. Exs. No 342, UPS L-125823). **Slovakia**. Carpati, Tatra Magna, in valle 'Velická dolina', supra lacum 'Velické pleso' dictum, alt. 1850 m.s.m., ad rupes graniticas, supra pulvinos musorum, 1969-09-10, A. Vězda (as *Catillaria dufourei*, Vězda, Lich. Sel. Exs. No 856, S F330939; UPS L-024587). **Sweden**. *Jämtland*: Snasahögen, 1912-07-12, G.O.A. Malme (as *Toninia squalescens*, Malme, Lich. Suec. Exs. No 314, H; UPS L-108908).

***Gilbertaria holomeloides* (Nyl.) M. Svensson & Fryday, comb. nov.** Fig. 3a, c, d  
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≡ *Lecidea holomeloides* Nyl., Flora 49: 369 (1866). *Biatorina holomeloides* (Nyl.) Arnold, Flora 53 (30-31): 474 (1871).—Type: [United Kingdom, Scotland,] Ben Lawers, [no date], [T.] Jones (holotype or syntype: H-Nyl 19139 = H9510514!).

*Thallus* widespreading but effuse, at most a thin, pale greyish to brown gelatinous film may be present; apothecia arising directly from the *Gymnomitrium* substrate. *Photobiont* chlorococcoid, 8–12(–16) µm with a thick hyaline wall 1–2 µm; thin-walled chlorococcoid algae 4–6 µm sometimes also occur.

*Apothecia* black, lecideine, sessile with a ± constricted base, strongly convex even when immature, orbicular 0.2–0.3(–0.5) mm diam., proper margin not apparent. *In section*, proper exciple not apparent. *Hymenium* 45–70 µm tall, hyaline or rarely light blue-green; *paraphyses* mostly (1–)1.5–2.5 µm wide, occasionally with solitary thicker paraphyses (–3.5 µm wide) interspersed among the narrower, more numerous ones, septate (cells 10–15 µm long), not or slightly constricted at the septa, often forked towards the apices, which are not swollen and immersed in a hymenial gel, sometimes anastomosing in their lower part; upper 5–10 µm (*epihymenium*) patchily blue (K+ brighter greenish-blue, N+ magenta), the pigment often confined to a gel-matrix above the paraphyse apices; lower part (*subhymenium*) merging imperceptibly into the hypothecium. *Hypothecium* massively developed (–250 µm deep), composed of randomly organized, hyaline hyphae c. 3 µm wide, patchily light-brown, rarely darker brown (K–), often with numerous dark blue-black streaks and spots (K+ blue-black, N+ magenta). All pigments ultimately N+ magenta. *Asci* *Biatora*-type, cylindrical c. 45 × 10 µm, becoming clavate when mature, 25 × 20 µm; *ascospores* hyaline, (0–)1-septate, (9–)11.7±1.7(–15) × (2.0–)3.4 ± 0.7(–4.5) µm; l/b ratio (2.2–)3.6 ± 0.3(–4.7), n = 37, straight or slightly bent, narrow ellipsoid with bluntly pointed apices. *Conidiomata* not observed.

*Ecology and distribution*: *Gilbertaria holomeloides* is a pioneer species of arctic-alpine environments, typically

growing on moribund *Gymnomitrium* mats in areas of late snow-lie. Accompanying lichen species are few or absent but may include *Ameliella grisea* Fryday & Coppins and small thalli of, for example, *Solorina crocea* (L.) Ach. and *Thamnolia vermicularis* (Sw.) Schaer. *Gilbertaria holomeloides* is currently known from the UK (Scotland), Sweden and Canada (Québec). In both Canada and the UK, it is known from only a single locality but in Sweden the species appears to be quite common. There may also be other collections that have been incorrectly identified as *Catillaria* (or *Lecidea*) *contristans*, such as the exsiccata specimen from the U.K. cited below. However, *G. holomeloides* has likely been overlooked in the past due to its small size and because of growing on a substrate where few other lichens occur. The species is likely to be much more widely distributed than the records listed below indicate.

