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Frequent circumarctic and rare transequatorial dispersals in the lichenised agaric genus *Lichenomphalia* (Hygrophoraceae, Basidiomycota)

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4 1 Frequent circumarctic and rare transequatorial dispersals in the lichenised agaric genus
5 2 *Lichenomphalia* (Hygrophoraceae, Basidiomycota)

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30 27 **Summary**

31 28 Species of the genus *Lichenomphalia* are mostly restricted to arctic-alpine environments with the
32 29 exception of *L. umbellifera* which is also common in northern forests. Although *Lichenomphalia*
33 30 species inhabit vast regions in several continents, no information is available on their genetic
34 31 variation across geographic regions and the underlying population-phylogenetic patterns. We
35 32 collected samples from arctic and subarctic regions, as well as from newly discovered
36 33 subantarctic localities for the genus. Phylogenetic, nonparametric permutation methods and
37 34 coalescent analyses were used to assess phylogeny and population divergence and to estimate the
38 35 extent and direction of gene flow among distinct geographic populations. All known species
39 36 formed monophyletic groups, supporting their morphology-based delimitation. In addition, we
40 37 found two subantarctic phylogenetic species (*L. sp.* and *L. aff. umbellifera*), of which the latter
41 38 formed a well-supported sister group to *L. umbellifera*. We found no significant genetic
42 39 differentiation among conspecific North American and Eurasian populations in *Lichenomphalia*.
43 40 We detected high intercontinental gene flow within the northern polar region, suggesting rapid
44 41 (re)colonization of suitable habitats in response to climatic fluctuations and preventing
45 42 pronounced genetic differentiation. On the other hand, our phylogenetic analyses suggest that
46 43 dispersal between northern circumpolar and subantarctic areas likely happened very rarely and
47 44 led to the establishment and subsequent divergence of lineages. Due to limited sampling in the
48 45 Southern Hemisphere, it is currently uncertain whether the northern lineages occur in
49 46 Gondwanan regions. On the other hand, our results strongly suggest that the southern lineages do
50 47 not occur in the circumpolar north. Although rare transequatorial dispersal and subsequent
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4 1 isolation may explain the emergence of at least two subantarctic phylogenetic species lineages in
5 2 *Lichenomphalia*, more samples from the Southern Hemisphere are needed to better understand
6 3 the phylogeographic history of the genus.
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9 5 **Key Words:** Arctic, biodiversity, climate change, coalescent methods, fungi, migration,
10 6 phylogeography, subantarctic.
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1. INTRODUCTION

One of the key questions in fungal phylogeography and biodiversity studies is whether disjunct populations inhabiting different continents belong to the same species. Beside the possible theoretical advancement in our knowledge regarding long-distance dispersal, studying intercontinental gene flow has practical implications for understanding the composition of past, present, and future communities during shifts in species distributions due to climatic changes. The capacity of a certain taxon for transoceanic dispersal will obviously have a profound effect on its intercontinental population structure and the potential emergence of divergent lineages.

There is considerable disagreement in the scientific community concerning the ability of fungi to disperse over long distances and become established (Brown and Hovmöller 2002; Feuerer and Hawksworth 2007; Galloway and Aptroot 1995; Kärnefelt 1990; Moncalvo and Buchanan 2008; Moyersoen et al. 2003; Printzen 2008). In recent years, molecular tools have revealed several examples of distinct phylogeographic lineages or cryptic species within fungal species complexes that were previously treated as single morphological species. The majority of boreal, temperate or tropical fungi subjected to genetic studies show strong phylogeographical patterns and limited dispersal, and there is an increasing amount of geographical endemism being discovered (e.g. Bergemann et al. 2009; Geml et al. 2008; Taylor et al. 2006 and references therein). In most studied fungi, the observed phylogenetic structures likely have arisen as a result of the lack of intercontinental dispersal, because allopatric clades often inhabit similar environments on different continents (e.g., Geml et al. 2008; Shen et al. 2002; Taylor et al. 2006). Exceptions to this general trend mostly come from fungi associated with humans, which are, therefore, more likely to be dispersed via shipment of goods: e.g., plant pathogens of agricultural crops (e.g. Couch et al. 2005), indoor fungi (e.g. Kauserud et al. 2006); and fungi that are almost exclusively clonal and produce very high quantities of airborne mitospores (e.g. Rydholm et al. 2006).

Similar studies on high-latitude agarics are virtually non-existent. Apart from our recent study (Geml et al. 2011), we are not aware of any studies published on the phylogeography of arctic basidiomycetes, not to mention possible bipolar connections. This is unfortunate, because fungi play critical roles in the functioning of high-latitude ecosystems (Callaghan et al. 2004; Printzen 2008). Studying dispersal and migration in high-latitude fungi, i.e. the degree to which they are able to exchange genes with populations inhabiting different geographical regions and to colonize suitable habitats, is relevant not only for the theoretical advancement in our knowledge regarding the dispersal abilities and evolutionary dynamics of fungi, but has practical implications for climate change studies. Climate warming is expected to cause a pole-ward shift in the distribution of many high-latitude species, and the dispersal capability of individual species will greatly influence the composition of future polar communities (Alsos et al. 2007).

Lichenomphalia Redhead, Lutzoni, Moncalvo and Vilgalys is a basidiomycete genus with omphalinoid fruiting bodies. The genus contains eight lichenised taxa that form symbioses with the unicellular green algal photobiont *Coccomyxa* (Zoller and Lutzoni 2003). The genus has been shown to be monophyletic, with *L. umbellifera* as sister to the remaining *Lichenomphalia* species (Lutzoni 1997). Although more recent studies have questioned the monophyly of the genus (Lawrey et al. 2009), there is no unequivocal evidence pro or contra. *Lichenomphalia* species are generally restricted to arctic-alpine environments with the notable exception of *L. umbellifera*, which is also found in boreal and northern temperate rain forests and is considered to be the most broadly distributed and ecologically most plastic species in the genus (Kranner and Lutzoni 1999; Redhead et al. 2002). In this study, we sampled populations across the northern

1 circumpolar distribution of three species that are widespread in the arctic regions: *L. alpina*, *L.*
2 *hudsoniana*, and *L. umbellifera*. In addition, we also included samples from newly discovered
3 subantarctic populations on Campbell Island tentatively identified in the field as *L. sp.* and *L. aff.*
4 *umbellifera* based on morphological characteristics of the basidiomes. We examined genetic
5 diversity and phylogeographic structure in *Lichenomphalia* in an effort to answer the following
6 questions: 1) Is there phylogeographic structure in the Northern Hemisphere similar to the
7 continental endemism seen in most temperate and boreal agaric species; 2) Is the
8 phylogeographic history of northern and southern lineages different from bipolar patterns seen in
9 other fungi?

