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RESEARCH PAPER

Parallel Miocene dispersal events explain the cosmopolitan distribution of the Hypogymnioid lichens

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Abstract

Aim: Contemporary species' distributions are shaped by both geography and historical events, such as extinction, diversification in specific areas and long-distance dispersals. In the most diverse family of lichen-forming fungi, Parmeliaceae, the Hypogymnioid clade, is an example of an evolutionary lineage comprised of species occurring in temperate to subpolar regions in both hemispheres. Here, we elucidate the timing of diversification events and the impact of historical events on the species distribution in this lineage.

Location: Worldwide.

Taxon: Genera *Arctoparmelia*, *Brodoa*, *Hypogymnia* and *Pseudevernia* (Parmeliaceae).

Methods: Our sampling focused on the most diverse genus of the clade, *Hypogymnia*, including c. 70% of the described species. We reconstructed phylogenetic relationships using a multi-locus data set, estimated divergence times, and inferred ancestral distributions.

Results: Our analyses suggest that the ancestor of the Hypogymnioid clade occurred in the Holarctic. In each of the four genera, all recovered as monophyletic here, diversification have occurred largely during the Miocene and Pliocene. A number of currently accepted species did not form monophyletic groups, especially in cases where specimens were collected from distinct geographic areas, with multiple, distinct clades corresponding to the geographic region of origin. Our results suggest that only a very few species in the Hypogymnioid clade have cosmopolitan distributions, all of which reproduces using vegetative propagules including both symbiotic partners.

Main conclusions: While the diversification occurred predominantly in the Northern Hemisphere during the Miocene, a long-distance dispersal event from the Northern to the Southern Hemisphere, resulted in diversification of a clade of species largely restricted to the Southern Hemisphere. Similar to other groups in this diverse family, our study highlights the need for re-evaluation of species boundaries among members of the Hypogymnioid clade.

KEYWORDS

Biogeography, diversification, *Hypogymnia*, lichen, Miocene, molecular evolution, molecular systematics, substitution rate

1 | INTRODUCTION

Many lichens have distinctive distribution patterns, such as truly cosmopolitan, broad and intercontinental distributions, including pantropical species or species occurring in the polar regions of both hemispheres (Culberson, 1972; Galloway, 2007), endemic at small geographic scales (Lücking et al., 2014), or disjunct distribution (Leavitt et al., 2013). More and more biogeographical studies attempting to understand factors influencing the widely disparate distributional patterns of lichen-forming fungi have occurred in recent years (see e.g. Leavitt, Esslinger, Divakar, & Lumbsch, 2012; Núñez-Zapata et al., 2017; Wei et al., 2017).

Phylogeny-based historical biogeography aims at understanding how past climatological and geological processes shaped current distributional patterns of species richness, dealing with evolutionary processes occurring over millions of years on a large scale, during which speciation, extinction, dispersal and vicariance are the key processes (Morrone & Crisci, 1995; Vilhena & Antonelli, 2015; Wiens & Donoghue, 2004). Phylogenetic reconstructions inferred from DNA sequence data, coupled with ancestral range estimation, are powerful tools used to infer which factors likely impact biogeographic patterns (Ree & Smith, 2008; Ronquist & Sanmartin, 2011; Sanmartin & Ronquist, 2004). While biogeographical studies on lichen-forming fungi demonstrate that both vicariance and long- or mid-distance dispersal events shape distributions of these symbiotic fungi (Amo de Paz, Crespo, Cubas, Elix, & Lumbsch, 2012; Leavitt et al., 2012; Otálora, Martínez, Aragón, & Molina, 2010), species with cosmopolitan distributions are rarer than earlier assumed. These results have led to an increased interest in historical biogeographical studies in lichen-forming fungi, especially in macrolichen groups, such as the family Parmeliaceae (Amo de Paz et al., 2012; Divakar et al., 2012; Núñez-Zapata et al., 2017), which is one of the largest families of lichen-forming fungi with c. 2,800 currently accepted species (Jaklitsch, Baral, Lücking, & Lumbsch, 2016). The family originated during the Cretaceous, with diversification of major clades during the Paleogene and a major increase in diversification during the Miocene (Kraichak et al., 2015). It has a worldwide distribution, occurring from tropical and temperate rainforests to deserts and Polar Regions (Divakar et al., 2015; Persoh & Rambold, 2002).