**Notes:** Nylander (1865, 1866) described *Lecidea contristans* and *L. holomeloides* from the same locality (Ben Lawers), but without comparing the two species. This, taken together with the anatomical similarity of the apothecia, probably contributed to *L. holomeloides* soon being treated as a synonym of *L. contristans*. As is clear from our phylogeny (Fig. 1), the two species are indeed closely related but well separated genetically. The most obvious morphological differences between *G. contristans* and *G. holomeloides* are the absence of a well-developed thallus and the smaller apothecia and ascospores in *G. holomeloides*. The ecology of the two species is also different as *G. contristans* grows in more dry situations on dying bryophytes on, for example, sloping rock-walls, whereas *G. holomeloides* tends to grow in more humid situations on the ground. *Gilbertaria astrapeana* is very similar to *G. holomeloides* but differs by having larger ascospores.

With its small, black and immarginate apothecia, *Gilbertaria holomeloides* is possible to mistake for a species of *Micarea*. The most similar species in that genus is *Micarea viridiatra*, which may grow in the same habitat as *G. holomeloides* and has similar pigmentation as well as 1-septate ascospores of about the same dimensions (Coppins 1985). It differs by having thin (1.3–1.7 µm wide), more richly branched and anastomosing paraphyses, by having pycnidia (unknown in *G. holomeloides*), by the absence of any brown pigment in the apothecia (Coppins 1985) and an ascus of the *Micarea*-type (our observations). *Megalania jemtlandica* is also superficially similar to *G. holomeloides* and may have a thin and varnish-like thallus when growing on dead *Gymnomitrium* but differs by having much larger ascospores (16–26 × 7–10 µm; Fryday 2004a).

**Additional specimens examined:** **Canada.** Québec: Nunavik, Detroit d'Hudson, 5.9 km au sud-est du fond de l'anse Erik, 62°49'30"00N, 77°30'59"9W, 263 m., avec *Gymnomitrium*, paroi ferrugineuse d'exposition ouest, 2015-08-10, J. Gagnon 127.15c (QFA). **Sweden.** Jämtland: Undersåker par., about 3 km NW of Storulvån Mountain

Lodge, the E top of Mt. Getryggen (Tjiejhtenrudtje), 63°18'32"27N, 12°32'17"99E, SWEREF99: 7008818 365221, elev. 1375 m, wind-swept alpine mountain top, on mosses on the ground, 2017-08-14, M. Svensson 3264 (UPS [TLC: negative]). Undersåker par., Mt. Välliste, just N of the track on the NE part of the mountain, 63°27'22"1N, 13°14'53"7E, SWEREF99: 7017262 406946, elev. 965 m, on dead or dying bryophytes on the ground, 2019-06-26, M. Svensson 3493 (MSC; UPS [TLC: negative]). Undersåker par., Sylarna, about 400 m NW of Sylarna Mountain Station, 63°04'49"6N, 12°26'75"8E, SWEREF99: 6993534 361838, elev. 1040 m, on soil and mosses in area of late snow-lie, 2019-07-03, M. Svensson 3513 (UPS [TLC: negative]). **Lule Lappmark:** Jokkmokk par., Padejlanta National Park, 11 km WNW of Staloluokta, N of the river Duvgejåhkå (Tukijåkkå, Tokijokk), between Mt. Stuorra Duvge (Stuor Tokivare, Stuorra Tuki) and Mt. Unna Duvge (Unna Toki, Unna Tuki), bare mountain region, 210 m E of small cabin, 67.34502, 16.4521, elev. 678 m, on bryophytes on small hill, 2020-07-31, M. Westberg PAD024 (UPS L-1019033); *ibid.*, E slope of Mt. Unna Duvge, bare mountain region, 1040 m NE of small cabin, 67.35321, 16.45813, elev. 791 m, on bryophytes on sloping siliceous rock, 2020-08-04, M. Westberg PAD324b (UPS L-1019036). **Pite Lappmark:** Arjeplog par., ridge along the NW part of the lake Ikkesjåvrr close to the border to Norway, on mosses on boulder in a late snow area, 66°53'N, 16°01'E, 2017-08-25, M. Westberg, L. Hedenäs & G. Odelvik PL336 (in collection of *Ameliella grisea*, UPS L-930873). **Torne Lappmark:** Jukkasjärvi par., Mt. Vassitjåkkå (= Vässeöhhkka), the top plateau, elev. 1490 m, 68°38'13"8N, 18°27'50"8E, på jord och klippphyllor på toppskulten, 1943-08-22, G.E. Du Rietz (UPS L-953210).