10 2. MATERIALS AND METHODS

11 2.1 Materials and molecular work

12 Specimens were collected in various locations in Europe, Asia, North America, and one
13 subantarctic island of New Zealand, or were obtained through herbarium loans (Table 1). DNA
14 was extracted from small samples of dried specimens using the DNeasy[®] Plant Mini Kit
15 (QIAGEN, Inc., Valencia, CA, U.S.A.). Sequences of the nuclear internal transcribed spacer
16 (ITS1+5.8S+ITS2) and the large subunit (LSU) region of the ribosomal DNA repeat were
17 generated, supplemented by translation elongation factor 1-alpha gene (EF1) sequences for a
18 subset of the *L. umbellifera* specimens. The primers and PCR and sequencing protocols have
19 been described previously (Geml et al. 2005; Geml et al. 2006). Sequences were deposited in
20 GenBank (Table 1). Available homologous *Lichenomphalia* sequences were downloaded from
21 GenBank and included in the analyses. DNA sequences were analysed for 80 *Lichenomphalia*
22 samples: *L. umbellifera* (n=49), *L. alpina* (n=7), *L. hudsoniana* (n=15), *L. grisella* (n=1), *L.*
23 *lobata* (n=2), *L. velutina* (n=1), and the subantarctic *L. sp.* (n=2) and *L. aff. umbellifera* (n=3).

24 2.2 Phylogenetic analysis

25 Sequence data obtained for both strands of each locus were edited and assembled for each
26 isolate using Aligner v. 1.3.4 (CodonCode Inc., Dedham, MA, U.S.A.) or Sequencher 4.5
27 (GeneCodes, Ann Arbor, MI, U.S.A.). We constructed two multiple sequence alignments using
28 MUSCLE (Edgar 2004) that were subsequently corrected manually. The first was a genus-wide
29 ITS and LSU alignment, while the second included ITS, LSU, and EF1 sequences of the *L.*
30 *umbellifera* complex (*L. umbellifera* and *L. aff. umbellifera*). We recognized genetically isolated
31 groups on the basis of concordance of multiple gene genealogies, applying phylogenetic species
32 recognition as outlined in Taylor et al. (2000). To determine if DNA sequence data from
33 different loci were phylogenetically congruent, we conducted a maximum likelihood (ML)
34 bootstrap analysis on each locus separately using PAUP* 4b10 (Swofford 2002). Topological
35 conflict was recognized as significant when members of a monophyletic group received
36 bootstrap values $\geq 70\%$ based on one locus and were shown to be significantly not monophyletic
37 with data from a different locus (Mason-Gamer and Kellogg 1996). Because we did not detect
38 significant conflicts among loci, we carried out heuristic searches on the combined datasets
39 under the maximum likelihood criterion, using PAUP*. For each dataset, the best-fit
40 evolutionary model was determined by comparing different evolutionary models with varying
41 values of base frequencies, substitution types, alpha-parameter of the gamma-distribution of
42 variable sites, and proportion of invariable sites via the Akaike information criterion (AIC) using
43 PAUP* and Modeltest 3.7 (Posada and Crandall 1998). Trees including multiple *Lichenomphalia*

1 species were rooted using *Arrhenia* species based on Lutzoni (1997). Phylogenetic analyses
2 restricted to the *L. umbellifera* complex were mid-point rooted. The bootstrap tests (Felsenstein
3 1985) were used with 1000 replicates, with “fast” stepwise-addition. The High Performance
4 Computing cluster maintained by the University of Alaska Fairbanks Life Sciences Informatics
5 Core (<http://biotech.inbre.alaska.edu/>) was used to run MUSCLE and PAUP*.

6 7 2.3 Coalescent analyses

8 We detected no or very little intraspecific variation in *L. alpina* s.str. (i.e., from the
9 Arctic) and *L. hudsoniana*, for which only 1 and 2 ITS sequence types were detected,
10 respectively. Therefore, coalescent analyses were carried out only for the northern circumpolar
11 *L. umbellifera*. Identical ITS sequences were collapsed into haplotypes, with retaining
12 information on their observed frequencies in the populations, using SNAP Map (Aylor et al.
13 2006) after excluding insertion or deletions (indels) and infinite-sites violations. Though well
14 represented across our samples, we did not use LSU data due to much lower levels of sequence
15 variation relative to ITS. The analyses presented here assume an infinite sites model, under
16 which a polymorphic site is caused by exactly one mutation and there can be no more than two
17 segregating bases. Base substitutions were categorized as phylogenetically informative or
18 uninformative, and as transitions or transversions. Site compatibility matrices were generated
19 from each haplotype dataset using SNAP Clade and Matrix (Bowden et al. 2008; Markwordt et
20 al. 2003) and no incompatibility was detected among all variable sites. Genetic differentiation
21 among geographical populations was analysed using SNAP Map, Seqtomatrix and Permtest
22 (Hudson et al. 1992) implemented in SNAP Workbench (Price and Carbone 2005). Permtest is a
23 nonparametric permutation method based on Monte Carlo simulations that estimates Hudson’s
24 test statistics (K_{ST} , K_S , and K_T) under the null hypothesis of no genetic differentiation. K_{ST} is
25 equal to $1 - K_S/K_T$, where K_S is a weighted mean of K_1 and K_2 (mean number of differences
26 between sequences in subpopulations 1 and 2, respectively) and K_T represents the mean number
27 of differences between two sequences regardless of the subpopulation to which they belong. The
28 null hypothesis of no genetic differentiation is rejected ($P < 0.05$) when K_S is small and K_{ST} is
29 close to 1. For these tests, specimens were assigned to groups depending on the geographical
30 scale of the research question. For estimating intercontinental gene flow in the Northern
31 Hemisphere, we assigned groups according to continents (North America or Eurasia, excluding
32 southern specimens), while, to estimate the level of genetic differentiation between arctic and
33 subantarctic populations, sequences were grouped according to the hemispheres of origin.

34 Subsequently, coalescent methods were used to determine whether there was any
35 evidence of transoceanic migration between pairs of populations inhabiting different continents.
36 Because the permutation tests indicated significant geographic structure and the phylogenetic
37 analyses indicated reciprocal monophyly for the northern and southern lineages, both of which
38 imply no current gene flow, we conducted coalescent analyses only for the arctic and boreal
39 populations to estimate migration between North America and Eurasia. We used MDIV (Nielsen
40 and Wakeley 2001), implemented in SNAP Workbench (Price and Carbone 2005), employing
41 both likelihood and Bayesian methods using Markov chain Monte Carlo (MCMC) coalescent
42 simulations to determine if the diversity patterns in different geographic areas were the result of
43 retention of ancestral polymorphism or recent gene flow. We estimated the migration parameter
44 (M), and the divergence time (T). M is defined as the effective number of migrants exchanged
45 between two populations each generation and it equals $2 \times$ the net effective population size (N_e)
46 multiplied by m (migration rate), while T is measured in coalescent units of $2N_e$ generations.