In spite of this progress, our current knowledge of evolutionary relationships and biogeography of species with contrasting distribution patterns is limited. About why species occurring in a distinct geographical area, more closely related to others in the same region than those occurring on other continents, either the product of multiple migrations into these areas, or some other reasons, it seems like remaining untested.

Within Parmeliaceae, the Hypogymnioid clade includes four foliose genera—*Arctoparmelia*, *Brodoa*, *Hypogymnia* and *Pseudevernia*. Species in the Hypogymnioid clade occur in arctic-alpine to temperate regions. The saxicolous genera *Arctoparmelia* and *Brodoa* contain a number of species with wide, often circumpolar distribution

(Goward, 1986; Hale, 1986), the corticolous genus *Pseudevernia* includes temperate species mostly restricted to a continent and adjacent areas (Egan, 2016; Hale, 1968; Nash & Elix, 2002). In contrast, *Hypogymnia* has a cosmopolitan distribution, occurring in temperate regions of both the northern and southern Hemisphere (Elix, 1979; Elvebakk, 2011; McCune, 2002; McCune, Martin, & Wang, 2003). *Hypogymnia* also comprises species with restricted distributional ranges, such as western North America, eastern Asia, and the southern Hemisphere or Eurasia (Elix, 1979; Elix & James, 1982; Hawksworth, 1973; Lai, 1980; McCune & Wang, 2014).

The Hypogymnioid clade represents an interesting lineage for investigating the origin of species distributions in lichen-forming fungi due to its distinctive distribution patterns. So far, only two studies addressed historical biogeography in the genus *Hypogymnia*: one study focused on phylogenetic relationship and biogeographic structure of this genus, inferring that major lineages have continental-scale distributions (Miadlikowska et al., 2011). However, this study was largely restricted to species from North America (25 spp.) and sampled only two genetic markers (ITS & *GPD1*); the other study used phenotypic data to address possible biogeographic patterns of South American species (Elvebakk, 2011), in which the author proposed that the Hypogymnioid clade likely originated in Laurasia.

Here, we assembled a multi-locus data set including five genetic markers and representing 70 species, i.e. 68% of the total described species in the Hypogymnioid clade to reconstruct the phylogeny. The resulting phylogeny was then used to estimate diversification times and ancestral ranges of the major lineages. Specifically, we address the following questions: (a) What are the evolutionary relationships in the Hypogymnioid clade? (b) When did early diversification events happen within this clade? and (c) How did the distributional ranges in the clade change through time and how can we explain the current wide distribution of some species and restricted distributional ranges of other taxa? We hypothesize that the major Hypogymnioid species likely originated in the Holarctic.

2 | MATERIALS AND METHODS

2.1 | Taxon sampling

We included totally 161 specimens corresponding to 70 species of the four genera in the Hypogymnioid clade: *Arctoparmelia* (two of five species) (Hale, 1986), *Brodoa* (all three species) (Goward, 1986), *Hypogymnia* (62 of c. 90 species) (Thell et al., 2012) and *Pseudevernia* (three of six species) (Egan, 2016). In addition, five species within Parmeliaceae were selected as outgroups based on previous studies (see Table S1.1 in Appendix S1).

2.2 | Molecular methods

Total genomic DNA was extracted from a small section of the thallus or apothecia using the DNeasy plant Mini Kit (Qiagen, Hilden,



Germany). Five markers were amplified: the nuclear ribosomal internal transcribed spacer region (ITS), nuclear ribosomal large subunit (nuLSU), mitochondrial ribosomal small subunit (mtSSU), glyceraldehyde-3-phosphate-dehydrogenase (GPD), and DNA replication licensing factor minichromosome maintenance complex component 7 (MCM7). Primers, PCR conditions, and sequencing were the same as described previously (Crespo et al., 2007; Schmitt et al., 2009). Newly obtained sequences were aligned with sequences downloaded from GenBank (www.ncbi.nlm.nih.gov), with sequences of each locus aligned separately using MAFFT (Kato, Asimenos, & Toh, 2009). For the ITS, nuLSU, GPD and MCM7 loci, we applied the G-INS-I alignment algorithm, "20PAM/K = 2" scoring matrix, and offset value = 0.0, with the remaining parameters set to default values and for the mtSSU we used the E-INS-I alignment algorithm, "20PAM/K = 2" scoring matrix, and offset value = 0.0. Ambiguous alignment positions were delimited and removed using Gblocks followed Wei et al. (2017).