**Exsiccatum: United Kingdom.** Scotland: [Mid Perthshire (VC 88):] supra terram prope cacumen montis Scotiae Ben Lawers, J.M. Crombie (as *Lecidea contristans*, Crombie, Lich. Brit. Exs. No. 177, UPS L-724606).

***Gilbertaria squalescens* (Nyl.) M. Svensson & Fryday, comb. nov.** Fig. 3b, e–j

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= *Lecidea squalescens* Nyl., Öfvers. Kgl. Vetensk.-Akad. Förhandl. 17: 297 (1860). *Toninia squalescens* (Nyl.) Th.Fr., Lich. Scand.: 340 (1874). *Thalloedema* [sic] *squalescens* (Nyl.) Stein in Cohn, Kryptog.-Flora von Schlesien 2 (2H): 174 (1879).—Type: [Norway] Dovre, [no date; on the isolectotype in UPS given as 1844] W.P. Schimper (lectotype: H-Nyl 18840 = H9510353!, designated by Timdal 1991 [ICN Art. 9.10]; isolectotypes: TUR-V 20271!, UPS L-797502!).

= *Thalloidima rimulosum* Th.Fr., Lich. Arct.: 174 (1860).—Type: [Norway,] Finnmark, Syd-Varanger, Jarfjorden, 1857-08-21, T.M. Fries (lectotype: UPS L-22985!, designated by Timdal 1991 [ICN Art. 9.10]; isolectotype: S F331961!).

= *Catillaria sphaeralis* Körb., Parerg. Lich.: 196 (1861). *Buellia sphaeralis* (Körb.) Anzi, Atti Soc. Ital. Sc. Natur. 9: 252 (1866). *Biatorina sphaeralis* (Körb.) Jatta, Sylloge Lich. Ital. Cryptog. Pars III: 565 (1911). *Bacidia sphaeralis* (Körb.) Erichsen, Flechtenfl. Nordwestdeutschl.: 154 (1957).—Type: [Czech Republic or Poland,] Sudetis, Schneekoppe, [no date,] [G.W.] Körber (lectotype: L-0056595, envelope marked ‘A’!, designated here, MBT10008588; isolectotypes: L-0063110!, UPS L-670616!).

= *Catillaria kivakkensis* Vain., Acta Soc. Faun. et Flor. Fennic. 57: 453 (1934).—Type: Rossia [= Russia], Karelia keretina, Kivakka, 1877, E. Wainio (holotype: TUR-V 22310! [TLC: negative]).

= *Lecidea subramosa* J. Lowe, Lloydia 2: 297 (1939).—Type: [U.S.A., New York, Adirondack Region,] Mount Marcy (near Lake Placid), elev. 4900 ft, on soil, 1933-08-23, J. L. Lowe 3130 (holotype: MICH!; Coppins and Fryday 2005).

*Thallus* of grey, bullate squamules 0.3–0.5(–0.8) mm diam. forming a ± contiguous crust up to 2–3 cm across, surface of squamules usually covered by a network of fine brown lines of a lichenicolous fungus, often miscoloured light yellowish to light yellowish brown in old herbarium material, K–, C–, Pd–, UV– or UV+ faintly grey or white. *Cortex* up to 20 µm thick, composed of hyaline, horizontally arranged cells c. 10 × 4 µm, larger squamules becoming hollow with a crust c. 0.1 mm thick. *Photobiont* chlorococcoid, cells 6–12 µm diam.

*Apothecia* black, strongly convex and marginless even when young, with a more or less constricted base; mature apothecia (0.3–)0.5–0.8 mm diam., often appearing to be formed from several confluent apothecia, 1.0–1.2 mm across. *In section, proper exciple* not apparent. *Hymenium* 50–70 µm tall; *paraphyses* 2–3(–4) µm wide, septate (cells 10–15 µm long), not constricted at the septum, slightly branched only towards the apices, which are not swollen and are immersed in a hymenial gel; upper 5–10 µm (*epihymenium*) patchily blue (K+ brighter greenish-blue, N+ magenta), the pigment extending down through the hymenium in broad streaks, usually with numerous hyphae of the lichenicolous fungus on the surface and these are also abundant at the base of the hypothecium. *Hypothecium* merging imperceptibly with the hymenium, massively developed (–350 µm deep), composed of randomly organized, hyaline hyphae, c. 3 µm wide, upper 50–75 µm dilute brown (K–, N+ dilute golden-brown) with darker spots, lower section ± hyaline. *Asci* *Biatora*-type, cylindrical c. 20–35 × 10 µm becoming somewhat clavate and 15 µm wide; *ascospores* hyaline, (0–)1(–3)-septate, (5–)8.5 ± 3.6(–14) × (2.5–)3.6 ± 0.6(–5) µm; l/b ratio (1.5–)2.5 ± 0.7(–4.7), *n* = 80, broadly ellipsoid, often with one end rounded and the other narrowing to a rounded point, sometimes ± dacryoid. *Conidiomata* not observed.