1 Data were simulated assuming an infinite sites model with uniform prior. We used 2,000,000
2 iterations in the chain for estimating the posterior probability distribution and an initial 500,000
3 iterations to ensure that sufficient genealogies were simulated before approximating the posterior
4 distribution. Subsequently, we reconstructed the genealogy with the highest root probability, the
5 ages of mutations, and the time to the most recent common ancestor of the sample using
6 coalescent simulations in Genetree v. 9.0 (Griffiths and Tavaré 1994).

8 3. RESULTS

10 3.1 Phylogenetic analyses

11 The combined ITS and LSU dataset consisted of 1566 characters, including gaps. There
12 were 614 variable sites, of which 502 were parsimony-informative. The General-Time-
13 Reversible model, with calculated proportion of invariable sites ($I=0.233$) and estimated alpha-
14 parameter ($=0.4806$) of gamma-distribution (GTR+I+G), was selected as the best-fit
15 evolutionary model. The phylogram with the highest likelihood value ($-\ln L=7076.8495$) is
16 shown in Fig. 1A. All sampled known species formed distinct, well-supported monophyletic
17 groups. In northern species, where samples were available from multiple geographic areas, we
18 did not find any genetic partitioning corresponding to the geographic origin of the samples. In
19 addition, the subantarctic samples grouped in two distinct phylogenetic species. One of these (*L.*
20 *sp.*) was quite different from any other species, while the other (*L. aff. umbellifera*) formed a
21 well-supported sister group to *L. umbellifera*.

22 In the *L. umbellifera* complex, the ITS, LSU, EF1, and the combined datasets consisted of
23 616, 610, 563, and 1789 characters, respectively, including gaps. The General-Time-Reversible
24 model, without calculated proportion of invariable sites and estimated alpha-parameter (GTR),
25 was selected as the best-fit evolutionary model. There were 74, 13, 64, and 151 variable
26 positions, respectively. The phylogram with the highest likelihood value ($-\ln L=3387.6449$) is
27 shown in Fig. 1B. All three genes supported the existence of two phylogenetic species lineages
28 corresponding to populations in the Northern and Southern Hemispheres: *L. umbellifera* and *L.*
29 *aff. umbellifera*, respectively. Apart from the clades resulting from the bipolar genetic
30 differentiation, there were no other well-supported clades.

32 3.2 Coalescent analyses

33 Estimates of Hudson's test statistics (K_{ST} , K_S , and K_T) using nonparametric permutation
34 method indicated no significant genetic differentiation among North American and Eurasian
35 populations of *L. umbellifera*. The genetic differences within and between continents were
36 $K_S=3.076$, $K_T=3.053$, resulting in $K_{ST}=-0.008$, $P=0.726$. In contrast, we detected strong genetic
37 structure among northern and subantarctic populations, where the values were $K_S=3.007$,
38 $K_T=7.873$, $K_{ST}=0.618$, $P<0.001$. After removing indels and infinite-sites violations from the
39 original ITS datasets, there were 21 ITS haplotypes in northern populations of *L. umbellifera*
40 (Table 2). MDIV showed evidence for high gene flow between North American and Eurasian
41 populations (Fig. 2) and estimated no population divergence (T not significantly different from
42 0). In simulations using Genetree, we assumed a moderately high level of migration ($M=0.1$)
43 among northern populations. As expected, the coalescent-based genealogy did not show any
44 historical population division in the Northern Hemisphere and was informative with respect to
45 inferring the mutational history and variation between and within geographical regions (Fig. 3).

4. DISCUSSION

Biogeographers have long been fascinated by species that have disjunct distributions, among which bipolar species or species pairs have received particular attention (e.g., Darwin 1859; Du Rietz 1940; Galloway and Aptroot 1995 and the references therein). Long-distance dispersal in cryptogams has remained controversial, particularly regarding the ability of cold-climate species to cross the tropical belt (Galloway and Aptroot 1995; Van Zanten and Pócs 1981). Based on our results, the phylogeographic structure of *Lichenomphalia* appears to have been shaped by extensive dispersals within one hemisphere combined with rare transequatorial dispersals that is different previously observed patterns in other fungi. On one hand, we observed a high level of intercontinental gene flow in the Northern Hemisphere, which is markedly different from the general patterns observed for boreal and temperate agarics, for which the lack of intercontinental gene flow generally results in the divergence of often morphologically cryptic species pairs on different continents. On the other hand, on the global scale, despite our limited sampling from the Southern Hemisphere, we did observe some geographic endemism, primarily at the hemispheric level. This, in turn, differs from patterns reported for other bipolar genera, predominantly ascolichens (e.g., Myllys et al. 2003; Seymour et al. 2007; Thell et al. 2002), where such bipolar genetic divergence has not been reported.

Intercontinental gene flow in Northern Hemisphere

The phylogeographic structure of arctic *Lichenomphalia* seems very different from mid-latitude agarics, as a pattern of multiple phylogenetic lineages with non-overlapping geographic distributions was not observed in the Northern Hemisphere. Instead, arctic populations of *Lichenomphalia* species for which we had samples from distant geographical regions were not genetically distinct. Of course, we acknowledge that three loci are insufficient to rule out significant genetic structure in other areas of the genome. Previously, Redhead and Kuyper (1987) had noted that *L. hudsoniana* (cited as *Botrydina viridis*) predominantly produced yellowish basidiomes in western North America, more orangish pilei in eastern North America, and only in Europe sometimes had lilac tints on their stipes. Nevertheless, the phylogeographic differentiation reported for mid-latitude agarics has also been based upon a limited number of loci, sometimes only on ITS. Our results suggest that, in response to climatic fluctuations, *L. umbellifera* has been able to migrate over considerable distances due to effective dispersal. The considerable genetic diversity observed in the Arctic indicates long-term survival at northern high latitudes, and that large and diverse populations have served as sources for migrants. The estimated migration rates and the absence of geographical population structure suggest continuing gene flow between northern continents that has prevented pronounced genetic differentiation. This was also supported by the lack of polymorphism in *L. alpina* and *L. hudsoniana* among all sampled populations, despite the highly elevated nucleotide substitution rate in the genus in general (Lutzoni and Pagel 1997). Similar patterns of circumpolar genetic diversity have recently been detected in arctic ectomycorrhizal fungi (Geml et al. 2011) and some other arctic organisms, for example in highly mobile animals such as the arctic fox, *Alopex lagopus* (Dalén et al. 2005) and the snowy owl, *Bubo scandiacus* (Marthinsen et al. 2008), and in the arctic-alpine lineage of the bog blueberry *Vaccinium uliginosum* (Alsos et al. 2005), as well as in the arctic-alpine lichens *Flavocetraria cucullata* and *F. nivalis* (Geml et al. 2010).

