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Lichenomphalia altoandina, a new species of Hygrophoraceae from the Chilean Altiplano

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ABSTRACT

Lichenomphalia is a lichenized agaric genus characterized by its omphalinoid basidiomes. *Lichenomphalia* species are associated with unicellular green algae in the genus *Coccomyxa* and are mainly distributed in polar and alpine habitats. The aim of this work is to describe *L. altoandina*, a new species from northern Chile that grows among cushion plants over 3000 m above sea level in the Andes Mountains. The species is remarkable for living in highly saline environments, in some cases virtually on salt crusts. *Lichenomphalia altoandina* differs from other known species and particularly from *L. aurantiaca*, the most morphologically similar species, in its smooth and broader stipe and its slightly larger spores. *Lichenomphalia altoandina* is also morphologicaly and ecologically more similar to the core *Lichenomphalia* clade. Our phylogenetic study based on nuclear rDNA ITS and partial 28S sequences shows that *L. altoandina* belongs to the *Protolichenomphalia* clade and is sister to an unknown lineage, *L.* aff. *umbellifera*, from New Zealand.

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basidiolichen; Basidiomycota; Chile; *Lichenomphalia aurantiaca, L. chromacea*; phylogeny

INTRODUCTION

Lichenomphalia Redhead, Lutzoni, Moncalvo & Vilgalys is a basidiolichen genus proposed by Redhead et al. (2002) that contains species with omphalinoid basidiomes that form symbiotic associations with unicellular green algae in the genus *Coccomyxa*. In the *Lichenomphalia* symbiosis, algae cells are not penetrated by haustoria, but instead they are surrounded by hyphae and nutrients are exchanged via dense cell-to-cell contact between mycobiont and photobiont (Oberwinkler 2012). *Lichenomphalia* species were formerly classified into genera based on thallus morphology whereby species with globose thalli were placed in the genus *Botrydina* and species with squamulose thalli were placed in the genus *Coriscium* (Oberwinkler 2012). *Lichenomphalia* is macroscopically characterized by basidiomes that are typically brightly colored or melanized with decurrent lamellae and a cartilaginous or tough stipe that is often pubescent (Lodge et al. 2014). Microscopically, *Lichenomphalia* is characterized by a lamellar trama that is bidirectional or subregular with a slightly thickening hymenium. The basidiomes typically have hyaline, smooth, inamyloid basidiospores that are white in mass and are not metachromatic in cresyl blue and also lack cystidia and clamp connections (Lodge et al. 2014).

Ten *Lichenomphalia* species are currently recognized. Originally, Redhead et al. (2002) transferred eight lichenized *Omphalina* species into the new genus *Lichenomphalia* and later, two new species were described, *L. cinereispinula* Neville & Fouchier (Neville and Fouchier 2009) and *L. tasmanica* Kantvilas (Kantvilas and Jarman 2012). There are currently three described species in South America, *L. aurantiaca* (Redhead & Kuyper) Redhead, *L. lobata* (Redhead & Kuyper) Redhead, and *L. velutina* (Quél.) Redhead. *Lichenomphalia aurantiaca* and *L. lobata* were initially described as *Gerronema hudsoniana* (H.S. Jenn.) Singer and as *Gerronema luteovitellinum* (Pilát & Nannf.) Singer (Singer 1970). Both species were collected in the Colombian Andes Mountains. *Lichenomphalia lobata* has also been recorded from Venezuela (Singer 1970) and Ecuador (Palice et al. 2005). The third species, *L. velutina*, was described as *Omphalina defibulata* Singer (Singer 1952), from the Andean-Patagonian Forest in southern South America (Niveiro and Albertó 2012) and tentatively synonymized with *L. velutina* by Redhead et al. (2002).

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Taxa in this group were previously included in Omphalinoid genera of the Tricholomataceae, such as *Omphalina* or *Gerronema*. However, molecular phylogenetic analyses indicate that members of the genus *Lichenomphalia* belong to the family Hygrophoraceae, as do most of the other described basidiolichens (Lawrey et al. 2009; Lodge et al. 2014). Recently, Lodge et al. (2014) proposed the new subgenus *Protolichenomphalia* Lücking, Redhead & Novell, comprising *L. umbellifera* and related phylogenetic lineages, but maintaining the rest of the species in *Lichenomphalia* subgenus *Lichenomphalia*. The monophyly of *Lichenomphalia* is poorly resolved when *L. umbellifera* is included, and the genus appears paraphyletic in some analyses, depending on the methods, genes, and taxa used in the analysis (Lodge et al. 2006, 2014; Lawrey et al. 2009). However, each of the two subgenera has been strongly supported by most phylogenetic analyses (Lawrey et al. 2009; Geml et al. 2012; Lodge et al. 2014).

