

Standard Paper

Nimisora (Lecanoraceae, Ascomycota), a new genus for a common lecideoid epiphytic species from the central Iberian Peninsula

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Abstract

The new genus *Nimisora* Pérez-Ort., M. Svenss. & J. C. Zamora is introduced to accommodate a puzzling lecideoid epiphyte common in the central Iberian Peninsula. *Nimisora* is characterized by the following combination of characters: lecideoid apothecia, excipulum composed of sparingly branched radiating hyphae with narrow lumina, thick walls and swollen terminal cells, the presence of a brown K+ olivaceous green pigment in the epihymenium, an ascus tip similar to the *Bacidia*-type, and the presence of simple ellipsoid ascospores. Molecular analyses based on nrITS, nrLSU and mtSSU sequences unequivocally place the new genus within the *Lecanoraceae*; however, its phylogenetic affinities with other genera of the family remain largely unresolved. Comparisons with the morphologically closest genera are provided. The single species of the genus, *Nimisora iberica* Pérez-Ort., Turégano, M. Svenss. & J. C. Zamora sp. nov., is also described as new to science.

Keywords: Ascomycota; *Bacidia*-type ascus; lichen systematics; Spain

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Introduction

The genus *Lecidea* Ach. has long been used as a catch-all to group all species with crustose thalli, lecideoid apothecia, chlorococcoid photobionts and simple, colourless ascospores following the treatments of Zahlbruckner (1925, 1932). Studies on saxicolous lecideoid species proliferated in the second half of the 20th century, describing new genera for several groups with synapomorphies and making it clear that *Lecidea* Ach. s. str. is a predominantly saxicolous group (e.g. Hertel 1967, 1983, 1984, 1995, 2007; Hafellner 1984, 1993; Rambold 1989).

Epiphytic lecideoid taxa represent a polyphyletic group of species (Pérez-Ortega *et al.* 2010; Schmuell *et al.* 2011; Miadlikowska *et al.* 2014) whose taxonomy and systematics have been partially clarified in recent decades, giving rise to a large number of new genera, such as *Japewia* Tønsberg (Tønsberg 1990), *Japewiella* Printzen (Printzen 1999), *Palicella* Rodr. Flakus & Printzen (Rodríguez-Flakus & Printzen 2014), *Ramboldia* Kantvilas & Elix (Kantvilas & Elix 1994), *Puttea* S. Stenroos & Huhtinen (Stenroos *et al.* 2009), *Australidea* Kantvilas *et al.* (Kantvilas *et al.* 2021) and *Myochroidea* Printzen *et al.* (Printzen *et al.* 2008).

The taxonomy of lecideoid epiphytic genera has been largely based on features of the excipulum and hamathecium, ascus type and the presence of certain secondary metabolites

(Printzen *et al.* 2008; Rodríguez-Flakus & Printzen 2014; Rodríguez-Flakus 2020).

Interestingly, it has been shown, with the aid of molecular characters, that many of these new genera belong to the family *Lecanoraceae* (Pérez-Ortega *et al.* 2010; Schmuell *et al.* 2011; Miadlikowska *et al.* 2014; Rodríguez-Flakus & Printzen 2014; Zhao *et al.* 2016), with members characterized often by lecanorine apothecia and the presence of *Lecanora*-like asci. The systematics of the family *Lecanoraceae* is in continuous change, and although recent papers on systematics have been published dealing with the phylogenetic relationships among the major lineages of the clade, the deep relationships are far from being unravelled (e.g. Zhao *et al.* 2016; Yakovchenko *et al.* 2019; Ivanovich *et al.* 2021; Svensson *et al.* 2022).

In spite of recent efforts made to determine the phylogenetic positions of lecideoid epiphytic species, many of them still remain unplaced. During studies by two of the authors on the lichenicolous members of *Tremella* Pers. in the Iberian Peninsula, a new species (*Tremella diderichiana* Pérez-Ort. *et al.*) was described growing on a puzzling lecideoid epiphyte which was tentatively identified as *Lecidea* aff. *erythrophaea* (Zamora *et al.* 2016). The species appears to be quite common, especially on branches of *Cistus ladanifer* in the central Iberian Peninsula, and had also been previously determined as *Lecidea exigua* Chaub. (Aragón *et al.* 2004; Martínez & Aragón 2004). Here, we introduce it as a new genus in the family *Lecanoraceae*, *Nimisora* Pérez-Ort., M. Svensson & J. C. Zamora, and a new species, *Nimisora iberica* Pérez-Ort., Turégano, M. Svenss. & J. C. Zamora, providing insights into its phylogenetic relationships based on ribosomal DNA data and morphology.

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Material and Methods

Morphological analyses

Specimens were examined using a Leica S9i dissecting microscope with an in-built digital camera. Hand-cut sections of apothecia and thalli were observed using either an Olympus BX51 with Nomarski differential interference contrast (DIC) or a Nikon Eclipse E200 microscope fitted with a set of polarized filters. Images were captured with a Leica DMC 4500 digital camera fitted to the Olympus microscope. Colour reactions were observed using 50% HNO₃ (N), 10% KOH (K), 8% sodium hypochlorite (C), paraphenyldiamine (PD) and Lugol's iodine solution (256977.1609 PanReac AppliChem) (I), the latter both with (K/I) and without pretreatment with K. The measurements of ascospores were made on material mounted in water and are presented as minimum– (mean ± standard deviation) –maximum values followed by the number of measurements (*n*) and number of specimens (*s*). Thin-layer chromatography analyses were carried out following standard methods using solvent C (Orange *et al.* 2001).

Molecular methods

Apothecial sections were excised from seemingly un-parasitized thalli and placed in microcentrifuge tubes. They were stored at –80 °C for 1 h after which they were pulverized using a Qiagen TissueLyser II and glass beads. DNA was extracted using E.Z.N.A.® Forensic DNA Kit (Omega Bio-Tek), following the instructions of the manufacturer. A fragment of the nuclear ribosomal DNA comprising the internal transcriber spacer (nrITS: ITS1, 5.8S, and ITS2) and domains D1–D3 of the nuclear large ribosomal subunit (nrLSU), as well as a fragment of the mitochondrial small subunit ribosomal DNA (mtSSU) of *c.* 800 bp, were amplified using the following primer pairs: ITS1-F (White *et al.* 1990) and ITS4_KYO2 (Toju *et al.* 2012) for nrITS, LR0R and LR5 (Vilgalys & Hester 1990) for the nrLSU, and mrSSU1 and mrSSU3r (Zoller *et al.* 1999) for the mtSSU. Amplification reactions were prepared for a 15 µl final volume containing 7.5 µl of MyTaq™ Red Mix (Bioline), 0.5 µl of each of the primers at 10 µM, 5.5 µl of H₂O, and 1 µl of template DNA. PCR conditions for the amplification of the nrITS and nrLSU were as follows: 5 min at 95 °C; 10 cycles of 30 s at 95 °C, 30 s at 66 °C, 1 min 30 s at 72 °C; 34 cycles of 30 s at 95 °C, 30 s at 56 °C, 1 min 30 s at 72 °C; and 10 min at 72 °C. Conditions for the amplification of the mtSSU were: 10 min at 94 °C; 34 cycles of 45 s at 95 °C, 45 s at 50 °C, 1 min 30 s at 72 °C; 5 min at 72 °C. Additionally, DNA was extracted for one specimen of the new taxon and one of *Japewiella tavaresiana* (H. Magn.) Printzen and the nrITS and mtSSU amplified following the methods described in Svensson & Fryday (2022). PCR products were purified using Exo SAP-IT (USB Europe GmbH), following the manufacturer's instructions. The samples were sequenced with Sanger dideoxy-technology by Macrogen Inc. (Macrogen Europe, Madrid, Spain) using the same PCR primers. Contigs were assembled and edited using either AliView v. 1.1 (Larsson 2014) or Geneious® Prime v. 2020.0.3.