*Ecology and distribution:* *Gilbertaria squalescens* is primarily an alpine species, typically growing on tufts of bryophytes (especially *Andreaea* spp.) on slightly sloping, acid rock surfaces (including seepages) in open to somewhat shaded situations. Accompanying species include *Frutidella caesioatra*, *Gilbertaria contristans*, *Lecanora leptacina* Sommerf. and *Lepraria neglecta* (Nyl.) Erichsen. *Gilbertaria squalescens* is known from North America and far eastern Russia as well as Central and Northern Europe. It may have a northern, circumpolar distribution.

*Notes:* *Lecidea squalescens* and *Thalloidima rimulosum* were both described in 1860 (Fries 1860; Nylander 1860). Part 6 of *Öfversigt af Kongl. Vetenskaps-akademiens förhandlingar*, which contains the description of *L. squalescens*, has the publication date June 1860, whereas the publication of *Lichenes Arctoi*, in which *T. rimulosum* was described, took place between ‘Mai–Dec. 1860’ (Stafleu and Cowan 1976). It is thus not clear which of the two names has priority. However, in his later treatment of the species, Fries (1874) gave *L. squalescens* priority and listed *T. rimulosum* as a synonym. As long as the precise dates of publication are unknown, we accept Fries’ decision (see also Timdal 1991).

As mentioned by Liška (2013), four specimens of *Catillaria sphaeralis* that likely are part of the original material are available in L, one in Körber’s *Typenherbar* and three in his *Stammherbar*. In addition, we located a specimen in UPS that is likewise likely to be part of the original material (UPS L-670616). The specimen from the *Typenherbar* (L-0056594) is labelled ‘Lectotype’, but we are not aware of any earlier lectotypification of *C. sphaeralis*. It is a typical specimen of *Gilbertaria contristans*. Of the three specimens from the *Stammherbar*, one (L-0063110) is *G. squalescens*, one (L-0056595) contains unsorted bryophyte tufts with both *G. contristans* and *G. squalescens* and the last (L-0837153) may represent *G. squalescens* but is not in good condition. The very small specimen in UPS is also *G. squalescens*. The rather short protologue of *C. sphaeralis* (Körber 1861) is consistent with both *G. contristans* and *G. squalescens* and it is likely that Körber included both species in his concept of *C. sphaeralis*.

Since its description in 1861, *Catillaria sphaeralis* has mostly been treated as a synonym, either of *Catillaria contristans/dufourii* (Hafellner and Türk 2016; Nimis 2016; Vainio 1934;) or of *Toninia squalescens* (Fries 1874). A typification of *C. sphaeralis* on a collection containing either *G. contristans* or *G. squalescens* would thus, in both cases, be consistent with the protologue and with how the name has been used. Since *C. sphaeralis* is an older name than *Lecidea contristans*, a typification of *C. sphaeralis* on that species would mean reducing the epithet *contristans* to synonymy. In the interests of nomenclatural stability, we view the designation of a lectotype containing *G. squalescens* as more appropriate. The collections L0063110 and UPS L-670616

are both very small, and we have therefore chosen to designate part of the collection L0056595 as the lectotype of *C. sphaeralis*. As mentioned above, this collection contains both *G. contristans* and *G. squalescens*. We have therefore sorted the two species into separate envelopes, marked 'A' for *G. squalescens* (designated as lectotype) and 'B' for *G. contristans*.

*Gilbertaria squalescens* has often been confused with *G. contristans*, see discussion under the latter species. When growing on very small tufts of *Andreaea* or other bryophytes, *G. squalescens* may sometimes occur as smaller morphs, with a less developed thalli and smaller apothecia. Such a specimen was described as the new species *Catillaria kivakkensis* by Vainio (1934), who noted the similarities to *C. dufourii* (= *Gilbertaria contristans*). Small specimens of *G. squalescens* can be distinguished from *G. contristans* by the shape and colour of the areoles and by the smaller (especially shorter) ascospores.