Lichenomphalia species are mainly distributed in polar and alpine habitats, including tropical mountain regions (Kranner and Lutzoni 1999; Lawrey et al. 2009; Redhead et al. 2002; Geml et al. 2012). *Lichenomphalia umbellifera*, the most broadly distributed and ecologically plastic species in the genus, is found in boreal and northern temperate rainforests of the Northern Hemisphere (Kranner and Lutzoni 1999; Redhead et al. 2002), whereas a closely related, yet undescribed phylogenetic linage occurs in the Southern Hemisphere (New Zealand) (Geml et al. 2012).

In this work, we describe a newly discovered *Lichenomphalia* species from northern Chile that occurs more than 3000 m above sea level (MASL) in the Andes Mountains. This new species is found among cushion plants in highly saline environments and in some cases can be found associated with salt crusts. We provide a description, illustrations, phylogenetic analyses, and comments on the biogeography of this species.

MATERIALS AND METHODS

Collections.—Samples were collected and processed according to Rossman et al. (1998). Macroscopic descriptions are based on fresh material according to Largent (1986) and Lodge et al. (2004). Color abbreviations follow Kornerup and Wanscher (1978). Microscopic features are described from material mounted in KOH (5%), phloxine (1%), Congo Red (1%), and Melzer's reagent. The following notations are used: x, for the arithmetic mean of the spore length and width; Q, for the quotient between length and width indicated as a range of variation; Qx, for the mean of Q values; and n, for the number of spores measured. Voucher specimens have been deposited in the Herbarium of the Museo Nacional de Historia Natural de Santiago, Chile (SGO), and the Instituto de Botánica del Nordeste (CTES). Herbarium acronyms follow Thiers (2016).

DNA extraction, amplification, and sequencing.—Genomic DNA was isolated from dried basidiome tissue using the DNAeasy Plant Minikit (Qiagen, Valencia, California, USA) following the manufacturer's recommendations. Two nuclear rDNA regions were obtained by polymerase chain reaction (PCR): the ITS1-5.8S-ITS2 region (ITS) was amplified with primers ITS1F (Gardes and Burns 1993) and ITS4 (White et al. 1990), and a 5′-portion of the ribosomal large subunit RNA region (28S) was amplified with primers LROR (Vilgalys and Hester, 1990) and LR5 (Moncalvo et al. 2000). PCR amplification was performed with 12.5 µL GoTaq Colorless Mastermix (Promega, Madison, Wisconsin, United States), 2.5 µL of each 10 µM primer, 2.5 µL of 1 mg/mL bovine serum albumin (BSA), 2 µL of DNA template, and distilled nuclease-free water for a 25-µL reaction. The PCR protocol followed that of Lodge et al. (2014), with an annealing temperature of 50 °C for both regions. Forward and reverse strands were purified and sequenced by Macrogen Inc. (Seoul, Korea). Sequences were visualized and assembled into contigs using the DNA Baser v4 assembly software (Heracle BioSoft S.R.L., Arges, Romania). Identity of the sequences was confirmed by the BLAST tool (http://www.ncbi.nlm.nih.gov/).

Phylogenetic analyses.—An initial BLAST search suggested that the new species belonged to the genus *Lichenomphalia*. To confirm this, preliminary phylogenetic placement within the family Hygrophoraceae was inferred based on the study by of Lodge et al. (2014), using GenBank sequences for the DNA regions ITS and 28S for one representative of every species reported by the authors (Supplementary Table 1 and Supplementary Fig. 1). The phylogenetic position of the new species within *Lichenomphalia* was inferred through an analysis using the available ITS and 28S sequences of the genus reported by Geml et al. (2012). Sequences used were obtained from GenBank (Supplementary Table 1). We replicated the two alignment steps carried out by Geml et al. (2012), in which we first aligned the whole genus *Lichenomphalia* and then restricted the alignment for the *Protolichenomphalia* clade. These two alignment steps were made in order to sequentially improve the homology assessment of the sequences used.