Sequence alignments

Preliminary BLAST searches (Altschul *et al.* 1997) pointed to members of the *Lecanoraceae* as the closest hits for these sequences. Thus, to find the phylogenetic position within the

family we aligned our data with sequences of the main genera and groups of *Lecanoraceae* (Rodríguez-Flakus & Printzen 2014; Zhao *et al.* 2016). Multiple sequence alignments for each genomic region were performed using MAFFT v. 7.490 (Katoch *et al.* 2002) as implemented on the CIPRES Science Gateway (Miller *et al.* 2011) using default parameters. Ambiguous positions were removed using Gblocks v. 0.91b (Castresana 2000) at http://phylogeny.lirmm.fr/phylo.cgi/one_task.cgi?task_type=gblocks, using all the options available for the least stringent selection.

Phylogenetic analysis

Single-locus trees were inferred using maximum likelihood (ML) in the IQ-TREE web server (Trifinopoulos *et al.* 2016). A visual inspection of the topologies revealed no incongruence between them, that is, there were no supported nodes that were incompatible with each other. Node support was calculated using 1000 ultrafast bootstrap replicates (BS), implying that only BS values > 95% should be considered indicative of compatibility (Hoang *et al.* 2018). Thus, the single-locus alignments were concatenated into a single alignment using Geneious® Prime v. 2020.0.3 for subsequent analyses. This alignment was analyzed using ML and Bayesian phylogenetic inference (BI) methods. Maximum likelihood analysis was performed in RAXML-HPC2 v. 8.2.4 (Stamatakis 2014) as implemented on the CIPRES Science Gateway (Miller *et al.* 2011), dividing the alignment into five partitions: nrITS1, 5.8S, nrITS2, nrLSU and mtSSU. The GTRGAMMA substitution model was used for all partitions. We searched the best-scoring ML tree and conducted a rapid bootstrap analysis with 1000 pseudoreplicates to evaluate nodal support in one single run. The BI analysis was performed in MrBayes v. 3.2.7a (Ronquist *et al.* 2012) as implemented on the CIPRES Science Gateway (Miller *et al.* 2011). The same partitions used in the ML analysis were implemented in the BI analysis. We inferred the topology and sampled across the substitution model space with the reversible-jump Markov chain Monte Carlo (MCMC) method (Huelsenbeck *et al.* 2004). The analysis was run using default priors, two parallel runs of four MCMC chains over 20 million generations, starting with a random tree and sampling one tree every 5000 generations. The first 25% of trees from each analysis was discarded as burn-in. Branch support (Bayesian posterior probability (PP)) was calculated using the consensus tree following the '50% majority rule' of the remaining trees. Nodes with ML bootstrap value ≥ 70% and PP ≥ 0.95 were considered phylogenetically supported.

Results

We generated 10 new sequences: 4 nrITS, 2 nrLSU and 4 mtSSU (Table 1). The corresponding alignments were 632, 803 and 898 bp long, respectively; 368, 563, 545 of which remained after the Gblocks removal of ambiguously aligned regions and gaps. Maximum likelihood and Bayesian analyses retrieved single best and 50% majority-rule trees respectively with similar topologies, so only the tree recovered using maximum likelihood inference is shown in Fig. 1. Overall supported relationships among species were rather similar to those inferred in previous works with a limited number of loci (e.g. Pérez-Ortega *et al.* 2010; Rodríguez-Flakus & Printzen 2014; Malíček *et al.* 2020; Davydov *et al.* 2021); that is, although most of the genera and morphological groups are well-supported, the relationships among them remain uncertain. All specimens from the new

Table 1. Sequence data used for the phylogenetic analysis (Fig. 1), with GenBank Accession numbers and voucher information. Sequences generated in this study are in bold.

Taxon	Country/voucher	ITS	LSU	mtSSU
<i>Bryonora castanea</i>	Sweden, Westberg PAD321 (UPS)	OM423658	OM423613	OM417201
<i>B. pruinosa</i>	Sweden, Westberg et al. PL101 (UPS)	OM423663		OM417205
<i>B. septentrionalis</i>	Sweden, Westberg et al. PL272 (UPS)	OM423667	OM423617	OM417209
<i>Carbonea vitellinaria</i>	Sweden, Svensson 3962 (UPS)	MZ474887		MZ468128
<i>C. vorticosa</i>	Antarctica, Türk 43031 (SZU)	JN873869		
<i>Cetraria islandica</i>	Canada, Lutzoni & Miadlikowska AFTOL-ID 211 (DUKE)	JQ301699	DQ912334	DQ912277
<i>Cladonia sulcata</i>	Australia, Lumbsch, Parmen & Widhelm HTL 19975i (F)	GQ500913	GQ500959	GQ500949
<i>Frutidella caesiopatra</i>	Norway, Andersen 91 (BG)		AY756349	AY567765
<i>F. furfuracea</i>	Norway, Tønsberg 34616 (hb. Schmull)	HQ650669	HQ660546	HQ660574
<i>Japewia tornensis</i>	Canada, Printzen s. n. (BG)	HQ650656		HQ660559
<i>Japewiella tavaresiana</i>	Ireland, Hertel 39505 (M)	MG925975		
<i>J. tavaresiana</i>	Portugal, Vicente (UPS L-1072779)	OQ930477		
<i>Lecanora anoapta</i>	USA, Leavitt 405_US (BRY-C)	MT938979		MT939206
<i>L. bicincta</i>	Australia, Trinkaus 102 eb36 (GZU)	AY541264		
<i>L. bipruinosa</i>	USA, Knudsen 19071.1	ON447588	ON391433	ON367860
<i>L. campestris</i>	Sweden, U225 (LD)	AF159930		DQ787362
<i>L. cateilea</i>	Canada, Goward & Poelt s. n. eb70 (GZU)	AY541250		
<i>L. densa</i>	USA, Pérez-Ortega & Spribille SPO14 (FR)	GU480097		
<i>L. dispersoareolata</i>	Switzerland, Li 92_LLJ20 (KUN-L)	ON179980	ON180240	ON180357
<i>L. farinacea</i>	Australia, Lumbsch 19971b (F)	JN943726	JN939511	JQ782670
<i>L. formosa</i>	China, ZX 20129045-2	KT453771	KT453773	KT453819
<i>L. horiza</i>	Spain	KT453772		KT453821
<i>L. intricata</i>	Bolivia, Rodriguez-Flakus 3751 (KRAM)	OL603994	OL663862	OL604075
<i>L. intumescens</i> I	Czech Republic, Malíček 8480 (hb. Malíček)	KY548040		KY502441
<i>L. intumescens</i> II	Norway, Ekman 3162 (BG)		AY300841	AY567715
<i>L. nashii</i>	USA, Knudsen 19030	ON447553		ON367825
<i>L. physciella</i>	Antarctica, Sancho MAF_MK1_63	MK208766		MK205061
<i>L. polytropa</i>	USA, Alaska, F. Lutzoni et al. AFTOL-ID 1798 (DUKE)	HQ650643	DQ986792	DQ986807
<i>L. rupicola</i>	Bolivia, Flakus 29512 (KRAM)	OL604023	OL663884	OL604104
<i>L. saligna</i>	Germany, Cezanne & Eichler 10884 (FR)	MT938988		MT939217
<i>L. subcarnea</i>	Sweden, Arup L97580 u274 (hb. Arup)	AY541267		
<i>L. subintricata</i>	Japan, Printzen 15562 (FR)	MT939010		MT939239
<i>L. sulphurea</i>	Sweden, Arup L96006 U212 (LD)	AF070030	DQ787355	DQ787356
<i>L. swartzii</i>	Norway, Grube MG102 (GZU)	DQ451654		
<i>L. symmicta</i>	Germany, Printzen CP999a, U205 (FR)	AF070024		KJ152466
<i>L. tropica</i>	Thailand, Papong 6440 (F)	JN943720		JQ782699
<i>L. varia</i>	U188	AF070028		
<i>Lecidella effugiens</i>	China, ZX 20141148-2	KT453747	KT453786	KT453833
<i>L. elaeochromoides</i>	China, ZX 20141142	KT453750	KT453790	KT453836
<i>L. euphorea</i>	China, ZX 20140638	KT453742	KT453798	KT453844
<i>Miriquidica complanata</i>	Poland, Szczepanska 935 (hb. Szczepanska)	KF562187	KF562179	
<i>M. garovaglii</i>	Slovakia, Szczepanska 538 (hb. Szczepanska)	KF562188		AY567711