2.3 | Phylogenetic analysis

Phylogenetic analyses were performed using the five-locus data set. We used a maximum likelihood (ML) approach to detect potential conflicts between individual markers with a threshold of $\geq 70\%$ bootstrap support (Lutzoni et al., 2004). Since no conflict was evident, it was assumed that the data sets were congruent and could be combined for subsequent phylogenetic analyses. The single-gene and partitioned matrix were analysed and the gene topologies were reconstructed using the program RAxML 8.2.6 (Stamatakis, 2014) as implemented on the CIPRES Web Portal (http://www.phylo.org/sub_sections/portal/; Miller, Pfeiffer, & Schwartz, 2010), with the GTRGAMMA model, a parameter (Γ) for rate heterogeneity among sites and without a parameter for estimating the proportion of invariable sites (Rodriguez, Oliver, Marin, & Medina, 1990). Support values were assessed using the "rapid bootstrapping" option with 1,000 replicates. All loci were treated as separate partitions. Only clades that received bootstrap support $\geq 70\%$ were considered strongly supported. Phylogenetic trees were drawn using the program FigTree 1.4.2. (Rambaut, 2009). Alignments are available at TreeBase (<http://www.treebase.org>) under study number 22675.

2.4 | Dating analysis

We estimated divergence dates using the program BEAST 2.4.3 (Bouckaert et al., 2014). The most likely tree derived from the five-locus RAxML phylogenetic analysis as the starting tree for each data set was used. In BEAST, the partitioned alignment data set was analysed with unlinked substitution models across the loci and a relaxed clock model (uncorrelated lognormal) for each partition. A Yule prior was assigned to the branching process. The concatenated data set was partitioned into five partitions corresponding to each locus using PARTITIONFINDER 1.1.1 (Lanfear, Calcott, Ho, & Guindon, 2012) to infer the best-fitting substitution model:

TrNef+I+G for ITS, nuLSU, GPD and MCM7, and TIM+I+G for mtSSU, allowing unlinked parameter estimation and independent rate variation. Simulations suggest that complex model evolution inferred from a limited sample of characters may be heavily biased (Posada & Crandall, 2001), therefore we did not further partition GPD and MCM7 loci by codon position. Since these models are unavailable in BEAST, we used similar models to those of best-fitting substitution models i.e. SYM+I+G for ITS, nuLSU, GPD and MCM7, and GTR+I+G for mtSSU. Due to the lack of appropriate fossil evidence for the Hypogymnioid clade, we used the molecular evolution rates for ITS estimated for *Melanelixia* (2.43×10^{-9} substitution/site/year) (Leavitt et al., 2012) and 0.70 (nuLSU) and 0.69 (mtSSU) $\times 10^{-9}$ substitution/site/year obtained for Parmeliaceae (Amo de Paz et al., 2012), to estimate the time to the most recent common ancestor (MRCA) for all clades. Substitution rates for the other loci were co-estimated along the run under a uniform, normal, lognormal and an exponential prior distribution. Exploratory analyses provided similar results among these analyses (results not shown), hence we selected the lognormal prior for final analysis (Thorne & Kishino, 2002). Additionally, a secondary calibration constraining the Hypogymnioid clade (Divakar et al., 2015) at 31.67 Ma (23.85–40.62 Ma, 95% highest posterior density, HPD) was implemented (Divakar et al., 2017).

To explore the effects of distribution priors and different calibration points on the results, we used different schemes: (a) the distributions of priors were modelled using uniform, normal, lognormal and exponential priors (Ho & Phillips, 2009), and (b) the divergence time estimates were compared between the three different calibrations; ITS rate versus LSU rate versus secondary calibration. Exploratory analyses provided highly similar results among different modelled analyses (see Appendix S2 for details; Table S2.2), hence we selected the normal distribution prior and these three calibration points for final analysis.