The lichenised nature may make *Lichenomphalia* particularly suitable for intercontinental dispersal. The small globules of the crustose thallus detach easily and can act as vegetative propagules (Kranner and Lutzoni 1999), allowing vertical transmission of the alga from

1 generation to generation and providing more autonomy than basidiospores. Moreover,
2 *Lichenomphalia* taxa often colonize disturbed soils that are likely to be exposed above snow
3 level and subjected to strong winter winds. For example, *L. umbellifera* is often found on top of
4 cryogenic earth hummocks and is particularly abundant when the soil of the hummocks has been
5 exposed due to erosion or other perturbations. Finally, most mushrooms have mycelia that grow
6 within the substrate and reproduce mostly via spores produced by ephemeral fruiting bodies,
7 whereas the mycelium of these lichen-forming fungi occurs above ground, forming a symbiotic
8 thallus to allow photosynthesis by the algal partner. These symbiotic crustose-globular thalli are
9 also long-lived, offering year-round dispersal opportunities of the fungal and algal partners. The
10 thalli are also pre-adapted to tolerate desiccation and exposure to UV light (Kranner and Lutzoni
11 1999; Zoller and Lutzoni 2003) which would benefit high altitude aerial dispersal, while pre-
12 adaptation to freezing would facilitate winter dispersal at the ground level (Savile 1972).

13 Besides the dispersal of thallus fragments, dispersal of basidiospores probably is
14 important, as expected for many fungi. However, the symbiotic nature of *Lichenomphalia* means
15 that after dispersal of its basidiospores, the fungus and the photobiont have to re-establish the
16 lichenized state, a slow and complex process (Zoller and Lutzoni 2003). Wind dispersal of spores
17 and thallus fragments should be particularly effective in the Arctic as a result of open landscapes,
18 strong winds, and extensive snow and ice cover, as has also been suggested for arctic fungi,
19 plants and lichenized ascomycetes (Alsos et al. 2007; Geml et al. 2010; Geml et al. 2011; Savile
20 1962, 1972, 1982). In this regard, sea ice may be of particular importance for intercontinental
21 dispersal, as it provides a frozen surface bridging the continents and archipelagos. Besides wind,
22 other possible means of dispersal include spores and thallus fragments being carried by
23 migratory animals, driftwood, and drifting sea ice. Despite the very low number of
24 phylogeographic studies on arctic fungi, the gradually emerging picture indicates that arctic
25 fungi may differ substantially from their low- and mid-latitude relatives regarding the extent of
26 intercontinental migration, which has important implications for studies on the biodiversity,
27 ecology and conservation of arctic fungi in general.

28 29 *Northern vs. southern lineages*

30 Among fungi, many biogeographic studies comparing populations in the Northern vs.
31 Southern Hemispheres have focused on bipolar ascolichens that form a ubiquitous component of
32 high-latitude vegetation. In general, bipolar lichen species tend to be circumpolar in the north
33 and only known from scattered localities in the Southern Hemisphere, although there are
34 exceptions (Printzen 2008). The unequal distributions of landmasses and sampling efforts are
35 likely to have contributed to this pattern.

36 In contrast to the high intercontinental gene flow observed in northern high latitudes, we
37 found no phylogenetic species shared between the polar regions. Our phylogenetic analyses
38 indicate pronounced genetic divergence between the sampled northern and southern lineages.
39 Due to limited sampling in the Southern Hemisphere, it is currently uncertain whether the
40 northern lineages occur in Gondwanan regions. On the other hand, our results strongly suggest
41 that the southern lineages do not occur in the circumpolar north. The genealogical concordance
42 suggests that the diverging arctic and subantarctic sister lineages (e.g., *L. umbellifera* vs. *L. aff.*
43 *umbellifera*) have or are still undergoing phylogenetic speciation. This pronounced genetic
44 differentiation between the polar regions is different from patterns seen in bipolar species of
45 fungi for which comparable data have been obtained. Despite their moderate to high intraspecific
46 nucleotide diversity, these latter species generally exhibit no genetic differentiation between

1 southern and northern populations that are thought to have originated from very recent dispersal
2 between the polar regions (Geml et al. 2010; Myllys et al. 2003; Seymour et al. 2007; Thell et al.
3 2002). In the majority of these studies, southward colonisations were inferred based on
4 phylogeographic structure and comparisons of genetic diversity, with the exception of the lichen
5 *Usnea sphacelata* (Seymour et al. 2007). Although our data are compatible with the hypothesis
6 of colonisation of the Southern Hemisphere from northern populations in *Lichenomphalia*, more
7 data from southern populations are needed to test this hypothesis. The molecularly sampled
8 southern lineages are currently only represented by two species from one subantarctic island. It
9 is, therefore, possible that these lineages are distributed over a larger area in the Southern
10 Hemisphere and that they may have colonized southern islands from southern mid-latitude
11 mainland areas or *vice versa*. Strong wind currents over the southern oceans have been
12 repeatedly shown to play a major role in the long-distance dispersal of fungi and other
13 cryptogams (e.g. Brown and Hovmøller 2002; Moncalvo and Buchanan 2008; Moyersoen et al.
14 2003) and migrating birds are suspected of transporting organisms as well (Savile 1972).
15 Similarly, in another agaric, *Galerina patagonica*, specimens from Campbell Island and South
16 America had identical ITS sequences, suggesting very recent transoceanic dispersal (Taylor,
17 Laursen and Horak unpubl. data).

18 Estimating divergence time is difficult in fungi because of the scarcity of fossils suitable
19 for calibration and because of the substantial nucleotide substitution rate heterogeneity across
20 lineages (Berbee and Taylor 2001; Taylor and Berbee 2006). Extrapolating from divergence time
21 estimates published for other groups is particularly difficult in *Lichenomphalia*, because the
22 genus has been shown to have significantly higher mutation rates than closely related, non-
23 lichenised genera, possibly associated with the transition from free-living to mutualist lifestyle
24 requiring exposure of the mycelium to ultraviolet light (Lutzoni and Pagel 1997; Zoller and
25 Lutzoni 2003). Therefore, we cannot estimate the divergence times between the northern and
26 southern phylogenetic species lineages with high confidence. On the other hand, our current
27 knowledge is sufficient to distinguish between alternative scenarios that have been represented
28 by two major schools of thought regarding the distribution of bipolar taxa. The first explains
29 bipolar distribution with migration across the tropics either by “mountain-hopping” during
30 glacial periods (Darwin 1859; Kristiansen and Vigna 1996) or via recent long-distance dispersal,
31 presumably by migrating animals or air currents (Galloway and Aptroot 1995). According to the
32 second, presently disjunct populations are thought to be the remnants of formerly continuous
33 populations that were broken up by vicariance events mainly as a result of continental drift
34 and/or climatic changes (e.g., Du Rietz 1940; Kärnefelt 1990; Thomson 1995). Proponents of
35 this latter view have claimed that many bipolar species are old and probably originated in the
36 early Cenozoic (Kärnefelt 1990; Thomson 1995).