(Continued)

Table 1. (Continued)

Taxon	Country/voucher	ITS	LSU	mtSSU
<i>Myriolecis dispersa</i>	Lókös Ld8 (KRAM)	JQ993733		
<i>M. semipallida</i>	Estonia, Jüriado Ls10 Jan. 2009	JQ993743		
<i>Nimisora iberica</i> S6011	Spain, Pérez-Ortega 8183 (MA-Lichen)	OQ930480	OQ930482	OQ930451
<i>N. iberica</i> P20	Spain, Zamora s. n. (UPS L-1072683)	OQ930478		
<i>N. iberica</i> S6010	Spain, Pérez-Ortega 8753 (MA-Lichen 26680)	OQ930479	OQ930481	OQ930450
<i>N. iberica</i> S6009	Spain, Pérez-Ortega 8273 (MA-Lichen 26676)			OQ930449
<i>Palicella filamentosa</i>	Germany, Hauck s. n. (hb. FH)	HQ650663	HQ660543	HQ660568
<i>P. schizochromatica</i>	USA, Hauck s. n. (hb. FH)	HQ650652	HQ660532	HQ660555
<i>Parmelia sulcata</i>	New Zealand, Knight 60594 (OTA)	GU994574	GU994621	GU994669
<i>Protoparmeliopsis muralis</i>	Austria, BGK247	KC791770		KJ766466
<i>P. zareii</i>	Iran, Zarei-Darki (1111) SK 480 (KW-L)	KP059049		KP059056
<i>Pulvinora pringlei</i>	USA, McCune 36799 (OSC & ALTB)	MW257114	MW257114	MW257153
<i>P. stereoallina</i>	Russia, Davydov 14820 (ALTB)	MW257112	MW257112	MW257152
<i>Pyrrhospora querneae</i>	Sweden, Ekman 3019 (BG)	AF517930	AY300858	AY300908
<i>Ramboldia brunneocarpa</i>	Australia, Elix 36756 (F)	EU075542	EU075520	EU075528
<i>R. russula</i>	Costa Rica, Lücking 17640 (F)	EU075547	EU075524	EU075533
<i>Rhizoplaca haydenii</i> subsp. <i>arbuscula</i>	USA, St. Clair & Knight C55028 (BRY)	HM577304	KT453813	KT453857
<i>R. melanophthalma</i>	Iran, Sohrabi MS014624 (H)	JX948275		KT453858
<i>R. parilis</i>	USA, Porter C55078 (BRY)	HM577309	KT453814	KT453859
<i>R. peltata</i>	USA	KT453722	KT453815	KT453860
<i>Scoliosporum fabisporum</i>	South Africa, Fryday 11123 (PRE)		NG_071258	MT611934
<i>S. umbrinum</i>	Austria, Wilfling 2873 m2873 (GZU)	AY541277		AY567719
<i>Stereocaulon pileatum</i>	Norway, Tønberg 27339 (BG)	AF517927	AY756335	AY567718

taxon form a well-supported (BP = 100, BPP = 1) monophyletic group sister to the species of the genus *Ramboldia* included in the analyses, although this relationship was not supported by either of the two inference analyses, so the exact phylogenetic position of *Nimisora* within the *Lecanoraceae* remains unclear.

Taxonomy

Morphoanatomical, chemical and molecular data support the description of a new genus and species of lichenized fungus in *Lecanoraceae*.

Nimisora Pérez-Ort., M. Svenss. & J. C. Zamora gen. nov.

MycoBank No.: MB 848883

The genus is characterized by the following combination of characters: crustose thalli, lecideoid apothecia with a proper excipulum composed of thick-walled radiating hyphae, with widened terminal cells, hymenium of simple to branched paraphyses widened at the apex, brown to dark green K+ olivaceous pigment in the epihymenium and excipulum, an ascus similar to the *Bacidia*-type and simple, broadly ellipsoid, colourless ascospores.

Type species: *Nimisora iberica* Pérez-Ort., Turégano, M. Svenss. & J. C. Zamora

Etymology. The genus is named after Prof. Pier Luigi Nimis (University of Trieste) for his 70th birthday, and in gratitude of his great contribution to lichenology and especially to the knowledge of lichens in the Mediterranean region.

Nimisora iberica Pérez-Ort., Turégano, M. Svenss. & J. C. Zamora sp. nov.

MycoBank No.: MB 848884

An epiphytic species without a well-developed cortex, granulate to areolated crustose thalli, lecideoid apothecia with a proper excipulum composed of radiating thick-walled, sparingly branched hyphae and dark brown to dark green pigment, hymenium composed of simple to branched paraphyses with widened apices with brown caps, epihymenium with a brown to dark green K+ olive green pigment, ascus similar to the *Bacidia*-type, ascospores simple, broadly ellipsoid, colourless, usually straight, 10–15 × 4–7 µm, with no lichen substances detected by TLC.