For all analyses, DNA sequences were aligned by the L-INS-i method implemented in MAFFT version 7 (Sievers et al. 2011; Katoh and Standley 2013). Phylogeny

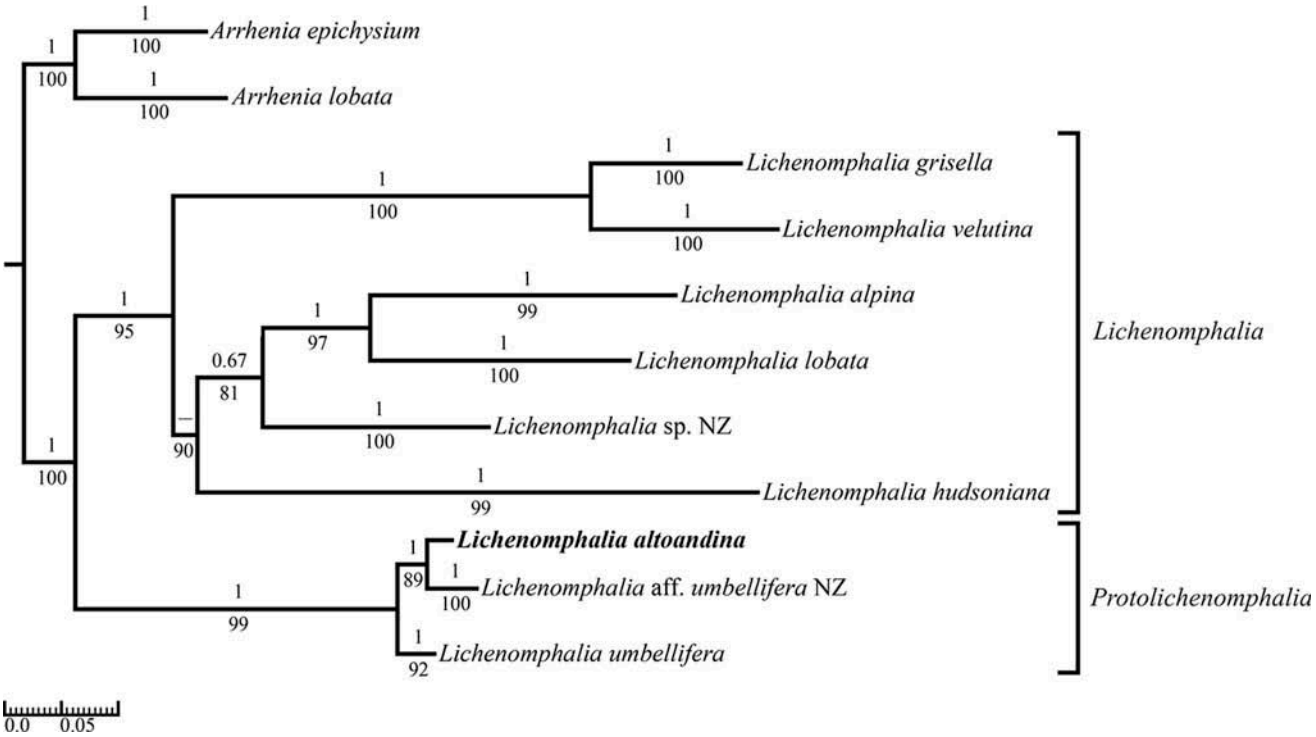

Figure 1. The 50% majority rule consensus tree obtained from nuc rDNA ITS and 28S sequences by Bayesian and ML inference. Numbers above branches are Bayesian posterior probabilities, and numbers below branches are ML bootstrapping values. Terminal nodes represent collapsed monophyletic groups of individuals of each taxon, with support values shown on their branches. Brackets show the subgenera proposed by Lodge et al. (2014). The phylogeny was rooted with *Arrhenia* spp.