37 Based on our results, it is very likely that the northern and southern lineages diverged
38 relatively recently and cannot represent the remnants of formerly continuous populations that
39 were broken up by vicariance events in the early Cenozoic. A much more plausible explanation
40 is migration across the tropics either by “mountain-hopping” and/or via direct long-distance
41 dispersal, although additional samples from the southern continents, especially from South
42 America, are needed to test this hypothesis. Anecdotal evidence for taxa morphologically similar
43 to *L. umbellifera* and *L. alpina* in Colombia and Venezuela (Jesús Hernández, pers. comm.)
44 supports this argument. On the other hand, *L. aurantiaca*, a taxon morphologically similar to *L.*
45 *alpina*, was described from Colombia (Singer 1970; Redhead and Kuyper 1987) and it is,
46 therefore, possible that the name *L. alpina* is misapplied for South American collections. The

possible presence of *L. umbellifera* in Gondwanan regions is similarly uncertain, because a morphologically similar taxon, *L. chromacea*, is a Southern Hemisphere species known from Southeast and Southwest Australia (Anonymous 2011a; Cleland 1924; Fuhrer 1985, 2005; Grey and Grey 2001; Grgurinovic 1997; May and Wood 1997; Redhead and Kuyper 1987, 1988) and this taxon may or may not be conspecific with the South American specimens labelled as *L. umbellifera*. However, another undoubted Australian *Lichenomphalia* identified as “*Omphalina ericetorum*” is illustrated and differentiated from *L. chromacea* in the books by Fuhrer (1985, 2005). Additionally, there are many scattered records of various synonyms of *L. umbellifera* from Australia (May and Wood 1997), some doubtful records from New Zealand (Horak 1971), voucher specimens of taxa under the names *L. alpina* and *L. umbellifera* from New Zealand’s main islands (Anonymous 2011b), records of “*Omphalia umbellifera*” from New Zealand’s subantarctic islands (Chilton 1909; Horak 1982), including South Georgia (Pegler, Spooner and Smith 1981; Horak 1982; Redhead 1989). Therefore, southern reports of *L. alpina* and *L. umbellifera* are suspect until verified via molecular and thallar comparisons. Similarly, at least some of the records by Grgurinovic (1997) are suspect because she reports the presence of clamp connections. Clamp connections are absent in previously documented *Lichenomphalia* including specimens of *L. chromacea* examined by Redhead (in Redhead and Kuyper 1987, 1988). If present it would be novel. However, at least one other southern *Lichenomphalia* is definitely known from Tierra del Fuego, Argentina, under the name *Omphalina defibulata* Singer (Horak 1979; Singer 1952; Redhead et al. 2002). Redhead (in Redhead et al. 2002) examined an isotype and confirmed it was a *Lichenomphalia* and placed it in the *L. grisella-velutina* complex characterized by narrow thallar hyphae. Molecular data from this lineage from the south is not available. The only other reports of *Lichenomphalia* from South America are of *L. lobata* from Colombia and Ecuador (Singer 1970 [as *Gerronema hudsonianum*]; Redhead and Kuyper 1987; Palice et al. 2005). Two samples from Ecuador (Palice et al. 2005) are included in our analyses. It is possible that our southern phylogenetic species (*L. sp.* and *L. aff. umbellifera*) correspond in part to *L. aurantiaca* and *L. chromacea* and possibly a third taxon based on the morphological similarities and differences mentioned above. Unfortunately, no publicly available genetic data exist on *L. aurantiaca* and *L. chromacea* for comparison. Therefore, future studies should clarify the status and phylogenetic position of these species and whether the unidentified southern lineages in our analyses correspond to any of these taxa.

Based on their recent, but pronounced divergence, it is possible that northern vs. southern species pairs, particularly *L. umbellifera* and *L. aff. umbellifera*, separated during the glacial cycles of the Pleistocene, when northern tundra and boreal forest areas were geographically closer to their southern cold-climate equivalents, making transequatorial dispersal more likely. Such a scenario is currently the most accepted biogeographical hypothesis for plant bipolar disjunctions: i.e. dispersal during the cold periods of the Pleistocene, when polar regions expanded on both hemispheres, either by long-distance dispersal, presumably by migrating animals or air currents (Galloway and Aptroot 1995), or via “mountain-hopping”, particularly along the north-south mountain chains (Escudero et al. 2010; Kristiansen and Vigna 1996; Raven 1963; Van Steenis 1962; Vollan et al. 2006). Animals may play a particularly important role in occasional transequatorial dispersal of spores and/or thallus fragments, because many migratory bird species travel between the polar regions. In the bipolar crowberries (*Empetrum*), which have fleshy bird-dispersed fruits, a fossil-calibrated relaxed molecular clock has recently been used to model the sequence evolution in two nuclear low-copy genes and two plastid DNA regions (Popp et al. 2011). The median estimates of the time to the most recent common ancestor for

1 northern and southern hemisphere *Empetrum* were 0.56-0.93 Ma, and 0.26-0.59 Ma for the
2 southern hemisphere plants only. The southern clade was imbedded in a large and widespread
3 northern clade, with Northwestern American *Empetrum* consistently identified as sister to the
4 southern clade. This implies that a single mid-Pleistocene long-distance dispersal event, possibly
5 via birds migrating from Alaska to southernmost South America, could explain the extreme
6 bipolar disjunction.

7 Despite the above uncertainties, it is clear that Campbell Island was almost certainly
8 colonized by at least two *Lichenomphalia* lineages via transoceanic dispersal either from another
9 southern landmass or perhaps directly from the Northern Hemisphere. Although the times of
10 colonisation of Campbell Island could substantially differ according to the alternative scenarios,
11 all scenarios support our argument: i.e. the frequency of dispersal appears to be scale-dependent:
12 subject to the limitations of our markers, intercontinental gene flow appears to be high in the
13 same climatic belt (e.g. the northern circumpolar), while transequatorial dispersal is rare,
14 ultimately leading to allopatric speciation, a pattern also demonstrated in *Empetrum* (Popp et al.
15 2011). Not surprisingly, our sampling efforts likely do not cover the entire distribution ranges of
16 the studied *Lichenomphalia* species, partly because the complete ranges are unknown and
17 because of the logistical difficulties of obtaining specimens spanning different continents and
18 hemispheres. Therefore, future works incorporating collections from additional geographic areas
19 will likely improve our current understanding of the phylogeography of the genus.