Analyses were performed using four independent MCMC runs of 50 million generations, with a sampling tree every 1,000 generations followed Wei et al. (2017) and are detailed in Appendix S2.

2.5 | Ancestral range estimation

We estimated ancestral range probabilities using the R package 'BioGeoBEARS' (Matzke, 2014) based on the dated tree obtained in BEAST. Species distributions were obtained from selected literatures (Bitter, 1901; Elix, 1979; Lai, 1980; McCune, Divakar, & Upreti, 2012; McCune & Wang, 2014) and unpublished results of the first author. Elvebakk (2011) and Miadlikowska et al. (2011) reported, mainly based on some *Hypogymnia* species, continental-scale distribution. Since a number of species occur either in northern and central Asia or Europe and adjacent areas, we separated those areas in the analysis. The ranges for each species were assigned to eight major geographic regions: North America (A), Europe and adjacent areas (B), northern and central Asia (C), eastern Asia and Indo-Malayan region (D), Neotropics (E), Africa and Middle East (F), southern South America (G) and Australasia (H).

'BioGeoBEARS' implements likelihood versions of the biogeographic models DEC (dispersal–extinction–cladogenesis) (Clarke, 2008; Ree & Sanmartin, 2009), DIVA (dispersal–vicariance analysis) (Ronquist, 1997), and BAYAREA (Landis, Matzke, Moore, & Huelsenbeck, 2013), with two free parameters describing anagenesis: the rate of dispersal (d , range expansion) and the rate of extinction (e , range contraction) (Ree & Smith, 2008) but differed in their treatment of cladogenetic events in which ancestral and daughter distributional ranges overlap. We did not consider the third free parameter (j , or "jump") that has been criticized by Ree & Smith (2018).

The analyses were performed using the dated tree, pruned to contain only one specimen of each monophyletic species and in cases where a nominal taxon was found to have well-supported phylogeographic substructure, we treated each lineage comprised of specimens from a distinct geographic region as separate species-level lineages. All ranges were allowed, considering the scenario of a wide distribution in the past of any of the studied taxa and assuming equal rates of dispersal between any two regions. Results were compared using the Akaike information criterion with correction (AICc), considering the relatively small sample size in this study (i.e. 68% of the total described species), which gives a sense of the relative probability of each model based on the preferred model corresponding to the minimum AICc value.

3 | RESULTS

3.1 | Phylogenetic analysis

A total of 500 new sequences (119 ITS, 106 nuLSU, 101 mtSSU, 84 GPD and 90 MCM7) were generated for this study (Table S1.1). The aligned data matrix was 3,228 bp in length (ITS: 442; nuLSU: 726; mtSSU: 759; GPD: 731; and MCM7: 570). The concatenated ML tree had a LnL (= -22,233) and single locus trees showed no conflicts (data not shown). In the ML topology, the Hypogymnioid clade and all four currently accepted genera are strongly supported as monophyletic (see Appendix S3; Figure S3.3). The two North American *Pseudevernia* species included here, viz. *P. consocians* and *P. intensa*, did not form separate monophyletic groups.

Within the genus *Hypogymnia*, two strongly supported monophyletic groups—clade "A" and "B" (Figures S3.3, Figure 1) were recovered. Clade "A" includes species endemic to NE Asia (Clade "A1") and North America clade "A2". Clade "B" consisted of two widespread clades (clades "B1" and "B2"), a clade of species restricted to the Southern Hemisphere (clade "B3"), and a clade with species mainly from far East Asia and the Holarctic (clade "B4").