reconstruction was conducted with the software MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) for Bayesian analyses and RaxML 8.1.24 (Stamatakis 2006) for maximum likelihood (ML) analyses. The general time reversible model with invariable sites and gamma distribution of heterogeneity (GTR+I+G) was used in both analyses. Bayesian analyses consisted of two independent runs of 10 million generations with four chains each (three heated and one cold). Trees were saved every 1000 generations in each run, after discarding 25% of the trees as the burn-in. ML analysis was carried out using default settings with random seeds and allowing the program to estimate the model parameters. For each phylogeny, a 50% majority rule consensus tree was constructed from the retained trees. Support for clades was provided by posterior probabilities (PP) calculated from default priors in the Bayesian analysis, and a rapid bootstrapping search over 1000 iterations (BS) in the ML analysis. All of the analyses were run in CIPRES (Miller et al. 2010).

RESULTS

Molecular phylogenies.—Our phylogenetic analysis confirmed the placement of the new species within genus *Lichenomphalia* as suggested by BLAST searches and preliminary analyses. Furthermore, the phylogeny is consistent with the placement within the subgenus *Protolichenomphalia* (1.0 PP, 99 BS) proposed by Lodge et al (2014), as a sister species of *L.* aff. *umbellifera* from New Zealand (1.0 PP, 89 BS) (Fig. 1).

TAXONOMY

Lichenomphalia altoandina Sandoval-Leiva & Niveiro, sp. nov. Figs. 2a–c, 3a–d, 4a–b

MycoBank MB 815457

Typification: CHILE. ARICA Y PARINACOTA: Municipality General Lagos, close to the locality of Colpitas, 17°56′51.15″S, 69°25′56.71″W, 4154 MASL, on dead cushions of *Zameioscirpus atacamensis* and *Oxychloë andina* with *Deyeuxia curvula* and *Carex* sp. in a saline wetland, 28 Dec 2012, *P. Sandoval-Leiva 192* (**holotype** SGO 160478). Isotype CTES 568351. GenBank KT371534 (ITS) and KT371535 (28S).

Diagnosis: Characterized by its orange basidiomata growing gregariously in highly saline environments, broadly ellipsoidal spores, 8–10.5 × 5–7 µm, long clavate basidia, 33–68 × 6–9.5 µm and insconspicuous *Botrydina*-type lichenized thallus. Differs from *L. aurantiaca*, the morphologically most similar species, in that *L. altoandina* has a glabrous and wider stipe, slightly larger spores, and more elongated basidia. *Lichenomphalia altoandina*