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4 1 Fig. 1. A) Maximum-likelihood phylogram of *Lichenomphalia* species (-lnL=7076.8495)
5 2 inferred from the combined ITS+LSU rDNA dataset. The tree was rooted using *Arrhenia* based
6 3 on phylogenetic results from a study with broader taxon sampling (Lutzoni 1997). Bootstrap
7 4 values greater than 70% are shown above the branches. Geographic distribution of the supported
8 5 clades is marked by N (“northern”) and S (“southern”). B) Maximum-likelihood phylogram of *L.*
9 6 *umbellifera* (-lnL=3387.6449) inferred from the combined ITS+LSU+EF dataset. The tree is
10 7 midpoint-rooted. The only bootstrap value greater than 70% is shown on the longest branch.
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13 9 Fig. 2. Geographical locations of *L. umbellifera* samples in the Northern Hemisphere and
14 10 intercontinental migration estimates. Shading indicates areas that were glaciated during the Last
15 11 Glacial Maximum. Inserts show sporocarps of *L. umbellifera* and the posterior probability
16 12 distribution of migration ($M=2N_e m$) estimated between Eurasia and North America using
17 13 Markov chain Monte Carlo coalescent simulations in MDIV. For each dataset, the data were
18 14 simulated assuming an infinite sites model, using 2,000,000 iterations in the chain, and an initial
19 15 500,000 iterations to ensure that a sufficient number of genealogies were simulated before
20 16 approximating the posterior distribution.
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23 18 Fig. 3. Coalescent-based genealogy of haplotypes found in arctic and boreal *L. umbellifera*
24 19 samples with the highest root probabilities (likelihood scores: $L = 9.9356 \times 10^{-52}$, $SD = 2.1275 \times$
25 20 10^{-49}) showing the distribution of mutations for the ITS region. The inferred genealogy is based
26 21 on 2,000,000 simulations of the coalescent with a Watterson’s (1975) estimate of $\Theta = 3.2$.
27 22 The time scale is in coalescent units of $2N_e$, where N_e is the effective population size. Mutations
28 23 and bifurcations are time ordered from the top (past) to the bottom (present). Mutation
29 24 designations correspond to the site numbers in Table 2. Numbers below the tree designate the
30 25 distinct haplotypes, their observed frequencies in total and on the different northern continents.
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1 Table 1. Geographical origin and GenBank accession numbers of *Lichenomphalia* specimens
 2 included in this study. Asterisks (*) refer to previously published data.

Isolate code	Origin	GenBank accession number		
		ITS	LSU	EF1
<i>L. alpina</i>				
FL930816-8	Iqaluit, Baffin Island, Nunavut, Canada	U66447*	U66447*	-
GAL1264	Barrow, Alaska, U.S.A	GU810972	GU811048	-
GAL1550	Barrow, Alaska, U.S.A	GU810973	GU811049	-
GAL2126	Barrow, Alaska, U.S.A	GU810974	GU811050	-
GAL2689	Longyearbyen, Svalbard, Norway	GU810975	GU811051	-
GAL2712	Longyearbyen, Svalbard, Norway	GU810976	GU811052	-
GAL4855	Denali National Park, Alaska, U.S.A	GU810977	GU811053	-
<i>L. grisella</i>				
FL930822-6	Schefferville, Québec, Canada	U66443*	U66443*	-
<i>L. hudsoniana</i>				
FL920728-4a	Mont Albert, Québec, Canada	U66446*	U66446*	-
FL930724-3	Nuuk, Greenland	AY293950*	-	-
FL930822-3	Schefferville, Québec, Canada	AY293951*	-	-
FL930724-6	Nuuk, Greenland	AY293952*	-	-
FL930811-6	Disko Island, Greenland	AY293953*	-	-
FL930805-6	Myvatn, Iceland	AY293954*	-	-
GAL1209	Barrow, Alaska, U.S.A	GU810978	GU811054	-
GAL2128	Barrow, Alaska, U.S.A	GU810979	GU811055	-
GAL3265	Atkasuk, Alaska, U.S.A	GU810980	GU811056	-
GAL4558	Denali National Park, Alaska, U.S.A	GU810981	GU811057	-
GAL7548	Nome, Alaska, U.S.A	GU810982	GU811058	-
GAL14648	Imnavait Creek, Alaska, U.S.A.	GU810983	GU811059	-
GAL14655	Toolik Lake LTER site, Alaska, U.S.A.	GU810984	GU811060	-
GAL18249	Barrow, Alaska, U.S.A	JQ065873	JQ065875	-
Gulden247/86	Ny-Ålesund, Svalbard, Norway	JQ065874	-	-
<i>L. lobata</i>				
Palice2327	Ecuador	AY542866*	AY542866*	-
Palice3275	Ecuador	AY542867*	AY542867*	-
<i>L. umbellifera</i>				
Dlaber 5/7/1989	Schwarzwald, Baden-Wurtenberg, Germany	GU810951	-	-
DU0011853	Iqaluit, Baffin Island, Nunavut, Canada	GU810943	GU811028	-
DU0011863	Iqaluit, Baffin Island, Nunavut, Canada	GU810942	GU811027	-
DU0011879	Abisko, Lappland, Sweden	GU810945	GU811030	-
FL930724-1	Nuuk, Greenland	AY293958*	-	-
FL930724-2	Nuuk, Greenland	AY293959*	-	-
FL930805	Myvatn, Iceland	AY293961*	-	-
FL930810-2	Disko Island, Greenland	AY293955*	-	-
FL930817-2	Iqaluit, Baffin Island, Nunavut, Canada	U66445*	-	-
FL930822-2	Schefferville, Québec, Canada	AY293956*	-	-
FL930822-4	Schefferville, Québec, Canada	AY293960*	-	-