Type: Spain, Madrid, Mataelpino, *Cistus ladanifer* thicket close to road M-617, 40°43'57"N, 3°58'16"W, 1135 m, on *Cistus ladanifer*, 16 September 2021, S. Pérez-Ortega 11512 (MA-Lichen 26675—holotype!) [TLC: nil, thallus with *Tremella diderichiana*].

(Fig. 2A–M)

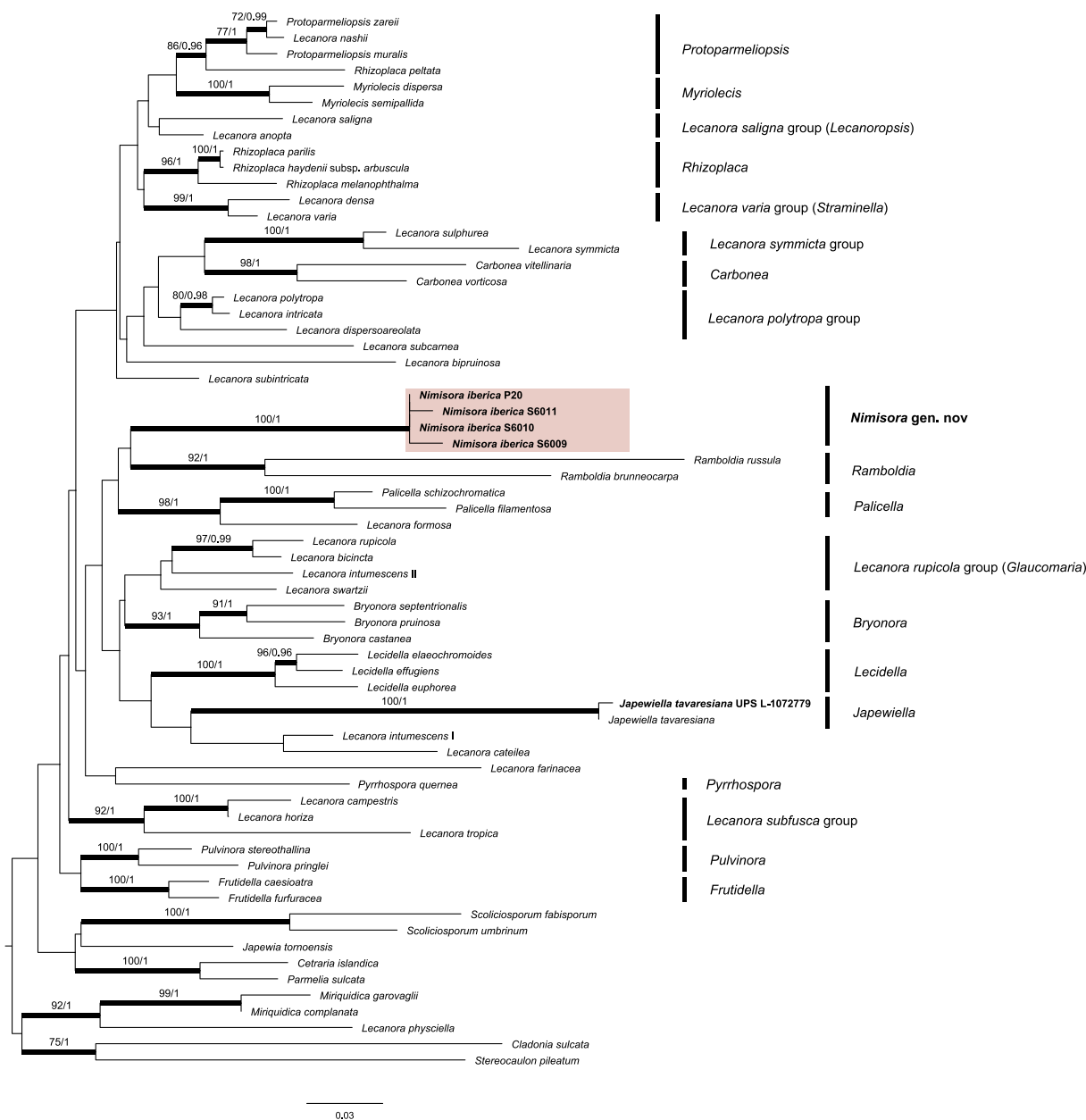


Figure 1. Most likely tree inferred by maximum likelihood (ML) analysis of the ITS, nrLSU and mtSSU regions of *Lecanoraceae* species. Sequences generated in this study and the new genus, *Nimisora*, are indicated in bold. Thick branches indicate nodes with phylogenetic support in both analyses (ML bootstrap values $\geq 70\%$ / posterior probability ≥ 0.95). In colour online.

Thallus crustose, episubstratal, granulose to minutely areolated, forming roundish to elongate patches up to 22 mm long and 10 mm wide, rarely coalescing. Granules roundish up to 350 μm diam., areoles roundish to elongate or angular in outline, average diam. of 0.03–0.42 mm, up to 0.55 mm in height reaching 0.7 mm when growing on *Pinus* branches, flattened to convex, greenish grey to light grey, or whitish, green when wet, matt, sometimes with a brownish tinge, without well-developed cortex, thallus hyphae I–. *Soralia* or *isidia* absent. Algal layer irregular, often expanded throughout the thallus and in contact with the substratum. *Photobiont* chlorococcoid, globose, algal cells up to 15 μm diam.

Apothecia common, more or less roundish in outline, sessile, immersed and with some thallus remains when very young, constricted at the base, single or in groups up to 7 or 8, usually 0.3–

0.6 mm diam. (up to 0.9 mm). *Disc* very variable in colour, even within the same thallus, from light cream-brown to reddish brown or dark brown, flat to weakly convex, matt, epruinose, margin visible, usually darker than the disc, dark brown to black, thinner with age but almost always conspicuous, rarely excluded. *Proper excipulum* laterally 20–45 μm in section, composed of radially arranged septate hyphae, hyphae up to 6 μm diam., widening at the apex up to 10 μm , individual cells up to 10 μm long, lumina up to 2 μm wide; excipulum colourless within or with a dark green or dark brown pigment in the outer part of the hyphae, apical cells with a much darker pigmentation, K+ dark olive green or dark brown, N+ dark pink. *Hypothecium*, 15–35 μm high, of roundish to angular hyphae 4–6 μm wide, with very thin walls, colourless. *Epithymenium* olive green to light to dark brown, pigment present in the gelatinous matrix and the apical

