

# Umbilicariaceae (lichenized Ascomycota) – Trait evolution and a new generic concept

Evgeny A. Davydov,<sup>1</sup> Derek Peršoh<sup>2</sup> & Gerhard Rambold<sup>3</sup>

<sup>1</sup> Altai State University, Lenin Ave. 61, Barnaul, 656049 Russia

<sup>2</sup> Ruhr-Universität Bochum, AG Geobotanik, Gebäude ND 03/170, Universitätsstraße 150, 44801 Bochum, Germany

<sup>3</sup> University of Bayreuth, Plant Systematics, Mycology Dept., Universitätsstraße 30, NW 1, 95445 Bayreuth, Germany

Author for correspondence: Evgeny A. Davydov, [eadavydov@yandex.ru](mailto:eadavydov@yandex.ru)

ORCID EAD, <http://orcid.org/0000-0002-2316-8506>; DP, <http://orcid.org/0000-0001-5561-0189>

DOI <https://doi.org/10.12705/666.2>

**Abstract** To reconstruct hypotheses on the evolution of Umbilicariaceae, 644 sequences from three independent DNA regions were used, 433 of which were newly produced. The study includes a representative fraction (presumably about 80%) of the known species diversity of the Umbilicariaceae s.str. and is based on the phylograms obtained using maximum likelihood and a Bayesian phylogenetic inference framework. The analyses resulted in the recognition of eight well-supported clades, delimited by a combination of morphological and chemical features. None of the previous classifications within Umbilicariaceae s.str. were supported by the phylogenetic analyses. The distribution of the diagnostic morphological and chemical traits against the molecular phylogenetic topology revealed the following patterns of evolution: (1) Rhizinomorphs were gained at least four times independently and are lacking in most clades grouping in the proximity of *Lasallia*. (2) Asexual reproductive structures, i.e., thalloconidia and lichenized dispersal units, appear more or less mutually exclusive, being restricted to different clades. Two major ontogenetic types of thalloconidial development (thallobred versus rhizinobred) exist, reflecting their non-homologous origin. Both types of thalloconidial formation were gained multiple times. (3) “Gyrodisc-omphalodisc” apothecia are plesiomorphic in Umbilicariaceae. The apothecial type is a relatively variable trait, because the main types of apothecia switched at least six times in evolution. Multiple evolutionary changes from the gyrodiscs to leiodiscs, by reduction of carbonized hymenial structures, seem likely. (4) Ascospore characters, such as spore number per ascus, spore size, and septation type and degree are strongly correlated. Eight non-septate small ascospores per ascus represent a plesiomorphic trait. The results indicate parallel evolutionary trends from “gyrodisc-omphalodisc” to leiodisc apothecia, from octospority to mono- or bispority and from unicellular to multicellular-muriform ascospores. The other types of apothecia and ascospores evolved multiple times. This suggests that the concept of Umbilicariaceae s.str. has to be refined. The new classification includes eight subgenera in the only genus *Umbilicaria*: subg. *Actinogyra* (type: *U. muehlenbergii*), subg. *Agyrophora* (type: *A. atropuina*), subg. *Floccularia* subg. nov. (type: *U. deusta*), subg. *Gyrophora* (type: *U. vellea*), subg. *Iwatakia* subg. nov. (type: *U. esculenta*), subg. *Lasallia* (type: *L. pustulata*), subg. *Umbilicaria* (type: *U. hyperborea*), and subg. *Umbilicariopsis* subg. nov. (type: *Umbilicaria polyrhiza*). Furthermore, four new combinations are proposed: *Umbilicaria daliensis* comb. nov., *U. hispanica* comb. nov., *U. sinorientalis* comb. nov., *U. xizangensis* comb. nov.

**Keywords** apothecia; ascospores; classification; likelihood; morphology; mtLSU; nrITS/5.8S; nrSSU nrDNA; *RPB2*; rhizinomorphs; thalloconidia

**Supplementary Material** The Electronic Supplement (Tables S1–S5; Figs. S1–S9) and DNA sequence alignments are available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>)

## ■ INTRODUCTION

The lichen family Umbilicariaceae was long considered to be composed of two genera, *Umbilicaria* Hoffm. and *Lasallia* Mérat, together comprising about one hundred species of mostly umbilicate growth habit (Savicz, 1950; Poelt, 1962; Wei & Jiang, 1993) (Fig. 1). Species of Umbilicariaceae are predominantly saxicolous and mostly found in regions of higher latitudes or altitudes. Bendiksby & Timdal (2013) recently extended the family circumscription by including the two new genera *Xylopsora*

Bendiksby & Timdal and *Fulgidea* Bendiksby & Timdal, both composed of a few lignicolous species with squamulose growth habit (Umbilicariaceae s.l.). However, classification of species belonging to Umbilicariaceae in the traditional view (i.e., Umbilicariaceae s.str.) remained unclear. A previous molecular study (Davydov & al., 2010) suggested that *Lasallia* represents a well-defined genus, based on morphological and molecular traits, whereas *Umbilicaria* appeared paraphyletic.

Major progress in clarifying the relationships among Umbilicariaceae species was achieved by molecular phyloge-

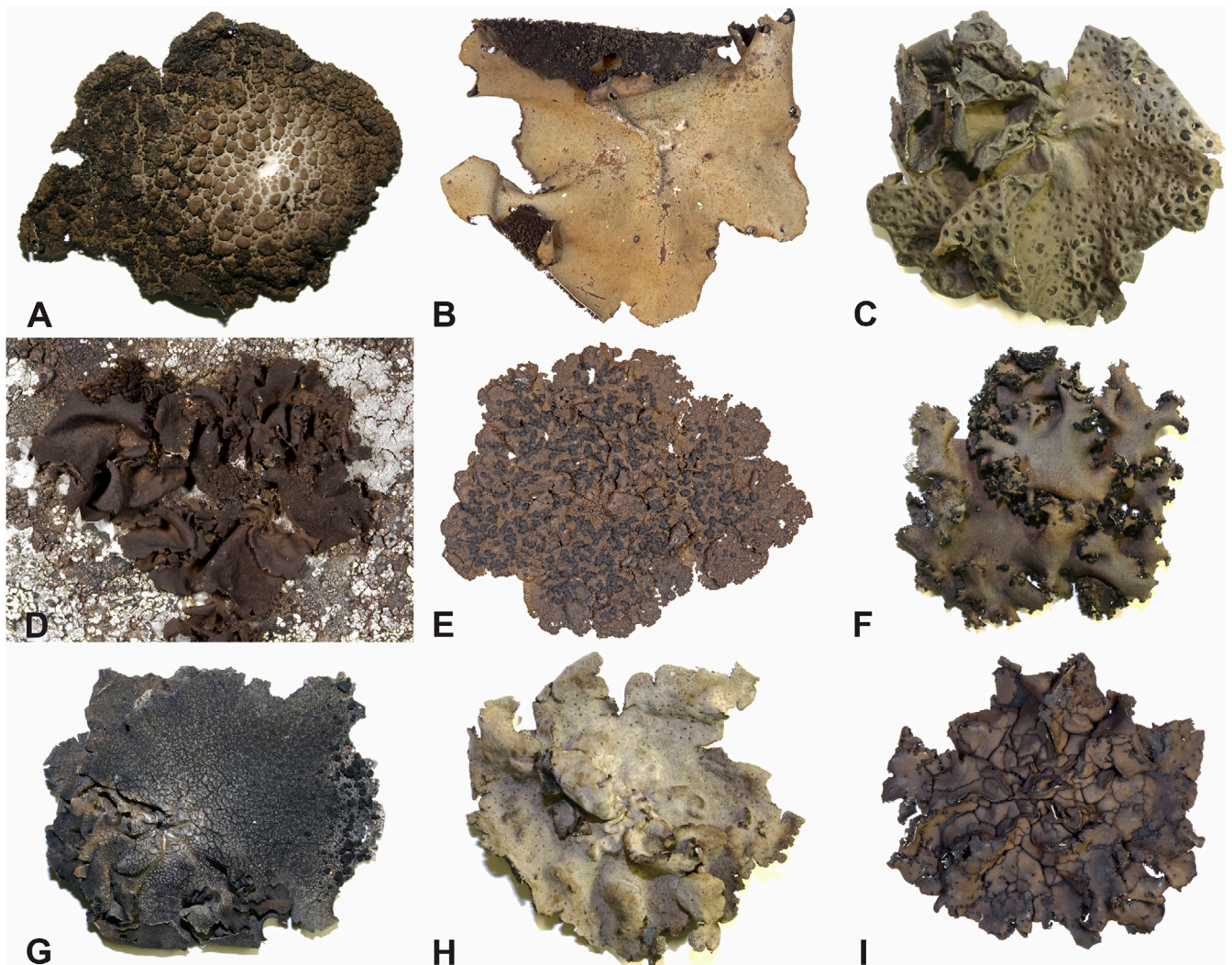
netic analyses over the last years (Niu & Wei, 1993; Ivanova & al., 1999; Romeike & al., 2002; Ott & al., 2004; Krzewicka & al., 2009; Davydov & al., 2010; Hestmark & al., 2011; McCune & Curtis, 2012; McCune & al., 2014). Molecular phylogenies based on multiple markers (Miadlikowska & al., 2014) supported the paraphyletic status of *Umbilicaria*. Those authors recommended broader taxon sampling before drawing taxonomic conclusions with respect to the generic concept of Umbilicariaceae.

The presence of sterile, more or less carbonized hyphal or paraphysal elements within the hymenial layer, which is characteristic for the whole family, results in the formation of four major apothecial types (Scholander, 1934; Llano, 1950). Most *Umbilicaria* species have eight-spored asci with unicellular spores. Only a few taxa facultatively produce bicellular or oligocellular, i.e., submuriform ascospores. Species of *Lasallia* are usually characterized by mono- or bispored asci, with multicellular-muriform, i.e., eumuriform, ascospores (Davydov & al., 2010). Many species of the Umbilicariaceae s.str. develop

rather characteristic mitosporic dispersal units, so-called “thalloconidia”, which were shown to be highly species-specific (Hasenhüttl & Poelt, 1978; Hestmark, 1991a, b).

Secondary metabolism of Umbilicariaceae s.str. has been studied rather extensively since Nylander (1869). Most species contain simple orcinol compounds such as depsides, tridepsides, and  $\beta$ -orcinol depsidones being synthesized via the acetyl-polymalonyl pathway (Hale, 1983). Chemical data for 56 species were published by Narui & al. (1996) and geographic variation in lichen substances was studied by Golubkova & Shapiro (1979) and Feige & al. (1987).

Evolution, distribution, and structural or functional coupling of the phenotypic traits in Umbilicariaceae is clarified in the present study. Extensive analyses of three independent DNA regions of different levels of variation, i.e., nuclear ITS/5.8S and *RPB2*, as well as mtLSU sequences were conducted. With 79 analysed taxa, the study presumably includes about 80% of the known species of Umbilicariaceae s.str. (see Taxonomic treatment).



**Fig. 1.** Species of Umbilicariaceae s.str.: **A**, *Umbilicaria pustulata* (subg. *Lasallia*); **B**, *U. esculenta* (subg. *Iwatakia*); **C**, *U. muehlenbergii* (subg. *Actinogyra*); **D**, *U. deusta* (subg. *Floccularia*); **E**, *U. hyperborea* (subg. *Umbilicaria*); **F**, *U. polyrhiza* (subg. *Umbilicariopsis*); **G**, *U. leiocarpa* (subg. *Agyrophora*); **H**, *U. vellea* (subg. *Gyrophora*); **I**, *U. pulvinaria* (subg. *Gyrophora*). — Photos: E.A. Davydov.



## ■ MATERIALS AND METHODS

**Material.** — We analyzed recently collected and herbarium specimens from different regions of the world (Appendix 1). DNA was extracted from 186 specimens of Umbilicariaceae s.str. and of 6 specimens of outgroup taxa, i.e., 4 for the *RPB2*+ITS+mtLSU dataset and 2 for the nuSSU dataset (Appendix 1). Freshly collected specimens were obtained from and deposited in the lichen herbaria ABL, ALTB, E, FR, H, INEP, KPABG, LE, M, MAF, VLA, and WSL, as well as the private collections of F. Fernandez-Mendoza, D. Masson, B. McCune, S. Pérez-Ortega, O.B. Blum and L.S. Yakovchenko. Voucher specimens are available in the herbaria listed. Duplicates of specimens from private collections were deposited in ALTB (Appendix 1).

**DNA extraction and amplification.** — Up to twelve apothecia were separated from the thallus under a magnifying lens, washed in drops of sterile water and transferred to sterile 1.5 ml reaction tubes. For specimens lacking apothecia, central thallus sections of up to 25 mm<sup>2</sup> were excised. Rhizinomorphs and thalloconidia were removed to avoid potential contamination with DNA from endolichenic fungi. The samples were frozen in liquid nitrogen and powderized in the tubes using sterile pestles. The DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) or ChargeSwitch gDNA Plant Kit (Invitrogen, Carlsbad, California, U.S.A.) were used for DNA extraction as recommended by the manufacturers, except that 80 µl of prewarmed (60°C) distilled water was used to elute DNA from the Qiagen spin columns in a single step.

Four genetic markers were amplified: the ITS region (ITS1, 5.8S, and ITS2 rRNA gene regions), SSU rRNA gene, *RPB2* (between six and seven conserved parts), and a partial sequence of the large subunit of the mitochondrial ribosomal DNA (mtLSU). ITS, *RPB2* and mtLSU were amplified in a single reaction, whereas SSU nrDNA was amplified in two parts. Primers and cycling conditions for amplification of all genes are listed in Table 1. Sequences were produced on Li-Cor 4200 or Sanger ABI 37390xl sequencers. The program Geneious v.6.0 (Biomatters, New Zealand) was used for assembling partial and complementary sequences. Consensus sequences were exclusively compiled from double-stranded sequenced parts of the sequences. Sequence alignments were complemented with Umbilicariaceae sequences from GenBank (<http://www.ncbi.nlm.nih.gov>; Sep 2013; Appendix 1). For the alignments, 644 sequences of Umbilicariaceae and outgroup taxa were used, 433 of which were newly obtained and 211 downloaded from GenBank (Appendix 1).

**Phylogenetic analyses.** — Phylogenetic trees were reconstructed using a maximum likelihood (ML) and a Bayesian phylogenetic inference framework. We rooted the trees using *Boreoplaca ultrafrigida* Timdal, *Hypocenomyce scalaris* (Ach.) M.Choisy, *Ophioparma ventosa* (L.) Norman, and *Xylopsora friesii* (Ach.) Bendiksby & Timdal, as outgroup. This selection is based on the studies of Bendiksby & Timdal (2013) and a five-gene analysis by Miadlikowska & al. (2014), in which these species of Umbilicariales form sister clades to Umbilicariaceae s.str. For the SSU dataset, we used 38 taxa

as outgroup, selected on the basis of the five-gene phylogeny of Pezizomycotina by Spatafora & al. (2006). One full-length sequence for each Pezizomycotina clade was downloaded from GenBank and aligned with newly produced sequences of *Pertusaria alpina* Hepp ex H.E.Ahles and *Ochrolechia parella* (L.) A.Massal. Nucleotide diversity and Tajima's D were calculated for each dataset using DnaSP v.5 (Librado & Rozas, 2009).

Optimal substitution models and partitions (Table 1) were inferred for the following subsets: ITS1, 5.8S, ITS2, *RPB2* 1st, 2nd, and 3rd codon positions, and mtLSU, using PartitionFinder v.1.1.1 (Lanfear & al., 2012).

The unambiguously alignable regions of 89 specimens (85 ingroup, 4 outgroup) for which all three marker regions were obtained were used to calculate ITS, *RPB2*, and mtLSU single-marker phylograms (not shown) with RAxML v.8.0.26 (Stamatakis, 2006, 2014). These were tested for conflicts. All phylograms were similar regarding well-supported clades; only two minor conflicts were found (Appendix 2). The analysis was re-run without the incongruent species, which were later added to the resulting phylogram. The combined data matrix consists of 1917 sites, 662 of which were variable, and used for RAxML and Bayesian analyses. In addition we present the combined analysis including the two conflicting species (Electr. Suppl.: Fig. S1) because its topology did not deviate from the tree topologies calculated without these species.

The most likely tree and 1000 bootstrap replicates were calculated using RAxML using the raxmlGUI software v.1.3.1 (Silvestro & Michalak, 2012) and applying the GTRGAMMAI model of substitution to the subsets. Bayesian inference was carried out using Metropolis coupled Markov Chain Monte Carlo (MCMCMC) as implemented in MrBayes, v.3.2.3 (Ronquist & al., 2012). Three independent analyses were run applying different models for partitions (Table 1), each running for 100 million generations (200 million for combined dataset) in six chains, and every 200th generation was sampled. A burn-in value of 50% was specified to calculate standard deviation; the same value was used for the final 50% majority-rule consensus tree calculated with the sumt command implemented in MrBayes v.3.2.3.

Character evolution was reconstructed using Mesquite v.3.2 (Maddison & Maddison, 2017). Modules “Trace Character Over Trees” and “Reconstruct Ancestral States” with the parameter “maximum likelihood reconstruction of ancestral states” were used to identify plesiomorphies and apomorphies.

**Phenotypic analyses.** — Morphological and chemical traits were examined and compared with published data (Llano 1950; Hestmark, 1990; Wei & Jiang, 1993; Narui & al., 1996). Morphology and anatomy were analysed by applying standard light microscopic methods. For each species, general morphology, structure of the upper and lower thallus cortex, special structures, occurrence and localization of thalloconidia, types of lichenised dispersal units and apothecial morphology were recorded. Thallus and apothecial anatomy were investigated under a light microscope, using freezing microtome sections mounted in water and lactophenol-cotton-blue. Measurements of ascospores ( $n = 20$  per specimen, sections mounted in water)

were performed under a light microscope. Secondary metabolites were analysed by applying standard thin-layer chromatography techniques (Culberson & Kristinsson, 1970; Elix & Stocker-Wörgötter, 2008).

**Statistics.** — The states of 12 diagnostic morpho-anatomical and chemical traits of Umbilicariaceae representing nominal data were coded (Table 2) and analysed using MS Excel. Associations between every character pair were tested using cross tabulation. We used chi-squared tests of the null hypothesis of no association between characters (Fienberg, 1980). Cramer’s V was calculated to test the strength of association of the cross tabulations; the phi coefficient was calculated in addition when both variables were binary.

The minimum number of switches from one character state to another was counted from the resulting phylogenetic tree to compare the constancy of selected phenotypic traits in the course of the phylogeny.

The phylogenetic distinctness of character states was calculated based on phylogenetic distances extracted from the Bayesian tree. We looked for indices reflecting phylogenetic relationship between species sharing a certain trait because most biologically and diagnostically important traits appeared non-monophyletic. Warwick & Clarke (1995) introduced the concept of taxonomic distinctness into marine ecology, as a measure of the average degree to which species in a community are related to each other. This index has been extensively used in ecology to measure phylogenetic relatedness of species in communities (Clarke & Gorley, 2015). We calculated this index to measure phylogenetic distinctness among species sharing specific traits. By comparing the average phylogenetic distance among all species in the phylogenetic tree with the average distance among species sharing a certain trait, we assessed phylogenetic distinctness of the traits. The distance matrix was calculated on the T-REX server (Boc & al., 2012),

**Table 1.** Summary statistics, PCR settings and substitution models used for the different datasets.

Name	ITS	SSU	<i>RPB2</i> (partial)	mtLSU (partial)	ITS+ <i>RPB2</i> +mtLSU
Regions	ITS1-5.8S-ITS2		Between 6 and 7 conservative regions (Liu & al., 1999)	ML3–ML4 (Zoller & al., 1999)	–
PCR Settings					
Primers	1203F-5' / ITS 4-3' 1055F-5' / ITS 4-3' ITS 1F-5' / ITS 4-3'	AS-5' / 1293R-3' AS-5' / 1400R-3' 819F-5' / ITS2-3' 1203F-5' / ITS 2-3' 1203F-5' / ITS 4-3'	<i>RPB2</i> -980F-5' / <i>fRPB2</i> -7cR-3'	ML 3-A-5' / ML 4-A-3'	–
References	White & al., 1990 Gargas & Taylor, 1992 Gardes & Bruns, 1993 Huss & al., 1999	Medlin & al., 1988 White & al., 1990 Gargas & Taylor, 1992 Döring & Triebel, 1998	Liu & al., 1999 Reeb & al., 2004	Printzen, 2002	–
Denaturation	95°C (2 min)	95°C (2 min)	95°C (2 min)	95°C (2 min)	–
Amplification	35 cycles 94°C (20 s) 52°C (1 min) 72°C (2 min)	35 cycles 94°C (20 s) 52°C (1 min) 72°C (2 min)	35 cycles 94°C (20 s) 61°C (1 min) 72°C (2 min)	35 cycles 94°C (20 s) 52°C (1 min) 72°C (2 min)	–
Extension	72°C (15 min)	72°C (15 min)	72°C (15 min)	72°C (15 min)	–
Datasets					
Alignment length [bp]	442	1516	738	739	1917
Variable sites	191	77	293	174	662
Nucleotide diversity $\pi$	0.06536	0.00745	0.09490	0.04930	0.07934
Tajima’s D	–1,59188	–1,7431	–0,70351	–1,33333	
Number of sequences (ingroup):					
total/original	317/162	29/22	118/108	130/127	83/83
Number of taxa total/originally sequenced					
	78/69	21/19	64/64	71/70	53/53
Substitution model	ITS1, 2: GTR+G; 5.8S: K80+I+G	SYM+I+G	pos. 1: HKY+G; pos. 2, 3: K80+I+G	HKY+I+G	As for separate markers

averaging distances for species. Calculation of phylogenetic distinctness was performed for each character state using the module “Univariate Diversity Indices (DIVERSE)” implemented in the Primer-E software v.7 (Clarke & Gorley, 2015). For the states of each character, average taxonomic distinctness ( $\Delta^+$ ) and its variation ( $\lambda^+$ ) were calculated. Average phylogenetic distinctness ( $\Delta^+$ ) indicates the average phylogenetic distance between all pairs of species (Clarke & Warwick 1998). Variation in phylogenetic distinctness ( $\lambda^+$ ) is a measure of the evenness of distribution in the phylogenetic tree. To analyse trait distribution across the phylogenetic tree, these measures were compared between species possessing a certain trait and the entirety of species in the phylogenetic tree.

## ■ RESULTS

**Phylogenetic reconstructions.** — DNA extracts from freshly collected specimens or samples stored in the herbarium for less than five years were mostly successful. The major taxon grouping was similar in the phylogenetic reconstructions of all markers. ITS and nuSSU-based trees (Electr. Suppl.: Figs. S2–S5) were highly resolved and contained a considerable number of clades, including representatives of one to few species, but species-rich clades were unsupported. The phylogenies based on *RPB2* and mtLSU (Electr. Suppl.: Fig. S6–S9) were less resolved, showing a smaller number of well-supported species-rich clades. A concatenated *RPB2*, ITS, and mtLSU sequence dataset provided phylograms with high support for most clades (Fig. 2). It was used as the basis for reconstructing trait evolution. As complete SSU rRNA gene sequences could be generated only from a few species representatives, these data were used only for testing results from the analyses based on the concatenated *RPB2*+ITS+mtLSU sequence dataset.

**Major clades based on *RPB2*+ITS+mtLSU dataset.** — In the Bayesian analysis of the *RPB2*+ITS+mtLSU dataset, the average standard deviation of split frequencies had fallen to 0.11067 at termination (200 million generations). The topology of the Bayesian 50% majority-rule consensus tree was similar to that of the tree calculated by RAxML. Both phylograms are combined in Fig. 2.

Umbilicariaceae s.str. are monophyletic in each Bayesian and RAxML analysis of nuSSU and *RPB2*+ITS+mtLSU datasets. The phylogenetic analysis of three independent DNA regions of different variability resulted in the recognition of six well-supported major clades of Umbilicariaceae (Fig. 2). The names of clades correspond to the respective subgenera (see Taxonomic treatment).

**Species-level structure of the six major clades.** — Species not present in the concatenated analyses, but grouped with support in the corresponding clades in single-locus phylogenies (Electr. Suppl.: Figs. S2, S3, S6–S9), were considered part of these clades.