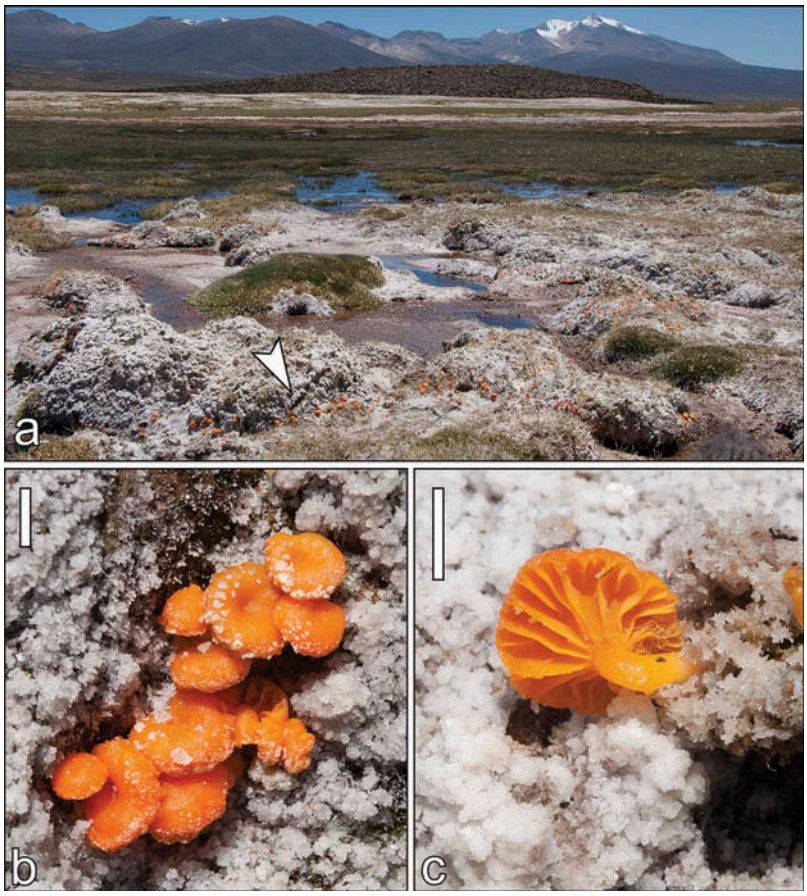

Figure 2. *Lichenomphalia altoandina*. a. Collecting site of the holotype of *L. altoandina* in saline high Andean wetlands in Chilean Altiplano, showing basidiomes emerging from cushions of vegetation (white arrow). b–c. Solitary and clustered basidiomes growing within salt crust. Bars = 1 cm (b–c).

differs from *L.* aff. *umbellifera*, from New Zealand, the phylogenetically most closely related species, in that the latter shows a disc-shaped lichenized thallus and in the coloration of the basidiomata.

Etymology: The epithet refers to "altoandino," a phytogeographical term used to refer to highland environments in the Andes Mountains and their vegetation.

Description: Basidiomata omphalinoid, gregarious. Pileus up to 32 mm broad, convex when young, becoming umbilicate, orange (5A5–7), moist, entire margin neither striate nor sulcate. Context fleshy, thin. Odor and taste not recorded. Lamellae decurrent, ventricose to arcuate, distant, orange (5A4–5), up 4 mm broad, not or scarcely intervenose, with lamellulae of varying lengths. Stipe central to slightly eccentric, 7–20 mm long × 2– 5 mm broad, cylindrical to laterally flattened, equal or tapering towards the base, light orange (5A3) to orange (5A4), smooth or occasionally with scattered hairs at the base. Spore print not observed. Lichened thallus inconspicuous.

Spores 8–10.5(–12) × (4.5–)5–7(–8) µm (x = 10 × 6.5 µm, Q = 1.2–1.8, Qx = 1.5, n = 150, N = 3), broadly ellipsoid to subglobose, lacrymoid to obovoid, hyaline, smooth, thin-walled, without germ pore, non-amyloid, non-metachromatic. Basidia (24–)33–68 × 6–9.5 µm clavate to long clavate, 1-, 2-, 3-, or 4-spored, originating at different heights in the hymenium, lacking clamp connection at basal septum and forming a hymenium up to 80 um deep. Pleurocystidia and cheilocystidia absent. Hymenophoral trama irregular, hyaline hyphae 2.5–6 µm diam. Pileipellis a cutis, with cylindrical prostrate intermixed hyphae, 3.5–5.5 µm diam. Stipitipellis a cutis of subparallel 2–4 µm diam., hyaline, thin-walled hyphae. Caulocystidia 30–55 × 4–6 µm, cylindrical with rounded or slightly attenuated apex, occasionally branched at the base, secondarily septate, scattered. Clamp connections absent. Lichenized thallus globose, *Botrydina*-type formed by globular clusters of algal cells surrounded by paraplenctenchymatous hyphae, 60–150 µm diam, interconnected by 2–5 µm diam hyaline hyphae, on the stipe base or on the surrounding substrate.

Additional specimens examined: CHILE. ARICA Y PARINACOTA: Municipality General Lagos, near to locality of Colpitas, 17°57′25.61″S, 69°26′25.93″W, 4127 MASL, 28 Dec 2012, *P. Sandoval-Leiva s/n* (SGO