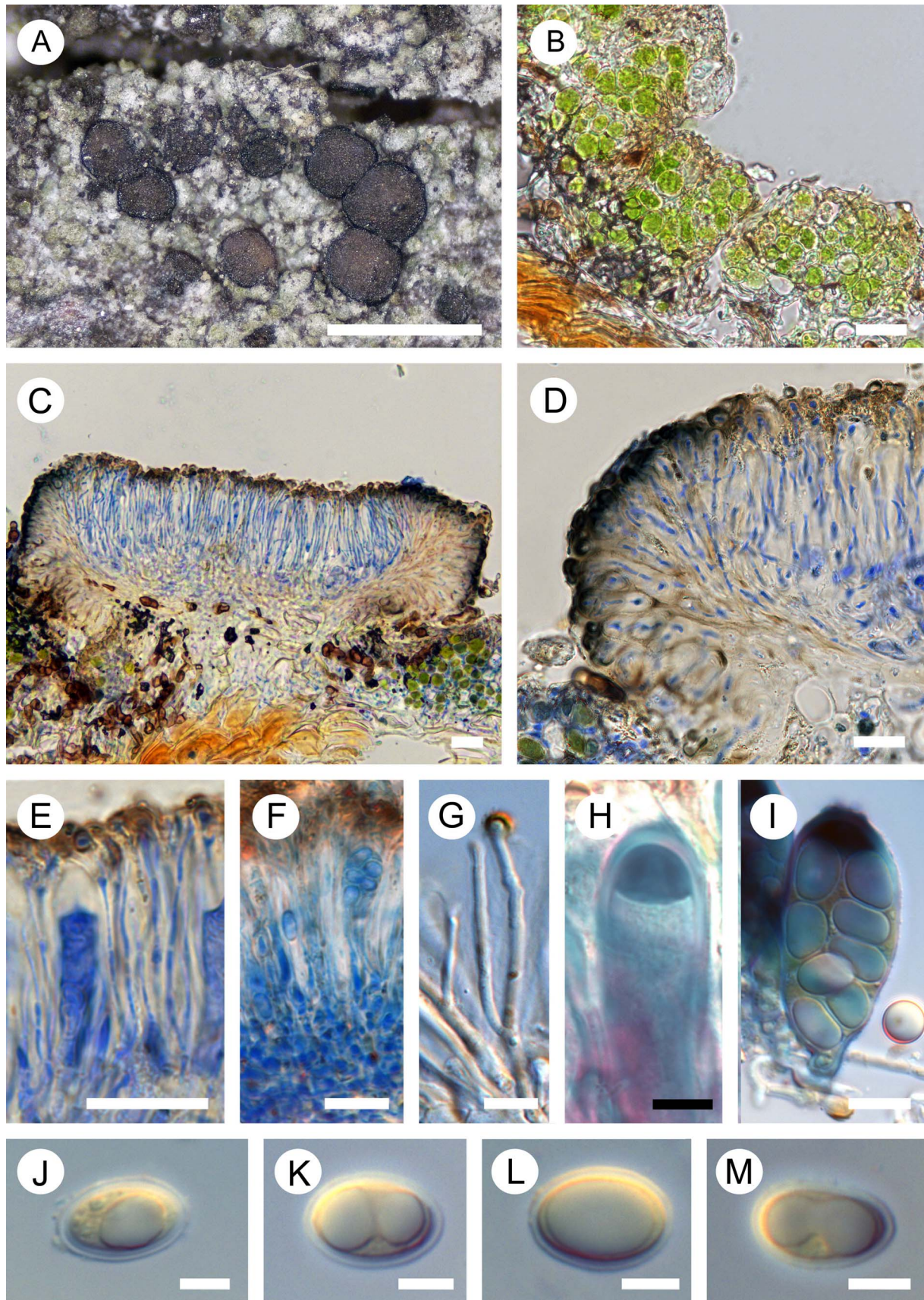


Figure 2. *Nimisora iberica* (S. Pérez-Ortega 11512). A, habitus. B, thallus section. C, section of apothecium. D, detail of excipulum. E, detail of the hymenium. F, subhymenium. G, paraphyses. H, detail of ascus tip. I, mature ascus. J–M, ascospores. C–F, lactophenol cotton blue. H & I, KOH and Lugol's iodine solution. J–M, Lugol's iodine solution. G & I–M, differential interference contrast. Scales: A = 1 mm; B, C, E & F = 20 μ m; D = 10 μ m; G–M = 5 μ m. In colour online.

cell walls of paraphyses, 5–10 µm thick, K+ dark olive green, N+ dark pink, without granules or with scarce granules refracting polarized light. *Hymenium* hyaline, 35–50 µm thick, I+ dark blue. *Paraphyses* simple to branched, especially in the upper part, rarely anastomosing, 1.5–2.5 µm wide, lumina up to 1 µm wide, apical cells capitate, 3–4 µm wide, with dark brown pigmentation in upper internal walls, with a gelatinized sheath c. 1 µm thick around the caps, dissolving in K. *Asci* clavate, 32–45 × 8–10 µm when mature, tholus strongly amyloid, with poorly developed or no ocular chamber, with a pale conical axial mass usually with a dark layer around the axial mass (*Bacidia*-type). *Ascospores* simple, very rarely 1-septate, hyaline, ellipsoid to broadly ellipsoid, straight, rarely curved, with a single wall (c. 0.5 µm) and lacking gelatinous epispore, 10–(11.03 ± 1.07)–15 × 4–(5.71 ± 0.65)–7 µm ($n = 35, s = 5$).

Conidiomata not seen.

Chemistry. No substances detected by TLC.

Ecology. The species is common on twigs of *Quercus rotundifolia* in the centre of the Iberian Peninsula, and especially on twigs of *Cistus ladanifer*, being rarer in other areas of the supramediterranean belt of the Peninsula. It is accompanied by other species typical of twigs in the area such as: *Blastenia xerothermica* Vondrák *et al.*, *Evernia prunastri* (L.) Ach., *Lecanora carpinea* (L.) Vain., *L. chlorotera* Nyl., *L. varia* (Hoffm.) Ach., *Lecidella elaeochroma* (Ach.) M. Choisy, *L. euphorea* (Flörke) Hertel, *Melanohalea exasperata* (De Not.) O. Blanco *et al.*, *Physcia adscendens* H. Olivier, *Rinodina pyrina* (Ach.) Arnold, or *R. sophodes* (Ach.) A. Massal. The species is also the host of *Tremella diderichiana*, a lichenicolous basidiomycete which forms characteristic minute whitish galls on the thallus of *N. iberica* (Zamora *et al.* 2016).