Within clade "A", clade "A1" consists of NE Asian endemics. All have physodic acid and mostly lack physodalic acid (P-), though physodalic-containing chemotypes are known in this group. The remaining two subclades have low bootstrap support (<70%) except the major clade (Clade "A2", 79%), all of which are North American endemics except for *H. hultenii*, occurring in North America and northern Europe. Within clade "B", four strongly supported subclades can be distinguished. Clade "B1" (bootstrap 87%) is geographically diverse, including one widespread species (*H. tubulosa*), Macaronesian island endemics (*H. tavaresii* and *H. madeirensis*), one narrow Asian endemic (*H. fujiisanensis*), one North American endemic (*H. wilfiana*), and one European species with possible disjuncts in North America and Asia (*H. farinacea*). Clade "B2" (bootstrap 100%) contains only *H. physodes*, which is geographically widespread, apparently with no close relatives. Clade "B3" (bootstrap 100%): contains species restricted to the southern hemisphere, plus one sorediate species more widespread and occurring in the northern Hemisphere (*H. pulverata*). All of the common Austral species occur in this clade. Clade B4 (bootstrap 83%) contains mostly Asian endemics with three widespread northern species (*H. austerodes*, *H. bitteri* and *H. subobscura*) and one widespread mostly northern species (*H. vittata*). No clear morphological or chemical synapomorphies are associated with either Clade A or B.

Several species fall into poorly supported clades (bootstrap values <70%). One clade includes: *H. canadensis*, *H. rugosa*, *H. aff. incurvoides 2* and *H. krogiae*. This group of mainly North American species are morphologically coherent in the dichotomous branching and dark lobe interiors, but had no further information other than belonging to clade "A". The specimen *H. aff. pulverata 1* is in an unresolved position in clade "B", and is phylogenetically distinct from other specimens identified as *H. pulverata* recovered in clade "B3". Interestingly, *Hypogymnia aff. incurvoides 1* is morphologically similar to *H. aff. incurvoides 2* but distantly related, since they fall in different clades, "B" and "A", respectively.

3.2 | Dating and ancestral ranges estimation

The mean node ages and divergence date ranges (95% HPD) of the clades are shown in Table S4.4 in Appendix S4 and Figure 1. The divergence of *Pseudevernia* was estimated to have occurred during the Oligocene at 31.43 Ma (29.54–33.47 Ma, node Ca), whereas the stem node of *Brodoa* was estimated at 26.04 Ma (21.18–30.25 Ma, node a). All other diversification events of supported clades were estimated during the Miocene and early Pliocene. The split of *Arctoparmelia* from *Hypogymnia* was estimated at 23.47 Ma (18.56–27.92 Ma, node b). The separation of the two major clades (A & B) within *Hypogymnia* was estimated at 18.86 Ma

FIGURE 1 Chronogram derived from the maximum clade credibility tree estimated for the sampled species of the Hypogymnioid clade. The chronogram was estimated from a multilocus data within a coalescent-based framework in BEAST. Light grey bars indicate the 95% highest posterior density (HPD) interval for the divergence times estimates. Values above branches indicate ages, and below branches are Bayesian posterior probability (PP) from the BEAST analysis; only clades supported in the BEAST analysis are presented. Letters inside circles refers to nodes as in Table S4.4. The calibration point (Ca) is indicated at the corresponding node

	LnL	No of parameters	d	e	AICc	AICc_wt
DEC	-290.2	2	0.0120	0.00000	584.40	0.00
DIVALIKE	-296.3	2	0.0130	0.00000	596.60	0.00
BAYAREALIKE	-265.6	2	0.0064	0.03000	535.40	1.00

TABLE 1 Parameter inference, log-likelihoods (LnL) and relative probabilities using AICc and AICc_wt (model weight) of each of three BioGeBears models. d: rate of dispersal (range expansion), e: rate of extinction (range contraction)

(14.49–22.97 Ma, node d) with subsequent diversification within those clades during the Miocene (Table S4.4). Divergence analysis shows that diversification within the four genera started also from the Miocene (Figure 1).

The relative probabilities of three models of the ancestral range analyses are summarized in Table 1. Overall, the most likely biogeographical model was the BAYAREALIKE model (LnL = -265.6, AICc = 535.40, AICc weight = 1.00). This model (Table S4.4, Figure 2) showed a most probable Holarctic ancestral range for the common ancestor of the Hypogymnioid clade either in Europe and North America (AB, prob = 0.22) or Europe, North America and eastern Asia and Indo-Malayan region (ABD, prob = 0.18). The most probable ancestral areas for all genera and the two main clades within *Hypogymnia* are in the Holarctic: (a) Europe (B, prob = 0.67) or Europe and North America (AB, prob = 0.30) for *Brodoa*, (b) Uncertain for *Pseudevernia*, (c) Europe, North America and northern and central Asia (ABC, prob = 0.56), Europe and northern and central Asia (BC, prob = 0.17), or Europe and North America (AB, prob = 0.11) for *Arctoparmelia*, (d) Europe and North America (AB, prob = 0.68), and Europe, North America and eastern Asia and Indo-Malayan region (ABD, prob = 0.14) for *Hypogymnia*, (e) North America for clades A and A2 of *Hypogymnia*, (f) Europe and North America for clades B, B1 and B2. The southern Hemisphere was estimated as ancestral range for clade B3, whereas eastern Asia and Indo-Malayan region was estimated as the most probable ancestral area for clade B4 (Table S4.4, Figure 2).