*Gilbertaria squalescens* could also be mistaken for *Frutidella caesioatra*, which likewise grows on dying bryophytes on acid rock in alpine situations. However, the thallus of the latter species is not composed of bullate areoles but of more or less isidioid granules and the apothecia are usually blue-grey pruinose. In addition, *F. caesioatra* clearly differs from *G. squalescens* anatomically by, for example, having simple ascospores, by having a red-brown pigment in the hypothecium and by having a secondary metabolite chemistry with sphaerophorin and xanthones (Gilbert 2009; Kalb 1994). *Protomicarea limosa* is also somewhat similar, but differs by having unicellular ascospores, a reddish brown pigment in the hypothecium, an ascus of the *Psora*-type and a thallus that usually contains pannarin (Coppins 2009; Hafellner and Türk 2001). Species of *Micarea* with similar pigmentation and well-developed thallus occurring in the same habitat (e.g. *Micarea lignaria*) may be distinguished by thin (ca. 1.5 µm wide), usually richly branched and anastomosing paraphyses and by other ascospore characters.

The lichenicolous fungus that occurs as a superficial, dark hyphal net on the thallus of many collections of *G. squalescens* appears to be a species of *Moriola* Norman. This fungus also infects the apothecia of the lichen, which become brown-coloured and, if the infection is heavy, distorted (Fig. 3j). The fungus exhibits a simple form of lichenisation with the hyphae forming hollow spherical structures up to 100 µm diam. that are filled with algal cells (Fig. 3i). Norman (1872) coined the name 'goniocyts' for these structures but this name has subsequently also been applied to a variety of other structures that comprise both fungal and algal cells (e.g. Sérusiaux 1985; Spribille et al. 2014). Similar fungi, growing on *Stereocaulon* spp., were previously reported as lichenicolous by Zhurbenko and Triebel (2008), and have been suggested to be species of the pyrenomycete lichenicolous genus *Merismatium* Zopf (Triebel 1989). However, they are also quite frequent, apparently non-

lichenicolous, on damp soil and among bryophytes in alpine environments (Fryday 1997, 2004b) but are rarely collected or reported. Several species have been described (Bachmann 1925; Norman 1872) that are separated by their perithecial characters but, unfortunately, we have yet to discover any fruiting bodies on the species associated with *G. squalescens*. Fryday (1997), however, reported ascospores with the dimensions 15–18 × 5.5–6 µm for the free-living alpine species.