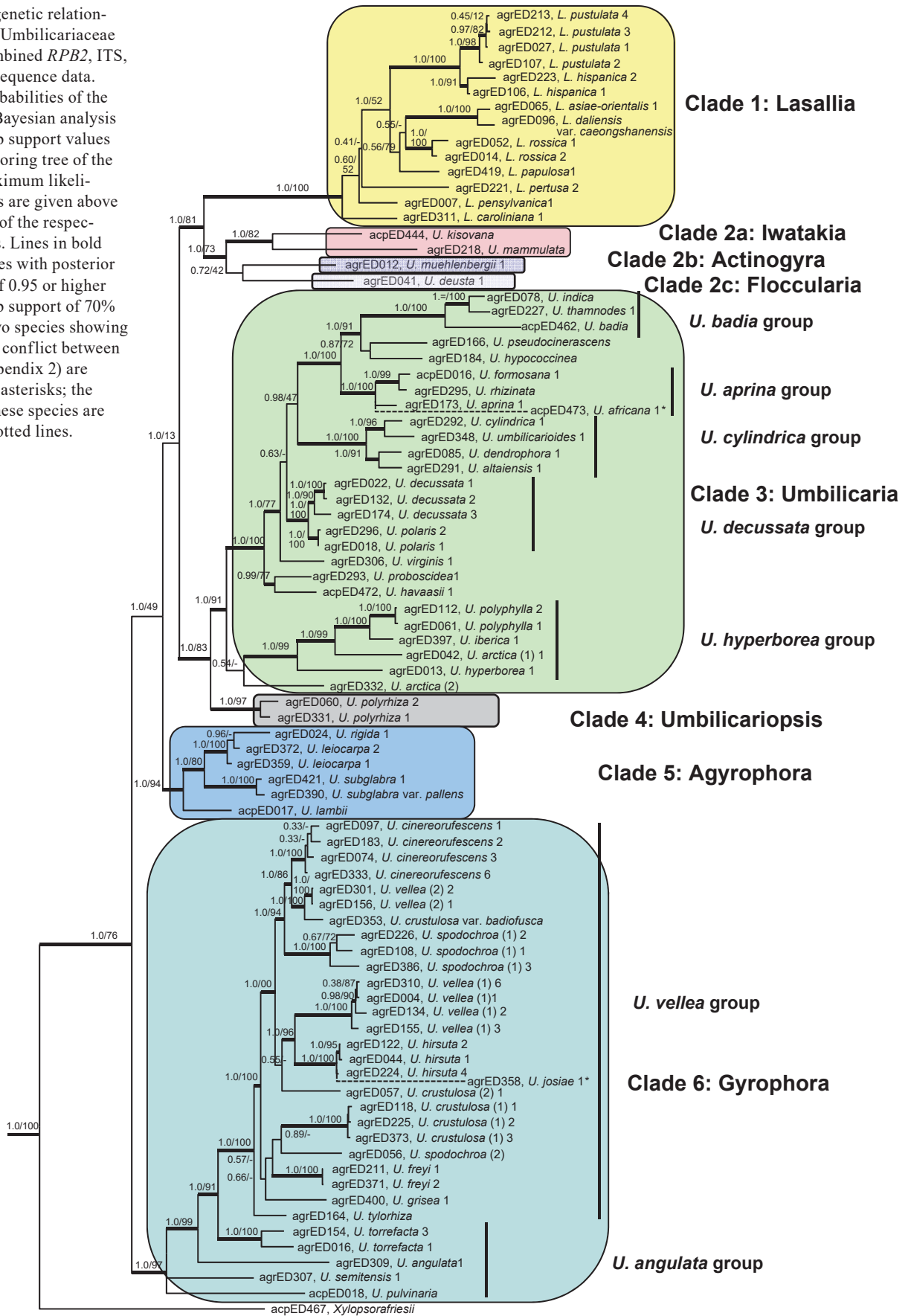
**Clade 1 (subg. *Lasallia*).** — *Lasallia* clade (Bayesian analysis: 1.0 PP; RAxML: 100% BS) unifies representatives of *Lasallia* in its former circumscription, including its type, *L. pustulata* (L.) Mérat (Fig. 1A). The trees calculated from different datasets were in full accordance regarding the topology and the present circumscription of *Lasallia*.

**Clade 2 (subg. *Iwatakia*, subg. *Floccularia*, subg. *Actinogyra*).** — Clade 2 combines *Umbilicaria kisovana* (Zahlbr. ex Asahina) Zahlbr., *U. mammulata* (Ach.) Tuck., *U. muehlenbergii* (Ach.) Tuck., and *U. deusta* (L.) Baumg. with considerable support (1.0 PP; 73% BS) and rather long branch lengths. Assignment of species to clade 2 by single-locus analyses: ITS, *RPB2*: *U. esculenta* (Miyoshi) Minks, *U. yunnana* (Nyl.) Hue. Morphological traits are heterogenous in clade 2. Single-marker analyses, however, resulted in several smaller clades,

**Table 2.** Coding of diagnostic morphological and chemical characters of Umbilicariaceae.

Character number	Character	States and terminology
Ch 1	Rhiziomorph (or rhizine) presence	Two states: absent (0); present (1)
Ch 2	Rhiziomorph (or rhizine) type	Four states: simple to branched (0); thalloconidial (1); fasciculate (2); true rhizines (3)
Ch 3	Thalloconidia presence	Two states: absent (0); present (1)
Ch 4	Thalloconidia origin	Two states: thallobred (0); rhizinobred (1)
Ch 5	Thalloconidia septation presence and type	Three states: 0–1-septate (0); (2–)6–10-septate (1); (4–)20- to multiseptate (2)
Ch 6	Lichenized propagules presence	Two states: absent (0); present (1). Species occasionally possessing thalyls developed on rhiziomorphs have not been mentioned as having lichenized propagules due to inconstancy of the character
Ch 7	Apothecia presence	Two states: rare (0); common (1)
Ch 8	Apothecia morphology	Three states: gyrodisc or omphalodisc (0); actinodisc (1); leiodisc (2)
Ch 9	Ascospore number per ascus	Two states: 8 per ascus (0); 1–2 per ascus (1)
Ch 10	Ascospore septation type	Three states: unicellular to bicellular (0); unicellular to submuriform (1); eumuriform (2)
Ch 11	Ascospore size class	Three states: small-sized: 7–16 × 4–8 μm (0); mean-sized: 16–30 × 8–20 μm (1); large-sized: 30–100 × 20–40 μm (2)
Ch 12	β-orcinol depsidones presence	Two states: absent (0); present (1)

**Fig. 2.** Phylogenetic relationships among Umbilicariaceae based on combined *RPB2*, *ITS*, and *mLSU* sequence data. Posterior probabilities of the MCMCMC Bayesian analysis and bootstrap support values of the best scoring tree of the RAxML maximum likelihood analysis are given above or to the left of the respective branches. Lines in bold indicate clades with posterior probability of 0.95 or higher and bootstrap support of 70% or higher. Two species showing phylogenetic conflict between markers (Appendix 2) are marked with asterisks; the position of these species are marked by dotted lines.



20.0



i.e., subclades 2a with taxa of more homogenous morphology, as well as 2b and 2c containing one species each.

**Clade 3 (subg. *Umbilicaria*).** — The *Umbilicaria* clade comprises sequences of *Umbilicaria* species, including the generic type *U. hyperborea* (Ach.) Hoffm. (Fig. 1E), and combines several lineages of closely related species such as the *U. hyperborea* group (*U. arctica* (Ach.) Nyl., *U. herrei* Frey, *U. hyperborea*, *U. iberica* Sancho & Krzewicka, *U. nylanderiana* (Zahlbr.) H.Magn., *U. polyphylla* (L.) Baumg.), the *U. cylindrica* group (*U. altaiensis* J.C.Weï & Y.M.Jiang, *U. cylindrica* (L.) Delise ex Duby, *U. dendrophora* (Poelt) Hestmark, *U. maculata* Krzewicka & al., *U. umbilicarioides* (Stein) Krog & Swinscow), the *U. decussata* group (*U. decussata* (Vill.) Zahlbr., *U. polaris* (Schol.) Zahlbr.), the *U. aprina* group (*U. africana*, *U. antarctica* Frey & Lamb, *U. aprina*, *U. formosana*, *U. kappeni* Sancho & al., *U. krascheninnikovii* (Savicz) Zahlbr., *U. rhizinata*), and the *U. badia* group (*U. badia* Frey, *U. indica* Frey, *U. thamnodes* Hue).

*Umbilicaria hypococcinea* (Jatta) Llano and *U. pseudocinerascens* J.C.Weï & Y.M.Jiang group together as sister to the *U. badia* group. *Umbilicaria proboscidea* (L.) Schrad. and *U. havaasii* Llano form a clade sister to the remainder of clade 3 except the *U. hyperborea* group. The precise phylogenetic placement of *U. virginis* Schaer. remains obscure due to its different phylogenetic positions across phylograms based on different datasets. Its intermediate morphology fits to more than one group within the *Umbilicaria* clade. Taxa assigned by single-locus analyses: ITS, mtLSU: *U. antarctica*, *U. herrei*, *U. kappeni*, *U. krascheninnikovii*.

**Clade 4 (subg. *Umbilicariopsis*).** — *Umbilicaria polyrhiza* clade (Fig. 1F) is sister to clade 3 with rather strong support (1.0 PP; 83% BS), but clearly differs morphologically (see discussion).

**Clade 5 (subg. *Agyrophora*).** — The *Agyrophora* clade combines representatives of *Umbilicaria* sect. *Anthracinae* sensu Imshaug and *U. lambii* Imshaug. The *Agyrophora* clade is well supported by the ITS and *RPB2* analyses (Electr. Suppl.: Figs. S2, S3, S6, S7). The mtLSU analysis, however, shows that clade 5 split into three subclades (Electr. Suppl.: Figs. S8, S9). Taxa assigned by single-locus analyses: ITS and mtLSU: *U. cinerascens* (Arnold) Frey, *U. laevis* (Schaer.) Frey, *U. lyngei* Schol., and *U. ruebeliana* Du Rietz & Frey; *RPB2* and mtLSU: *U. microphilla* (Laurer) A.Massal.

**Clade 6 (subg. *Gyrophora*).** — The *Gyrophora* clade comprises sequences of the *Umbilicaria vellea* group as well as the *U. angulata* group (*U. angulata* Tuck., *U. pulvinaria* (Savicz) Frey, *U. semitensis* Tuck., *U. torrefacta* (Lightf.) Schrad.). The *U. vellea* group is monophyletic, whereas the *U. angulata* group consists of paraphyletic lineages forming the sister group(s) to the *U. vellea* group (Fig. 2). Two species groups are morphologically distinguishable. However, analyses of single-marker datasets do not fully support this segregation. *Umbilicaria americana* Poelt & T.H.Nash, being sister to *U. angulata* and *U. semitensis* in the *RPB2* dataset, is morphologically more similar to the *U. vellea* group.

Three species appear non-monophyletic. Sequences of *U. crustulosa* s.l. (*U. crustulosa*-1, *U. crustulosa*-2, and

*U. crustulosa* var. *badiofusca*) group in three different well-supported clades. Despite their similar thallus morphology, apothecial and rhizinomorph traits differ. Two individuals assigned to *U. vellea* (“*U. vellea*-2”) from the Khibiny Mtns have a morphology similar to other specimens of *U. vellea* (“*U. vellea*-1”), but have clearly darker rhizinomorphs and group with *U. crustulosa* var. *badiofusca* Frey. The sequence of one specimen of *U. spodochroa* (Ehrh. ex Hoffm.) Ach. from Turkey (Izmir, V. John, H) groups apart from the other specimens.

Taxa assigned by single-locus analyses: ITS: *U. loboperipherica* J.C.Weï & al.; ITS+mtLSU: *U. phaea* Tuck. ITS sequences of the endemic South American species *U. calvescens* Nyl., *U. haplocarpa* Nyl., *U. dichroa* Nyl., and *U. leprosa* (Zahlbr.) Frey were obtained from GenBank. They group in a well-supported clade (1.0 PP; 89% BS, Electr. Suppl.: Figs. S2, S3) together with *U. cf. phaea*, also from South America. However, the relationship of *U. phaea* s.str. to other phylogenetic groups remains obscure. We assigned *U. phaea* and its relatives to the *U. vellea* clade based on published phylogenetic analyses of three markers (Hestmark & al., 2011; Miadlikowska & al., 2014). Three ITS sequences of *U. nodulospora* McCune & al. obtained from GenBank group together (1.0 PP; 96% BS), but their relationship to other phylogenetic groups lacked statistical support. Therefore, these species are not treated in detail here, even though an affiliation to clade 6 appears plausible according to morphological traits.

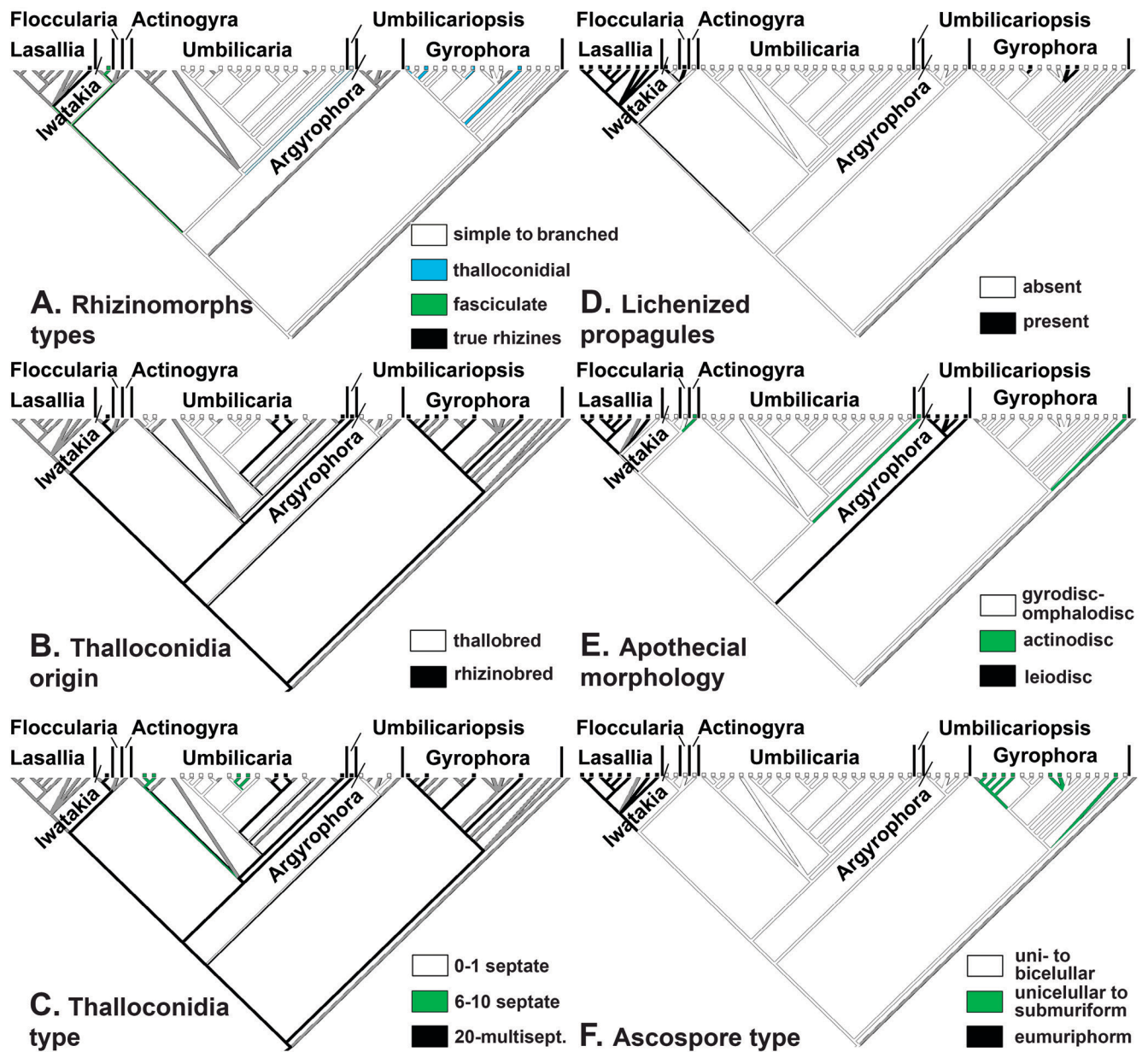
**Classification of phenotypic traits.** — The phylogenetic analysis of taxon and trait evolution was at first based on a narrow classification of traits. This provided evidence for multiple origins of certain phenotypic traits. For subsequent comparisons of morphological traits and phylogenetic relationship, we applied a more generalized classification of the traits (Table 2).

Rhizinoid structures were classified into four different types – “simple to branched”: non-branched to dichotomously or irregularly branched, cylindrical or complanate; “thalloconidial”: simple to irregularly branched, dissolving into clumps of septate thalloconidia; “fasciculate”: short and richly branched, with distal branches several times thinner than the basal branch; and “true rhizines”: relatively long, sparsely branched, attaching the thallus. Classification of thalloconidia septation follows Hestmark (1990). Apothecia types were classified mainly after Scholander (1934) and Llano (1950), but since omphalodisc and gyrodisc types are morphologically highly congruent, they may reflect only successional steps of apothecial ontogeny (Henssen, 1970). The “gyrodisc” and “omphalodisc” type are combined into one character state. Ascospore septation is classified as proposed by Davydov & al. (2010) with two types for multiseptate spores. “Submuriform” are spores with relatively few longitudinal and transverse septa and 12(–25) cells in optical section, usually restricted to the distally positioned spores within the ascus. “Eumuriform” are regularly developed multicellular-muriform spores subtype with (25–)30 or more septa and exceeding 50–100 cells in optical section.

**Co-occurrence and dependency of major phenotypic traits.** — The cross tabulation analysis shows a strong degree of association (Table 3) between presence of rhizinomorph and

apothecial morphology. This is due to the absence of rhizinomorphs in most species with leiodisc apothecia. The strong association of rhizinomorph type with ascospore morphology (Cramer’s V = 0.58 for ascospore septation and 0.62 for size class) is due to the co-occurrence of absence of rhizinomorphs with large-sized muriform ascospores in the *Lasallia* clade and rhizinomorphs of the “fasciculate” type with mean-sized simple spores in the *Iwatakia* clade. A strong association (Cramer’s V = 0.71) was revealed for thalloconidia origin and septation. While thallobred thalloconidia are non-septate or have few (6–10) septa, rhizinobred thalloconidia are always multiseptate.

Absence of thalloconidia is moderately associated with presence of lichenized propagules and vice versa (Table 3). When species exclusively reproducing by ascospores are excluded from the analysis, the association increases significantly ( $\phi = -0.85$ ; Cramer’s V = 0.60). The same degree of association (Table 3) is found for absence of thalloconidia and presence of apothecia. Most species having thalloconidia rarely produce apothecia. An association between production of lichenized propagules and apothecia is not obvious due to an only moderate association of lichenized propagules presence and rarity of apothecia ( $\phi = -0.39$ ; Cramer’s V = 0.28). The presence of



**Fig. 3.** Reconstruction of the evolution of traits, based on tree Fig. 2. **A,** Rhizinomorphs (presence and types); **B,** Thalloconidia (origin); **C,** Thalloconidia (presence and types); **D,** Lichenized propagules presence **E,** Apothecia morphology (type); **F,** Ascospores (type). — Grey, character lacking.



lichenized propagules is strongly associated with spore type, size, and number per ascus. This resulted from co-occurrence of lichenized propagules with 1–2 large-sized eumuriform spores per ascus in the Lasallia clade. The strong association of apothecial morphology with ascospore number, septation and size is due to the associated presence of gyrodisc-omphalodisc apothecia and octosporic asci with small non-septate spores. Associations are strong between apothecial morphologies and ascospore number, septation and size (Table 3). While the pairwise comparisons indicate strong correlations between single characters, additional multivariate interdependencies can not be excluded.

#### Phylogenetic distribution of major phenotypic traits. —

Rhizinomorphs occur in all clades except Agyrophora and Lasallia (Fig. 3A). Clades Umbilicaria, Umbilicariopsis, and Gyrophora mostly include species bearing rhizinomorphs. Most species of the Umbilicaria and Gyrophora clades often develop rhizinomorphs of the “simple to branched” type which is, according to the maximum likelihood reconstruction using Mesquite, a plesiomorphic trait (Fig. 3A). The “thalloconidial” type appears in clades Umbilicaria and Gyrophora along with the “simple to branched” type and exclusively in clade Umbilicariopsis. Only the “fasciculate” type occurs in Iwatakia. True rhizines appear in one species of the Lasallia clade.

Maximum likelihood reconstruction using Mesquite software (not shown) suggests that the absence of thalloconidia is a plesiomorphic trait. Thalloconidia in clades Gyrophora, Umbilicariopsis, and Iwatakia (except *U. yunnana* with non-septate thalloconidia), if present, are rhizinobred and multiseptate. The Umbilicaria clade includes all thalloconidial septation types. Only some species of the Agyrophora clade

have thallobred non-septate thalloconidia. The Lasallia clade includes species lacking thalloconidia (Fig. 3B, C).

Most, or, if lobules are regarded as propagules, all species of clades Lasallia, Iwatakia, and Floccularia have lichenized dispersal units, which are lacking in the clades Umbilicaria (apart from *U. kappeni*), Umbilicariopsis, and Agyrophora. Lichenized propagules are also rather common in Gyrophora (Fig. 3D).

Gyrodisc-omphalodisc apothecia occur in all clades, prevail in clades Iwatakia and Gyrophora, and are found in all species of the Umbilicaria clade. Our maximum likelihood reconstruction suggests that gyrodisc-omphalodisc apothecia represents a plesiomorphic trait. All but one representative of clades Lasallia and Agyrophora each have leiodisc apothecia. Three known species with actinodisc apothecia are found in different clades, i.e., Actinogyra, Umbilicariopsis, and Gyrophora (Fig. 3E).

Unicellular (to rarely bicellular) ascospores predominate in all clades except Lasallia and represent a plesiomorphic trait (Fig. 3F). Oligocellular-muriform ascospores occasionally occur in clades Agyrophora and Gyrophora. Multicellular-muriform ascospores are found in clade Lasallia. Eight-spored asci are exclusively found in all clades except Lasallia, where all but one species have mono- or bisporic asci.

The distribution pattern of the classes of secondary metabolites only partly coincides with monophyletic clades within Umbilicariaceae.  $\beta$ -orcinol depsidones were found in three different clades (Agyrophora, Gyrophora, Umbilicaria). In the *U. cylindrica* group (Umbilicaria clade) and the Agyrophora clade species with  $\beta$ -orcinol depsidones co-occur with chemodeficient strains. In species of the remaining clades, only

**Table 3.** Associations of diagnostic chemical and morphological characters Ch1 to Ch12 of the investigated species on the basis of Nominal Cramer's V and phi coefficients calculated from the cross tabulation.

	Ch1	Ch2	Ch3	Ch4	Ch5	Ch6	Ch7	Ch8	Ch9	Ch10	Ch11	Ch12	phi coefficient	
Ch1		–	0.21	0.47		–0.21	0.02		<b>–0.37</b>			–0.07		
Ch2	–													
Ch3	0.15	0.35		–		<b>–0.30</b>	<b>–0.39</b>		–0.25			–0.003		
Ch4	0.34	0.45	–			0.25	–0.31		–			0.04		
Ch5	<b>0.34</b>	0.37	–	<b>0.71</b>										
Ch6	0.15	0.15	<b>0.15</b>	0.17	0.17		<b>–0.39</b>		0.24			–0.20		
Ch7	0.02	0.25	<b>0.28</b>	0.22	0.26	<b>0.28</b>			–			0.13		
Ch8	<b>0.42</b>	0.18	<i>0.14</i>	0.26	0.25	0.09	–							
Ch9	<b>0.26</b>	–	<i>0.18</i>	–	–	0.17	–	<b>0.40</b>				–0.14		
Ch10	<b>0.25</b>	<b>0.58</b>	0.25	0.19	0.15	0.17	–	<b>0.31</b>	<b>0.66</b>					
Ch11	<b>0.31</b>	<b>0.62</b>	<i>0.19</i>	0.12	0.13	0.16	–	<b>0.32</b>	<b>0.66</b>	<b>0.67</b>				
Ch12	0.05	0.14	0.002	0.03	0.12	0.14	0.09	0.06	0.10	0.16	0.21			
Cramer's V coefficient														

The statistical significance tested with Pearson's Chi-square test (significance level 0.1% [in bold] or 1% [in bold italic]).

For empty cells the format of data is not appropriate to calculate the phi-coefficient.

Cramer's V gives a value between 0 and +1 in proportion to the strength of association, whereas phi coefficient ranges from –1 to +1, where +1/–1 indicates perfect agreement or disagreement, and 0 indicates no relationship.

orcinol depsides occur; our maximum likelihood reconstruction (not shown) suggests that this trait is plesiomorphic.

In summary, our results suggest that the states of all characters, except for ascospore number, switched multiple times during the evolution of the Umbilicariaceae (Table 4).

**Phylogenetic distinctness of character states.** — Phylogenetic distances ( $\Delta+$ ) between the character states rhizinomorphs, thalloconidia, lichenized propagules and  $\beta$ -orcinol depsidones presence and absence, and apothecia commonness and rareness are close to the phylogenetic distance among all sequences in the tree ( $\Delta+$  = 55.5; Electr. Suppl.: Table S2). These character states also show high variation in phylogenetic distinctness ( $\lambda+$ ). This reflects a largely stochastic distribution on the tree and occurrence in different phylogenetic lineages. Phylogenetic distances between types of rhizinomorphs, thalloconidia, and apothecia are lower. Species having “thalloconidial” rhizinomorphs ( $\Delta+$  = 36.2;  $\lambda+$  = 373.4) are more closely related than are species with “simple to branched” rhizinomorphs ( $\Delta+$  = 50.1;  $\lambda+$  = 540.3). Species with non-septate thalloconidia ( $\Delta+$  = 37.2;  $\lambda+$  = 261.3) are, on average, phylogenetically closer than species with oligoseptate ( $\Delta+$  = 36.9;  $\lambda+$  = 418.8) and especially multiseptate ( $\Delta+$  = 50.3;  $\lambda+$  = 502.4) thalloconidia. Species having actinodisc ( $\Delta+$  = 38.8;  $\lambda+$  = 22.3) or leiodisc apothecia ( $\Delta+$  = 39.4;  $\lambda+$  = 325.9) are, on average, less distantly related to each other than are species with gyrodisc-omphalodisc apothecia ( $\Delta+$  = 53.6;  $\lambda+$  = 434.4). Phylogenetic distances and their variation are lowest in the analysis for 1–2 eumuriform large ascospores ( $\Delta+$  = 24.7;  $\lambda+$  = 55.8;  $\Delta+$  = 24.8;  $\lambda+$  = 49.8;  $\Delta+$  = 24.8;  $\lambda+$  = 49.8) reflecting close phylogenetic relationships among clade *Lasallia* species sharing these traits. Species with submuriform ascospores ( $\Delta+$  = 28.5;  $\lambda+$  = 174.6) are, on average, more distantly related than are species with eumuriform ascospores.