Additional specimens examined. **Spain:** Madrid: Tres Cantos, Parque Central, *Pinus radiata* forest, 40°36'7"N, 3°42'16"W, 718 m, on *Pinus radiata* twig, 2021, S. Pérez-Ortega 12116 & E. Arróniz (MA-Lichen 26684) [TLC: nil]; Manzanares el Real, *Cistus ladanifer* in the surroundings of the reservoir, 40°44'24"N, 3°50'30"W, 901 m, on *Cistus ladanifer*, 2021, S. Pérez-Ortega 11207, M. Arróniz & E. Arróniz (MA-Lichen 26683) [TLC: nil]; San Agustín de Guadalix, Dehesa de Moncalvillo, siliceous outcrops (gneiss) and *Cistus ladanifer* thicket near La Sima creek, 40°42'6"N, 3°38'46"W, 843 m, on *Cistus ladanifer*, 2021, S. Pérez-Ortega 11260 (MA-Lichen 26682) [TLC: nil]; Olmeda de las Fuentes, *Quercus rotundifolia* forest, 40°20'47"N, 3°12'4"W, 821 m, on *Q. rotundifolia* twig, 2018, S. Pérez-Ortega 8790 (MA-Lichen 26881) [TLC: nil]; Madrid, *Quercus rotundifolia* forest near the road M-612 from Fuencarral to El Pardo, 40.511531°N, 3.750402°W, 679 m, on *Q. rotundifolia* twig, 2018, S. Pérez-Ortega 8753 (MA-Lichen 26680) [TLC: nil]; El Boalo, *Cistus ladanifer* thicket near San Isidro hermitage, 40°43'46"N, 3°55'12"W, 1000 m, on *Cistus ladanifer*, 2021, S. Pérez-Ortega 11404, M. Arróniz & E. Arróniz (MA-Lichen 26679) [TLC: nil, with *Tremella diderichiana*]; El Berruoco, Pradera del Amor, granitic boulders and *Cistus ladanifer* thicket close to M-127 road, 40°52'55"N, 3°34'38"W, 1013 m, on *Cistus ladanifer*, 2018, S. Pérez-Ortega 8183 & S. Prats i Font (MA-Lichen 26685) [TLC: nil]; *ibid.*, S. Pérez-Ortega 8186 & S. Prats i Font (UPS) [TLC: nil, with *Tremella diderichiana*]; *ibid.*, S. Pérez-Ortega 8185 & S. Prats i Font (G) [TLC: nil, with *Tremella diderichiana*]; Tres Cantos, Soto de Viñuelas,

40°37'5"N, 3°40'14"W, 689 m, on *Q. rotundifolia* twig, 2020, S. Pérez-Ortega 10797, M. Arróniz & E. Arróniz (MA-Lichen 26677) [TLC: nil]; Colmenar Viejo, gneiss outcrops in Cerro San Pedro, 40°43'12"N, 3°43'52"W, 1014 m, on *Cistus ladanifer*, 2021, S. Pérez-Ortega 11766, E. Arróniz & M. Arróniz (MA-Lichen 26678) [TLC: nil]. *La Rioja:* Sojuela, mixed forest of *Q. pyrenaica* and *Q. rotundifolia*, 42°21'33"N, 2°33'16"W, 814 m a.s.l., on *Q. rotundifolia* twig, 2019, S. Pérez-Ortega 8273 (MA-Lichen 26676) [TLC: nil]. *Castilla-La Mancha:* Ciudad Real, Retuerta del Bullaque, Cabañeros National Park, Viñuelas, *Quercus pyrenaica* forest, 30SUJ7159, 800 m, on dead *Quercus pyrenaica*, 1996, I. Fernández, F. J. Sarrión & J. A. Maroto 297 (MA-Lichen 14845); Ciudad Real, Villamanrique, 38.416507°N, -2.999149°W, on dead branches of *Cistus ladanifer*, 3 iii 2018, J. C. Zamora (UPS).

Other species examined. *Lecanora symmicta* (Ach.) Ach. **Spain:** Castile and León: Segovia, Riofrío de Riaza, Riaza valley, Majada Larga, 30TVL6564, 1720 m, on *Juniperus nana*, 1994, G. Aragón, I. Martínez & T. Rojas IMM 202/94 (MA-Lichen 4938).

Lecidella elaeochroma. **Spain:** Castilla y Len: Burgos, Torrecilla del Monte, *Quercus rotundifolia* forest with *Juniperus oxycedrus* and *Quercus faginea*, 42°4'19"N, 3°42'38"W, 948 m, on *Quercus rotundifolia*, 2018, S. Pérez-Ortega 9315 & A. Berlinches de Gea (MA-Lichen).

Lecidella euphorea. **Spain:** Madrid: Madrid, *Quercus rotundifolia* close to the road M-612, 40.511531°N, 3.750402°W, 679 m, on *Quercus rotundifolia*, 2017, S. Pérez-Ortega 10612 & M. Comte (MA-Lichen).

Pyrrhospora quereana (Dicks.) Körb. **Spain:** Islas Baleares: San Josep de sa Talaia, *Pinus halepensis* forests near the top of Sa Talaia, 38°54'53"N, 1°16'39"E, 445 m, on *Pinus halepensis*, 2017, S. Pérez-Ortega 5590 (MA-Lichen 26862).

Ramboldia elabens (Fr.) Kantvilas & Elix. **Spain:** Castilla-La Mancha: Toledo, Hontanar, Montes de Toledo, Estena River, *Quercus rotundifolia* forest, 30SUJ6380, 875 m, on dead trunk of *Juniperus oxycedrus*, 1995, G. Aragón 1006/95, J. L. Izquierdo & I. Martínez (MA-Lichen 7157).

Traponora varians (Ach.) J. Kalb & Kalb (sub *Lecidea exigua* Chaub.). **Spain:** Navarra: Oronoz Mugaire, Señorío de Bértiz, 30TXN1579, on *Quercus robur* branches, J. Etayo (MA-Lichen 3845). *Galicia:* Pontevedra, Niño do Corvo, 41°56'58"N, 8°48'37"W, 293 m, on *Pyrus cordata*, 15 viii 2021, D. Fernández-Costas & A. García-Morales (MA-Lichen 26863); Pontevedra, Niño do Corvo, Mirador de Tamuxe, 41°54'59"N, 8°49'34"W, 25 m, on *Castanea sativa*, 25 vii 2021, D. Fernández-Costas & A. García-Morales (MA-Lichen 26864).

Discussion

The lecideoid epiphytic species described here has been treated equivocally in the literature as *Lecidea exigua* (= *Traponora varians*) (e.g. Martínez & Aragón 2004) or *L. aff. erythrophaea* (e.g. Zamora *et al.* 2016). Records of these species from the Mediterranean region of the Iberian Peninsula should therefore be re-evaluated.

Our phylogenetic analyses showed that *Nimisora iberica* belongs to the family *Lecanoraceae*. A number of epiphytic lecideoid species have been shown to belong to the *Lecanoraceae* in recent years (e.g. Pérez-Ortega *et al.* 2010; Rodríguez-Flakus & Printzen 2014; Schmuil *et al.* 2011). Unfortunately, our analyses

Table 2. Characters distinguishing *Nimisora* from similar genera in the *Lecanoraceae*. Characters for genera mostly follow Aptroot (2009), Rodríguez-Flakus & Printzen (2014), Rodríguez-Flakus (2020) and Cannon *et al.* (2022).