**Selected additional specimens examined: Austria.** *Tirol*: Kùhthai, 1872-08 [F. Arnold] (UPS L-170621). **Canada.** *Québec*: Nunavik, Detroit d'Hudson, 10.8 km au sud-sud-ouest du fond de la baie Kangirsukutaq, 62°38'79"N, 76°9'24'93"W, 415 m., dépôt glaciaire mi-versant, 2015-08-12, J. Gagnon 142.2f (QFA [TLC: negative]). **Norway.** *Finnmark*: Sør-Varanger, Elvenaes, 1864-07-28, T.M. Fries (UPS L-797515). *Hordaland*: Ulvik, Finse, Flakavassnuten, elev. 1700 m, 1916-07-20, G.E. Du Rietz (UPS L-599025); Flakavassnutens topp, 1916-07-20, G.E. Du Rietz (UPS L-598810). *Møre og Romsdal*: Rauma, Grytten hd, Trollstien, alt. 850 m, on moss, 1947-07-08, A.H. Magnusson 20717 (UPS L-797500 [TLC: negative]). *Nord-Trøndelag*: Rognvik hd, Mellingsfjeld, håll i reg. subalp., 1939-06-21, S. Ahlner (S F331959 [TLC: negative]). *Sør-Trøndelag*: Oppdal, Dovre, Vaarstien, 1863-08-06, T.M. Fries (with *G. contristans*, UPS L-797503, L-797504); Dovre, Jerkind, Geteryggen, 1863, T.M. Fries (with *G. contristans*, UPS L-797509). *Nordland*: Vega par., Vega Island, Sundsvoll, S of the farms, on moss on big boulder, 1973-06-24, G. Degelius V-312 (UPS L-797512 [TLC: negative]). **Russia.** *Sibiria Septentrionalis*: sinus Kongam ad fretum Bering, 64°50' lat. bor., 173° long. occid. (Greenw.), 1879-07-28-30, E. Almquist (S F331956). **Sweden.** *Härjedalen*: Storsjö par., Helagsfjällets topp, alt. 1796 m, 1913-07-18, G.E. Du Rietz (UPS L-167816 [TLC: negative]). Tännäs par., Funäsdalsberget, 1866, S. Almquist (UPS L-797487 [TLC: negative]; with *G. contristans*, S F332018). *Jämtland*: Kall par., Anjeskutan, 1914-07-07, A.H. Magnusson (UPS L-797491 [TLC: negative]). Kall par., St. Mjölkvattnet, Tjourn [= Tjovren], klippan N om bron strax nedanför bron, 'Rhizocarpon-bältet', 1942-08-24, S. Ahlner, (S F332011 [TLC: negative]). Kall par., Sösjöfjällen, north of Näverhön, 63.96919N 12.98386E, on moss cushions on rocky ground, 2020-08-24, M. Westberg JMT131 (UPS L-1026518). Undersåker par., Mt Middagsvalen, SW slope, ca 1.5 km NW of Vallbo, elev. 855 m, 63°13'983"N, 13°04'343"E, on bryophytes, 2015-08-21, A. Nordin 7797 (UPS L-721939). Undersåker par., Vällista [= Mt. Välliste], 1914-06, E.P. Vrang (UPS L-167820 [TLC: negative]; with *G. contristans*, UPS L-797489). Åre par., 3.5 km SW of Oppdalsvallen, by the water fall Silverfallet, just above the tree limit, elev. 750 m, 63°25'120"N, 12°32'646"E, 2017-08-15, M. Svensson 3272 (UPS). Åre par., Åreskutan, in summe montis, 1917-08-08, G. O. Malme (S F331982 [TLC:

negative]); close to path c. 150 m S of the summit, elev. 1380 m, 63°42999N, 13°09542E, on bryophytes in crevice, 2012-08-31, A. Nordin 7451 (UPS L-587792); c. 500 m SW of the summit, elev. 1325 m, 63°42836N, 13°08603E, 2013-08-15, A. Nordin 7561 (UPS L-632750 [TLC: negative]); c 570 m SW of the summit, elev. 1260 m, 63°42720N, 13°08566E, 2018-07-26, on mosses over siliceous rock, M. Westberg UCDLR149 (UPS L-931311); about 640 m S of Toppstugan, south-facing, alpine mountain slope, elev. 1265 m, 63°42539N, 13°09219E, on bryophytes on the ground, 2018-07-26, M. Svensson 3443 (UPS [TLC: negative], MSC); about 575 m SW of Toppstugan, elev. 1300 m, 63.42712N 13.08563E, on bryophytes, 2018-07-26, M. Svensson 3440 (UPS); about 570 m S of Toppstugan, elev. 1275 m, 62.42544N 13.09416E, on bryophytes, 2018-07-26, M. Svensson 3442 (UPS). Åre par., Snasahögen, 1914-06-24, A.H. Magnusson (with *G. contristans*, UPS L-797490). *Lule Lappmark*: Kvikkjokk par., in saxis muscosis infra Skärff [= Skierfe], 1871, P.J Hellbom & E.V.M. Hellbom (with *G. contristans*, S F332030). *Torne Lappmark*: Jukkasjärvi par., the valley Kärkevage (= Geargeväggi), ca 2.5 km NNW of Lake Trollsjön, elev. 750 m, 68°24217N 18°19253E, on bryophytes on vertical rock wall of large boulder, 2019-08-01, M. Svensson 3581 (UPS [TLC: negative]). Jukkasjärvi par., 3 km N of Riksgränsen, about 750 m E of Riksrose 266c, elev. 540 m, 68°27169N 18°7425E, on bryophytes on vertical rock wall, 2019-07-31, M. Svensson 3633 (UPS [TLC: negative]). Jukkasjärvi par., Vassitjåkko [= Vässeöhhkka], regio alpina, on moss, 1921-07-24, A.H. Magnusson 5786a (UPS L-797496). *Värmland*: Gustav Adolf par., S of Stjärnudden, over thin earth on a boulder near a brook, 1980-06-09, S.W. Sundell 13882 (UPS L-122572 [TLC: negative]). Norra Finnskoga par., ca 10 km N of Höljes, 61°00N, 12°37E, elev. 320 m, on big boulders in open situation, 1986-05-31, G. Thor 6473 (UPS L-174177 [TLC: negative]). *Ångermanland*: Hämsand par., Hämnön, 1873, S. Almquist & E. Almquist (UPS L-797488 [TLC: negative]). *Åsele Lappmark*: Vilhelmina par., 15 km WNW of Klimpfjäll, 120 m S of the bridge over river Saxån, the N slope of Mt Stihke, elev. 763 m, 65.11755N 14.50871E, alpine heath on rather calcareous soil, on mosses on stone slab, 2017-07-26, M. Westberg ULR128 (UPS L-880141). **Switzerland**. Monte Susten, ad terram, [no date,] Gisler (UPS L-170618). **USA Alaska**: Hoonah-Angoon District, Glacier Bay National Park, Dundas Bay, 58.3437°N, 136.3990°W, 350 m, snow bed in gully, granitic rock, 2012-07-25, A. Fryday 10156 (MSC). *New Hampshire*: Coos Co., Mt. Washington, low point on trail to Mt Clay, 44°16.75'N, 71°18.74'W, 1400 m, over bryophytes on east-facing rock with seepage, 2008-08-27, A. Fryday 9172 [TLC: negative], 9175 [TLC: negative], 9177 [TLC: negative] (MSC).