## DISCUSSION

**Phylogenetic resolution.** — Umbilicariaceae s.str. forms a monophyletic group, based on a nuSSU sequence dataset including 29 sequences of 22 taxa of Umbilicariaceae and 38 taxa of Pezizomycotina (Electr. Suppl.: Figs. S4, S5), which is in accordance with studies focusing on higher taxonomic levels (e.g., Peršoh & al., 2004, Hofstetter & al., 2007; Miadlikowska & al., 2014). The backbone of the Umbilicariaceae s.str., however, was still poorly resolved in these previously published trees, and therefore delimitations of and relationships among the respective species groups largely remained unclear. A phylogram obtained from the 2–5 markers and 30 species dataset (Miadlikowska & al., 2014) revealed two well-supported clades: one including representatives of the core of *Umbilicaria*, the *Agyrophora* clade, and the *Gyrophora* clade, and the other including *Lasallia* and *Iwatakia* clades. The broader taxon sampling in the present study and the use of three markers for all specimens provided a better resolved backbone, whereas all single-marker phylograms revealed an unresolved backbone but the same well-supported branches forming rather similar topologies.

**Interclade and intraclade tree topology.** — High statistical support for the major clades and a well-resolved backbone of the phylogenetic tree (Fig. 2) enable the analysis of co-occurrences of phenotypic traits as well as a reconstruction of general evolutionary trends. The distribution of selected biological and diagnostically relevant features among the clades are summarized in Table S1 (Electr. Suppl.), whereas morphological descriptions for the accepted groups (subgenera) are given in the section Taxonomic treatment below and in Table S3 (Electr. Suppl.). These descriptions also consider species missing in the phylogenetic analyses but added to the clades based on morphological congruence. A discussion of morphological characteristics and geographical distribution is presented below, based mostly on species included in our analyses but some additional, morphologically similar species were included as well.

**Clade 1 (subg. *Lasallia*).** — The circumscription of the genus *Lasallia* based on ITS sequence data has been discussed in detail by Davydov & al. (2010). The present study, however, includes a wider spectrum of taxa. *Lasallia caroliniana* (Tuck.) Davydov & al. – the only species in subg. *Lasallia* with octosporic asci – is sister to the remaining taxa of the *Lasallia* clade. The clade combines several well-supported subclades of taxa with distinct geographic distributions. Both *L. caroliniana* and *L. pennsylvanica* (Hoffm.) Llano are found in north Asia and North America. *Lasallia pertusa* (Rass.) Llano propagates only via soredia and soredial isidia and is widely distributed in Asia and East Africa. A further well-supported clade includes two East Asian isidiate species – *L. asiae-orientalis* Asahina and *L. daliensis* J.C.Wei. Together they consistently group as sister to the morphologically similar species of the following two clades. The north Asian species *L. rossica* Domb. consistently groups with the Afroamerican species *L. papulosa* (Ach.) Llano. These two species are highly similar according to their morphological traits. The ITS sequence data show some

**Table 4.** Minimal numbers of switches of diagnostic morphological and chemical traits as inferred from the phylogenetic tree in Fig. 2.

Character	Minimal number of switches
Ch 1: Rhizinomorph (or rhizine) presence	7
Ch 2: Rhizinomorph (or rhizine) type*	8
Ch 3: Thalloconidia presence	15
Ch 4: Thalloconidia origin	6
Ch 5: Thalloconidia septation presence and type*	8
Ch 6: Lichenized propagules presence	5
Ch 7: Apothecia presence	2
Ch 8: Apothecia morphology*	6
Ch 9: Ascospore number per ascus	1
Ch 10: Ascospore septation type*	4
Ch 11: Ascospore size class*	7
Ch 12: $\beta$ -orcinol depsidones presence	9

\* Multistate characters

degree of polymorphism between two morphotypes of *L. rossica*, but specimens with lightly pigmented, more areolate and less papillose lower thallus surfaces appear to be conspecific with those of the more geographically widespread phenotype. The most terminal clade combines the two European species, *L. hispanica* (Frey) Sancho & Crespo and *L. pustulata*. The latter species was also reported for Asia from a single locality in the Khangai Mts. (Byazrov, 1986; LE-L5923!).

**Clade 2.** — The species of clade 2 are most heterogeneous morphologically (Fig. 1B–D; Electr. Suppl.: Table S3) and the clade obtained the lowest bootstrap support (73%) of all major clades. In single-marker analyses, the monophyletic Iwatakia clade, combining four species, groups close to representatives of *U. muehlenbergii* and *U. deusta*, but with insufficient support and rather heterogeneous branch lengths (Electr. Suppl.: Figs. S2, S3, S6–S9), reflecting a distant relationship. Finally, the geographical distribution appears also quite heterogeneous in this group. Phylograms, morphology and geographical distribution therefore indicate the necessity of segregating species into more homogeneous groups, as suggested in the following.

**Clade 2a (subg. *Iwatakia*).** — *Umbilicaria mammulata* and *U. esculenta* (Fig. 1B) are sister species of east Asian and North American distribution, respectively. Their sister taxon, *U. yunnana*, differs by the presence of abundant angular apothecia and a deviating type of thalloconidiogenesis. All three species have in common relatively large spores and the same type of rhizinomorphs. Despite their similarity to the “*U. vellea*” group in gross morphology, *U. mammulata* and *U. esculenta* differ in the type of rhizinomorphs and thalloconidia and are, in agreement with Hasenhüttl & Poelt (1978) and Poelt & Nash (1993), considered to be only distantly related to that group. *Umbilicaria kisovana* groups within the Iwatakia clade, but differs by having a small and thin lobulate thallus lacking rhizinomorphs and thalloconidia and having small ascospores. It is morphologically similar to *U. esculenta* at early stages of ontogeny (both species often grow in the same habitat), but *U. kisovana* forms patches of densely growing small thalli, whereas thalli of *U. esculenta* are monophyllous and expanded. Species of the *U. esculenta* group occur in regions with high humidity in forest clearings. *Umbilicaria esculenta* and *U. kisovana* occur in East Asia and *U. mammulata* occurs in eastern North America in landscapes with rock outcrops and boulders. *Umbilicaria yunnana* is a Taiwanese-Himalayan endemic in mountain forests and is characterized by its corticolous growth, known only for this species and *Lasallia mayebarae* (Satô) Asahina. Thus, these species are well characterized by ecological and biogeographical traits.

**Clade 2b (subg. *Actinogyra*).** — *Umbilicaria muehlenbergii* (Fig. 1C) differs from the remaining species of clade 2 in that its lower surface is covered with trabeculae (flattened filaments), it lacks thalloconidia and it has actinodisc apothecia. Groupings with any other species in single-marker datasets are insufficiently supported, reflecting its isolated position. The species occurs both in Asia and North America, is most common on boulders in mountain forests, and is distributed more widely than species of the Iwatakia clade

**Clade 2c (subg. *Floccularia*).** — *Umbilicaria deusta* (Fig. 1D) is morphologically rather similar to subg. *Lasallia* due to its isidiate and often pustulate thallus, but differs by its unicellular ascospores. The lack of rhizinomorphs and thalloconidia are also common traits of *U. deusta* and subg. *Lasallia* species. However, a relationship to subg. *Lasallia* or to any other species group lacks evidence from molecular data. The species habitually resembles *U. kisovana*, which, however, does not group with *U. deusta* in any analysis. The species is widely distributed in the Holarctic.

**Clade 3 (subg. *Umbilicaria*).** — Species of the Umbilicaria clade have a uniform morphology (Electr. Suppl.: Table S3); the characteristic feature of this group is their elevated pruinose or reticulate-ridged upper thalline center, which can be prominent or only rarely observed for some species (e.g., *U. hyperborea*, *U. polyphylla*). Species are generally widely distributed in high mountainous and subpolar regions in both hemispheres or only in the Holarctic. Himalayan species (*U. badia* group, *U. hypococcinea*, *U. pseudocinerascens*) group together with high support (1.0 PP; 95% BS), indicating a common origin. The apparent non-monophyletic origin of Eurasian and North American *U. arctica* specimens should be investigated in more detail, based on a broader and geographically more balanced sampling.

**Clade 4 (subg. *Umbilicariopsis*).** — *Umbilicaria polyrhiza* is sister to *Umbilicaria* s.str. but differs morphologically (Fig. 1F; Electr. Suppl.: Table S3) and seems to represent an isolated phylogenetic lineage. The species has actinodisc apothecia, multiseptate thalloconidia on the tips of richly branched to coralloid rhizinomorphs, and a rough areolated lower surface. The species has a multiregional oceanic distribution.

**Clade 5 (subg. *Agyrophora*).** — The species of the Agyrophora clade have rather uniform thallus morphology (Fig. 1G) and all but *Umbilicaria ruebeliana* have leiodisc apothecia and simple ascospores. The species are distributed in the high-mountain or subpolar regions of the Northern Hemisphere; *U. subglabra* (Nyl.) Llano also occurs in the Southern Hemisphere. The crustose or squamulose *U. lambii* is sister to the remaining species of the *U. leiocarpa* clade. Additional species represent pairs of morphologically similar species, each species in the pair differing in their mode of reproduction (Electr. Suppl.: Table S1): *U. leiocarpa* DC.–*U. rigida* (Du Rietz) Frey and *U. subglabra*–*U. subglabra* var. *pallens* (Nyl.) Frey. Species within each of these pairs are not well separated, differ in only a small number of nucleotides and therefore may be conspecific. However, more extensive sampling is required to draw unambiguous taxonomic conclusions.

**Clade 6 (subg. *Gyrophora*).** — The diagnostic characters for the species of the *Umbilicaria vellea* group and *U. angulata* group overlap. The *U. angulata* group is morphologically segregated by brown thalli and angular gyrodisc to actinodisc apothecia.

*Umbilicaria vellea* group. — Taxa belonging to the monophyletic *U. vellea* group s.str. are morphologically rather uniform (Fig. 1H; Electr. Suppl.: Table S3). Poelt & Nash (1993) considered several species to belong to the *U. vellea* group due to their commonly occurring rhizinomorphs, multicellular



thalloconidia, gyrodisc apothecia, and usually simple ascospores, which are, however, oligocellular-muriform in *U. cinereorufescens*. Our results reveal that multicellular thalloconidia occur only in some of the species of the *U. vellea* group, and that species lacking thalloconidia (i.e., *U. crustulosa* (Ach.) Frey, *U. freyi* Codogno & al., *U. grisea* Hoffm., *U. hirsuta*, *U. josiae*, *U. loboperipherica*, *U. spodothroa*) also should be included. The status of non-monophyletic species requires further investigation, based on more samples. *Umbilicaria vellea*-2 probably belongs to the enigmatic *U. tylorhiza* (Nyl.) Nyl., the holotype of which (H-9503606!) probably represents a senescent thallus. The *U. vellea* group combines widely distributed bipolar (e.g., *U. cinereorufescens* (Schaer.) Frey, *U. grisea*, *U. hirsuta*, *U. vellea* (L.) Hoffm.) as well as endemic taxa (e.g., *U. crustulosa*-2(?), *U. crustulosa* var. *badiofusca*, *U. josiae* and *U. vellea*-2(?)) from Europe, and *U. loboperipherica* and *U. squamosa* J.C.Wei & Y.M.Jiang from Southeast Asia.

*Umbilicaria angulata* group. – This paraphyletic group combines morphologically similar species with a smooth and brownish upper thalline surface and a papillate lower surface, simple rhizinomorphs and filaments, and lack of thalloconidia. Apothecia are angular, star-like gyrodisc or “actinodisc”. Angular gyrose apothecia are similar to actinodisc apothecia in their radial growth, but differ in having an apothecial margin. This subtype of apothecia links typical round gyrodisc apothecia with star-like actinodisc apothecia. Species of the *U. angulata* group have eight hyaline, unicellular spores per ascus, except for *U. semitensis*, which has submuriform ascospores. Gyrophoric and lecanoric acids occur throughout the group, instead of or in addition to  $\beta$ -orcinol depsidones (stictic, norstictic,  $\alpha$ -metylsalacinic acids). The group combines species of wide distribution in the Western Hemisphere, i.e., *U. phaea* and *U. angulata* (North and South American), *U. torrefacta* (Circumboreal), with the endemic taxa *U. pulvinaria* (Far East), and *U. semitensis* (California and southern Oregon).

**Comparison with morphology-based classification concepts.** — Over time, the classification of Umbilicariaceae s.str. was rearranged several times (see historical overviews in Llano, 1950 and Davydov, 2007). Two major intrafamilial classification concepts exist, one proposed by Frey (1933, 1949) and modified by Imshaug (1957) and Motyka (1964), and a second by Scholander (1934) and Llano (1950), modified by Wei (1966) and Wei & Jiang (1993). However, most of the suggested genera, subgenera or sections are non-monophyletic in the phylogeny of the present study (Electr. Suppl.: Table S4). Frey’s sect. *Anthracinae*, sect. *Glabrae*, sect. *Polymorphae*, and sect. *Velleae* appear in several clades each. Imshaug (1957) split sect. *Anthracinae* sensu Frey into sect. *Anthracinae* sensu Imshaug (grouping only in the Agyrophora clade of the present phylogeny) and sect. *Decussatae* (Schol. ex Llano) Imshaug (grouping in the Umbilicaria clade). Subgenera according to Wei & Jiang (1993) are also not congruent with the tree topology (Electr. Suppl.: Table S4). The results therefore do not support any of the previously proposed intrafamilial classifications.

All algorithms applied resulted in the recognition of a monophyletic origin of the sequences included of the genus *Lasallia*. The most prominent distinctive trait of the species

of the *Lasallia* clade is the increase in ascospore septation (multicellular-muriform) together with an enlargement of the spores and the reduction of spore number (except for *L. caroliniana*). This apomorphy appears functionally significant in that it increases cytoplasmal resources for single meiospores and may, therefore, be advantageous in the early stage of fungal growth. Thus, *Lasallia* represents a taxon within the Umbilicariaceae characterized by a derived and presumably functionally meaningful morphological trait (Davydov & al., 2010). However, the clade is nested within the *Umbilicaria* sequences. Therefore, *Umbilicaria* forms a paraphyletic grouping of clades, a finding previously reported based on a smaller number of taxa (Ivanova & al., 1999; Davydov & al., 2010; Miadlikowska & al., 2014). Our analyses reveal eight well-supported main clades delimited by a combination of morphological and chemical features. The taxonomic consequences of this finding require further discussion. A subdivision of the family Umbilicariaceae requires either the acceptance of *Umbilicaria* as a paraphyletic genus or the establishment of several new monophyletic entities at the genus or subgenus level.

The first solution requires acceptance of two genera – *Lasallia* and *Umbilicaria* – as they are recognized today, and segregating of the latter genus into seven subgenera. This concept would perfectly reflect the phylogenetic situation, with one out of eight lineages, i.e., *Lasallia*, showing an evolutionarily significant apomorphy. The problem with this scheme is the paraphyletic status of *Umbilicaria*, which was either accepted (Davydov & al., 2010) or considered unacceptable (Miadlikowska & al., 2014) earlier.

The second approach would fully solve the problem of paraphyly and is generally followed in modern publications in which authors propose separate taxa for strongly monophyletic (holophyletic) groups based on morphological or molecular characters. Creation of a number of relatively small genera often follows the comprehensive molecular phylogenetic analyses of a particular family or genus, such as Parmeliaceae (Thell & al., 2012), Megasporaceae (Nordin & al., 2010), Teloschistaceae (e.g., Arup & al., 2013; Kondratyuk & al., 2014a, b), Collemataceae (Otálora, 2014) and many others. Unfortunately, since no fully consistent genus concept exists in mycology, the differences between genera and other species groups (series, sections, subgenera, or non-taxonomical groupings) have been treated on a subjective basis by the experts (authors, reviewers, and editors). The fact that the generic name is a part of the binary scientific name assigns high importance to the generic level classification. Some well-established species-rich genera as *Cladonia* Hill ex P.Browne, *Peltigera* Willd., and *Usnea* Dill. ex Adans. so far remain as taxonomic units (Truong & al., 2013; Athukorala & al., 2016; Magain & al., 2017), but still include phylogenetically distinct smaller entities.

A natural, i.e., phylogenetically defined, classification of Umbilicariaceae s.str. may be achieved by rearrangements at the generic or subgeneric level. The finding that most major phylogenetic lineages are supported by morphological traits would favour a rearrangement at the generic level. The diagnostic characters and character combinations identified for every clade allow for placing new species into one of the eight

clades with high certainty and without the help of DNA data. However, several uncertainties would remain. First, the phenotypic characterization of clades 2 and 6 still remains ambiguous, due to the high homoplasy of characters in the phylogeny. Second, some species groups, e.g., endemic Southeast Asian and New Zealand species, have not yet been included in phylogenetic analyses or are represented only by ITS sequences (Appendix 1). New species and possibly new markers to the analyses may result in re-consideration of clades 2 and 6.

The erection of new genera, therefore, appears to be premature, while separating a single genus (i.e., *Lasallia*) also appears implausible. We propose to combine *Lasallia* and *Umbilicaria* into one genus *Umbilicaria* s.l., and to segregate eight subgenera to obtain units for naming phylogenetic lineages for future discussions. While the concept of *Umbilicaria* as the only genus in Umbilicariaceae s.str. appears to be broad in comparison to other Lecanoromycetes (cf. *Parmelia* s.l.), this new phylogenetic classification of Umbilicariaceae s.str. is a first step towards a consistent phylogeny of Umbilicariaceae, based on monophyletic taxa. If the current trend of splitting continues and further phylogenetic and anatomical results provide further support for the clades obtained here, subgenera could easily be raised to genus level.

Names are available for some well-delimited clades suggested as subgenera here, such as *Actinogyra* for *Umbilicaria muehlenbergii*, *Gyrophora* for the *Umbilicaria vellea* and *U. angulata* groups, and *Agyrophora* for species of clade 5. New subgeneric names are required for species of clade 2a, for *U. deusta*, and *U. polyrhiza*.

**Co-occurrence, dependency and functional coupling of major phenotypic traits.** — As a result of our phylogenetic analysis, functional coupling for the rhizinoid, asexual reproductive structures and lichenized dispersal units became evident. The gain of rhizinomorphs gave rise to the production of rhizinobred thalloconidia. Rhizinomorphs are therefore considered a precondition for the development of this different kind of thalloconidia. Our statistical analysis of trait associations (Table 3) revealed not only such primary dependencies, but also the structural or functional interdependencies of traits that are not connected directly, i.e., phylogenetic dependency. For example, rhizinomorph presence is associated with apothecial and ascospore morphology and the occurrence of lichenized propagules is strongly associated with ascospore characteristics. The strong degree of association of thalloconidia origin and septation was considered by Hestmark (1990, 1991a) as structural dependence, due to the existence of “architectural” (space conditional) constraints determining the degree of septation. Species possessing multiseptate rhizinobred thalloconidia or lichenized dispersal units, i.e., parasoredia and schizidia, occur in the clade which forms the sister group to all other Umbilicariaceae (*Gyrophora* clade). In Umbilicariaceae clades of the sister group to the *Lasallia* clade (*Iwatakia* plus *Floccularia* clades), thalloconidia combine with schizidia, lobules or isidia, and in the *Lasallia* clade, taxa completely shift from non-lichenized to lichenized asexual dispersal units (Fig. 3B–D). Correlation analyses of these four types of rhizinomorph and asexual reproductive structures

(Table 3) largely support the view of replacement of functional structures and functional coupling. The association between producing apothecia, thalloconidia and lichenized propagules (Table 3) may be the result of a functional coupling of traits. For species having thalloconidia or lichenized propagules, the significance of propagation by ascospores is decreased (Hestmark, 1991b, c). Functional coupling also concerns sexual reproductive structures. Ascospore traits, such as number per ascus, size and septation are strongly associated (Table 3). Moreover, reduction to mono- or bispority is associated with increase in spore septation and size. This is also associated with reduction of carbonized hymenial structures, mainly in the *Lasallia* clade. While multicellular-muriform ascospores (both in eight- and one-spored asci) are always large, the size of oligocellular-muriform spores classified as “small-sized” (*Umbilicaria ruebeliana*) or “mean-sized” (subg. *Gyrophora*) are similar to unicellular spores of some species of subg. *Iwatakia* and subg. *Floccularia* (Electr. Suppl.: Table S1). In parallel, an evolutionary progression towards reduction of spore number per ascus and an increase of septa number per ascospore is observed, as had also been shown for *Rhizocarpon* Ramond ex DC. (Rambold & al., 1998). Increased cellularity entails the gain of additional compartments with secondary nuclei and additional cytoplasmic resources. Ascospore number reduction results in a decrease of the relative number of independent meiospore units in favour of additional cytoplasmic resources per meiospore. In addition, a reduction of carbonized hymenial hyphal and paraphysal structures, i.e., a shift towards leiodisc apothecia, is observed. This apothecial type in subg. *Lasallia* is likely the result of outbreeding due to presence of large ascospores, since the reduction of carbonized structures at the hymenial surface enables a free passage of the epihymenial zone of large-sized spores when released.

**Evolution of major phenotypic traits.** — The distribution of biologically and diagnostically important traits against the background of the molecular phylogenetic tree can help to define the phylogenetic (plesiomorphic vs. apomorphic) status of the various character states. The maximum likelihood reconstruction (Fig. 3A) as well as morphology of the taxa positioned closest to the root of the main phylogenetic lineages suggest that rhizinomorphs represent a plesiomorphic trait. *Umbilicaria caroliniana*, *U. lambii* and *U. pulvinaria* are attached by the umbilicus and a lamellar-trabecular net of the underthallus or rhizines. Rhizinomorphs therefore may represent a reduced form of this underthalline structure. There are no parallelisms in rhizinomorph appearance in the different clades. Switching between presence and absence of the rhizinomorphs apparently occurred at least seven times, and at least eight times between the rhizinomorph types (Table 3). These results suggest that rhizinomorphs were lost and gained more than once during the evolution of Umbilicariaceae and evidently led to different morphological types, which consequently represent non-homologous structures.

The plesiomorphic status of thalloconidia absence looks plausible in Umbilicariaceae because they are lacking in taxa positioned close to the root of the Umbilicariaceae and phylogenetically related outgroup taxa (*Boreoplaca*, *Xylopsora*,

etc.) lack them. Species with thalloconidia are dispersed over the tree with the exception of the *Lasallia* clade, always along with other propagation types. The number of assumed gains and losses of thalloconidia (15) is the highest for any trait (Table 4). The production of thalloconidia requires no additional morphological structures, as they are produced by the lower cortex, parathecium or rhizinomorphs. Thalloconidia may not always develop during ontogenesis of some species (*Umbilicaria aprina*, *U. krascheninnikovii*, *U. subglabra*, *U. umbilicarioides*). It is likely that some species pairs (e.g., *U. decussata*–*U. polaris*, *U. leiocarpa*–*U. rigida*, *U. subglabra*–*U. subglabra* var. *pallens*) represent two morphotypes of one biological species, individuals of which exhibit a sexual and asexual life habit, respectively, which was possibly induced in the early stages of ontogenesis. Divergence by alternation of the reproduction mode, as shown for several species pairs (Poelt, 1970; Hestmark, 1991b), may be a result of fixation of such shifts during evolution and isolation of populations. The genetic potential for producing thalloconidia appears prevalent in Umbilicariaceae because this trait has evolved in separate clades of morphologically homogenous species (*Iwatakia*, *Umbilicaria*, *Agyrophora*, *Gyrophora*). Phylogenetic distinctness of the character states thalloconidia presence and absence ( $\Delta^+ = 55.5$ ; 49.2; Electr. Suppl.: Table S2) is close to the phylogenetic distance among all sequences in the tree ( $\Delta^+ = 55.5$ ). This reflects a distant relationship of species having thalloconidia. Within clades, however, the types of thalloconidia are uniform and seem to have evolved once. Species with thallobred (or similar rhizobred) thalloconidia from different clades differ in details of thalloconidiogenesis, indicating multiple evolution of thalloconidia. The presence of thalloconidia would then represent a synapomorphic trait. These findings are in agreement with the conclusion of Hestmark (1990, 1991a) that the thallobred and rhizinobred thalloconidia are not homologous and that the corresponding two types of thalloconidiogenesis emerged more than once during the evolution of Umbilicariaceae. While the presence of thalloconidia is highly variable, thalloconidia septation type is more conserved (eight switches, despite being a multistate character) and phylogenetically distinct. Species with non-septate thalloconidia are, on average, phylogenetically closer than species with septate thalloconidia. Species with a certain septation type often group with non-thalloconidial species, but rarely with species having other types of thalloconidia septation. The traits thallobred thalloconidia, non-septate and oligoseptate thalloconidia are more phylogenetically distinct.