4 | DISCUSSION

Our study provides the most comprehensive insight to-date into phylogenetic relationships and biogeography in the Hypogymnioid clade in Parmeliaceae. Here, the monophyly of the four currently accepted genera in this clade was supported, as found previously with smaller ingroup taxon samplings (Divakar et al., 2015, 2017; Miadlikowska et al., 2014). These results also supported the presence of distinct distributional patterns and clear phylogeographical structure in *Hypogymnia*, consistent with previous studies suggesting continental-scale distribution in the genus (Elvebakk, 2011; Miadlikowska et al., 2014).

The fossil record of Hypogymnioid lichens is relatively poor (Kaasalainen, Schmidt, & Rikkinen, 2017; Taylor, Krings, & Taylor, 2015). Therefore, we used molecular sequence data from extant taxa to infer the historical biogeography of the Hypogymnioid clade, which have been widely used to better understand biogeographic

patterns in other clades of Parmeliaceae (Divakar et al., 2015; Leavitt et al., 2012; Wei et al., 2017).

In our study, we implemented the divergent time of 31.67 Ma for the Hypogymnioid node as a secondary calibration point because this age was obtained based on three lichen fossil calibrations, i.e. *Alectoria*, *Anzia* and *Parmelia* (Divakar et al., 2017), and got the age at this node as 31.43 Ma (Oligocene). Our study indicates that early diversification events of the *Hypogymnia* clade occurred in the Northern Hemisphere, especially North America and Europe, and then dispersed to Australia and Asia. The other three genera are mainly restricted to the Northern Hemisphere with a few sorediate species being widely distributed and extending to the southern Hemisphere.

Some species were supported as widely distributed, including *H. tubulosa* and *H. vittata*, reproduce with asexual diaspores called soredia that disperse the fungal and photosynthetically active partner at the same time. The observation that sorediate species have higher dispersal capacity was reported (Bjerke, 2003; Elvebakk, 2011; Elvebakk, Fritt-Rasmussen, & Elix, 2007). Some sorediate species, such as *Hypogymnia austerodes*, have a wide distribution in the Northern Hemisphere (Elvebakk, 2011), which is also supported by our study. In Clade B4 (Figures S3.3), the sorediate species *H. austerodes* and *H. bitteri* are widespread. *Hypogymnia austerodes*, common in the Northern Hemisphere, is also found in southern South America and Australasia (Elvebakk, 2011). Our results suggest that this group originated from Asia (D, Figure 2) or Asia and Europe (BD, Figure 2) during the late Miocene (Figure 1), then extended and spread southwards. As shown in Figure S3.3, the other two strongly supported clades, B1 and B2, are also composed of sorediate species with worldwide distribution.

Two major disjunctions distribution in the *Hypogymnia* clade can be found: (a) European-North American vs. eastern Asia and Indo-Malayan region species and (b) amphitropical disjunctions (north and south of tropical climates, but not within, except at high elevations). The latter disjunctions have been proposed of relatively recent origin as a result of long-distance dispersal occurring during the late Pliocene or Pleistocene in lichens (Fernández-Mendoza & Printzen, 2013; Galloway & Aptroot, 1995; Myllys, Stenroos, Thell, & Ahti, 2003; Wirtz, Printzen, & Lumbsch, 2008), and during Miocene in plants (Ickert-Bond, Rydin, & Renner, 2009; Lia, Confalonieri, Comas, & Hunziker, 2001; Simpson, Tate, & Weeks, 2005). Our study suggests a long-distance dispersal event from the Northern to the Southern Hemisphere happened during the Miocene. This underlines that similar contemporary distribution patterns can be caused by different processes at different times (Donoghue, Bell, & Li, 2001). So, based on current evidence, it appears that a single