	<i>Nimisora</i>	<i>Lecidella</i>	<i>Palicella</i>	<i>Japewia</i>	<i>Japewiella</i>
Exciple	Radial hyphae with thick walls and narrow cylindrical lumina, rarely anastomosed, apically strongly swollen with a brown pigment. Granules rare, not abundant	Radial hyphae cylindrical, ellipsoid to globose lumina, apically weakly swollen, strongly gelatinized. Granules often present	Radial hyphae with narrow cylindrical lumina, strongly gelatinized, apically weakly to strongly swollen. Oil droplets in taxa from the Northern Hemisphere	True exciple reduced, weakly gelatinized, similar in structure to the hamathecium	Radial hyphae, anastomosed with thick gelatinous walls. Granules often present
Pigments	Unknown brown pigment in epihymenium and external part of the excipulum, K+ dark olivaceous green	Cinereorufa-green in epihymenium and external part of the excipulum, K+ vivid green. Brown to yellowish brown pigments sometimes in hypothecium and inner part of excipulum	Cinereorufa-green, K+ vivid green, and an unknown brown pigment in epihymenium and external part of the excipulum	Brown, K+ fuscous brown, sometimes covered by a thick colourless gelatinous layer	Orange to greenish brown, K+ greenish, N+ rose-red
Paraphyses	Simple to branched, rarely anastomosed, apically widened with a brown pigment around the tip. Hymenium not interspersed	Simple, apically widened. Hymenium interspersed or not	Branched, rarely anastomosed, without apical widening	Richly branched and anastomosed, apically widened with a brown pigment around the tip. Hymenium not interspersed, often with yellowish droplets	Sparingly branched and anastomosed except in the lower part, apically widened with a brown pigment around the tip
Ascus type	<i>Bacidia</i> -like	<i>Lecidella</i> - <i>Bacidia</i>	From <i>Bacidia</i> -type to intermediate of <i>Lecanora</i> - <i>Lecidella</i> types	<i>Lecidella</i> - <i>Bacidia</i>	<i>Lecidella</i>
Ascospores	Simple, broadly ellipsoid	Simple, broadly ellipsoid	Simple, rarely one septate, narrowly ellipsoid	Ovoid-ellipsoidal to globose, the wall thick, distinctly multilayered in K	Broadly ellipsoid with thick homogeneous walls
Chemistry	No substances	Atranorin (major), terpenoids (\pm), xanthonones (\pm)	Atranorin (major), usnic acid, terpenoids (\pm), aliphatic acids (\pm), pannarin (\pm), and thiophanic acid in <i>P. lueckingii</i>	Secalonic acid and eumitrin (\pm), fatty acids (\pm), lobaric acid (\pm), or no substances	Atranorin (major), depsides (major) and xanthonones (\pm)

have not been able to ascertain the closest relative of *Nimisora*, as its relationship to other groups within *Lecanoraceae* were not supported. Molecular data gathered in this study seem largely insufficient to build a solid phylogenetic hypothesis for the family, just as in previous studies on the systematics and taxonomy of the *Lecanoraceae* (e.g. Pérez-Ortega *et al.* 2010; Rodríguez-Flakus & Printzen 2014; Davydov *et al.* 2021).

Morphologically, the new genus shows clear similarities with many other genera of lecideoid epiphytic species but, in our opinion, the combination of the structure of the proper exciple, paraphyses, pigments and ascus type make *Nimisora* characteristic enough to be separated as a new independent genus.

Ascus types, defined by a combination of ascus characteristics, especially the staining patterns shown at the apex after KI application, have been widely used in the taxonomy and systematics of the *Lecanoraceae* and *Lecideaceae* for the last six decades (Hafellner 1984; Rambold & Triebel 1992). However, the interpretation of ascus type is sometimes not straightforward, as intermediate stages occur within the same groups and even at different developmental stages in the same species (Rambold 1995; Rodríguez-Flakus 2020). This is the case for several of the taxa anatomically related to *Nimisora*, where the ascus types do not

seem to conform exactly to one of the proposed ideal types (Hafellner 1984). Likewise, the ascus of *Nimisora* is similar to the *Bacidia*-type; however, the strongly amyloid reaction of the tholus may make observation and interpretation of the ascus type difficult, and low concentrations of Lugol's often help with examination of the ascus tip structure.

Nimisora shares morphological and anatomical features with species from *Lecidella* Körb., *Japewia*, *Japewiella*, *Palicella* and *Traponora* Aptroot (Knoph 1990; Tønsberg 1990; Printzen 1999; Aptroot 2009; Rodríguez-Flakus & Printzen 2014).

Lecidella is the most similar genus to *Nimisora* (Table 2). They share a number of characters, although the thalli of the two genera are characteristically different, with *Lecidella* species usually having well-developed verrucose to areolate thalli and much larger apothecia than *Nimisora*, with a distinctive black colour and showing well-developed thick margins when young. Anatomically, *Nimisora* and *Lecidella* have an excipulum composed of radiating hyphae which thicken at the apices. In addition, *Nimisora* and *Lecidella* have sparsely branched paraphyses, although in *Nimisora* they usually terminate in a widened cell surrounded by a dark brown pigment, which is not present in *Lecidella*. *Lecidella* species typically have the

Cinereorufa-green pigment (Meyer & Printzen 2000) in the epihymenium and the outer excipulum, reacting K⁺ vivid green, N⁺ purple, whereas *Nimisora* has an unknown dark brown or dark green pigment that reacts K⁺ dark olive green, N⁺ dark pink. The genera also apparently have different ascus types. It has been stated that *Lecidella* species have a *Lecanora*-type ascus (e.g. Cannon *et al.* 2022) or *Lecidella*-type ascus (Rodríguez-Flakus & Printzen 2014), a modification of the *Lecanora*-type in which the axial mass does not reach the upper part of the ascus tip and is usually broadened. However, according to our observations, species such as *L. elaeochroma* or *L. euphorea* show an ascus type similar to the *Bacidia*-type reported here for *Nimisora*. Following Ekman *et al.* (2008), we do not recognize the *Biatora*-type since the presence of a darker layer surrounding the axial mass is a very variable character, even within species. Finally, *Lecidella* species often have atranorin as the major substance, usually accompanied by terpenoids and/or xanthenes, whereas no TLC-detectable substance is known so far from *Nimisora*.

Palicella also shows clear similarities with *Nimisora* (Table 1). It is noteworthy that all species of *Palicella* (except *P. lueckingii* Rodr. Flakus) and *N. iberica* have apothecia that show a great chromatic variation, often within the same specimen (Rodríguez-Flakus & Printzen 2014; Rodríguez-Flakus 2018). Excipular hyphae in *Palicella*, although also radiating, do not have thick hyphal walls. Unlike *Nimisora*, dark-pigmented *Palicella* species have the Cinereorufa-green pigment in the epihymenium and outer excipulum. Furthermore, the paraphyses are not or only slightly apically thickened, except in *P. lueckingii* (Rodríguez-Flakus & Printzen 2014; Rodríguez-Flakus 2018). In addition, the ascospores are narrowly ellipsoid (except in *P. lueckingii*), sometimes 1-septate, whereas in *Nimisora* they are broadly ellipsoid and extremely rarely septate. The species of *Palicella* have a *Lecanora/Lecidella*-type ascus, although *Bacidia*-like asci can also be found in young specimens (see Printzen & May 2002). Finally, *Palicella* species have atranorin as the major compound, whereas in *P. lueckingii* thiophanic acid is the major compound, often together with usnic acid or terpenoids (Rodríguez-Flakus & Printzen 2014; Rodríguez-Flakus 2018). Holarctic species are known to contain aliphatic substances (paraensic acids; Pérez-Ortega *et al.* 2010), confined apparently to apothecia (Palice *et al.* 2011), and South American species have pannaric acid as crystals in the epihymenium (Rodríguez-Flakus & Printzen 2014; Rodríguez-Flakus 2018).