Thus, the specification of the trait is more conserved than its presence, due to structural dependencies from the thalloconidial formation type, which is a relatively constant trait in the phylogeny (six switches) (Table 4).

Most of the clades (except those containing one species) combine representatives with sexual reproduction and asexual reproduction by thalloconidia or lichenized dispersal units. The presence of lichenized propagules in Umbilicariaceae has evolved at least five times and is predominant only in the *Lasallia* clade. The phylogenetic distinctness of lichenized propagula presence and absence is low ( $\Delta^+ = 49.2$ ; 50.5; Electr. Suppl.:

Table S2) because of its presence in phylogenetically distant lineages. Similarly, as with thalloconidia, some evolutionary trends are evident within certain species groups. Several clades combine two closely related species reproducing sexually and by lichenized propagules, respectively, such as *Umbilicaria hirsuta*–*U. josiae*, *U. freyi*–*U. crustulosa*-2, *U. spodochroa*-1–*U. grisea*, and *U. pustulata*–*U. hispanica*. The possession of lichenized propagules therefore initiates species divergence by alteration of the reproduction mode. Only a few species reproduce exclusively by vegetative propagules (Electr. Suppl.: Table S1). The lack of ascumata therefore is an apomorphy.

All clades except the monospecific subgenera include at least one species having gyrodisc-omphalodisc ascumata. Moreover, this trait is also predominant in taxa of *Xylopsora*. Therefore, it appears plausible that the gyrodisc-omphalodisc apothecium is plesiomorphic in Umbilicariaceae. Apothecia types accordingly switched during phylogeny at least six times (Table 4). Any of three representatives of Umbilicariaceae having actinodisc apothecia, i.e., *Umbilicaria pulvinaria*, *U. polyrhiza*, and *U. muehlenbergii*, group separately and represent apomorphies in different phylogenetic lineages. The phylogenetic distinctness of the trait actinodisc apothecia ( $\Delta^+ = 38.8$ ) is similar to the leiodisc ( $\Delta^+ = 39.4$ ), which also appears in different clades. Based on the previously applied categories, apothecial morphology appeared to be diagnostically useful at the genus level only to some extent. This conclusion by earlier authors (e.g., Frey, 1931, 1933; Henssen, 1970; Hestmark & al., 2011) could be supported by the present results. Whereas gyrodisc-omphalodisc apothecia contain octosporic asci, leiodisc apothecia may contain asci either with eight unicellular small spores (*Agyrophora* and *Gyrophora* clades, *Umbilicaria sholanderii*) or with 1–2 eumuriform large spores (*Lasallia* clade), which supports the recognition of their independent evolution and non-homologous relation.

Ascospore numbers and types are mostly consistent within clades but vary little outside the *Lasallia* clade. Unicellular (to rarely bicellular) ascospores predominate in all clades except *Lasallia*, as well as in outgroup taxa, and represent the symplesiomorphic trait. Ascospore number per ascus changed only once (Table 4), and one additional switch is most likely a reversal (Davydov & al., 2010). Ascospore characters are the phylogenetically most distinct ones in the analysis (Electr. Suppl.: Table S2). All species with large eumuriform ascospores belong to the monophyletic *Lasallia* clade, combining all mono- or bisporic species. An exception is *U. caroliniana* with eight spores per ascus, which is nevertheless strongly supported as belonging to *Lasallia* by its eumuriform ascospores. However, species with submuriform spores appear in subg. *Gyrophora* and subg. *Agyrophora*. These differ by size class (Electr. Suppl.: Table S1) and are non-monophyletic. Due to such homoplasies, the traits “ascospore type” and “ascospore number” do not fully reflect evolutionary relationships in Umbilicariaceae. A comparable combination of ascospore traits is given in *Rhizocarpon*, where nuRNA ITS and mtRNA SSU gene sequences analyses (Ihlen & Ekman, 2002) revealed that ascospore septation types did not correspond to monophyletic groups.



The production of orcinol depsides as secondary metabolites is common in Umbilicariaceae (Table 1). Both depsides and  $\beta$ -orcinol depsidones are synthesized via the acetyl-poly-malonyl pathway from orcellinic acid with different numbers of biosynthesis steps; 1 to 4 steps for depsides and 4 to 5 steps for  $\beta$ -orcinol depsidones (Electr. Suppl.: Table S5). The synthesis of  $\beta$ -orcinol depsidones differs from the very first step on and requires a number of fermentation reactions (Chooi & al., 2008).

The presence of secondary compounds is very variable, with a minimum of nine switches between traits (Table 4). Fungal secondary metabolites are encoded by clusters of sequentially arranged genes (Keller & Hohn, 1997). The presence or absence of a compound in the phenotype cannot fully address evolutionary questions, because a chemical phenotype is determined not only by the presence of genes required for the production of a compound, but by the expression of the entire pathway leading to the compound. It is not clear to what extent expression patterns are determined genetically, or whether an entire pathway or parts of it can evolve or degenerate repeatedly (Grube & Blaha, 2003). As a consequence, it is impossible to say which character state is plesiomorphic in Umbilicariaceae. Several species of subg. *Umbilicaria* and subg. *Gyrophora* (e.g., *U. proboscidea*, *U. virginis*, *U. torrefacta*) may contain either orcinol depsides or additional  $\beta$ -orcinol depsidones. This fact of multiple switches from one type of polyketide to another, according to the present phylogeny, suggests that a change in the control of gene expression (e.g., Calo & al., 2014) may be more likely than functionally relevant nucleotide substitutions in the coding genes. Additional knowledge of polyketide synthase genes and their regulation will be necessary to identify the course of evolution of secondary metabolism. Regarding the occurrence of  $\beta$ -orcinol depsidones in a few species present in different clades, there is no direct evidence for overall phylogenetic and chemotaxonomic congruency. The presence of  $\beta$ -orcinol depsidones was not found to be significantly associated with any analysed morphological trait (Table 3).

Most conservative are character states of ascospores and apothecia (1 to 7 switches), while those concerning asexual propagation and secondary metabolism are most variable (up to 5 to 15 switches). The ascospore septation type, postulated as most suitable for distinguishing the subg. *Lasallia*, is quite conserved (4 gains and losses, despite being a multistate character). However, other generic markers, such as the predominant number of spores per ascus, the presence and predominant type of apothecia, rhizomorphs or thalloconidia, may have few or many gains and losses. High number of gains and losses, especially within the same clade, may reflect that changes of character states require just minor genetic changes.

**Macroevolutionary trends.** — Umbilicariales have the shortest branches to the base of Lecanoromycetes in the nuSSU phylogram (Electr. Suppl. Fig. S4, S5). This indicates a relatively old phylogenetic age of the order. This hypothesis is supported by a recent molecular clock analysis (Prieto & Wedin, 2013) where Umbilicariales branched off from the main lineages of Lecanoromycetes prior to the major diversification of the latter. Our results indicate some possible macroevolutionary trends,

which are outlined in the following, but which require verification in future studies. Lichenization and the umbrella-like, umbilicate growth habit may have enabled Umbilicariaceae to occupy extreme ecological niches, in which they may have rapidly radiated since the early stages of their evolution. Within epilithic microbial and lichen communities, their growth habit is highly effective with regard to competition for light, space, and water (Degelius, 1940; Larson, 1984; Harris, 1996; Hestmark, 1997), mainly because umbilicate thalli with their horizontally expanding unattached margins do not overgrow, but overlap neighbouring thalli. Moreover, overlapping and shadowing of less active distal parts of umbilicate thalli, which grow from their centres, is less invasive compared to the growth of crustose and foliose lichens (Hestmark & al., 1997). The production of thalloconidia provides additional advantages in competition for substrate colonization, particularly within-habitat colonization (Hestmark, 1991c), and may therefore have been advantageous since the early stages of the evolution of this family.

It is remarkable that subg. *Gyrophora*, being sister to the remaining taxa in the present phylogeny, combines species with a wide range of ascoma and ascospores traits, i.e., all apothecial morphology types as well as both simple and muriform ascospore types. Species of subg. *Gyrophora* may or may not have a trabeculate network or rhizomorphs, the latter with or without non-septate to multiseptate thalloconidia. Both orcinol depsides and  $\beta$ -orcinol depsidones can be produced by species of subg. *Gyrophora*. Other taxa appear to be more specialized regarding these traits. Thus, subg. *Gyrophora* may represent an unspecialized ancestral group in Umbilicariaceae s.str., in which most diagnostic characters have been realized already. *Umbilicaria pulvinaria* (Fig. 11) and *U. semitensis* are sister to the remaining taxa within subg. *Gyrophora*. These species as well as the related *U. angulata* share the rare trait of a dense mat of trabeculae and tangled black cylindrical to flattened rhizines. This loose ‘underthallus’ may also be useful for attaching the polyphyllous crustose-like thallus of *U. pulvinaria* and *U. angulata* var. *compacta* Krog (Krog, 1968) to their substrates. Moreover, *U. pulvinaria* and *U. semitensis* have a rather restricted distribution: Kamchatka Peninsula and Sakhalin Island (Davydov & al., 2011), and California and southern Oregon (McCune & Curtis, 2012), respectively. They are therefore likely to represent paleoendemics. The fact that both species inhabit the territories of recent volcanism and geologically young rocks (2000 to 100,000 years old) might just underline their high degree of adaptability. It is remarkable that the species sister to the remaining taxa in the *Agyrophora* clade, *Umbilicaria lambii*, is also polyphyllous and thickly crustose to squamulose. Imshaug (1957) treated this species as most basal in Umbilicariaceae and placed it in sect. *Vellea*, which, however, obtained no support in the present analyses. The species has a restricted likely paleoendemic distribution in the Pacific Northwest of North America, including British Columbia, Alberta, south to Montana and northern California (McCune & Geiser, 2009). If the umbilicate habit is synapomorphic in Umbilicariaceae s.str., the presence of species with a similar crustose-like thalline habit in monotypic or low diverse clades sister to all remaining taxa of the respective

group in different phylogenetic lineages may indicate their plesiomorphic status. Consequently such a habit was present in the common ancestor of Umbilicariaceae s.str. The species of subg. *Lasallia*, which groups least distant to subg. *Umbilicaria*, i.e., *U. caroliniana*, produces big cushion-like thalli. It is also not clearly umbilicate but attached to the substrate by a small umbilicus and true rhizines. In North America, *U. caroliniana* has a relictual disjunct distribution, occurring in Alaska and the Yukon Territory (Llano, 1950; Brodo & al., 2001). In East Asia, the species is known from Kamchatka and Japan to eastern Siberia. The traits named for *U. caroliniana* also converge with the ancestral traits. No taxon or group of taxa converging with the ancestral traits can be identified in the *Umbilicaria* s.str. clade. *Umbilicaria kisovana* stands out sharing plesiomorphic traits with subg. *Umbilicaria* and therefore appears to be ancestral within the subg. *Iwatakia*.

## ■ TAXONOMIC TREATMENT

New system of the family Umbilicariaceae:

***Fulgidea*** Bendiksby & Timdal in Taxon 62: 952. 2013 – Type: *Fulgidea oligospora* (Timdal) Bendiksby & Timdal.

***Umbilicaria*** Hoffm., Descr. Pl. Cl. Crypt. 1: 8. 1789 – Type: *Umbilicaria hyperborea* (Ach.) Hoffm. [typ. cons. ICBN 1999].

***Umbilicaria*** subg. ***Actinogyra*** (Schol.) Savicz in Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Akad. Nauk. S.S.S.R. 4: 107. 1950 ≡ *Actinogyra* Schol. in Nyt. Mag. Naturvidensk. 75: 28. 1934 – Type: *Umbilicaria muehlenbergii* (Ach.) Tuck. Clade 2b

**Diagnostic characters.** – Thallus medium to large, never pustulate, upper surface smooth and brownish; lower surface papillate, grey-brown, lacking rhizinomorphs and thalloconidia, covered by a thick lamellate-trabeculate network. Apothecia subimmersed, actinodisc with asci containing eight simple, small hyaline spores. North American – Asian.

**Included species.** – *Umbilicaria muehlenbergii* (Ach.) Tuck.

***Umbilicaria*** subg. ***Agyrophora*** Nyl. in Flora 61: 247. 1878 – Type: *Agyrophora atropruinosa* (Schaer.) Nyl. [= *Umbilicaria leiocarpa* DC.].

Clade 5

**Diagnostic characters.** – Thallus small to medium, never pustulate, without lichenized propagules; upper surface areolate, rarely reticulate, matt, grey; lower surface smooth to areolate, lacking rhizinomorphs, often with thallobred non-septate thalloconidia. Apothecia sessile to stipitate subimmersed to sessile, leiodisc, rare omphalodisc, containing asci with eight small simple or rare submuriform spores.

**Included species.** – *Umbilicaria cinerascens* (Arnold) Frey, *U. leiocarpa* DC., *U. laevis* (Schaer.) Frey, *U. lambii* Imshaug, *U. microphylla* (Laur.) A.Massal., *U. ruebeliana* (Du

Rietz & Frey) Frey, *U. lyngei* Schol., *U. rigida* (Du Rietz) Frey, *U. subglabra* (Nyl.) Harm., *U. zahlbrucknerii* Frey.

***Umbilicaria*** subg. ***Floccularia*** Davydov, Peršoh & Rambold, **subg. nov.** [MB 821406] – Type: *Umbilicaria deusta* (L.) Baumg.

Clade 2c

**Diagnostic characters.** – Thallus small to medium, thin, weakly pustulate, curled and lobed, margins often downwardly recurved; upper thallus brownish-black, matt, and smooth, with isidiose to subsquamulose structures concolorous with the upper cortex; lower surface brighter in colour, smooth, with deep depressions, lacking rhizinomorphs and thalloconidia. Apothecia sessile, gyrodisc, with asci containing hyaline unicellular spores. Secondary metabolites: gyrophoric, lecanoric, and umbilicarinic acids.

**Etymology.** – The name refers to the typical habit of *Floccularia deusta* with abundant granular to flattened-squamulose isidia. The epithet “*flocculosa*” had priority over “*deusta*” until the type of *Lichen deustus* L. had been conserved (Jørgensen & al., 1994; Gams, 1996).

**Included species.** – *Umbilicaria deusta* (L.) Baumg.

***Umbilicaria*** subg. ***Gyrophora*** (Ach.) Frey in Rabenh. Krypt.-Fl. 9(4, 1): 209. 1933 ≡ *Gyrophora* Ach., Methodus: 100. 1803 – **Type (designated here):** *Umbilicaria vellea* (L.) Ach. Clade 6

**Diagnostic characters.** – Thallus medium to large, rigid, never pustulate or reticulate; upper thallus surface smooth, granulose to parasorediate or schizidiolate, occasionally areolate, centrally never reticulate; lower surface and rhizinomorphs papillose or areolate, trabeculae emerging from the umbilicus often present; rhizinomorphs with or without 6–50-septate thalloconidia, sometimes with thalylles. Apothecia subimmersed to sessile, gyrodisc or omphalodisc, occasionally leiodisc or actinodisc. Asci containing eight hyaline unicellular or brown oligocellular-muriform spores. Secondary metabolites: gyrophoric, lecanoric, and umbilicarinic acids, sometimes also β-orcinol depsidones. Mostly Holarctic with European and South American endemic elements.

**Included species.** – *Umbilicaria americana* Poelt & T.H.Nash, *U. angulata* Tuck., *U. calvescens* Nyl., *U. cinereo-rufescens* (Schaer.) Frey, *U. crustulosa* (Ach.) Frey, *U. crustulosa* var. *badiofusca* Frey, *U. dichroa* Nyl., *U. freyi* Codogno & al., *U. grisea* Ach., *U. haplocarpa* Nyl., *U. hirsuta* (Sw.) Ach., *U. josiae* Frey, *U. koidzumii* Yasuda ex Satô, *U. leprosa* (Zahlbr.) Fray, *U. loboperipherica* J.C.Weï & al., *U. murihikuana* D.J.Galloway & Sancho, *U. nodulospora* McCune & al., *U. phaea* Tuck., *U. pulvinaria* (Savicz) Frey, *U. semitensis* Tuck., *U. soralifera* (Frey) Krog & Swinscow, *U. spodochroa* Ehrh. ex Hoffm., *U. squamosa* J.C.Weï & Y.M.Jiang, *U. tylorhiza* Nyl., *U. torrefacta* (Lightf.) Schrad., *U. vellea* (L.) Ach.

***Umbilicaria*** subg. ***Iwatakia*** Davydov, Peršoh & Rambold, **subg. nov.** [MB 821405] – Type: *Umbilicaria esculenta* (Miyoshi) Minks.

Clade 2a

*Diagnostic characters.* – Thallus medium to large or rarely small, never pustulate or reticulate, often bearing schizidia; upper surface smooth to finely areolate, greyish to brownish; lower surface brown to black, verrucose to areolate, usually with short and richly branched rhizinomorphs with relatively wide base and thin distal branches, possessing multicellular thalloconidia, or thalloconidia thallobred and non-septate. Apothecia subimmersed to sessile, gyrodisc, containing asci with eight simple small to mean-size spores.

*Etymology.* – The name refers to “iwatake”, the Japanese name for the edible lichen *Umbilicaria esculenta*.

*Included species.* – *Umbilicaria esculenta* (Miyoshi) Minks, *U. kisovana* (Zahlbr. ex Asahina) Zahlbr., *U. mammulata* (Ach.) Tuck., *U. yunnana* (Nyl.) Hue.

*Umbilicaria* subg. *Lasallia* (Mérat) Frey in Rabenh. Krypt.-Fl. 9(4/1): 208. 1933 ≡ *Lasallia* Mérat, Nouv. Fl. Env. Paris, ed. 2, 1: 202. 1821 – Type: *Lasallia pustulata* (L.) Mérat. Clade 1

*Diagnostic characters.* – Thallus medium to large, pustulate; upper surface smooth to areolate or echinose, brown to grey, with lobules or isidia; lower surface papillose or areolate, lacking rhizinomorphs, but with true rhizines, lacking thalloconidia; apothecia sessile to stipitate, leiodisc or rarely gyrodisc, containing asci with 1–2, rarely 8 large eumuriform spores. Mostly Holarctic with European, North American, South African and East Asian endemic elements.

*Included species.* – *Umbilicaria asiae-orientalis* (Asahina) Satô, *U. brigantium* Zschacke, *U. caroliniana* Tuck., *U. chiriquiensis* (Llano) Llano, *U. daliensis* (J.C.We) Davydov, Peršoh & Rambold, **comb. nov.** ≡ *Lasallia daliensis* J.C.We in Acta Mycol. Sin 1(1): 21. 1982, *U. hispanica* (Frey) Davydov, Peršoh & Rambold, **comb. nov.** ≡ *Lasallia brigantium* var. *hispanica* Frey in Ber. Schweiz. Bot. Ges. 59: 443. 1949, *U. mayebarae* Satô, *U. membranacea* Laurer, *U. papulosa* (Ach.) Nyl., *U. pensylvanica* Hoffm., *U. pertusa* Rass., *U. pustulata* (L.) Hoffm., *U. rossica* (Domb.) N.S.Golubk., *U. sinorientalis* (J.C.We) Davydov, Peršoh & Rambold, **comb. nov.** ≡ *Lasallia sinorientalis* J.C.We in Acta Mycol. Sin. 1(1): 23. 1982, *U. xizangensis* (J.C.We & Y.M.Jiang) Davydov, Peršoh & Rambold, **comb. nov.** ≡ *Lasallia xizangensis* J.C.We & Y.M.Jiang in Acta Phytotax. Sin. 20: 500. 1982.

*Umbilicaria* subg. *Umbilicaria*

Clade 3

*Diagnostic characters.* – Thallus small to medium, non-pustulate; upper surface smooth to areolate with elevated pruinose or reticulate ridged center (only rarely observed for some species), brown or grey to blackish; lower surface smooth to areolate; rhizinomorphs frequently present, simple or moderately dichotomously or irregularly branched, cylindrical or complanate, with smooth surface; thalloconidia thallobred or in addition rhizinobred, non-septate to oligoseptate or rarely rhizinobred and multicellular. Apothecia sessile to stipitate, gyrodisc and omphalodisc, occasionally leiodisc, with 8-spored asci, containing uni- to bicellular spores. Secondary metabolites:

orcinol depsides gyrophoric, lecanoric, and umbilicarinic acids regularly present; β-orcinol depsidone occasionally present. Bipolar or holarctic with endemic elements.

*Included species.* – *Umbilicaria africana* (Jatta) Krog & Swinscow, *U. altaiensis* J.C.We & Y.M.Jiang, *U. antarctica* Frey & Lamb, *U. aprina* Nyl., *U. arctica* (Ach.) Nyl., *U. badia* Frey, *U. cristata* C.W.Dodge & G.E.Baker, *U. cylindrica* (L.) Delise ex Duby, *U. decussata* (Vill.) Zahlbr., *U. dendrophora* (Poelt) Hestmark, *U. durietzii* Frey, *U. formosana* Frey, *U. havaasii* Llano, *U. herrei* Frey, *U. hyperborea* (Ach.) Hoffm., *U. hypococcinea* (Jatta) Llano, *U. iberica* Sancho & Krzewicka, *U. indica* Frey, *U. isidiosa* Krzewicka, *U. kappeni* Sancho & al., *U. krascheninnikovii* (Savicz) Zahlbr., *U. maculata* Krzewicka & al., *U. minuta* J.C.We & Y.M.Jiang, *U. nanella* Frey & Poelt, *U. nepalensis* Poelt, *U. nylanderiana* (Zahlbr.) H.Magn., *U. polaris* (Schol.) Zahlbr., *U. polyphylla* (L.) Baumg., *U. proboscidea* (L.) Schrad., *U. pseudocinerascens* J.C.We & Y.M.Jiang, *U. rhizinata* (Frey & Poelt) Krzewicka, *U. robusta* (Llano) D.J.Galloway & Sancho, *U. scholanderii* (Llano) Krog, *U. subaprina* Frey, *U. subumbilicarioides* J.C.We & Y.M.Jiang, *U. taibaiensis* J.C.We & Y.M.Jiang, *U. thamnoides* Hue, *U. umbilicarioides* (Stein) Krog & Swinscow, *U. virginis* Schaer.

*Umbilicaria* subg. *Umbilicariopsis* Davydov, Peršoh & Rambold, **subg. nov.** [MB 821407] – Type: *Umbilicaria polyrhiza* (L.) Ach.

Clade 4

*Diagnostic characters.* – Thallus medium to large; upper surface smooth, non-pustulate or pustulate, red-brown with abundant, erect, marginal rhizinomorphs; lower surface black, areolate, densely felted with richly branched rhizinomorphs; thalloconidia on the tips of the rhizinomorphs, multicellular. Apothecia adnate, actinodisc, containing asci with eight small simple hyaline spores.

*Etymology.* – The name reflects the close phylogenetic relationship to subg. *Umbilicaria*.

*Included species.* – *Umbilicaria polyrhiza* (L.) Ach.

*Xylopsora* Bendiksby & Timdal in Taxon 62: 952. 2013 – Type: *Xylopsora friesii* (Ach.) Bendiksby & Timdal.

## ■ ACKNOWLEDGEMENTS

We appreciate Prof. B. McCune for his valuable comments and improving of the text and to anonymous reviewers for helpful feedback on an earlier version of this work. The curators of the herbaria cited above as well as Prof. B. McCune, Dr D. Masson, Dr F. Fernandez-Mendoza, Dr S. Pérez-Ortega, Dr O.B. Blum and Dr L.S. Yakovchenko are thanked for the loan of herbarium specimens. We are also indebted to Christina Leistner for technical assistance and to Prof. Patricia S. Muir for improving the English. The first author was supported by Russian Foundation for Basic Research (no. 14-04-00067). The work in Bayreuth University was supported by the DAAD (German Academic Exchange Service) and by the DFG (no. RA 731/13-1).