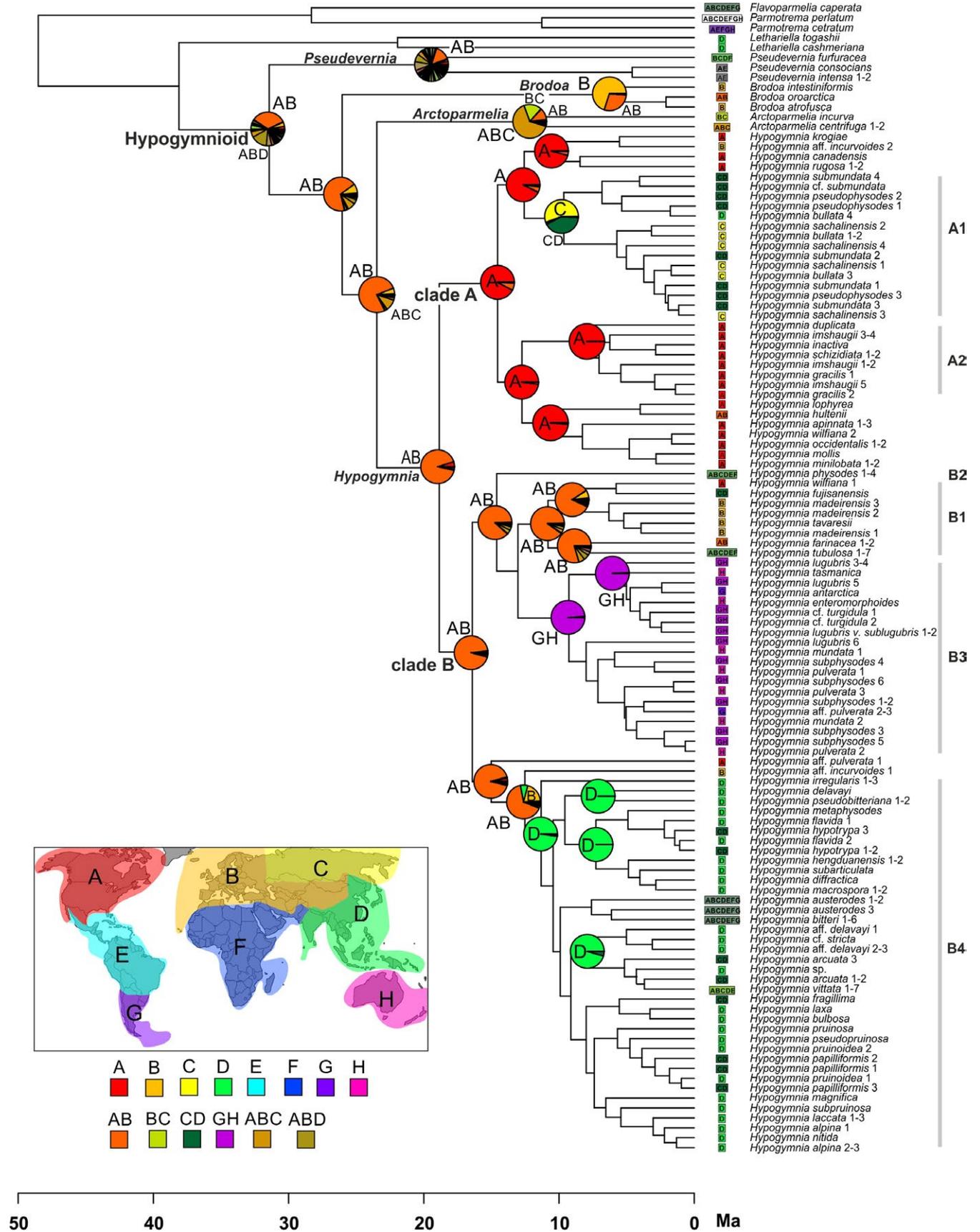


FIGURE 2 Maximum likelihood estimations of geographic range evolution in the Hypogymnioid clade according to the BAYAREALIKE model in a 'BioGeoBEARS' analysis. Pie charts at the nodes show the relative probabilities of possible geographic ranges (see Table S4.4 in Appendix S4 for ancestral areas details)

long-distance dispersal event during the Miocene led to the origin of a Southern Hemisphere clade of *Hypogymnia*.