The genus *Japewiella* is also anatomically similar to *Nimisora*, especially in terms of the excipulum and hamathecial structure. In both, the excipulum is formed by very thick-walled hyphae in a radial arrangement, although they are more branched and anastomosed in *Japewiella* than in *Nimisora*, in which the hyphae are unbranched or barely branched (Printzen 1999). Both genera have hamathecia composed of sparingly branched or anastomosed paraphyses with widened apical cells with brown walls. Regarding ascus type, it is stated in the literature that *Japewiella* has a *Lecidella*-type (Printzen 1999); however, plasticity there also exists and transitions to the *Bacidia*-type present in *Nimisora* are common. There are also differences in secondary chemistry: *Japewiella* species either contain atranorin and other depsides as major substances (Printzen 1999) or the β -orcinol depsidone norstictic acid (Allen & Lendemer 2015), whereas *Nimisora* does not contain any lichen substance detectable by TLC. In addition, our phylogenetic analyses indicate a rather distant relationship between the two genera (Fig. 1).

Japewiella may be superficially similar to *Nimisora* but it displays a large number of differences, such as an exciple not clearly different in structure from the hamathecium, which is composed of a network of highly branched and anastomosed paraphyses. Asci range from the *Lecidella*- and *Bacidia*-types (Tønsberg 1990), and ascospores have characteristic, thick multilayered walls (Tønsberg 1990; Printzen 1999; Malíček *et al.* 2020).

Other groups in the *Lecanoraceae* which show some similarities with *Nimisora* are *Ramboldia*, *Pyrrhospora querneae* and the *Lecanora symmicta* group.

Ramboldia was described by Kantvilas & Elix (1994) to accommodate a group of lignicolous species close to *Lecidea elabens* Fr., characterized by lecideoid apothecia, an unpigmented excipulum composed of radially branched and anastomosed hyphae, *Lecanora*-type asci and simple, hyaline, non-halonate ascospores. The group has later been revised to incorporate species formerly placed in *Pyrrhospora*, including saxicolous species and species with the anthraquinone russulone (Kantvilas & Elix 2007; Kalb *et al.* 2008). *Nimisora* differs from *Ramboldia* in the different ascus type and in the excipular hyphae which are much less branched and anastomosed than in *Ramboldia*, as well as in the very distinct chemistry of the latter genus.

Pyrrhospora querneae also has an excipulum with radiating hyphae, but they are usually not swollen at their ends and the tips are usually interspersed with red granules; it has the K⁺ purplish anthraquinone (7-chloroemodin) in the epithecium, a *Lecanora*-type ascus and ascospores typically turning yellow to brownish when mature.

The predominantly tropical genus *Traponora* also shows some similarities with *Nimisora* (Aptroot *et al.* 1997; Aptroot 2009). The main differences concern the anatomy of the apothecia, which in *Traponora* are irregular in shape, pruinose and surrounded by thallus remnants when young (Aptroot 2009), in contrast to the more roundish and regular apothecia in *Nimisora* which only show scarce thallus remnants in some very young specimens and never show pruina. The excipulum in *Traponora* is composed of narrow radiating hyphae, not swollen at the tips, and it has a *Lecanora*-type ascus (Aptroot 2009). *Traponora* is a genus with a mainly tropical distribution (Aptroot 2009), but *T. varians* is a species with a temperate distribution in Europe and North America (see below).

The species of the *Lecanora symmicta* group also have excipular margins with radiating hyphae but they form a network through frequent anastomoses and are weakly swollen in the apex, and they also have granules in the outer part. In addition, the pale pigments in the epithecium are K⁻, and the thalli contain usnic acid as the major compound.

Nimisora iberica can be confused in the field with *Lecidella elaeochroma* and *L. euphorea*, two species with which it often co-occurs. Confusion is especially possible with the former since it may have thalli with coloration similar to *N. iberica* and apothecia, especially in shade forms, ranging from dark brown to light brown. However, both species are easily distinguished from *Nimisora* by the presence of whitish or creamy crustose continuous to areolate thalli, much larger apothecia and the characteristic Cinereorufa-green pigment in the epihymenium and external part of the excipulum, reacting a K⁺ vivid green.

There has previously been confusion in the literature between *Nimisora iberica* and two other species, namely *Lecidea exigua* Chaub. and *L. erythrophaea* Sommerf. The former taxon was recently put into synonymy with *Traponora varians* (Cannon *et al.* 2022), a species now having a disjunct distribution occurring

on the Pacific Coast and Eastern Coast of North America (Hertel & Printzen 2004; León-González & Pérez-Pérez 2020), as well as in several areas of Europe such as Great Britain (Cannon et al. 2022), Italy (Nimis 2023), France (Roux 2012), and the Iberian Peninsula (e.g. Carballal & García-Morales 1991; Etayo & Gómez-Bolea 1992). *Traponora varians*, which according to our observations shares the same *Bacidia*-type ascus with *N. iberica*, can be distinguished from the new species by having a thallus usually surrounded by a black hypothallus, small lecideine apothecia which are orange to pale reddish brown, usually pruinose when young, and atranorin and unidentified xanthonones as the main secondary metabolites (Cannon et al. 2022). In addition, in Europe, *T. varians* seems to prefer more humid localities than *N. iberica*. The relationships between *T. varians* and the tropical species of the genus, as well as the relationships between the North American and European populations, need to be investigated further.

Lecidea erythrophaea has larger apothecia than *N. iberica* (0.25–0.75(–1) mm), typically with reddish brown discs (Hertel & Printzen 2004). In addition, *L. erythrophaea* has a thin, white thallus, lacks a K+ green pigment in the epihymenium, contains reddish brown oily granules in the exciple and has a distinctly different ascospore shape, with comparatively more narrowly ellipsoid ascospores up to 18 µm long and 3–4.5(–5) µm wide (Aptroot et al. 2009; Wirth et al. 2013).

The mostly lignicolous *Lecanora hypoptoides* (Nyl.) Nyl. also shares some similarities with *N. iberica*, such as the very similar ascus type (Palice et al. 2018). The two taxa can be differentiated by the poorly developed, often immersed, thallus in *L. hypoptoides*, as well as by the presence in this species of lecanorine apothecia when young, becoming biatorine with age (van den Boom & Brand 2008; Cannon et al. 2022). In addition, the presence of paraensic C and D acids is diagnostic of *L. hypoptoides* (van den Boom & Brand 2008; Palice et al. 2018).

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