## ■ LITERATURE CITED

- Arup, U., Søchting, U. & Frödén, P. 2013. A new taxonomy of the family Teloschistaceae. *Nordic J. Bot.* 31: 16–83. <https://doi.org/10.1111/j.1756-1051.2013.00062.x>
- Athukorala, S.N.P., Pino-Bodas, R., Stenroos, S., Ahti, T. & Piercey-Normore, M.D. 2016. Phylogenetic relationships among reindeer lichens of North America. *Lichenologist* 48: 209–227. <https://doi.org/10.1017/S0024282915000572>
- Bendiksby, M. & Timdal, E. 2013. Molecular phylogenetics and taxonomy of *Hypocenomyce* sensu lato (Ascomycota: Lecanoromycetes): Extreme polyphyly and morphological/ecological convergence. *Taxon* 62: 940–956. <https://doi.org/10.12705/625.18>
- Boc, A., Diallo, A.B. & Makarenkov, V. 2012. T-REX: A web server for inferring, validating and visualizing phylogenetic trees and networks. *Nucl. Acids Res.* 40(W1): W573–W579. <https://doi.org/10.1093/nar/gks485>
- Brodo, I.M., Duran Sharnoff, S. & Sharnoff, S. 2001. *Lichens of North America*. New Haven & London: Yale University Press.
- Byazrov, L.G. 1986. Dopolneniya k flore lishainikov Khangaya (MNR). 1. Semeistvo Umbilicariaceae Fee = Additions to the lichen flora in Khangai (Mongolian People's Republic). 1. The family Umbilicariaceae Fee. *Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol.* 91: 100–101. [In Russian]
- Calo, S., Shertz-Wall, C., Lee, S.C., Bastidas, R.J., Nicolás, F.E., Granek, J.A., Mieczkowski, P., Torres-Martínez, S., Ruiz-Vázquez, R.M., Cardenas, M.E. & Heitman, J. 2014. Antifungal drug resistance evoked via RNAi-dependent epimutations. *Nature* 513: 555–558. <https://doi.org/10.1038/nature13575>
- Chooi, Y.H., Stalker, D.M., Davis, M.A., Fujii, I., Elix, J.A., Louwhoff, S.H.J.J. & Lawrie, A.C. 2008. Cloning and sequence characterization of a non-reducing polyketide synthase gene from the lichen *Xanthoparmelia semivivida*. *Mycol. Res.* 112: 147–161. <https://doi.org/10.1016/j.mycres.2007.08.022>
- Clarke, K.R. & Gorley, R.N. 2015. *PRIMER v7: User manual/tutorial*. Plymouth: PRIMER-E.
- Culberson, C.F. & Kristinsson, H.A. 1970. A standardized method for the identification of lichen product. *J. Chromatogr.* 46: 85–93. [https://doi.org/10.1016/s0021-9673\(00\)83967-9](https://doi.org/10.1016/s0021-9673(00)83967-9)
- Davydov, E.A. 2007. Approaches to a classification of the family Umbilicariaceae (lichenised Ascomycota) by anatomical and morphological characters. *Turczaninowia* 10(3–4): 51–57.
- Davydov, E.A., Peršoh, D. & Rambold, G. 2010. The systematic position of *Lasallia caroliniana* (Tuck.) Davydov, Peršoh & Rambold comb. nova and considerations on the generic concept of *Lasallia* (Umbilicariaceae, Ascomycota). *Mycol. Progr.* 9: 261–266. <https://doi.org/10.1007/s11557-009-0636-y>
- Davydov, E.A., Tchabanenko, S.I., Makryi, T.V. & Khanin, V.A. 2011. The second confirmed record of *Umbilicaria pulvinaria* (lichenised Ascomycota) since its original description in 1914. *Turczaninowia* 14(2): 119–122.
- Degelius, G.N. 1940. Studien über die Konkurrenzverhältnisse der Laubflechten auf nacktem Fels. *Acta Horti Gothob.* 14: 195–219.
- Döring, H. & Triebel, D. 1998. Phylogenetic relationships of *Bulgaria* inferred by 18S rDNA sequence analysis. *Cryptog., Bryol. Lichénol.* 19: 123–136.
- Elix, J.A. & Stocker-Wörgötter, E. 2008. Biochemistry and secondary metabolites. In: Nash, T.H., III (ed.), *Lichen biology*, ed. 2. Cambridge: Cambridge University Press.
- Feige, G.B., Posner, B. & Geyer, M. 1987. Zur Chemotaxonomie von *Umbilicaria* sect. *Antracinae*. *Herzogia* 7: 649–674.
- Fienberg, S.E. 1980. *The analysis of cross-classified categorical data*, ed. 2. Cambridge, Massachusetts: M.I.T. Press.
- Frey, E. 1931. Weitere Beiträge zur Kenntnis der Umbilicariaceen. *Hedwigia* 71: 94–119.
- Frey, E. 1933. *Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz*, ed. 2, vol. 9(4, 1), *Cladoniaceae (unter Ausschluß der Gattung Cladonia) Umbilicariaceae*. Leipzig: Akademische Verlagsgesellschaft.
- Frey, E. 1949. Neue Beiträge zu einer Monographie des Genus *Umbilicaria*. (Hoffm.) Nyl. *Ber. Schweiz. Bot. Ges.* 59: 427–470.
- Gams, W. 1996. Report of the Committee for Fungi: 6. *Taxon* 45: 309–311. <https://doi.org/10.2307/1224675>
- Gardes, M. & Bruns, T.D. 1993. ITS primers with enhanced specificity for basidiomycetes – Application to the identification of mycorrhizae and rusts. *Molec. Ecol.* 2: 113–118. <https://doi.org/10.1111/j.1365-294x.1993.tb00005.x>
- Gargas, A. & Taylor, J.W. 1992. Polymerase chain reaction (PCR) primers for amplifying and sequencing nuclear 18S rDNA from lichenized fungi. *Mycologia* 84: 589–592. <https://doi.org/10.2307/3760327>
- Golubkova, N.S. & Shapiro, I.A. 1979. Vidi roda *Umbilicaria* Hoffm. em. Frey v SSSR i ikh khemotaksonomicheskoye izuchenie = Species generis *Umbilicaria* Hoffm. em. Frey in URSS cresentes et examinatio earum chemotaxonomica. *Novosti Sist. Nizsh. Rast.* 16: 133–153. [In Russian].
- Grube, M. & Blaha, J. 2003. On the phylogeny of some polyketide synthase genes in the lichenized genus *Lecanora*. *Mycol. Res.* 107: 1419–1426. <https://doi.org/10.1017/s0953756203008724>
- Hale, M.E. 1983. *The biology of lichens*, ed. 3. London: Arnold.
- Harris, P.M. 1996. Competitive equivalence in a community of lichens on rock. *Oecologia* 108: 663–668. <https://doi.org/10.1007/BF00329040>
- Hasenhüttl, G. & Poelt, J. 1978. Über die Brutkörner bei der Flechtengattung *Umbilicaria*. *Ber. Deutsch. Bot. Ges.* 91: 275–296.
- Henssen, A. 1970. Die Apothecienentwicklung bei *Umbilicaria* Hoffm. emend. Frey. *Vortr. Gesamtgeb. Bot.*, N.F., 4: 103–126.
- Hestmark, G. 1990. Thalloconidia in the genus *Umbilicaria*. *Nordic J. Bot.* 9: 547–574. <https://doi.org/10.1111/j.1756-1051.1990.tb00546.x>
- Hestmark, G. 1991a. Teleomorph-anamorph relationships in *Umbilicaria* I. Making the connections. *Lichenologist* 23: 343–359. <https://doi.org/10.1017/s0024282991000506>
- Hestmark, G. 1991b. Teleomorph-anamorph relationships in *Umbilicaria* II. Patterns in propagative morph production. *Lichenologist* 23: 361–380. <https://doi.org/10.1017/S0024282991000518>
- Hestmark, G. 1991c. To sex, or not to sex ... Structures and strategies of reproduction in the family Umbilicariaceae (Lecanorales, Ascomycetes). *Sommerfeltia Suppl.* 3: 1–47.
- Hestmark, G. 1997. Competitive behaviour of umbilicate lichens – An experimental approach. *Oecologia* 111: 523–528. <https://doi.org/10.1007/s004420050266>
- Hestmark, G., Schroeter, B. & Kappen, L. 1997. Intrathalline and size-dependent patterns of activity in *Lasallia pustulata* and their possible consequences for competitive interactions. *Funct. Ecol.* 11: 318–322. <https://doi.org/10.1046/j.1365-2435.1997.00086.x>
- Hestmark, G., Miadlikowska, J., Kauff, F., Fraker, E., Molnar, K. & Lutzoni, F. 2011. Single origin and subsequent diversification of central Andean endemic *Umbilicaria* species. *Mycologia* 103: 45–56. <https://doi.org/10.3852/10-012>
- Hofstetter, V., Miadlikowska, J., Kauff, F. & Lutzoni, F. 2007. Phylogenetic comparison of protein-coding versus ribosomal RNA-coding sequence data: A case study of the Lecanoromycetes (Ascomycota). *Molec. Phylogen. Evol.* 44: 412–426. <https://doi.org/10.1016/j.ympev.2006.10.016>
- Huss, V.A.R., Frank, C., Hartmann, E.C., Hirmer, M., Kloboucek, A., Seidel, B.M., Wenzler, P. & Kessler, E. 1999. Biochemical taxonomy and molecular phylogeny of the genus *Chlorella* sensu lato (Chlorophyta). *J. Phycol.* 35: 587–598. <https://doi.org/10.1046/j.1529-8817.1999.3530587.x>
- Ihlen, P.G. & Ekman, N.S. 2002. Outline of phylogeny and character evolution in *Rhizocarpon* (Rhizocarpaceae, lichenized Ascomycota) based on nuclear ITS and mitochondrial SSU ribosomal DNA sequences. *Biol. J. Linn. Soc.* 77: 535–546. <https://doi.org/10.1046/j.1095-8312.2002.00127.x>

- Imshaug, H.A.** 1957. Alpine lichens of western United States and adjacent Canada. I. The Macrolichens. *Bryologist* 60: 177–272. <https://doi.org/10.2307/3240365>
- Ivanova, N.V., DePriest, P.T., Bobrova, V.K. & Troitsky, A.V.** 1999. Phylogenetic analysis of the lichen family Umbilicariaceae based on nuclear ITS1 and ITS2 rDNA sequences. *Lichenologist* 31: 477–489. <https://doi.org/10.1017/s0024282999000638>
- Jørgensen, P.M.** 1994. (1094–1097) Proposals to reject four species names of lichenized fungi. *Taxon* 43: 462–464. <https://doi.org/10.2307/1222724>
- Jørgensen, P.M., James, P.W. & Jarvis, C.E.** 1994. (1112–1137) Proposals to reject or conserve 26 Linnaean names of lichenized ascomycetes. *Taxon* 43: 646–654. <https://doi.org/10.2307/1223554>
- Keller, N.P. & Hohn, T.M.** 1997. Metabolic pathway gene clusters in filamentous fungi. *Fungal Genet. Biol.* 21: 17–21. <https://doi.org/10.1006/fgbi.1997.0970>
- Kondratyuk, S.Y., Jeong, M.-H., Yu, N.-N., Kärnefelt, I., Thell, A., Elix, J.A., Kim, J., Kondratiuk, A. & Hur, J.-S.** 2014a. A revised taxonomy for the subfamily Caloplacoideae (Teloschistaceae, Ascomycota) based on molecular phylogeny. *Acta Bot. Hung.* 56: 93–123. <https://doi.org/10.1556/ABot.56.2014.1-2.10>
- Kondratyuk, S.Y., Kärnefelt, I., Thell, A., Elix, J.A., Kim, J., Jeong, M.-H., Yu, N.-N., Kondratiuk, A. & Hur, J.-S.** 2014b. A revised taxonomy for the subfamily Xanthorioideae (Teloschistaceae, Ascomycota) based on molecular phylogeny. *Acta Bot. Hung.* 56: 141–178. <https://doi.org/10.1556/ABot.56.2014.1-2.12>
- Krog, H.** 1968. The macrolichens of Alaska. *Norsk Polarinst. Skr.* 144: 1–180.
- Krzewicka, B., Garsía, M.A., Johansen, S.D., Sancho, L.G. & Martín, M.P.** 2009. Morphological and nuclear ribosomal DNA data support distinguishing two new species of *Umbilicaria* (Umbilicariaceae, Ascomycota) from Europe. *Lichenologist* 41: 631–648. <https://doi.org/10.1017/s0024282909990120>
- Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S.** 2012. PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molec. Biol. Evol.* 29: 1695–1701. <https://doi.org/10.1093/molbev/mss020>
- Larson, D.W.** 1984. Habitat overlap/niche segregation in two *Umbilicaria* lichens: A possible mechanism. *Oecologia* 62: 118–125.
- Librado, P. & Rozas, J.** 2009. DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 15: 1451–1452. <https://doi.org/10.1093/bioinformatics/btp187>
- Liu, Y.J., Whelen, S. & Hall, B.D.** 1999. Phylogenetic relationships among ascomycetes: Evidence from an RNA polymerase II subunit. *Molec. Biol. Evol.* 16: 1799–1808. <https://doi.org/10.1093/oxfordjournals.molbev.a026092>
- Llano, G.A.** 1950. *A monograph of the lichen family Umbilicariaceae in the Western Hemisphere*. Washington, D.C.: Department of the Navy.
- Maddison, W.P. & Maddison, D.R.** 2017. Mesquite: A modular system for evolutionary analysis, version 3.2. <http://mesquiteproject.org>
- Magain, N., Miadlikowska, J., Goffinet, B., Sérusiaux, E. & Lutzoni, F.** 2017. Macroevolution of specificity in cyanolichens of the genus *Peltigera* section *Polydactylon* (Lecanoromycetes, Ascomycota). *Syst. Biol.* 66: 74–99. <https://doi.org/10.1093/sysbio/syw065>
- McCune, B. & Curtis, M.J.** 2012. *Umbilicaria semitensis* (lichenized fungi: Umbilicariaceae) resurrected. *Bryologist* 115: 255–264. <https://doi.org/10.1639/0007-2745-115.2.255>
- McCune, B. & Geiser, L.** 2009. *Macrolichens of the Pacific Northwest*, ed. 2. Corvallis: Oregon State University Press.
- McCune, B., Di Meglio, J. & Curtis, M.J.** 2014. An unusual ascospore shape and a new species, *Umbilicaria nodulospora* (Umbilicariaceae), from California and Oregon. *Bryologist* 117: 170–178. <https://doi.org/10.1639/0007-2745-117.2.170>
- Medlin, L., Elwood, H.J., Stickel, S. & Sogin, M.L.** 1988. The characterization of enzymatically amplified eukaryotic 16S-like rRNA coding regions. *Gene* 71: 491–499.
- Miadlikowska, J., Kauff, F., Högnabba, F., Oliver, J.C., Molnár, K., Fraker, E., Gaya, E., Hafellner, J., Hofstetter, V., Gueidan, C., Otálora, M.A., Hodkinson, B., Kukwa, M., Lücking, R., Björk, C., Sipman, H.J., Burgaz, A.R., Thell, A., Passo, A., Myllys, L., Goward, T., Fernández-Brime, S., Hestmark, G., Lendemer, J., Lumbsch, H.T., Schmutz, M., Schoch, C.L., Sérusiaux, E., Maddison, D.R., Arnold, A.E., Lutzoni, F. & Stenroos, S.** 2014. A multigene phylogenetic synthesis for the class Lecanoromycetes (Ascomycota): 1307 fungi representing 1139 infragenetic taxa, 317 genera and 66 families. *Molec. Phylog. Evol.* 79: 132–168. <https://doi.org/10.1016/j.ympev.2014.04.003>
- Motyka, J.** 1964. *Flora Polska*, vol. 3(2), *Porosty (Lichenes)*. Warsaw: Państwowe Wydawnictwo Naukowe.
- Narui, T., Culberson, C.F., Culberson, W.L., Johnson, A. & Shibata, S.** 1996. A contribution to the chemistry of the lichen family Umbilicariaceae (Ascomycotina). *Bryologist* 99: 199–211. <https://doi.org/10.2307/3244550>
- Niu, Y. & Wei, J.C.** 1993. Variations in ITS2 sequences of nuclear rDNA from two *Lasallia* species and their systematic significance. *Mycosystema* 6: 25–29.
- Nordin, A., Savić, S. & Tibell, L.** 2010. Phylogeny and taxonomy of *Aspicilia* and *Megasporaceae*. 2010. *Mycologia* 102: 1339–1349. <http://dx.doi.org/10.3852/09-266>
- Nylander, W.** 1869. De reactionibus in genere *Umbilicaria*. *Flora* 52: 387–389.
- Otálora, M., Jørgensen, P. & Wedin, M.** 2014. A revised generic classification of the jelly lichens, Collemataceae. *Fungal Diversity* 64: 275–293. <https://doi.org/10.1007/s13225-013-0266-1>
- Ott, S., Brinkmann, M., Wirtz, N. & Lumbsch, H.T.** 2004. Mitochondrial and nuclear ribosomal DNA data do not support the separation of the Antarctic lichens *Umbilicaria kappenii* and *Umbilicaria antarctica* as distinct species. *Lichenologist* 36: 227–234. <https://doi.org/10.1017/s0024282904014306>
- Peršoh, D., Beck, A. & Rambold, G.** 2004. The distribution of ascus types and photobiontal selection in Lecanoromycetes (Ascomycota) against the background of a revised SSU rDNA phylogeny. *Mycol. Progr.* 3: 103–121. <https://doi.org/10.1007/s11557-006-0081-0>
- Poelt, J.** 1962. Bestimmungsschlüssel der Höheren Flechten von Europa. *Mitt. Bot. Staatssamml. München* 4: 301–571.
- Poelt, J.** 1970. Das Konzept der Artenpaare bei den Flechten. *Vortr. Gesamtegeb. Bot.*, N.F., 4: 187–198.
- Poelt, J. & Nash, T.H., III** 1993. Studies in the *Umbilicaria vellea* group (Umbilicariaceae) in North America. *Bryologist* 96: 422–430. <https://doi.org/10.2307/3243872>
- Prieto, M. & Wedin, M.** 2013. Dating the diversification of the major lineages of Ascomycota (fungi). *PLOS ONE* 8(6): e65576. <https://doi.org/10.1371/journal.pone.0065576>
- Printzen, C.** 2002. Fungal specific primers for PCR-amplification of mitochondrial LSU in lichens. *Molec. Ecol. Notes* 2: 130–132. <https://doi.org/10.1046/j.1471-8286.2002.00179.x>
- Rambold, G., Meier, C. & Thamerus, M.** 1998. A comparative study on structure and functionality of asci in species of *Rhizocarpon* (Lecanorales, Ascomycetes). *Cryptog. Bryol. Lichénol.* 19: 247–255.
- Reeb, V., Lutzoni, F. & Roux, C.** 2004. Contribution of *RPB2* to multi-locus phylogenetic studies of the Pezizomycotina (Euascomycetes, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Molec. Phylog. Evol.* 32: 1036–1060. <https://doi.org/10.1016/j.ympev.2004.04.012>
- Romeike, J., Friedl, T., Helms, G. & Ott, S.** 2002. Genetic diversity of algal and fungal partners in four species of *Umbilicaria* (Lichenized Ascomycetes) along a transect of the Antarctic Peninsula. *Molec. Biol. Evol.* 19: 1209–1217. <https://doi.org/10.1093/oxfordjournals.molbev.a004181>



- Ronquist, R., Teslenko, M., Van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Savicz, V.P. 1950. Konspekt k flore lishainikov sem. Umbilicariaceae v SSSR = Conspectus lichenum ad flora Umbilicariacearum in URSS. *Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Akad. Nauk S.S.S.R.* 6(7–12): 97–108. [In Russian].
- Scholander, P.F. 1934. On the apothecia in the lichen family Umbilicariaceae. *Nytt Mag. Naturvidensk.* 75: 1–132.
- Silvestro, D. & Michalak, I. 2012. raxmlGUI: A graphical front-end for RAxML. *Organisms Diversity Evol.* 12: 335–337. <https://doi.org/10.1007/s13127-011-0056-0>
- Spatafora, J., Sung, G.-H., Johnson, D., Hesse, C., O'Rourke, B., Serdani, M., Spotts, R., Lutzoni, F., Hofstetter, V., Miadlikowska, J., Reeb, V., Gueidan, C., Fraker, E., Lumbsch, T., Lücking, R., Schmitt, I., Hosaka, K., Aptroot, A., Roux, C., Miller, A.N., Geiser, D.M., Hafellner, J., Hestmark, G., Arnold, A.E., Büdel, B., Rauhut, A., Hewitt, D., Unterreiner, W.A., Cole, M.S., Scheidegger, C., Schultz, M., Sipman, H. & Schoch, C.L. 2006. A five-gene phylogeny of Pezizomycotina. *Mycologia* 98: 1018–1028.
- Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- Stamatakis, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30, 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Thell, A., Crespo, A., Divakar, P.K., Kärnefelt, L., Leavitt, S.D., Lumbsch, H.T. & Seaward, M.R.D. 2012. A review of the lichen family Parmeliaceae – history, phylogeny and current taxonomy. *Nordic J. Bot.* 30: 641–664. <https://doi.org/10.1111/j.1756-1051.2012.00008.x>
- Truong, C., Divakar, P.K., Yahr, R., Crespo, A. & Clerc, P. 2013. Testing the use of ITS rDNA and protein-coding genes in the generic and species delimitation of the lichen genus *Usnea* (Parmeliaceae, Ascomycota). *Molec. Phylog. Evol.* 68: 357–372. <http://dx.doi.org/10.1016/j.ympev.2013.04.005>
- Warwick, R.M. & Clarke, K.R. 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar. Ecol. Progr. Ser.* 129: 301–305. <https://doi.org/10.3354/meps129301>
- Wei, J.C. 1966. A new subgenus of *Lasallia* Mer. em. Wei. *Acta Phytotax. Sin.* 11(1): 1–8.
- Wei, J.C. & Jiang, Y.M. 1988. A conspectus of the lichenized Ascomycetes Umbilicariaceae in China. *Mycosystema* 1: 73–106.
- Wei, J.C. & Jiang, Y.M. 1993. *The Asian Umbilicariaceae (Ascomycota)*. Mycosystema Monographicum Series, No. 1. Beijing: International Academic Publishers.
- White, T.J., Bruns, T.D., Lee, S.B. & Taylor, J.W. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (eds.), *PCR protocols: A guide to methods and applications*. San Diego: Academic Press. <https://doi.org/10.1016/b978-0-12-372180-8.50042-1>
- Zoller, S., Lutzoni, F. & Scheidegger, C. 1999. Genetic variation within and among populations of the threatened lichen *Lobaria pulmonaria* in Switzerland and implications for its conservation. *Molec. Ecol.* 8: 2049–2059. <https://doi.org/10.1046/j.1365-294x.1999.00820.x>

#### Appendix 1. Voucher data and GenBank accession numbers for samples included in this study.

Taxon, voucher (given for newly generated sequences), accession number of ITS, *RPB2*, mtLSU, and nrSSU. \*, newly generated sequence; –, missing information. ED, collector E.A. Davydov.

*Boreoplasma ultrafrigida* Timdal, Korea, Mt. Sorak, L.S. Yakovchenko 1265 (ALTB), KY947736\*, KY972584\*, KY947872\* –, *Hypocenyomyce scalaris* (Ach. ex Lilj.) M.Choisy, Germany, Bavaria, B., P. & T. Dornes s.n. (M-0166177), KY947864\*, KY972691\*, KY947994\* –, *Lasallia asiae-orientalis* Asahina 1, China, Yunnan, A.A. Zavarzin s.n. (ALTB-L174), EU909470, KY972612\*, KY947908\* –, 2, Nepal, A. Cross AC9 (E), –, KY972588\*, KY947875\* –, *Lasallia caroliniana* (Tuck.) Davydov & al. 1, U.S.A., Alaska, B. McCune 30743 (OSC), KY947836\*, KY972665\*, KY947962\* –, 2, Russia, Khabarovsk Territory, I.F. Skirina s.n. (VLA-L13502), EU909475, –, –, 3, Russia, Irkutsk Region, S.E. Voronyuk (ALTB-L5632), –, KY972640\*, –, –, 4, Russia, Sokhondinsky Reserve, I.A. Galanina s.n. (VLA-L86), EU909464, KY972641\*, KY947936\* –, *Lasallia daliensis* var. *caelongshanensis* (J.C.Wei) J.C.Wei, China, Yunnan, A.A. Zavarzin s.n. (ALTB-L172), EU909471, KY972617\*, KY947912\* –, *Lasallia hispanica* (Frey) Sancho & Crespo 1, Spain, Madrid, L.G. Sancho & S. Pannewitz s.n. (M-0082659), EU909473, KY972619\*, KY947914\* –, 2, Spain, Madrid, A. Crespo s.n. (MAF-10313), KY947821\*, KY972649\*, KY947945\* –, 3, Spain, Madrid, A. Crespo s.n. (MAF-10315), –, KY972645\*, KY947941\* –, *Lasallia papulosa* (Ach.) Llano 1, South Africa, Cape Town, S.I. Tschabanenko s.n. (ALTB-L186), KY947860\*, KY972688\*, KY947990\* –, 2, South Africa, Cape Town, M.P. Andreev 041101 (ALTB-L159), –, KY972633\* –, –, 3, same collection (ALTB-L160), –, KY972634\* –, –, 4, same collection (ALTB-L161), –, KY972635\* –, –, *Lasallia pensylvanica* (Hoffm.) Llano 1, Russia, Tigiretsky Reserve, ED 5310 (ALTB), EU909462, KY972594\*, KY947882\* –, 2, Turkey, Anatolia, V. John s.n. (M-0082754), EU909472, –, –, 3, AF096202, –, –, 4, HM161513, –, –, *Lasallia pertusa* (Rass.) Llano 1, Russia, Altai, ED 5311 (ALTB), KY948000, –, KY947889\*, KY948000\* 2, China, Tibet, W. Obermayer 08338 (M-0082746), KY947820\*, KY972648\*, KY947944\* –, 3, AF096203, –, –, *Lasallia pustulata* (L.) Mérat 1, Finland, Uusimaa, T. Ahti & ED 5037 (ALTB), EU909467, KY972602\*, KY947893\* –, 2, Portugal, G.B. & I. Feige s.n. (M-0083314), EU909474, KY972620\*, KY947915\* –, 3, Spain, Madrid, A. Crespo s.n. (MAF-10320), KY947816\*, KY972643\*, KY947939\* –, 4, same locality, A. Crespo s.n. (MAF-10303), KY947817\*, KY972644\*, KY947940\* –, 5, same locality, A. Crespo s.n. (MAF-10303), KY947818\* –, –, *Lasallia rossica* Domb. 1, Russia, Laplandsky Reserve, I.N. Urbanavichene & G.P. Urbanavichus s.n. (ALTB-L155), EU909469, KY972607\*, KY947903\* –, 2, Russia, Altai, ED 5267 (ALTB), KY947999\*, KY972597\*, KY947887\*, KY947999\* 3, Russia, Tigiretsky Reserve, ED 5263 (ALTB), EU909461, –, –, 4, Russia, Altai, ED 5270 (ALTB), KY948003\* –, KY947895\*, KY948003\* 5, Russia, Sokhondinsky Reserve, I.A. Galanina s.n. (ALTB), EU909463, –, –, 6, Russia, Tigiretsky Reserve, ED 7537 (ALTB), KY947826\*, KY972654\*, KY947950\* –, 7, AF096201, –, –, *Ochrolechia parella* (L.) A.Massal., Russia, Tigiretsky Reserve, ED 5537, KY948009\* –, KY948009\* *Ophioparma ventosa* (L.) Norman, Norway, Spitsbergen, L.A. Konoreva s.n. (ALTB), KY947741\*, KY972590\*, KY947877\* –, *Pertusaria alpina* Hepp ex Ahles., Russia, Tigiretsky Reserve, ED 5540 (ALTB), KY948010\* –, –, KY948010\* *Umbilicaria africana* (Jatta) Krog & Swinscow 1, Ethiopia, Simien Mts. National Park, T. Lutsak s.n. (FR-220099), KY947743\*, KY972592\*, KY947879\* –, 2, Chile, XII Region, S. Perez-Ortega & F. Fernandez-Mendoza 1774 (Herb. Perez-Ortega), KY947844\* –, KY947971\* –, 3, HM161482, –, –, *Umbilicaria altaiensis* J.C.Wei & Y.M.Jiang 1, Russia, Altai, ED 7230 (ALTB), KY947827\*, KY972655\*, KY947951\* –, 2, Russia, Altai, ED 5357 (ALTB), KY947757\* –, KY947900\* –, 3, Russia, Altai, ED 5366 (ALTB), KY947764\* –, –, 4, Mongolia, Altai, ED 5363 (ALTB), KY947768\* –, –, 5, Austria, Tirol, R. Guderley & al. s.n. (M-0083187), KY947786\* –, –, 6, Austria, Tirol, H. Wittmann & al. s.n. (M-0083186), KY947787\* –, –, 7, Russia, Altai, ED 5307 (ALTB), KY947787\* –, –, *Umbilicaria americana* Poelt & Nash 1, U.S.A., Katmai National Park, J.K. Walton 13054 (KATM 492), –, KY972671\*, KY947968\* –, 2, AF096218, –, –, *Umbilicaria angulata* Tuck. 1, U.S.A., Oregon, B. McCune 30050 (OSC), KY947834\*, KY972663\*, KY947960\* –, 2, JQ764746, –, –, 3, JQ764734, –, –, 4, JQ764738, –, –, *Umbilicaria antarctica* Frey & Lamb 1, Antarctica, Barton, M.P. Andreev L03951 (ALTB), KY947849\* –, KY947978\* –, 2, AF096213, –, –, 3, AJ431604, –, –, 4, FN185922, –, –, 5, AY603123,