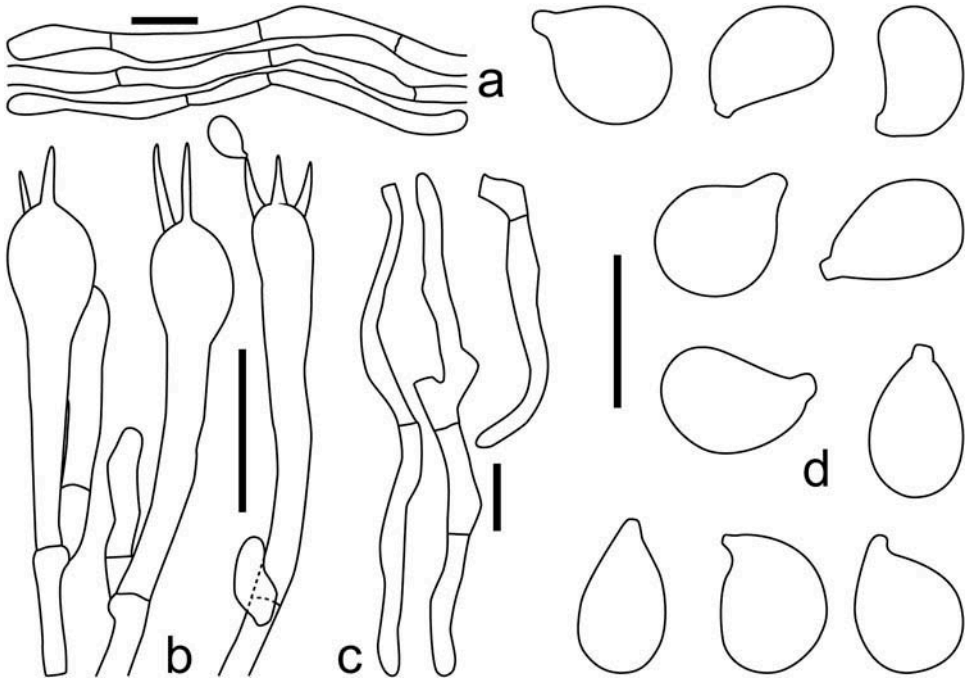

Figure 3. Microscopic features. *Lichenomphalia altoandina*. a. Pileipellis. b. Basidia. c. Caulocystidia. d. Spores. Bars =10 µm (a–d).

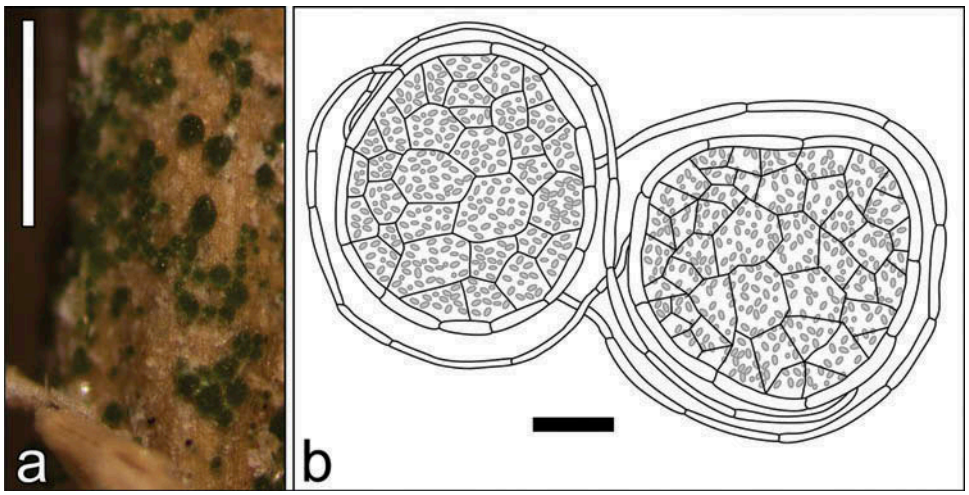

Figure 4. Lichenized thallus. a–b. Globular cluster surrounded by *Lichenomphalia* hyphae. Bars = 0.5 mm (a) and 10 µm (b).

164999). *Ibid*. 17°57′23.33″S, 69°26′25.38″W, 4123 MASL, 19 Dec 2012, *P. Sandoval-Leiva s/n* (SGO 165000). *Ibid*. 17°56′51.96″S, 69°25′58.48″W, 4158 MASL, 18 Dec 2013, *P. Sandoval-Leiva s/n* (SGO 165001). TARAPACA: Municipality Pica, near to locality of Lirima, 19°46′46.96″S, 68°49′25.89″W, 4486 MASL, 12 Jan 2012, *P. Saldivia 1388* (SGO 160485).

Distribution: Currently known only from northern Chile near Colpitas and Lirima but probably distributed in high elevation Andean Mountain wetlands throughout northern Chile.