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4	FL930822-8	Schefferville, Québec, Canada	AY293957*	-	-
5	GAL2616	Longyearbyen, Svalbard, Norway	GU810944	GU811029	-
6	GAL2667	Longyearbyen, Svalbard, Norway	GU810962	GU811038	-
7	GAL2687	Longyearbyen, Svalbard, Norway	GU810964	GU811040	-
8	GAL2690	Longyearbyen, Svalbard, Norway	GU810963	GU811039	-
9	GAL5374	Columbia Glacier, Alaska, U.S.A.	GU810934	GU811019	GU810993
10	GAL7544	Nome, Alaska, U.S.A.	GU810927	GU811012	GU810986
11	GAL8441	Kenai Lakes, Alaska, U.S.A.	GU810932	GU811017	GU810991
12	GAL8933	Denali National Park, Alaska, U.S.A.	GU810933	GU811018	GU810992
13	GAL9836	Kobuk National Park, Alaska, U.S.A.	GU810928	GU811013	GU810987
14	GAL12138	Adak Island, Alaska, U.S.A.	GU810936	GU811021	GU810995
15	GAL12214	Amchitka Island, Alaska, U.S.A.	GU810937	GU811022	GU810996
16	GAL12224	Amchitka Island, Alaska, U.S.A.	GU810938	GU811023	GU810997
17	GAL12274	Amchitka Island, Alaska, U.S.A.	GU810939	GU811024	GU810998
18	GAL12717	Kobuk National Park, Alaska, U.S.A.	GU810931	GU811016	GU810990
19	GAL14811	Imnavait Creek, Alaska, U.S.A.	GU810935	GU811020	GU810994
20	GAL14845	Toolik Lake LTER site, Alaska, U.S.A.	GU810930	GU811015	GU810989
21	GAL15152	Sitka, Alaska, U.S.A.	GU810926	GU811011	GU810985
22	GAL15669	Bonanza Creek LTER site, Alaska, U.S.A.	GU810929	GU811014	GU810988
23	GAL18192	Fairbanks, Alaska, U.S.A.	GU810940	GU811025	GU810999
24	GAL18247	Barrow, Alaska, U.S.A.	GU810941	GU811026	GU811000
25	Gulden 302/86	Ny-Ålesund, Svalbard, Norway	GU810961	GU811037	GU811007
26	Gulden 393/86	Ny-Ålesund, Svalbard, Norway	GU810960	GU811036	GU811006
27	HN4615	Longyearbyen, Svalbard, Norway	GU810965	GU811041	-
28	HN4616	Bjørndalen, Svalbard, Norway	GU810966	GU811042	-
29	L 3865	Pyasino Gulf, Taymyr Autonomous Okrug, Russia	GU810956	-	-
30	L 3915	Lake Baikal, Irkutsk Oblast, Russia	GU810958	-	-
31	L 201124	Khibiny Mtns., Province of Murmansk, Russia	GU810957	-	-
32	L 203055	Valaam, Republic of Karelia, Russia	GU810954	-	-
33	L 208257	Bolshevik Island, Severnaya Zemlya, Russia	GU810953	-	-
34	L 215201	Lisino-Korpus, Province of Leningrad, Russia	GU810959	-	-
35	L 215343	Lebedevka, Province of Leningrad, Russia	GU810955	-	-
36	LU113	Pechora, Republic of Komi, Russia	GU810952	-	-
37	O 64705	Ålesund, Møre og Romsdal, Norway	GU810948	GU811033	GU811003
38	O 66530	Nøtterøy, Vestfold, Norway	GU810950	GU811035	GU811005
39	O 72207	Dovre, Oppland, Norway	GU810949	GU811034	GU811004
40	O 72224	Hemnes, Nordland, Norway	GU810946	GU811031	GU811001
41	O 73818	Ulvik, Hordaland, Norway	GU810947	GU811032	GU811002
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49	<i>L. aff. umbellifera</i>				
50	GAL9512	Campbell Island, New Zealand	GU810967	GU811043	GU811008
51	GAL9517	Campbell Island, New Zealand	GU810968	GU811044	GU811009
52	GAL9547	Campbell Island, New Zealand	GU810969	GU811045	GU811010
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55	<i>L. velutina</i>				
56	FL930812-1	Disko Island, Greenland	U66454*	U66454*	-
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58	<i>L. sp.</i>				
59	GAL9540	Campbell Island, New Zealand	GU810971	GU811047	-
60	GAL9541	Campbell Island, New Zealand	GU810970	GU811046	-
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1 Table 2. Polymorphic sites in the ITS haplotypes of arctic and boreal *L. umbellifera* collapsed
 2 after removing indels and infinite-sites violations from the original ITS dataset for the
 3 subsequent coalescent analyses. Haplotype designations, position, site number, and designation
 4 of the given mutation are as shown in Fig. 3. Position refers to that in the original alignment, site
 5 type refers either transition (t), transversion (v), deletion (-) change with regard to the consensus
 6 sequence, while character type designation indicates whether the site is parsimony-informative
 7 (i) or not (-).
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Position	1111222233334444445555555556
	44778902221238033814566701223345790
	446134131487556339678901576042751586
Site number	111111111122222222223333333
	123456789012345678901234567890123456
Site Type	ttttttttttttttvtvtvtttttttttttvtvtvt
Character Type	-----i-----i---i---i-ii-----i---
Consensus	GTCTCTGTTCTCGTGGTGGGTGCGGCTGGACTTTCC
Haplotypes (Frequency)	
A (1)A.....
B (1)	ACT...A.....
C (1)	...CT...C.....A.C...T...T
D (18)C.....
E (1)C.C.....
F (1)C.....A.....
G (1)C.....A.A.....
H (2)C.....A.....
I (1)C.....A.....
J (1)CT...T.T...C...
K (1)T.....A.....
L (1)A...C.T.T...C...
M (1)G.TG.A...C.....
N (2)C.T.T...C...
O (1)C.C.T.T...GC...
P (1)A.....
Q (3)T.T...C...
R (7)T.....
S (1)A.....
T (1)T...C...
U (2)A...T...