## Appendix 1. Continued.

- , AY603135, –, 6, AY603124, –, AY603136, –, 7, AY603125, –, AY603137, –, *Umbilicaria aprina* Nyl. 1, Antarctica, Queen Mod Land, M.P. Andreev 42501 (ALTB-L158), KY947808\*, KY972636\*, KY947931\*, –, 2, Russia, Baikalsky Reserve, *Urbanavichus* G.P. s.n. (ALTB), KY947810\*, –, KY947933\*, –, 3, Norway, Svalbard, S. Perez-Ortega & S. Domaschke 1796 (ALTB), KY948014\*, –, KY947976\*, KY948014\*, 4, same collection, S. Perez-Ortega & S. Domaschke 1796 (ALTB), KY947859\*, –, KY947989\*, –, 5, HM161483, –, –, 6, HM161502, –, –, 7, FN185930, –, –, 8, FN185931, –, –, *Umbilicaria arctica* (Ach.) Nyl. (1) 1, Russia, Kola Penins., ED 5351 (ALTB), KY947754\*, KY972604\*, KY947898\*, –, 2, Russia, Kola Peninsula, A.A. Zavarzin s.n. (ALTB-L149), KY947996\*, –, KY947884\*, KY947996\*, 3, HM161454, –, –, *Umbilicaria arctica* (Ach.) Nyl. (2), U.S.A., Alaska, B. McCune 30832 (OSC), KY947839\*, KY972669\*, KY947966\*, –, *Umbilicaria badia* Frey, Nepal, Sharma & al. s.n. (E00321836), KY947738\*, KY972586\*, KY947874\*, –, *Umbilicaria calvescens* Nyl. 1, HM161506, –, –, 2, HM161507, –, –, 3, HM161508, –, –, 4, HM161458, –, –, 5, HM161459, –, –, 6, HM161484, –, –, 7, HM161485, –, –, 8, HM161460, –, –, 9, HM161461, –, –, 10, HM161462, –, –, 11, HM161463, –, –, 12, HM161486, –, –, *Umbilicaria cinerascens* (Arnold) Frey 1, Russia, Altai, ED 5361 (ALTB), KY947758\*, –, KY947902\*, –, 2, Russia, Altai, ED 5446 (ALTB), KY947779\*, –, –, *Umbilicaria cinereorufescens* (Schaer.) Frey 1, Russia, Baikalsky Reserve, G.P. Urbanavichus s.n. (ALTB), KY947778\*, KY972618\*, KY947913\*, –, 2, Russia, Baikalsky Reserve, G.P. Urbanavichus s.n. (ALTB), KY947811\*, KY972638\*, KY947934\*, –, 3, Russia, Altai, ED 651 (ALTB), KY947766\*, KY972613\*, KY947909\*, –, 4, Russia, Altai, ED 5275 (ALTB), KY948002\*, –, KY947894\*, KY948002\*, 5, Mongolia, Altai, ED 5283 (ALTB), KY947765\*, –, –, 6, U.S.A., Alaska, B. McCune 31407 (OSC), KY947840\*, KY972670\*, KY947967\*, –, 7, Nepal, Ch. Sheidegger s.n. (WSL), –, –, KY947992\*, –, 8, HM161503, –, –, 9, HM161511, –, –, *Umbilicaria crustulosa* (Ach.) Frey (1) 1, Norway, Hordaland, T. Tonsberg 28870 (M-0083255), KY948007\*, KY948077\*, KY947918\*, KY948007\*, 2, Spain, Madrid, A. Crespo s.n. (MAF-10294), KY947823\*, KY972651\*, KY947947\*, –, 3, France, D.M. Masson 83.4189 (ALTB), KY948016\*, KY972680\*, KY947981\*, KY948016\*, 4, AF096215, –, –, 5, HM161497, –, –, *Umbilicaria crustulosa* (Ach.) Frey (2) 1, Austria, W. Obermayer 7104 (H), KY947761\*, KY972609\*, KY947905\*, –, 2, France, D.M. Masson 31.3651 (ALTB), –, KY972687\*, –, 3, HM161498, –, –, 4, HM161499, –, –, *Umbilicaria crustulosa* var. *badiofusca* Frey, France, D.M. Masson 2B.3733 (ALTB), KY948012\*, KY972675\*, KY947972\*, KY948012\*, *Umbilicaria cylindrica* (L.) Delise ex Duby 1, Russia, Tigireksky Reserve, ED 7255 (ALTB), KY947828\*, KY972656\*, KY947952\*, –, 2, Russia, Laplandsky Reserve, I.N. Urbanavichene 03-0109 (ALTB), KY947773\*, –, –, 3, Russia, Teberdinsky Reserve, O.V. Blinkova 200700104 (ALTB), KY947776\*, –, –, 4, Russia, Altai, ED 5427 (ALTB), KY947802\*, –, –, 5, Russia, Altai, ED 5376 (ALTB), KY947803\*, –, –, 6, Russia, Tigireksky Reserve, ED 7255 (ALTB), KY947828\*, KY972656\*, KY947952\*, –, 7, Russia, Tigireksky Reserve, ED 7257 (ALTB), –, KY972684\*, –, –, 8, Ukraine, Carpaty Mts. Blum O.B. s.n. (ALTB) –, –, KY947869\*, –, 9, AF096199, –, –, 10, AF096209, –, –, 11, FN185933, –, –, 12, FN185934, –, –, 13, FN185938, –, –, 14, FN185982, –, –, 15, FN185942, –, –, *Umbilicaria decussata* (Vill.) Zahlbr. 1, Kazakhstan, Altai, D.A. German s.n. (ALTB-L153), KY948001\*, KY972600\*, KY947891\*, KY948001\*, 2, Russia, Altai, ED 5468 (ALTB), KY947795\*, KY972626\*, KY947922\*, –, 3, Antarctica, Hasuell Is., M.P. Andreev 41601 (ALTB-L157), KY947809\*, KY972637\*, KY947932\*, –, 4, Russia, Altai, ED 5464 (ALTB), KY947790\*, –, –, 5, Turkey, Anatolia, O. Beuss & al. s.n. (M-0083214), KY947785\*, –, –, 6, AF096214, –, –, 7, HM161501, –, –, 8, HM161510, –, –, *Umbilicaria dendrophora* (Poelt) Hestmark 1, Finland, H. Väre L 1777 (H), KY947772\*, KY972616\*, KY947911\*, –, 2, France, D.M. Masson 65.3254 (ALTB), KY947847\*, –, –, 3, HM161504, –, –, 4, HM161509, –, –, 5, HM161505, –, –, *Umbilicaria deusta* (L.) Baumg. 1, Russia, Altai, ED 5353 (ALTB), KY947753\*, KY972603\*, KY947897\*, –, 2, Russia, Baikalsky Reserve, G.P. Urbanavichus s.n. (ALTB), KY947774\*, –, –, 3, Russia, Laplandsky Reserve, I.N. Urbanavichene 03-0107 (ALTB), KY947775\*, –, –, 4, AF096206, –, –, *Umbilicaria dichroa* Nyl. 1, HM161464, –, –, 2, HM161465, –, –, *Umbilicaria esculenta* (Miyoshi) Minks, Korea, K.H. Moon 10001 (H), KY947856\*, KY972583\*, –, –, *Umbilicaria formosana* Frey 1, Russia, Primorye, I.S. Zhdanov s.n. (LE-L6823), KY947733\*, KY972580\*, KY947865\*, –, 2, China, Yunnan, A. Aptroot 55680 (ALTB), KY947806\*, –, KY947929\*, –, *Umbilicaria freyi* Codogno & al. 1, Spain, Madrid, A. Pintado & A. Argueello (MAF-10307), KY947815\*, KY972642\*, KY947938\*, –, 2, France, D.M. Masson 2B.3815 (ALTB), KY948015\*, KY972678\*, KY947979\*, KY948015\*, *Umbilicaria grisea* Ach. 1, France, D.M. Masson 2B.3813 (ALTB), KY948018\*, KY972686\*, KY947986\*, KY948018\*, 2, Ukraine, O.B. Blum (ALTB-L197), –, KY972666\*, –, 3, Ukraine, O.B. Blum (ALTB), KY947848\*, –, KY947977\*, –, 4, HM161491, –, –, 5, HM161493, –, –, 6, HM161500, –, –, *Umbilicaria haplocarpa* Nyl. 1, HM161466, –, –, 2, HM161467, –, –, 3, HM161468, –, –, 4, HM161469, –, –, 5, HM161470, –, –, 6, HM161471, –, –, 7, HM161472, –, –, 8, HM161474, –, –, 9, HM161475, –, –, 10, HM161476, –, –, 11, HM161487, –, –, 12, HM161477, –, –, *Umbilicaria havaasii* Llano 1, Russia, Lapland Reserve, A.V. Melekhin s.n. (KPABG-L11690), KY947742\*, KY972591\*, KY947878\*, –, 2, U.S.A., Oregon, B. McCune 27067 (H), KY947858\*, –, –, 3, JQ764739, –, –, *Umbilicaria herrei* Frey, U.S.A., Washington, B. McCune 32307 (OSC), KY947837\*, –, KY947963\*, –, *Umbilicaria hirsuta* (Sw.) Ach. 1, Russia, Altai, ED 5354 (ALTB), KY948004\*, KY972605\*, KY947899\*, KY948004\*, 2, Russia, Altai, ED 5449 (ALTB), KY947788\*, KY972624\*, KY947919\*, –, 3, Russia, Altai, ED 5449 (ALTB), KY947789\*, –, –, 4, Spain, Madrid, A. Crespo (MAF-L10300), KY947822\*, KY972650\*, KY947946\*, –, 5, HM161494, –, –, 6, HM161495, –, –, *Umbilicaria hyperborea* (Ach.) Hoffm. 1, Russia, Karelia, A.A. Zavarzin s.n. (ALTB-L148), KY947998\*, KY972596\*, KY947886\*, KY947998\*, 2, Russia, Altai, ED 5309 (ALTB), KY947744\*, –, –, 3, U.S.A., Washington, B. McCune 32306 (OSC), –, KY972667\*, KY947964\*, –, 4, Russia, Altai, ED 7444 (ALTB), –, –, KY947871\*, –, 5, AF096216, –, –, *Umbilicaria hypococeina* (Jatta) Llano, China, Yunnan, A. Aptroot 55687 (ALTB-L165), KY947812\*, KY972639\*, KY947935\*, –, *Umbilicaria iberica* Sancho & Krzewicka 1, France, D.M. Masson 2B.3791 (ALTB), KY948017\*, KY972685\*, KY947985\*, KY948017\*, 2, FN185964, –, –, 3, FN185965, –, –, 4, FN185966, –, –, *Umbilicaria indica* Frey, China, Yunnan, A.A. Zavarzin s.n. (ALTB-L170), KY948006\*, KY972614\*, KY947910\*, KY948006\*, *Umbilicaria josiae* Frey 1, France, D.M. Masson 31.3650 (ALTB), KY948013\*, KY972676\*, KY947974\*, KY948013\*, 2, France, D.M. Masson 09.3803 (ALTB), KY947852\*, KY972681\*, –, *Umbilicaria kappenii* Sancho & al. 1, AY603129, –, AY603142, –, 2, AY603131, –, –, *Umbilicaria kisovana* (Zahlbr. ex Asahina) Zahlbr., Russia, Primorye Territory, I.S. Zhdanov s.n. (ALTB-L190), KY947737\*, KY972585\*, KY947873\*, –, *Umbilicaria krascheninnikovii* (Savicz) Zahlbr. 1, Russia, Kamchatka, D.E. Himelbrant s.n. (ALTB), KY947752\*, –, KY947896\*, –, 2, Russia, Kamchatka, D.E. Himelbrant & I.S. Stepanchikova K-226-06 (H), KY947857\*, –, KY947988\*, –, 3, same region and collectors (LE-L7461), –, –, KY947957\*, –, *Umbilicaria laevis* (Schaer.) Frey, France, D.M. Masson 65.3580 (ALTB), KY947845\*, –, KY947973\*, –, *Umbilicaria lambii* Imshaug, Canada, M. Zhurbenko 02238 (ALTB-L193), KY947734\*, KY972581\*, KY947866\*, –, *Umbilicaria leiocarpa* DC. 1, France, D.M. Masson 2B.4194 (ALTB), KY947846\*, KY972677\*, KY947975\*, –, 2, France, D.M. Masson 65.3593 (ALTB), KY947850\*, KY972679\*, KY947980\*, –, 3, AF096211, –, –, *Umbilicaria leprosa* (Zahlbr.) Frey 1, HM161478, –, –, 2, HM161479, –, –, *Umbilicaria lyngei* Schol. 1, N. Greenland, E.S. Hansen s.n. (H), KY947771\*, –, –, 2, Russia, Altai, ED 5465 (ALTB), KY948008\*, –, KY947920\*, KY948008\*, 3, Russia, Altai, ED 5466 (ALTB), KY947792\*, –, –, 4, AF096217, –, –, *Umbilicaria maculata* Krzewicka & al. 1, Russia, Altai, ED 653 (ALTB), KY947793\*, –, –, 2, Russia, Altai, ED 1008 (ALTB), KY947794\*, –, –, 3, Russia, Altai, ED 5656 (ALTB), KY947813\*, –, KY947868\*, –, 4, Russia, Altai, ED 5656 (ALTB), KY947814\*, –, –, 5, France, D.M. Masson 04.4199 (ALTB), KY947863\*, KY972690\*, –, *Umbilicaria mammulata* (Ach.) Tuck., U.S.A., Minnesota, C.M. Wetmore 82463 (M-0083027), KY947819\*, KY972647\*, KY947943\*, –, *Umbilicaria microphylla* (Laurer) A.Massal., Austria, R. Turk & R. Reiter s.n. (M-0083177), –, KY972646\*, KY947942\*, –, *Umbilicaria muehlenbergii* (Ach.) Tuck. 1, Russia, Primorye Territory, S.V. Smirnov s.n. (ALTB-L154), KY947997\*, KY972595\*, KY947885\*, KY947997\*, 2, Russia, Altai, ED 5360 (ALTB), KY948005\*, –, KY947901\*, KY948005\*, 3, AF096204, –, –, *Umbilicaria nodulospora* McCune & al. 1, KJ740718, –, –, 2, KJ740719, –, –, 3, KJ740720, –, –, *Umbilicaria nylanderiana* (Zahlbr.) H. Magn. 1, –, –, KY947880\*, –, 2, Mongolia, Altai, ED 5657 (ALTB), –, –, KY947937\*, –, 3, Russia, Altai, ED 5295 (ALTB), KY947855\*, –, KY947987\*, –, 4, Russia, Tigireksky Reserve, ED 5456 (ALTB), KY947796\*, –, KY947923\*, –, 5, Argentina, Rio Negro, S. Perez-Ortega & F. Fernandez-Mendoza 1788 (Herb. Perez-Ortega), KY947841\*, –, KY947969\*, –, 6, AY603133, –, –, 7, AF096205, –, –, 8, HM161488, –, –, 9, HM161489, –, –, 10, FN185974, –, –, *Umbilicaria cf. phaea* Tuck., Chile, VII Region, S. Perez-Ortega & F. Fernandez-Mendoza 1789 (Herb. Perez-Ortega), KY947843\*, KY972674\*, –, –, *Umbilicaria phaea* Tuck. 1, U.S.A., California, J.C. Lendemer & K. Knudsen 14858 (H), KY947862\*, –, KY947993\*, –, 2, JQ764736, –, –, 3, JQ764741, –, –, 4, JQ764733, –, –, *Umbilicaria polaris* (Schol.) Zahlbr. 1, Russia, Tigireksky Reserve, ED 5306 (ALTB), KY947747\*, KY972599\*, KY947890\*, –, 2, Russia, Tigireksky Reserve, ED 7251 (ALTB), KY947830\*, KY972659\*, KY947955\*, –, 3, Russia, Altai, ED 5298 (ALTB), KY947759\*, –, –, 4, U.S.A., Montana, B. McCune 32070 (OSC), –, KY972672\*, –, 5, Russia, Tigireksky Reserve, ED 7301 (ALTB), –

## Appendix 1. Continued.

–, KY947870\*, – 6, AY603131, –, –, *Umbilicaria polyphylla* (L.) Baumg. 1, Finland, *V. Haikonen 21060* (H), KY947763\*, KY972611\*, KY947907\* – 2, Canada, British Columbia, *T. Spribille s.n.* (M-0083126), KY947784\*, KY972622\*, KY947917\* – 3, Great Britain, Scotland, *F. Bungartz s.n.* (M-0083113), KY947782\*, –, –, 4, Norway, *ED 5470* (ALTB), KY947798\*, –, –, 5, FN185975, –, –, 6, FN185976, –, –, 7, FN185977, –, –, 8, FN185978, –, –, 9, FN185979, –, –, *Umbilicaria polyrhiza* (L.) Ach. 1, U.S.A., California, *B. McCune 30433* (OSC), KY947838\*, KY972668\*, KY947965\* – 2, Finland, *V. Haikonen 20887* (H), KY947762\*, KY972610\*, KY947906\* – 3, Norway, *T. Tønsberg 28871* (M-0082944), KY947783\*, –, –, 4, JQ764737, –, –, *Umbilicaria proboscidea* (L.) Schrad. 1, Russia, Tigiretsky Reserve, *ED 7253* (ALTB), KY947829\*, KY972657\*, KY947953\* – *Umbilicaria pseudocin-  
erascens* J.C. Wei & Y.M. Jiang, China, Yunnan, *A. Aptroot 55686* (ALTB), KY947807\*, KY972632\*, KY947930\* – *Umbilicaria pulvinaria* (Savicz) Frey, Russia, Sakhalin I., *S.I. Chabanenko s.n.* (LE-L7943), KY947735\*, KY972582\*, KY947867\* – *Umbilicaria rhizinata* (Frey & Poelt) Krzewicka, Russia, Tigiretsky Reserve, *ED 7258* (ALTB), KY948011\*, KY972658\*, KY947954\*, KY948011\* – *Umbilicaria rigida* (Du Rietz) Frey 1, Norway, *ED 5367* (ALTB), KY947749\*, KY972601\*, KY947892\* – 2, AF096212, –, –, 3, HM161455, –, –, *Umbilicaria ruebeliana* (Du Rietz & Frey) Frey 1, France, *D.M. Masson 04.4198* (ALTB), KY947851\*, –, KY947982\* – 2, AF096219, –, –, *Umbilicaria semitensis* Tuck. 1, U.S.A., Oregon, *B. McCune 30048* (OSC), KY947833\*, KY972662\*, KY947959\* – 2, JQ764742, –, –, 3, JQ764735, –, –, 4, JQ764745, –, –, 5, JQ764743, –, –, *Umbilicaria spodochoera* Ehrh. ex Hoffm. (1) 1, Norway, *T. Tønsberg* (M-0082898), KY947780\*, KY972621\*, KY947916\* – 2, Spain, Madrid, *A. Crespo s.n.* (MAF-10297), KY947824\*, KY972652\*, KY947948\* – 3, France, *D.M. Masson 2A.3739* (ALTB), KY947853\*, KY972682\*, KY947983\* – 4, AF096207, –, –, *Umbilicaria spodochoera* Ehrh. ex Hoffm. (2), Turkey, Izmir, *V. John s.n.* (H), KY947760\*, KY972608\*, KY947904\* – *Umbilicaria subglabra* (Nyl.) Harm. 1, France, *Ph. Clerck 2215* (ALTB-L205), KY947861\*, KY972689\*, KY947991\* – 2, Russia, Altai, *ED 5313* (ALTB), KY947750\*, –, –, 3, Mongolia, Altai, *ED 5355* (ALTB), KY947755\*, KY972606\*, –, –, 4, Russia, Altai, *ED 1210* (ALTB), KY947756\*, –, –, 5, AF096200, –, –, *Umbilicaria subglabra* var. *pallens* (Nyl.) Frey, France, *D.M. Masson 09.4191* (ALTB), KY947854\*, KY972683\*, KY947984\* – *Umbilicaria thamnodes* Hue 1, China, Yunnan, *A. Aptroot 55697* (ALTB-166), KY947825\*, KY972653\*, KY947949\* – 2, China, Yunnan, *A.A. Zavarzin s.n.* (ALTB-L173), KY947769\*, KY972615\*, –, –, *Umbilicaria torrefacta* (Lightf.) Schrad. 1, Russia, Altai, *ED 5314* (ALTB), KY947746\*, KY972598\*, KY947888\* – 2, Russia, Laplandsky Reserve, *I. N. Urbanavichene 03-0111* (ALTB), KY947777\*, –, –, 3, Norway, *ED 5352* (ALTB), KY947799\*, KY972628\*, KY947925\* – 4, JQ764744, –, –, *Umbilicaria tylorhiza* Nyl., China, Yunnan, *A. Aptroot 56888a* (ALTB), KY947805\*, KY972631\*, KY947928\* – *Umbilicaria umbilicarioides* (Stein) Krog & Swinscow 1, Chile, XII Region, *S. Perez-Ortega & F. Fernandez-Mendoza 1773* (Herb. Perez-Ortega), KY947842\*, KY972673\*, KY947970\* – 2, South Africa, *F. Brusse s.n.* (M-0082846), KY947781\*, –, –, 3, AY603121, –, –, 4, AF096210, –, –, 5, FN185980, –, –, 6, FN185981, –, –, 7, FN185941, –, –, *Umbilicaria vellea* (L.) Ach. (1) 1, Russia, Altai, *ED 5305* (ALTB), KY947995\*, KY972593\*, KY947881\*, KY947995\* 2, Russia, Altai *ED 5469* (ALTB), KY947797\*, KY972627\*, KY947924\* – 3, Russia, Teberdinsky Reserve, *O.V. Blinkova 240700106* (ALTB), KY947800\*, KY972629\*, KY947926\* – 4, Russia, Altai, *ED 5294* (ALTB), KY947751\*, –, –, 5, Russia, Tigiretsky Reserve, *ED 5453* (ALTB), KY947791\*, KY972625\*, KY947921\* – 6, U.S.A., Flathead, *B. McCune 32390* (OSC), KY947835\*, KY972664\*, KY947961\* – 7, AF096208, –, –, 8, HM161490, –, –, *Umbilicaria vellea* (L.) Ach. (2) 1, Russia, Laplandsky Reserve, *I.N. Urbanavichene* (ALTB-5163), KY947801\*, KY972630\*, KY947927\* – 2, Russia, Laplandsky Reserve, *I.S. Zhdanov s.n.* (ALTB-196), KY947831\*, KY972660\*, KY947956\* – 3, FN185983, –, –, 4, FN185984, –, –, *Umbilicaria virginis* Schaer. 1, U.S.A., Montana, *B. McCune 32089* (OSC), KY947832\*, KY972661\*, KY947958\* – 2, Russia, Altai, *ED 5541* (ALTB), KY947804\*, –, –, 3, Russia, Altai, *ED 5422* (ALTB), KY947767\*, –, –, *Umbilicaria yunnana* (Nyl.) Hue 1, China, Yunnan, *A.A. Zavarzin s.n.* (ALTB-L169), KY947770\*, –, –, 2, KY947739\*, KY972587\*, –, –, *Xylopsora friesii* (Ach.) Bendiksby & Tindal, Russia, Murmansk Region, *G.P. Urbanavichus s.n.* (INEP-48), KY947740\*, KY972589\*, KY947876\* –.