DISCUSSION

Lichenomphalia altoandina is characterized by its orange basidiomes and gregarious fruiting in highly saline environments in the highlands of the Andes Mountains in northern Chile. The environment of *L. altoandina* is typical of the Altiplano ecosystems present in Bolivia, Chile, Argentina, and Peru, in the xerophytic Puna phytogeographical region (Josse et al. 2009). Climatically, this corresponds to the driest portion of the Andes Mountains, with extremely dry areas (Josse et al. 2009), and markedly seasonal rainfall in

summer (Kalin Arroyo et al. 1988; Teillier 1998). *Lichenomphalia altoandina* grows associated with highly saline ecosystems such as salt flats and salt lakes that are unique to the Altiplano (Chong 1988; Josse et al. 2009). Specifically, it has been collected growing on saline wetlands with cushion-forming plants such as *Deyeuxia curvula, Oxychloe andina*, and *Zameioscirpus atacamensis*, all endemic species of the Altiplano (Kirschner 2002; Dhooge et al. 2003; Rúgolo de Agrasar 2006).

Lichenomphalia altoandina is quite distinct from the most morphologically similar species, *L. aurantiaca*, because *L. altoandina* has larger spores [8.5–12 × 5.5–7.8 µm in *L. altoandina* vs. 5.3–8 × 5.8(–7) µm sensu Singer (1970) or 8–10 × 5.5–6.9 µm sensu Redhead and Kuyper (1987) in *L. aurantiaca*], has a wider stipe (2–5 mm in *L. altoandina* vs. 1–2 mm in *L. aurantiaca*), and has longer basidia [33–68 µm long in *L. altoandina* vs. 29–37 µm long in *L. aurantiaca* (Singer 1970; Redhead and Kuyper 1987)]. Because of the morphological similarities, we attempted to obtain DNA from the holotype specimen of *L. aurantiaca* and assess the phylogenetic relationship between these two species. Unfortunately, the only known specimens of *L. aurantiaca* were collected in 1968 and DNA sequencing was not successful.

Lichenomphalia aurantiaca and *L. altoandina* also differ in their ecology. The collection areas for these two species are approximately 2500 km apart, and although both grow in high altitude locations in the Andes Mountains, their known distribution areas show notable differences in climate, vegetation, and associated flora. *Lichenomphalia aurantiaca* is known only from the Northern Andes phytoregion (Josse et al. 2009) in the Colombian Páramo ecosystem. This is a wet ecosystem with 1500–2000 mm of rain that is distributed throughout the year (Vargas et al. 2002). This region lacks the extremely dry conditions and hypersaline salt flats where *L. altoandina* has been collected.

Our phylogenetic studies show that *L. altoandina* belongs to *Lichenomphalia* subgenus *Protolichenomphalia*, together with *L. umbellifera* from the Northern Hemisphere and *L.* aff. *umbellifera* from New Zealand. Our phylogeny shows strong statistical support for this relationship. Each of the species in this group has a unique morphology. *Lichenomphalia umbellifera* is distinguished by its basidiomata with a yellow-brown to gray pileus and a slender, purplish to yellow-brown stipe. Furthermore, it has different ecological requirements and a wider distribution, extending in high latitudes of both hemispheres (Bigelow 1970; Kuyper 1995; Barrasa and Rico 2001). The taxon *L.* aff. *umbellifera* may correspond to *L. chromacea* (Cleland) Redhead, Lutzoni, Moncalvo & Vilgalys based on morphological similarities (Geml et al. 2012). *Lichenomphalia chromacea* was described from southern Australia and resembles *L. altoandina* in its spore morphology and omphalinoid basidiomata. However, *L. chromacea* differs from *L. altoandina* in its yellow to pale orange-yellow basidiomata and its disc-shaped to slightly angular lichenized thallus, which forms an areolate crustose surface when crowded (Redhead and Kuyper 1987; Kantvillas and Jarman 2012).