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Figure 1

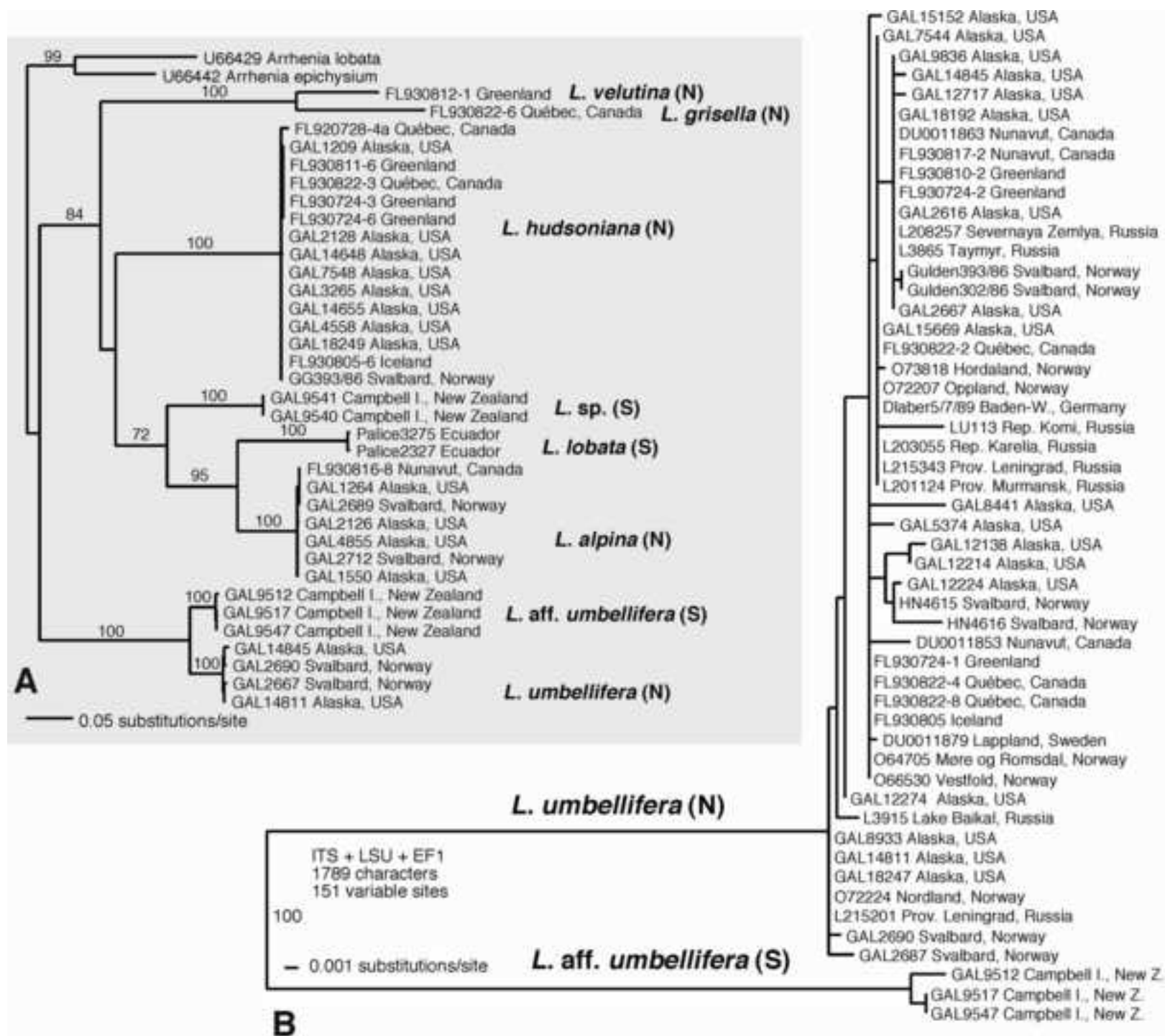
[Click here to download high resolution image](#)

Figure 2
[Click here to download high resolution image](#)

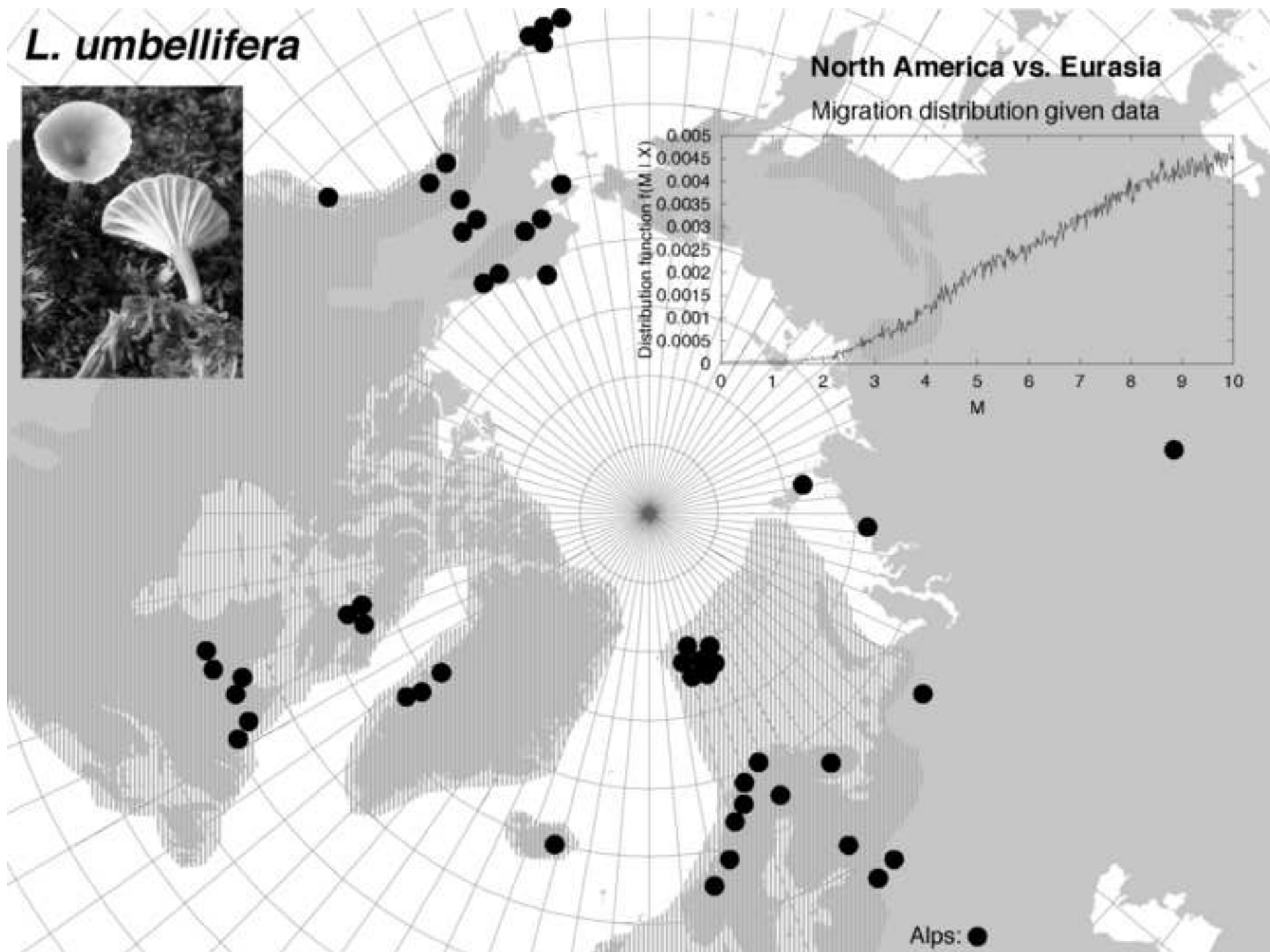


Figure 3