## Appendix 2. Conflicts between ITS, RPB2, and mtLSU single-marker phylograms.

Two conflicts were found: (1) *Umbilicaria hirsuta* is monophyletic in RPB2 and mtLSU analyses (99% and 92% BS, respectively) and *U. josiae* groups as a sister group (97% and 98% BS). However, in the ITS phylogram, KY947822 *U. hirsuta* groups with *U. josiae* (95% BS) and with a clade of two remaining sequences of *U. hirsuta* (99% BS). (2) All phylograms include well-supported clade *U. formosana–U. rhizinata* (BS ITS: 81%; RPB2: 85%; mtLSU: 99%). In the ITS analysis this clade groups with *U. africana* (86% BS) and with KY947808 *U. aprina* (43% BS), whereas in the mtLSU phylogram with *U. aprina* and *U. africana*. In the RPB2 analysis, the interactions between these three branches are unresolved due to low bootstrap support. Mentioned conflicts were considered as minor, because they appeared in the grouping of distal branches among sequences of taxa belonging to closely related species, and often have bootstrap support less than 90%.

# TAXON

International Journal of Taxonomy, Phylogeny and Evolution

Electronic Supplement to

## **Umbilicariaceae (lichenized Ascomycota) – Trait evolution and a new generic concept**

**Evgeny A. Davydov, Derek Peršoh & Gerhard Rambold**

*Taxon* 66: 1282–1303



**Table S1.** Distribution of the diagnostic morphological and chemical traits to the investigated species and clades recognized by the phylogenetic analyses.

Taxon	Clade no.	Ch1	Ch2	Ch3	Ch4	Ch5	Ch6	Ch7	Ch8	Ch9	Ch 10	Ch 11	Ch 12
<i>L. asiae-orientalis</i>	C1	0	–	0	–	–	1	0	2	1	2	2	0
<i>L. caroliniana</i>		1	3	0	–	–	0	1	0	0	2	2	0
<i>L. daliensis</i> var. <i>caeongshanensis</i>		0	–	0	–	–	1	1	2	1	2	2	0
<i>L. hispanica</i>		0	–	0	–	–	0	1	2	1	2	2	0
<i>L. papulosa</i>		0	–	0	–	–	0	1	2	1	2	2	0
<i>L. pennsylvanica</i>		0	–	0	–	–	0	1	2	1	2	2	0
<i>L. pertusa</i>		0	–	0	–	–	1	0*	–	–	–	–	0
<i>L. pustulata</i>		0	–	0	–	–	1	0	2	1	2	2	0
<i>L. rossica</i>		0	–	0	–	–	0	1	2	1	2	2	0
<i>U. esculenta</i>	C2a	1	2	1	1	2	1	0	0	0	0	1	0
<i>U. mammulata</i>		1	2	1	1	2	0	0	0	0	0	1	0
<i>U. yunnana</i>		1	2	1	0	0	0	1	0	0	0	1	0
<i>U. kisovana</i>		0	–	0	–	–	1	0	0	0	0	0	0
<i>U. muehlenbergii</i>	C2b	0	–	0	–	–	0	1	1	0	0	0	0
<i>U. deusta</i>	C2c	0	–	0	–	–	1	1	0	0	0	1	0
<i>U. africana</i>		1	0	1	0	1	0	0	0	0	0	0	0
<i>U. altaiensis</i>		1	0	0	–	–	0	0	0	0	0	0	0
<i>U. antarctica</i>		1	0	1	0	0	0	1	0	0	0	0	0
<i>U. aprina</i>		1	0	1	0	0	0	0	0	0	0	0	0
<i>U. arctica-1</i>		0	–	0	–	–	0	1	0	0	0	0	1
<i>U. arctica-2</i>		0	–	0	–	–	0	1	0	0	0	0	1
<i>U. badia</i>		1	0	1	0	0	0	1	0	0	0	0	0
<i>U. cylindrica</i>		1	0	0	–	–	0	1	0	0	0	0	1
<i>U. decussata</i>		0	–	1	0	0	0	0	0	0	0	0	1
<i>U. dendrophora</i>		1	0	1	1	2	0	0	0	0	0	0	1
<i>U. formosana</i>		1	0	1	0	0	0	1	0	0	0	0	0
<i>U. havaasii</i>		1	0&1	1	1	2	0	0	0	0	0	0	0
<i>U. herrei</i>		1	0	1	0	0	0	1	0	0	0	0	0
<i>U. hyperborea</i>		0	–	0	–	–	0	1	0	0	0	0	0
<i>U. hypococcinea</i>		1	0	0	–	–	0	1	0	0	0	0	0
<i>U. iberica</i>		0	–	1	0	1	0	0	0	0	0	0	0
<i>U. indica</i>		1	0	1	0	0	0	1	0	0	0	1	0
<i>U. kappenii</i>		1	0	0	–	–	1	0*	–	–	–	–	0
<i>U. krascheninnikovii</i>		1	0	1	0	0	0	1	0	0	0	0	0
<i>U. maculata</i>		1	0	0	–	–	0	1	0	0	0	0	0
<i>U. nylanderiana</i>		0	–	1	0	0	0	0	0	0	0	0	0
<i>U. polaris</i>	0&1	0	0	0	–	–	0	1	0	0	0	0	1
<i>U. polyphylla</i>		0	–	1	0	1	0	0	0	0	0	0	0
<i>U. proboscidea</i>		1	0	0	–	–	0	1	0	0	0	0	1
<i>U. pseudocinerascens</i>		0	–	1	0	0	0	1	0	0	0	–	0
<i>U. rhizinata</i>		1	0	1	0	1	0	1	0	0	0	0	0
<i>U. thamnodes</i>		1	0	1	0	0	0	0	0	0	0	1	0
<i>U. umbilicarioides</i>		1	0	1	1	2	0	1	0	0	0	0	1

Table S1. Continued.

Taxon	Clade no.	Ch1	Ch2	Ch3	Ch4	Ch5	Ch6	Ch7	Ch8	Ch9	Ch 10	Ch 11	Ch 12
<i>U. virginis</i>	C3	1	0	0	–	–	0	1	0	0	0	0	1
<i>U. polyrhiza</i>	C4	1	1	1	1	2	0	1	1	0	0	0	0
<i>U. cinerascens</i>	C5	0	–	1	0	0	0	0	2	0	0	0	0
<i>U. laevis</i>		0	–	0	–	–	0	1	2	0	0	0	0
<i>U. lambii</i>		0	–	0	–	–	0	1	2	0	0	0	0
<i>U. leiocarpa</i>		0	–	1	0	0	0	1	2	0	0	0	1
<i>U. lyngei</i>		0	–	1	0	0	0	0	2	0	0	0	1
<i>U. microphylla</i>		0	–	0	–	–	0	1	2	0	0	0	0
<i>U. rigida</i>		0	–	0	–	–	0	1	2	0	0	0	1
<i>U. ruebeliana</i>		0	–	0	–	–	0	1	0	0	1	0	0
<i>U. subglabra</i>		0	–	1	0	0	0	0	2	0	0	0	0
<i>U. subglabra</i> var. <i>pallens</i>		0	–	0	–	–	0	1	2	0	0	0	0
<i>U. americana</i>	C6	1	0	1	1	2	0	0	0	0	0	0	0
<i>U. angulata</i>		1	0	0	–	–	0	1	0	0	0	1	0
<i>U. cinereorufescens</i>		1	1	1	1	2	0	0	0	0	1	1	0
<i>U. crustulosa</i> var. <i>badiofusca</i>		1	0	0	–	–	0	1	0	0	1	1	0
<i>U. crustulosa</i> -1		1	0	0	–	–	0	1	0	0	1	1	0
<i>U. crustulosa</i> -2		1	0	0	–	–	0	1	0	0	1	1	0
<i>U. freyi</i>		1	0	0	–	–	1	0	0	0	0	0	0
<i>U. grisea</i>		0	–	0	–	–	1	0	0	0	0	0	0
<i>U. hirsuta</i>		1	0	0	–	–	1	0	0	0	0	0	0
<i>U. josiae</i>		1	0	0	–	–	0	1	0	0	0	0	0
<i>U. loboperipherica</i>		1	0	0	–	–	1	0	0	0	0	–	0
<i>U. phaea</i>		0	–	0	–	–	0	1	0	0	0	0	0
<i>U. pulvinaria</i>		1	0	0	–	–	0	1	1	0	0	0	0
<i>U. semitensis</i>		1	0	0	–	–	0	1	0	0	1	1	0
<i>U. spodochoa</i> -1		1	0	0	–	–	0	1	0	0	1	1	0
<i>U. spodochoa</i> -2		1	0	0	–	–	0	1	0	0	1	1	0
<i>U. torrefacta</i>		1	0	0	–	–	0	1	0	0	0	0	1
<i>U. tylorhiza</i>		1	1	1	1	2	0	0	0	0	0	0	0
<i>U. vellea</i> -1		1	0&1	1	1	2	0	0	0	0	0	0	0
<i>U. vellea</i> -2		1	0&1	1	1	2	0	0*	–	–	–	–	0
<i>U. calvescens</i>	C6 (?)	1	0	0	–	–	0	1	0	0	0	0	0
<i>U. dichroa</i>		0	–	0	–	–	1	1	2	0	0	0	0
<i>U. haplocarpa</i>		1	0	0	–	–	0	1	2	0	0	0	0
<i>U. leprosa</i>		0	–	0	–	–	1	0	0	0	0	0	0
<i>U. nodulospora</i>		1	0	0	–	–	0	1	0	0	0	0	0

The classification of characters follows the scheme as given in Tables 2 and S2.

\* apothecia unknown

**Table S2.** Phylogenetic distinctness of traits. Phylogenetic distances ( $\Delta^+$ ) and variation in taxonomic distinctness ( $\lambda^+$ ) are indicated.

	Character state	Number of taxa	$\Delta^+$	$\lambda^+$
ALL		59	55.5	372.3
Ch 1: Rhiziomorph (or rhizine) presence	0	25	50.9	289.2
	1	34	50.2	513.0
Ch 2: Rhiziomorph (or rhizine) type	0	30	50.1	540.3
	1	6	36.2	373.4
	2	1	0	0
	3	1	0	0
Ch 3: Thalloconidia presence	0	37	55.5	331.7
	1	22	49.2	410.0
Ch 4: Thalloconidia origin	0	13	39.0	295.9
	1	9	50.3	502.4
Ch 5: Thalloconidia septation presence and type	0	9	37.2	261.3
	1	4	36.9	418.8
	2	9	50.3	502.4
Ch 6: Lichenized propagules presence	0	45	50.5	357.9
	1	14	49.2	551.2
Ch 7: Apothecia presence	0	21	57.5	446.0
	1	38	54.9	329.8
Ch 8: Apothecia morphology	0	42	53.6	434.4
	1	3	38.8	22.3
	2	13	39.4	325.9
Ch 9: Ascospore number per ascus	0	50	51.8	344.7
	1	8	24.7	55.8
Ch 10: Ascospore septation type	0	42	49.4	316.2
	1	7	28.4	174.6
	2	9	24.8	49.8
Ch 11: Ascospore size class	0	36	47.0	299.7
	1	12	55.8	625.1
	2	9	24.8	49.8
Ch 12: $\beta$ -orcinol depsidones presence	0	47	58.3	411.2
	1	12	36.3	250.0

The classification of characters follows the scheme as given in Table 2.



**Table S3.** Characteristics of subgenera in Umbilicariaceae.

	subg. <i>Actinogyra</i>	subg. <i>Agyrophora</i>	subg. <i>Floccularia</i>	subg. <i>Gyrophora</i>	subg. <i>Iwatakia</i>	subg. <i>Lasallia</i>	subg. <i>Umbilicaria</i>	subg. <i>Umbilicariopsis</i>
Type	<i>Umbilicaria muehlenbergii</i>	<i>Agyrophora atropuinososa</i>	<i>Umbilicaria deusta</i>	<i>Umbilicaria vellea</i>	<i>Umbilicaria esculenta</i>	<i>Lasallia pustulata</i>	<i>Umbilicaria hyperborea</i>	<i>Umbilicaria polyrhiza</i>
<b>Character</b>								
<i>Thalline morphology</i>								
thallus size	medium to large	small to medium	small to medium	medium to large	medium to large	medium to large	small to medium	medium to large
thallus structure	never pustulate	never pustulate	pustulate	never pustulate	never pustulate	pustulate	never pustulate	non-pustulate or pustulate
upper surface structure and colour	smooth, brownish	areolate, matt, gray	smooth, brownish-black	smooth to finely areolate, whitish to brownish	smooth to finely areolate, greyish to brownish	smooth to areolate or echinose, brown to grey	smooth to areolate with elevated pruinose or reticulately ridged center brown or grey to blackish	smooth, red-brown
lower surface structure	papillose, covered by lamellate-trabeculate network	smooth or areolate	smooth, lacunose	papillose or areolate; trabeculae going from the umbilicus often present	verrucose to areolate	papillose or areolate	smooth to areolate	areolate
rhizinomorphs or rhizines presence and type	absent	absent	absent	simple to branched and/or thalloconidial or absent	fasciculate or absent	absent except one species ( <i>U. caroliniana</i> ) with true rhisinae	simple to branched and/or thalloconidial or absent	richly branched to coralloid
lichenized propagula presence and type	absent, occasionally shizidia	absent	laminal isidia	thallyles, soredia, parasoredia, shizidia	schizidia	isidia, lobulae	absent (or marginal isidia)	absent
<i>Thalloconidia</i>								
thalloconidia presence	absent	present or absent	absent	present or absent	present or absent	absent	present or absent	present
thalloconidia origin and septation	–	thallobred non-septate	–	rhizinobred multicellular	rhizinobred multicellular	–	thallobred or thallobred and rhizinobred non-septate to oligoseptate, but <i>U. umbilicarioides</i> – multiseptate rhizinobred	rhizinobred multicellular

Table S3. Continued.

	subg. <i>Actinogyra</i>	subg. <i>Agyrophora</i>	subg. <i>Floccularia</i>	subg. <i>Gyrophora</i>	subg. <i>Iwatakia</i>	subg. <i>Lasallia</i>	subg. <i>Umbilicaria</i>	subg. <i>Umbilicariopsis</i>
<i>Apothecial morphology</i>								
Apothecial disc type	actinodisc	leiodisc, but <i>A. ruebeliana</i> – omphalodisc	gyrodisc	omphalodisc and gyrodisc (but <i>U. dichroa</i> and <i>U. haplocarpa</i> – leiodisc; <i>U. pulvinaria</i> – actinodisc)	gyrodisc	leiodisc (but <i>U. caroliniana</i> and <i>U. sinensis</i> – gyrodisc)	omphalodisc and gyrodisc (but <i>U. scholanderii</i> – leiodisc)	actinodisc
Apothecia attaching type	subimmersed	sessile to stipitate	sessile	subimmersed to sessile	subimmersed to sessile	sessile to stipitate	sessile to stipitate	apothecia adnate
Spore number	8	8	8	8	8	1, 2, 8	8	8
Spore septation and size	simple, small	simple (but <i>U. ruebeliana</i> – submuriform), small	simple, mean-size	simple small to submuriform, mean-size	simple, mean-size to small	eumuriform, large	simple to one-septate, small	simple, small
<i>Secondary metabolites</i>								
	orcinol depsides	orcinol depsides, sometimes also $\beta$ -orcinol depsidones	orcinol depsides	orcinol depsides, sometimes also $\beta$ -orcinol depsidones	orcinol depsides	orcinol depsides	orcinol depsides, sometimes also $\beta$ -orcinol depsidones	orcinol depsides
<hr/>								
<b>Distribution</b>	North American–Asian	mostly Holarctic with European and North American endemic elements	bipolar	mostly Holarctic with European, East Asian and South American endemic elements	mostly East Asian	mostly Holarctic with European, South African and East Asian endemic elements	bipolar or Holarctic with East Asian, New Zealand, South and North American and Antarctic endemic elements	Holarctic

**Table S4.** Correspondence of the phylogenetic tree topology of Umbilicariaceae to previous intrafamilial classifications.

Clades	Frey (1949) with modifications of <sup>1</sup> Imshaug (1957) or <sup>2</sup> Motyka (1964)	Llano (1950), modified by Wei & Jiang (1993)
Clade 1	<i>Lasallia</i> subg. <i>Lasallia</i> <i>Umbilicaria</i> subg. <i>Gyrophoropsis</i> p. pte	<i>Lasallia</i> subg. <i>Lasallia</i> <i>Umbilicaria</i> sect. <i>Gyrophoropsis</i> p. pte
Clade 2a	<i>Umbilicaria</i> Subg. <i>Umbilicaria</i> , sect. <i>Glabrae</i> p. pte Subg. <i>Umbilicaria</i> , sect. <i>Vellea</i> p. pte	<i>Umbilicaria</i> Subg. <i>Umbilicaria</i> , sect. <i>Umbilicaria</i> p. pte
Clade 2b	Subg. <i>Umbilicaria</i> , sect. <i>Vellea</i> p. pte	Subg. <i>Actinogyra</i> p. pte
Clade 2c	Subg. <i>Umbilicaria</i> , sect. <i>Glabrae</i> p. pte	Subg. <i>Umbilicaria</i> , sect. <i>Umbilicaria</i> p. pte
Clade 3	<i>Umbilicaria</i> Subg. <i>Umbilicaria</i> , sect. <i>Anthracinae</i> p. pte (= Subg. <i>Umbilicaria</i> , sect. <i>Decussatae</i> <sup>1</sup> ) Subg. <i>Umbilicaria</i> , sect. <i>Glabrae</i> p. pte Subg. <i>Polymorphae</i> (= subg. <i>Umbilicaria</i> <sup>2</sup> ) Subg. <i>Umbilicaria</i> , sect. <i>Vellea</i> p. pte	<i>Umbilicaria</i> Subg. <i>Omphalodiscus</i> , sect. <i>Omphalodiscus</i> Subg. <i>Umbilicaria</i> , sect. <i>Umbilicaria</i> p. pte
Clade 4	<i>Umbilicaria</i> Subg. <i>Umbilicaria</i> , sect. <i>Vellea</i> p. pte Subg. <i>Actinogyra</i> p. pte <sup>2</sup>	<i>Umbilicaria</i> Subg. <i>Actinogyra</i> p. pte
Clade 5	<i>Umbilicaria</i> Subg. <i>Umbilicaria</i> , sect. <i>Anthracinae</i> p. pte Subg. <i>Umbilicaria</i> , sect. <i>Anthracinae</i> <sup>1</sup> Subg. <i>Gyrophoropsis</i> p. pte	<i>Umbilicaria</i> Subg. <i>Agyrophora</i> Subg. <i>Omphalodiscus</i> sect. <i>Spodochroae</i> p. pte
Clade 6	<i>Umbilicaria</i> Subg. <i>Gyrophoropsis</i> p. pte Subg. <i>Umbilicaria</i> , sect. <i>Vellea</i> p. pte Subg. <i>Umbilicaria</i> , sect. <i>Glabrae</i> p. pte	<i>Umbilicaria</i> Subg. <i>Actinogyra</i> p. pte Subg. <i>Agyrophora</i> Subg. <i>Umbilicaria</i> sect. <i>Gyrophoropsis</i> p. pte Subg. <i>Omphalodiscus</i> sect. <i>Spodochroae</i> p. pte Subg. <i>Umbilicaria</i> sect. <i>Umbilicaria</i> p. pte

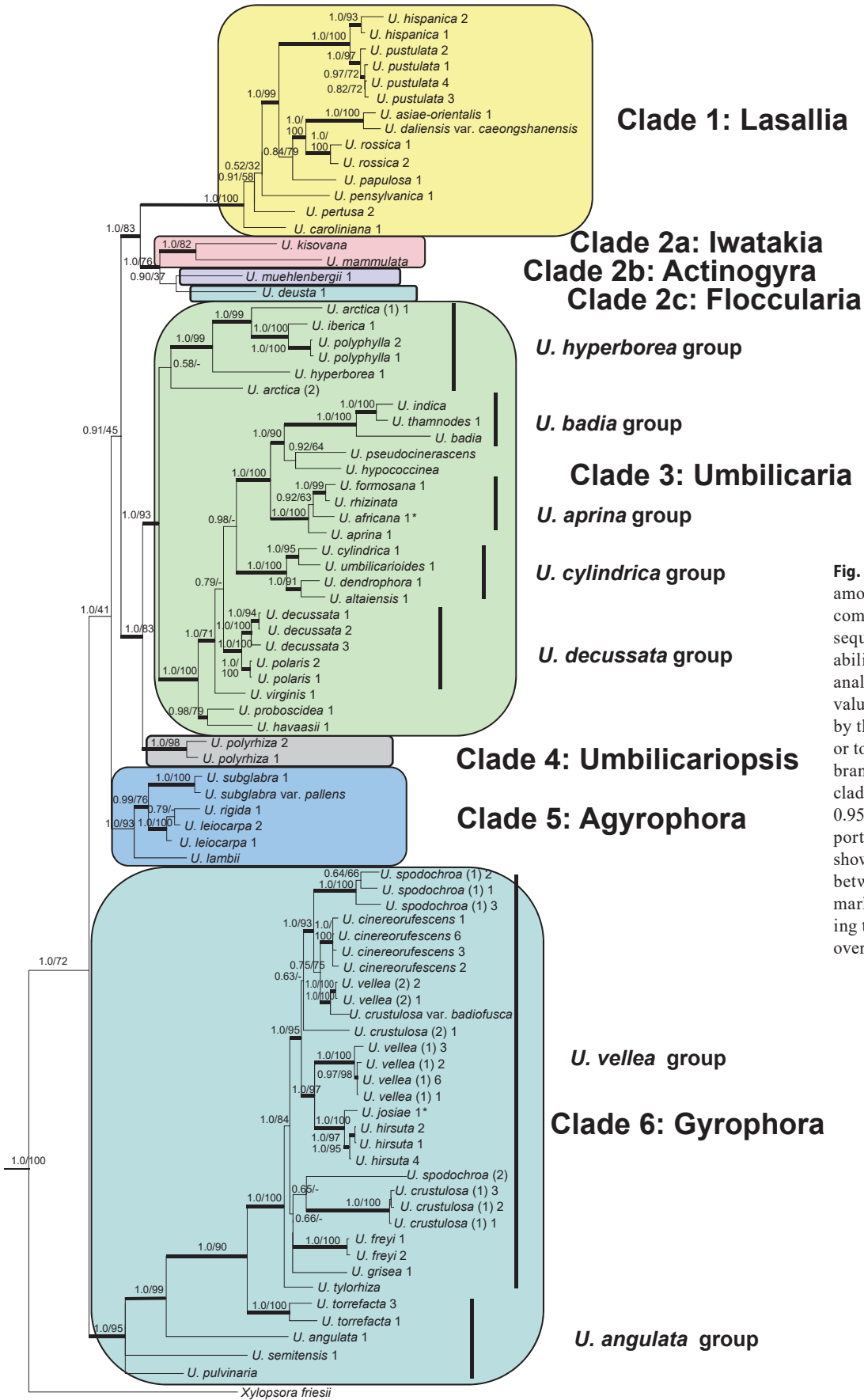
**Literature cited**

- Imshaug, H.A.** 1957. Alpine lichens of western United States and adjacent Canada. I. The Macrolichens. *Bryologist* 60: 177–272.  
<https://doi.org/10.2307/3240365>
- Motyka, J.** 1964. *Flora Polska*, vol. 3(2), *Porosty (Lichenes)*. Warsaw: Państwowe Wydawnictwo Naukowe.
- Wei, J.C. & Jiang, Y.M.** 1993. *The Asian Umbilicariaceae (Ascomycota)*. Mycosystema Monographicum Series, No. 1. Beijing: International Academic Publishers.