A number of lineages in *Hypogymnia* have more restricted distributional ranges, being restricted to Asia (clade "A1"), North America (clade "A2") or the Southern Hemisphere (clade "B3") (Figure S3.3), with the exception of *H. pulverata*, which is also known from Japan, China and easternmost Russia (Elix, 1979; Galloway, 2007). Our study showed that both clades "A1" and "A2" originated in North America ("A", Figure 2), with ancestors of "A1", dispersing into Asia during the middle and late Miocene (Figure 1). Clade "B3" (Figure S3.3) consisting of Southern Hemisphere species originated in North America and Europe (AB, Figure 2) or North America, Europe and Asia (ABD, Figure 2), and dispersed to the southern Hemisphere during the middle and late Miocene (Figure 1). Although most species of clade "B4" (Figure S3.3) initially originated in North America and Europe (AB, Figure 2) or North America, Europe and Asia (ABD, Figure 2), East Asia became the main distributional areas of this clade during the late Miocene. Strikingly, *Hypogymnia* species restricted to eastern Asia and the Indo-Malayan region belong to two distantly related clades, A1 and B4 (Figure S3.3) and hence species restricted to this area are composed of two different elements that reached eastern Asia and adjacent regions during the Miocene, which is consistent with other disjunct Northern Hemisphere distributions studied recently (Wen & Ickert-Bond, 2009; Núñez-Zapata et al., 2017).

The Hypogymnioid clade initially radiated during the early Oligocene, then successively diversified during the early Miocene (Figure 1). The early Miocene is a crucial time period with major paleoclimatic events (Zachos, Pagani, Sloan, Thomas, & Billups, 2001; Zachos, Shackleton, Revenaugh, Palike, & Flower, 2001), and the terrestrial climate became cooler with remarkable thermal seasonality (Mosbrugger, Utescher, & Dilcher, 2005). Major tectonic activity and orogeny also happened in the Northern Hemisphere during this period (Pagani, Freeman, & Arthur, 1999; Ramstein, Fluteau, Besse, & Joussaume, 1997). Global shifts in vegetation are seen during this time period, for example, alpine coniferous deciduous forests emerged (Ramstein et al., 1997), which are known as very common substrates for Hypogymnioid lichens, meanwhile, more open habitats also occurred (Ramstein et al., 1997). All those conditions, i.e. the suitable climate, terrain, habitat and substrate, may have contributed to the diversification of the Hypogymnioid clade.

In this study, we were able to infer novel perspectives into biogeographical patterns in Hypogymnioid lichens: (a) The Hypogymnioid clade, including four genera, i.e. *Arctoparmelia*, *Brodoa*, *Hypogymnia* and *Pseudevernia*, is a well-supported monophyletic clade, among which *Pseudevernia* is the earliest diverging lineage and *Hypogymnia* the sister group; (b) Hypogymnioid lichens originated during the early Oligocene, but the main diversification happened during the Miocene; and (c) the Hypogymnioid clade originated in the Holarctic, and experienced a long-distance dispersal event from the Northern to the Southern Hemisphere

during the Miocene, which gave rise to a clade of species in the Southern Hemisphere.

Besides, in this study, we found several distinct species-level lineages may be masked within a single nominal taxon without readily observed phenotypical characters (Appendix S3). While our taxon sampling was not specifically designed to address species delimitation in members of the Hypogymnioid clade, it is worth underlining whether there exist cryptic species in the near future.

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DATA ACCESSIBILITY

The Materials are available as Appendix S1. All sequence data generated for this study (Appendix S1) can be accessed via GenBank: <https://www.ncbi.nlm.nih.gov/genbank/>. Alignments are available at TreeBase (<http://www.treebase.org>). The comparison of the divergence time estimated for *Hypogymnia*, with a partitioned data set of five marker loci and a secondary calibration constraining the crown of the Hypogymnioid clade at 31.67 Ma is available as Appendix S2.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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