**Exsiccata: Norway.** *Hordaland*: Granvin par., Nesheimshorgen i Granvin, alt. 1100 m, på tyndt, delvis mosegrodd jordlag som hviler på skarvgrunn, 1937-08-02,

J.J. Havaas (Havaas, Lich. Exs. Norv. No. 617, UPS L-137518). **Poland**. Montes Tatri Alti, vallis Dolina Roztoki, ad saxa granitica prope Siklawa, 1610 m.s.m., 1959-08-24, Z. Tobolewski (Tobolewski, Lichenotheca Polonica no. 237, S F331955 [TLC: negative]; UPS L-574300). **Slovakia**. Carpati, Tatra Magna, in alpe 'Velká Svišťovka', alt. 1800 m.s.m, 1964-05-28, supra Grimmias et Andreaeas in rupibus graniticis, A. Vězda (Vězda, Lich. Sel. Exs. No. 259, UPS L-23990).

### Key to *Gilbertaria*

- 1 Thallus granular-areolate to squamulose..... 2
- 1\* Thallus at most a thin, gelatinous film ..... 3
- 2 Thallus of grey, bullate squamules; ascospores usually < 10 µm long..... *G. squalescens*
- 2\* Thallus granular-areolate; ascospores usually > 10 µm long.....*G. contristans*
- 3 Ascospores 14–17 × 3–4 µm ..... *G. astrapeana*
- 3\* Ascospores 9–15 × 2–4.5 µm ..... *G. holomeloides*

### Discussion

The taxonomic status of *Catillaria contristans* and *Toninia squalescens* has been unclear for a long time. As we demonstrate here, more than two species were hidden under these names, and they represent a previously unrecognized, but well-defined genus. The monophyly and phylogenetic position of *Gilbertaria* within the *Sphaerophoraceae* were both highly supported in all the Bayesian and maximum likelihood analyses, regardless of which alignment method was used. This indicates that our results are robust to different alignment strategies and modelling choices.

The phylogenetic position of *Gilbertaria* may seem surprising since no anatomical character seems to suggest an affinity to the *Sphaerophoraceae*. The traditional circumscription of this family includes macrolichens with prototunicate asci formed within mazaedia, such as occur in the genera *Bunodophoron*, *Leifidium* and *Sphaerophorus* (e.g. Wedin 1993), but studies of anatomy (Döring et al. 1999; Döring and Wedin 2000) and molecular phylogenies (Wedin and Döring 1999; Wedin et al. 2000) have both supported the emendation of the family to include the two non-mazaediate, Southern Hemisphere genera *Austropeltum* and *Neophyllis*. This enlargement made the *Sphaerophoraceae* more heterogeneous, including species of various growth forms and with different ascus types, different apothecial development types and different types of apothecial stalks (e.g. podetia, pseudopodetia; Döring and Wedin 2000). However, detailed developmental and morphological studies identified the presence of a trait possibly common to all members of the family:

the presence of ‘boundary tissue’; that is, a tissue of sometimes pigmented, plasma-rich hyphae that forms a boundary between generative and vegetative tissue (Döring et al. 1999; Döring and Wedin 2000). The layers forming this boundary tissue have been assessed as homologous within the *Sphaerophoraceae* and this character was consequently suggested to be a synapomorphy for the family (Döring and Wedin 2000; Wedin et al. 2000). We have failed to identify any structure that would qualify as boundary tissue in *Gilbertaria*. This can at least partly be attributed to scale: in contrast to the large macrolichens of the rest of the family, *Gilbertaria* is a genus of small crustose lichens with a comparatively poorly developed thallus. This is especially true of two of the species (*G. astrapeana* and *G. holomeloides*) that have very poorly developed, film-like thalli. In such cases, boundaries between generative tissue (apothecia) and vegetative tissue (thalli) are a question of individual hyphae, rather than well-defined and well-differentiated layers of hyphae. The two larger species (*G. contristans* and *G. squalescens*) both have a more differentiated thallus with a discernible cortex. However, in these species, the structures are comparatively very thin (i.e. up to 20 µm thick) and there is little scope for the development of complex, layered tissue. The presence of boundary tissue within the *Sphaerophoraceae* may thus be connected to growth form, either as a prerequisite, or as a consequence, of the evolution of large, complex thalli.

The basal position of *Gilbertaria* in the *Sphaerophoraceae*, as well as its deviating anatomy from the other genera of the family, suggests that a separate family could be described to accommodate it. However, quite apart from the dubious benefits of erecting a new family consisting of one genus of four species, this would also leave the question of what to do with the other basal genera of the *Sphaerophoraceae*. *Neophyllis*, and especially *Austropeltum*, like *Gilbertaria*, are not only clearly different from the mazaediate genera of the rest of the *Sphaerophoraceae*, but also from each other. At the present time, we consider that retaining all three genera in the *Sphaerophoraceae* is the most prudent course of action, but this may need to be revisited in the future. Generally, a larger taxon sampling and an increased number of markers are needed to fully evaluate the boundaries and relationship of the families currently considered to belong in the *Sphaerophorineae*, along with others that may be shown to be referable there by future research.

This revision formally recognizes four species of *Gilbertaria*, but our phylogeny indicates that more species may be involved. The ‘*Catillaria contristans*’ used by Kistenich et al. (2018), corresponding to *Gilbertaria* sp. in Fig. 1, is apparently closely related but at the same time well separated genetically from *G. astrapeana*, *G. contristans* and *G. holomeloides*. We have examined the specimen from which the sequences were generated (Timdal 11347, O-L163408!) and found the specimen to be similar to *G.*

*contristans*, but possibly differing by having somewhat larger thallus areoles that partly appear almost coralloid. Since we have only seen one specimen that could be clearly attributed to this entity, we refrain from describing this as a new species.

There are also indications of genetic structuring within *Gilbertaria squalescens*, with three different sub-clades (Fig. 1): one comprising *G. squalescens* 1–5, one *G. squalescens* 7–14 and one with *G. squalescens* 6. The genetic differences between these three groups are consistent but very small, usually just a few bp per marker, and in the protein-coding genes restricted to the third codon position. There is no apparent correlation between the genetic pattern and geographical distribution: although most of the sequenced collections of *G. squalescens* are from Scandinavia, specimens from North America are present in both the larger sub-clades (*G. squalescens* 2 and 14). Despite thorough morphological and anatomical investigations of the sequenced specimens, we have not found any clear differences between the sub-clades, and thus prefer to treat them as one species pending further studies.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11557-022-01838-5>.

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**Author contribution** Both authors contributed to the study conception and design. Both authors collected specimens, did morphological and anatomical work, and contributed to the descriptions. MS did the molecular lab work and performed the phylogenetic analyses. The manuscript was written by both authors together. Both authors read and approved the final manuscript.

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**Data availability** Sequence data are deposited in GenBank. The collections cited, including all types, have been deposited in public herbaria, as indicated by herbarium acronyms. The alignments used for the phylogenetic analyses have been submitted as Supplementary material.

## Declarations

**Conflict of interest** The authors declare no conflict of interest.

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