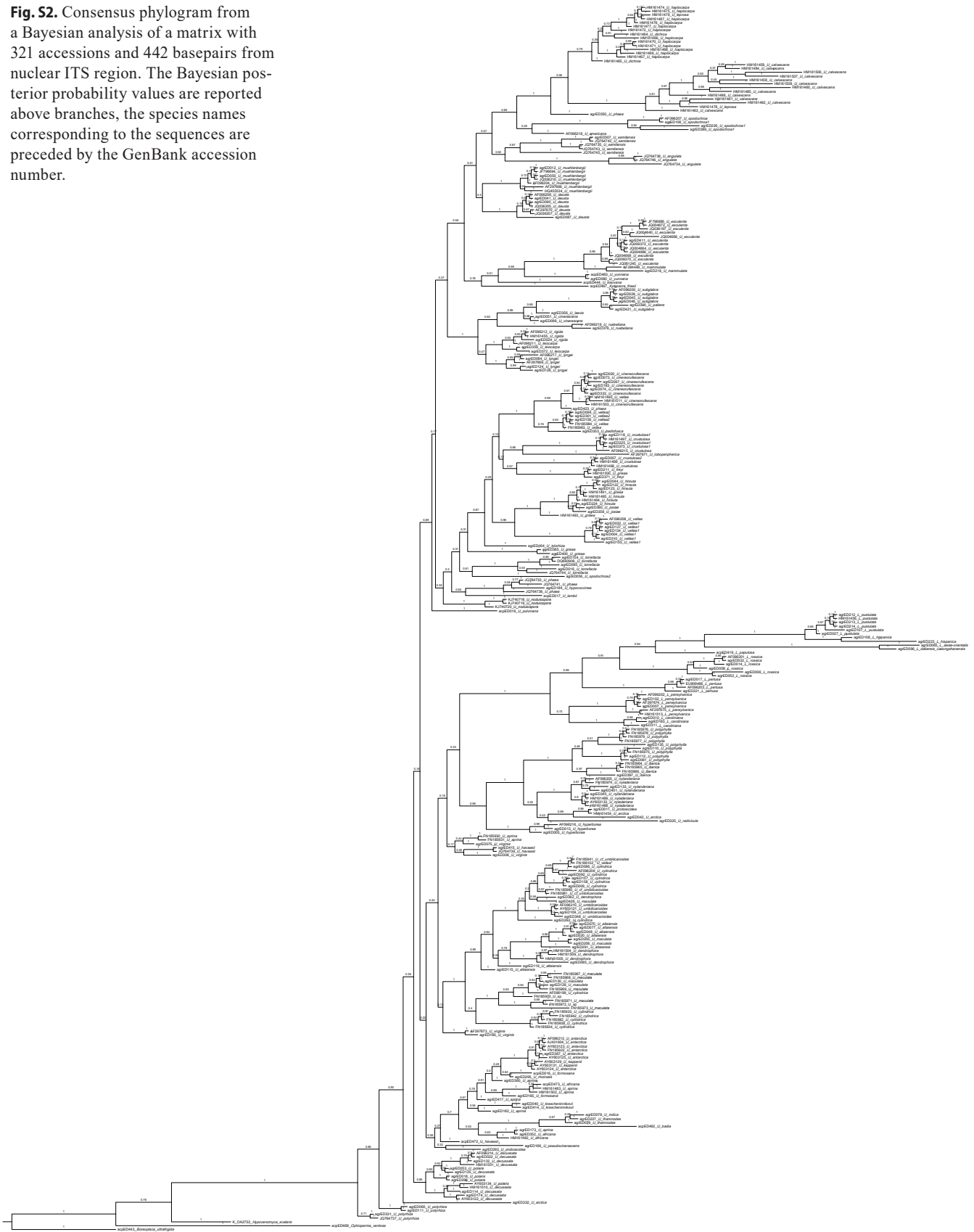
**Table S5.** Number of biosynthetic steps for secondary compounds synthesis from orcellinic acid.

Compound	Additional compound	Process	Resulting compound	Number of biosynthesis steps for synthesis from orcellinic acid
Orcellinic acid	Orcellinic a.	dehydration	Lecanoric a.	1
Lecanoric a.	Orcellinic a.	dehydration	Gyrophoric a.	2
Gyrophoric a.		methylation	Umbilicarinic a.	3
Gyrophoric a.		methylation	Ovoic a.	3
Gyrophoric a.		hydroxylation	Hiasic a.	3
Gyrophoric a.		5-hydroxylation, smiles rearrangement	Crustinic a.	4
Gyrophoric a.		3-hydroxylation, smiles rearrangement	Lasallic a.	4
Orcellinic a.		C-methylation	$\beta$ -Orcellinic a.	1
$\beta$ -Orcellinic a.		O-methylation	Methyl $\beta$ -Orcellinate	2
Methyl $\beta$ -Orcellinate	Methyl $\beta$ -Orcellinate	dehydration	Methyl 4-O-Demethylbarbatate	3
Methyl 4-O-Demethylbarbatate		oxidation	Atranorin	4
$\beta$ -Orcellinic a.	$\beta$ -Orcellinic a.	dehydration	4-O-demethylbarbatic	2
4-O-demethylbarbatic		oxidation	Hypoprotocetraric	3
Hypoprotocetraric		oxidation	Norstictic a.	4
Norstictic a.		O-methylation	Stictic a.	5



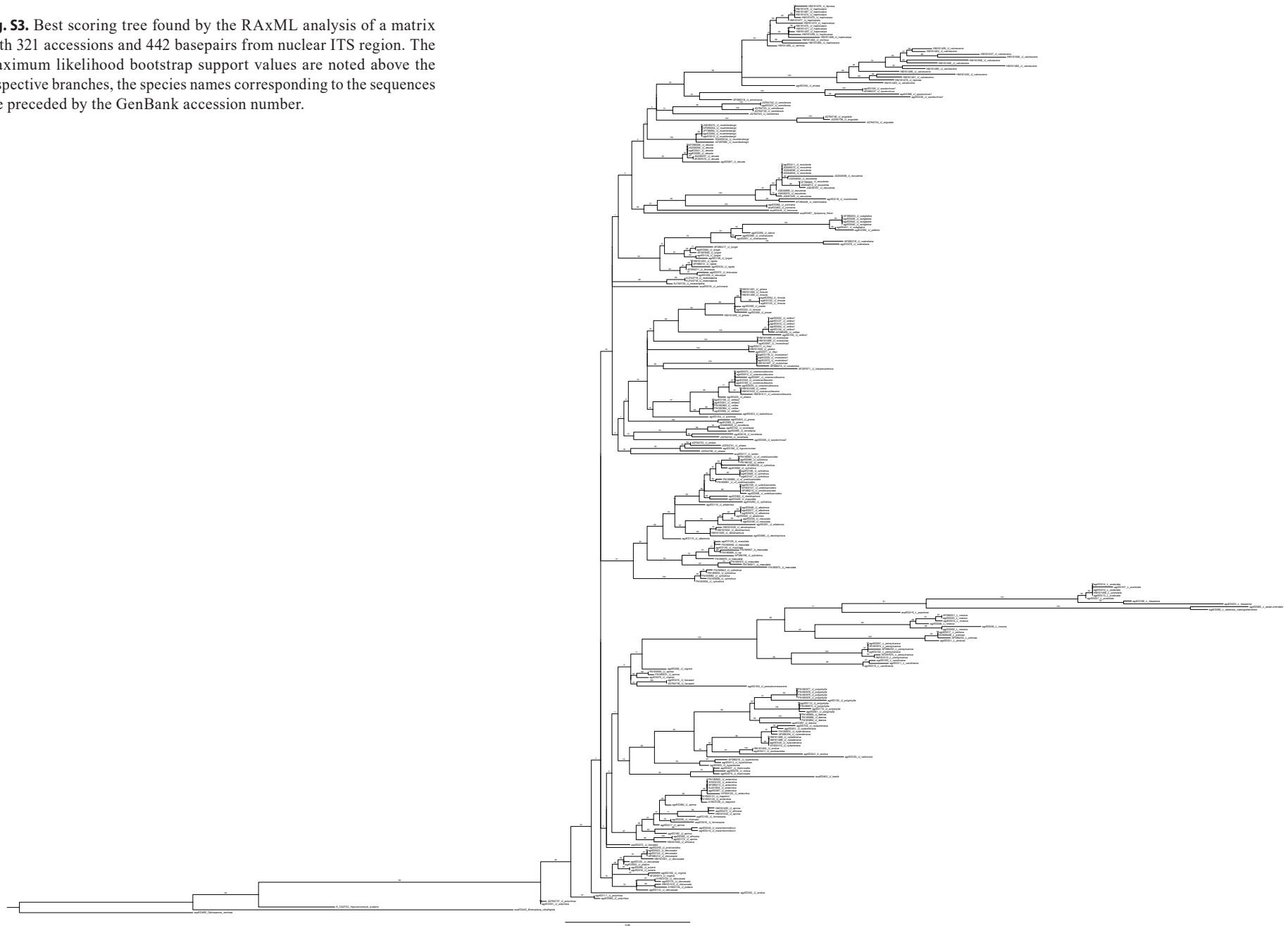
**Fig. S1.** Phylogenetic relationships among Umblicariaceae based on combined *RPB2*, ITS, and mtLSU sequence data. Posterior probabilities of MCMCMC Bayesian analysis and bootstrap support values of best scoring tree found by the RAxML are noted above or to the left of the respective branches; Lines in bold indicate clades with posterior probability 0.95 or higher and bootstrap support 70% or higher. Two species showing phylogenetic conflict between markers (Appendix 2) marked with asterisk; including those species had no impact overall tree topology.

**Fig. S2.** Consensus phylogram from a Bayesian analysis of a matrix with 321 accessions and 442 basepairs from nuclear ITS region. The Bayesian posterior probability values are reported above branches, the species names corresponding to the sequences are preceded by the GenBank accession number.



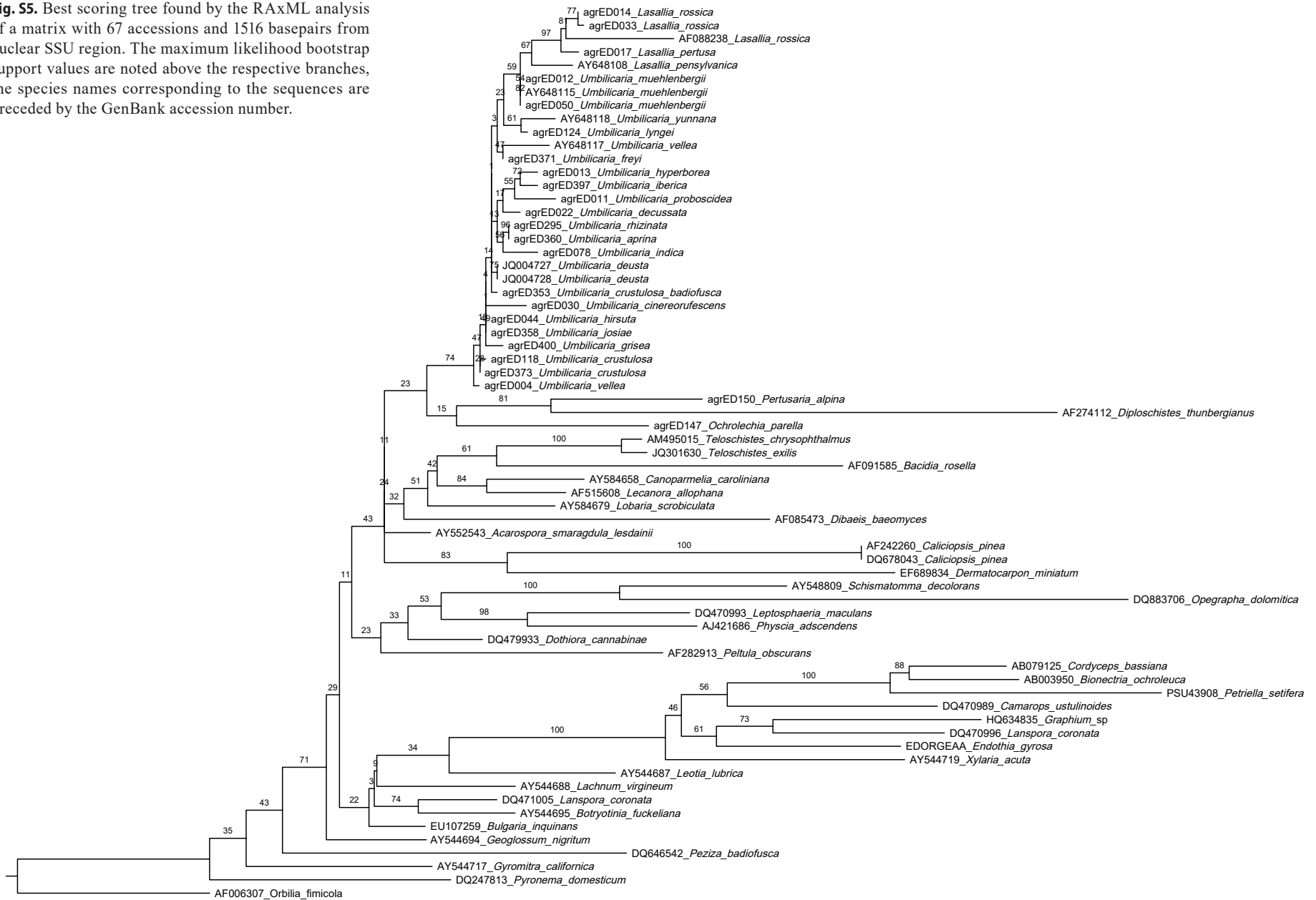


**Fig. S3.** Best scoring tree found by the RAxML analysis of a matrix with 321 accessions and 442 basepairs from nuclear ITS region. The maximum likelihood bootstrap support values are noted above the respective branches, the species names corresponding to the sequences are preceded by the GenBank accession number.



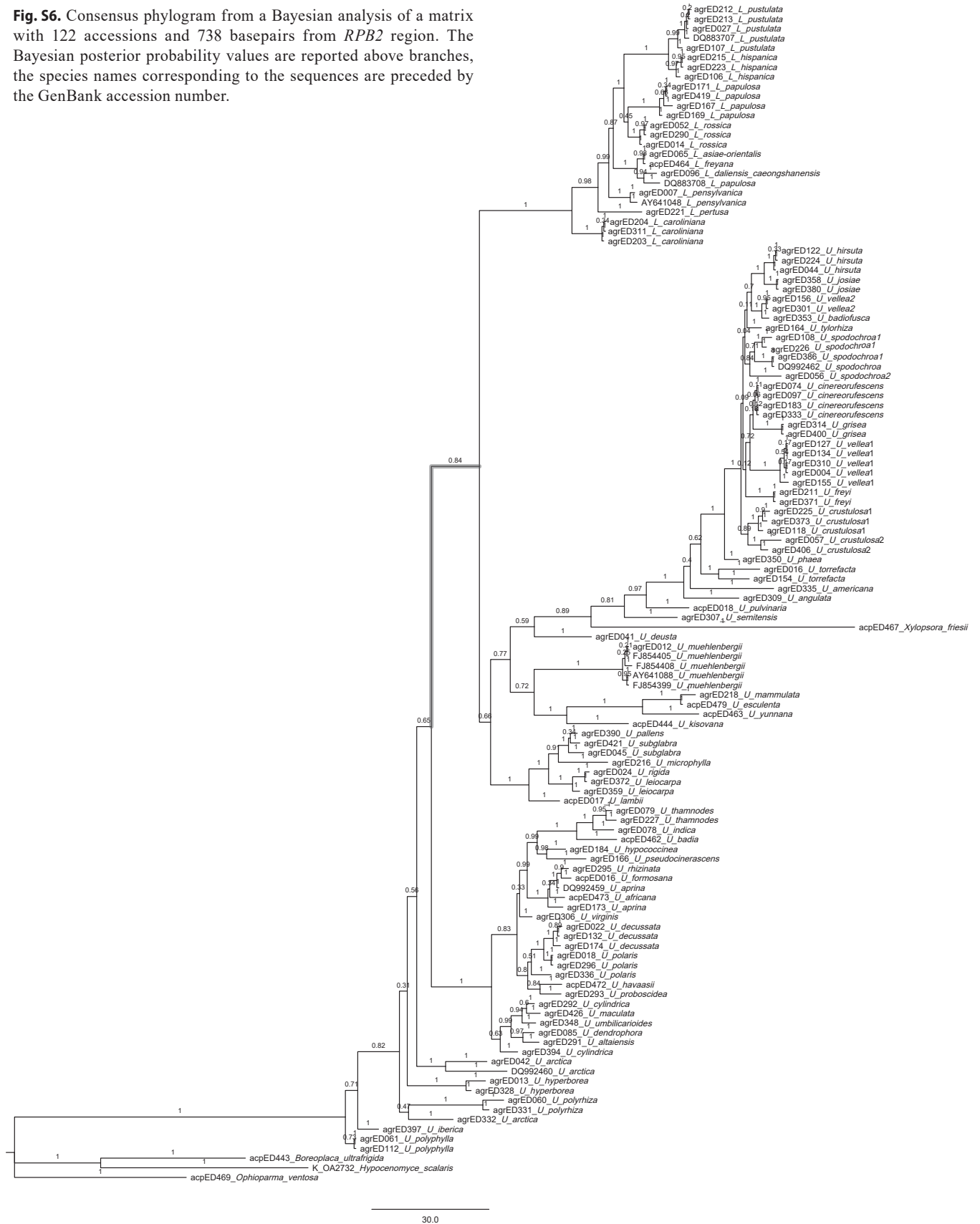


**Fig. S5.** Best scoring tree found by the RAxML analysis of a matrix with 67 accessions and 1516 basepairs from nuclear SSU region. The maximum likelihood bootstrap support values are noted above the respective branches, the species names corresponding to the sequences are preceded by the GenBank accession number.



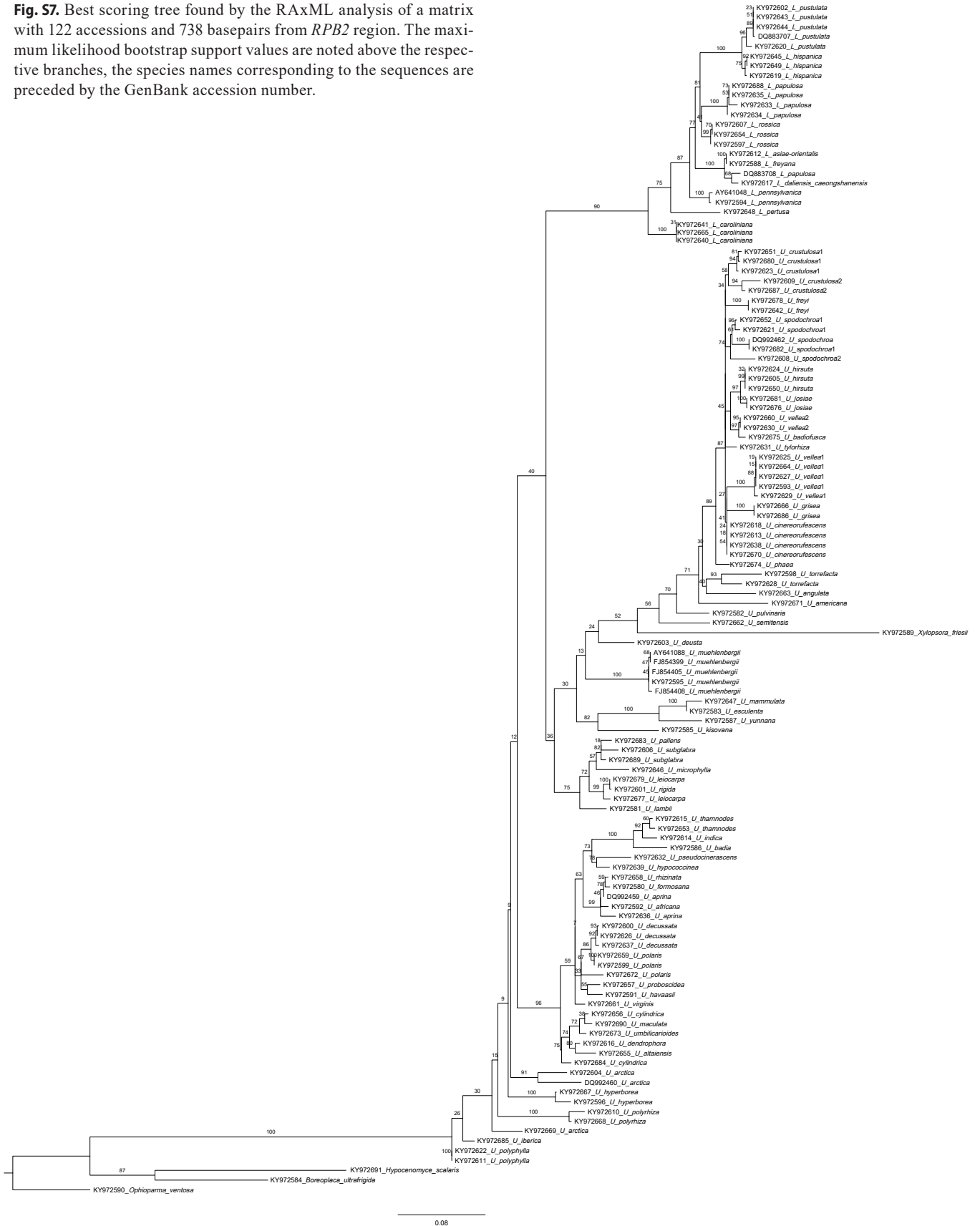
0.03

**Fig. S6.** Consensus phylogram from a Bayesian analysis of a matrix with 122 accessions and 738 basepairs from *RPB2* region. The Bayesian posterior probability values are reported above branches, the species names corresponding to the sequences are preceded by the GenBank accession number.

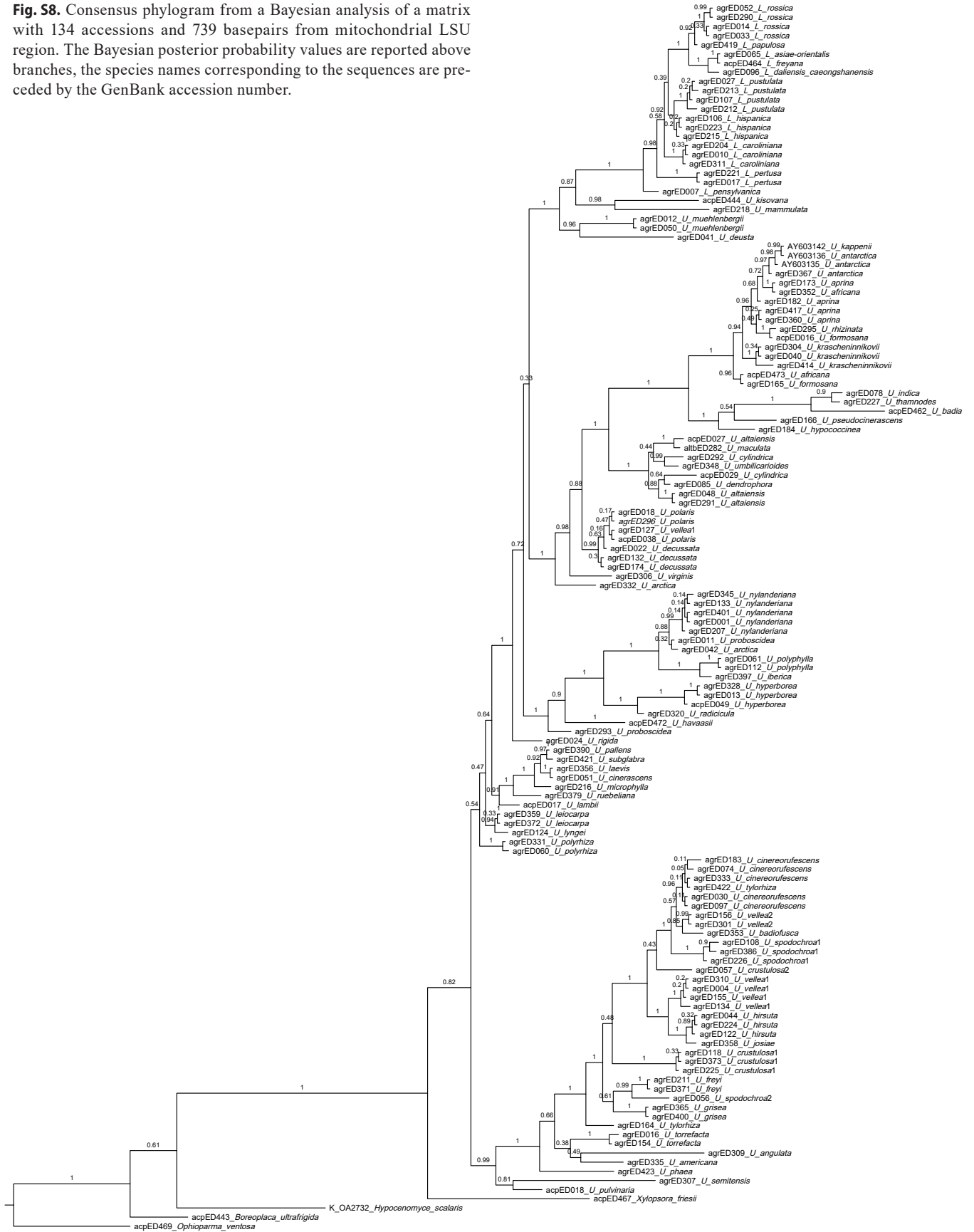




**Fig. S7.** Best scoring tree found by the RAXML analysis of a matrix with 122 accessions and 738 basepairs from *RPB2* region. The maximum likelihood bootstrap support values are noted above the respective branches, the species names corresponding to the sequences are preceded by the GenBank accession number.



**Fig. S8.** Consensus phylogram from a Bayesian analysis of a matrix with 134 accessions and 739 basepairs from mitochondrial LSU region. The Bayesian posterior probability values are reported above branches, the species names corresponding to the sequences are preceded by the GenBank accession number.



**Fig. S9.** Best scoring tree found by the RAXML analysis of a matrix with 134 accessions and 739 basepairs from mitochondrial LSU region. The maximum likelihood bootstrap support values are noted above the respective branches, the species names corresponding to the sequences are preceded by the GenBank accession number.