Other *Lichenomphalia* species that are morphologically similar to *L. altoandina* include *L. hudsoniana* (H. S. Jenn.) Redhead, Lutzoni, Moncalvo & Vilgalys, *L. lobata*, and *L. alpina* (Britzelm.) Redhead, Lutzoni, Moncalvo & Vilgalys. Nevertheless, they are morphologically different and phylogenetically fall into *Lichenomphalia* subgenus *Lichenomphalia* (Fig. 1). *Lichenomphalia hudsoniana* is similar to *L. altoandina* in size and coloration of the basidiomata but differs in having a pubescent stipe, smaller spores [7–8.5(–9) × 4–4.5 µm], and a squamulose vegetative thallus of the *Coriscium*-type (Bigelow 1970; Barrasa and Rico 2001). *Lichenomphalia alpina* [(= *L. luteovitellina* (Pilát & Nannf.) Redhead, Lutzoni, Moncalvo & Vilgalys)] has bright yellow basidiomata that are superficially similar to *L. altoandina*, but it has a lichenized thallus of the *Botrydina*-type (Bigelow 1970). However, Barrasa and Rico (2001) reported that *L. alpina* has egg-yellow to orange basidiomata that are similar to those of *L. altoandina*. Nevertheless, the spores of *L. alpina* are markedly narrower (4–4.5 µm in *L. alpina* vs. 5–7 µm in *L. altoandina*) (Bigelow 1970; Redhead and Kuyper 1987). Other similar *Lichenomphalia* species differ from *L. altoandina* in their basidiomata coloration and lichenized thallus type. Among them, *L. lobata* from northern South America (Singer 1970; Palice 2005) and *L. tasmanica* from Tasmania (Kantvillas and Jarman 2012) are distinguished from *L. altoandina* by their bright yellow basidiomata and squamulose lichenized thalli of the *Coriscium*-type. Species within the *L. velutina–L. grisella* complex (Lutzoni 1997) are characterized by grayish basidiomata with incrusted pigments in the pileipellis and velutinous stipes (Redhead et al. 2002). Similar features can also be found in *L. cinereispinulosa* Neville & Fouchier (Neville and Fouchier 2009). However, these taxa are clearly different from *L. altoandina*.

Lichenomphalia altoandina has morphological and ecological characters that are more similar to taxa in subgenus *Lichenomphalia*, as indicated by Lodge et al. (2014) and Redhead et al. (2002). However, our phylogenetic analyses show that *L. altoandina* belongs to

Lichenomphalia subgenus *Protolichenomphalia*. The highly pigmented basidiomes, thickened hyphal walls, and preference for higher light intensity habitats could presumably be adaptations to high radiation and desiccation (Lodge et al. 2014).

Although taxon sampling for the Southern Hemisphere taxa in subgenus *Protolichenomphalia* is limited, the phylogenetic analyses show a clear geographic structure that is contrary to what was seen for *L. umbellifera* s.s. populations in the Northern Hemisphere, where no geographic structure was detected. Geml et al. (2012) discussed the high level of intercontinental gene flow among *L. umbellifera* s.s. populations and pointed out the strong phylogeographic separation between *L. umbellifera* s.s. and *L.* aff. *umbellifera* in New Zealand, which seems to be an uncommon pattern in fungi. In this sense, the sister relationship between *L. altoandina* and *L.* aff. *umbellifera* not only reinforces the phylogeographic divergence but also suggests some geographic genetic structure among the Southern Hemisphere populations that contrasts with the Northern Hemisphere pattern. Nevertheless, more phylogeographic analyses are necessary to better understand this pattern.

Geml et al. (2012) pointed out that their results are compatible with the hypothesis of Southern Hemisphere colonization from Northern Hemisphere populations. Although our results are also compatible with this hypothesis, they also suggest the possibility of intercontinental dispersion within the Southern Hemisphere. Contrary to the patterns observed in *Galerina patagonica*, we observed differences in ITS sequences between South American and New Zealand populations (Geml et al. 2012). However, these could be due to an older transoceanic dispersal or higher nucleotide substitution rate heterogeneity among lineages. Nevertheless, in both cases, it is very likely that the divergence among these taxa occurred relatively recently, suggesting a post-Gondwanan origin of these lineages. Lack of DNA sampling among tropical and Australian populations does not allow us to infer dispersal processes of the genus from the Northern to the Southern Hemisphere, which has been suggested to be either mountain-hopping (maybe across the Andes Mountain) or long distance dispersal (Geml et al. 2012).

Finally, this finding is a contribution that extends the southern distribution of the *Lichenomphalia* subgenus *Protolichenomphalia* to South America. It has also contributed to a better understanding of some biogeographic patterns in the genus that could serve to address the hypothesis of *Lichenomphalia* dispersal from the Northern to the Southern Hemisphere.

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