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Patagonean *Polyozellus alinae* sp. nov.: the first representative of the genus in the Southern Hemisphere

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Abstract

The genus *Polyozellus* was originally described by Murrill to accommodate the pileate-cantharelloid taxa of Thelephoraceae. However, molecular data indicate that most resupinate taxa previously considered as belonging to the genus *Pseudotomentella* form a monophyletic group that includes the pileate taxa in *Polyozellus*. Accordingly, *Polyozellus* is now recognized as a more diverse genus, including both pileate and resupinate ectomycorrhizal fungi. Until now, all of the known *Polyozellus* species have been restricted to the Northern Hemisphere. Repeated excursions to the *Nothofagaceae* forests in the Andean Patagonia revealed interesting resupinate specimens with simple septa and dimitic hyphal system that morphologically fit the classic concept of *Pseudotomentella* but do not match any of the described species. Here, using morphological and phylogenetic analyses, we show that this taxon is a new species of *Polyozellus*. This is the first *Polyozellus* species described from the Southern Hemisphere, and its occurrence (along with many other endemic taxa) highlights the importance of Patagonian forests as a biogeographically unique hotspot of fungal diversity.

Keywords: Resupinate, Ectomycorrhizal, Biogeography, *Nothofagus*, *Pseudotomentella*

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Introduction

Andean Patagonia is a distinctive biogeographic region that is shared by Argentina and Chile and extends between 33° and 55° latitudes on both sides of the Andes. In contrast to the rest of South America, which primarily hosts neotropical biota with biogeographic connections to North America and Africa, the mountain ranges of Patagonia host fauna, flora, and funga derived from the temperate southern Gondwana landmasses[1,2]. Trees belonging to the family Nothofagaceae are found in temperate forests limited to southern South America in the Western Hemisphere, New Zealand, Australia, New Guinea, New Caledonia, and in high-elevation forest types found in tropical Australasia in the Eastern Hemisphere[3]. Nothofagaceae trees are often dominant in the forests where they occur, and this group helps define the Antarctic biogeographical region. Nothofagaceae are also unique because all known taxa form ectomycorrhizal (ECM) associations with fungi, and trees in this lineage are associated with a wide array of endemic ECM fungal taxa[2,4]. The funga of these Nothofagaceae forests found in the Southern Hemisphere include characteristic austral ECM Basidiomycota such as *Descolea*[5], *Psathyloma*[6], and *Austropaxillus*[7], and ECM Ascomycota such as *Amylascus*[8], *Geomorium*[9], and *Ruhlandiella*[10]. The ECM communities of Nothofagaceae forests are also consistently dominated by Cortinariaceae, including the neotenic hypogeous and secotioid species that are most diverse and abundant in this biogeographic region[11], as is also the case with some secotioid *Inocybe*[12].

Soil DNA and root-tip barcoding have shown that Thelephorales are abundant ECM partners in Patagonian forests[4,13]. Recent reports have begun to clarify the identity of Southern Andean representatives of Thelephorales, which also include non-mycorrhizal groups[14,15].

The genus *Polyozellus* was originally described by Murrill[16] to accommodate pileate-cantharelloid taxa of Thelephoraceae. However, molecular analyses based on the DNA regions LSU, nrSSU, RPB2, and mtSSU have shown that most resupinate taxa that were previously regarded as belonging to the genus *Pseudotomentella* belong to a monophyletic group that includes the pileate taxa in *Polyozellus*[17]. Accordingly, *Polyozellus* is now recognized as a more diverse genus, containing 28 species (according to Index Fungorum) and including both pileate and resupinate ECM taxa as well as orchid mycorrhizal fungi based on molecular data[18]. This is similar to the classical genera *Tomentella* and *Thelephora* (Thelephoraceae; Thelephorales), which were considered distinct based on their basidiome configurations: resupinate in *Tomentella* and fan-shaped to funnel-shaped to coralloid in *Thelephora*[19]. However, molecular phylogenetic data have shown that basidiome configurations are evolutionarily labile and that taxa from both *Tomentella* and *Thelephora* are more appropriately regarded as belonging to a single genus, *Thelephora*, which now contains resupinate and pileate mycorrhizal species with diverse hymenophoral configurations, and is symbiotically associated with a wide range of broad-leaf and conifer trees and even herbaceous plants such as orchids[20].

Polyozellus has previously been considered restricted to the Northern Hemisphere. *Tomentellopsis larsenii* (Kõljalg & Dunstan) Kõljalg, previously considered as belonging to the genus *Pseudotomentella*, was discovered in the Southern Hemisphere[17]. Recently, *T. rosannae* Kuhar & Gresl. has also been reported from the Southern Hemisphere[15]. However, further molecular studies are needed to confirm their phylogenetic affinities. Even when resupinate taxa

are included, *Polyozellus* has not previously been reported from the Southern Hemisphere[17].

During repeated expeditions by our team, collections of large resupinate basidiomes with notable color variations within the same basidiome (ranging from olive green to dark brownish red) were found attached to clumps of soil, decayed clusters of leaf litter, and decomposed wood. Upon microscopic inspection, the dimitic subiculum of thick-walled skeletal hyphae, the simple-septate generative hyphae, and the conspicuously apiculate basidiospores were evident, which are features matching the morphology of *Pseudotomentella*. A literature search could not identify any species described that matches the morphology of these collections. Phylogenetic analyses of the internal transcribed spacer (ITS) ribosomal DNA (rDNA) confirmed the phylogenetic affiliation within the modern genus *Polyozellus*. We describe this taxon here as the new species *Polyozellus alinae* sp. nov. based on morphology and phylogenetic analyses.

Materials and methods

The studied specimens were collected from four collection sites in the Los Lagos Region (Chile) in April 2017 from mixed and pure stands of *Nothofagus pumilio* and *N. dombeyii*, within the framework of a multi-year sampling project covering the full latitudinal range of Nothofagaceae forests in Patagonia. Characteristics such as detachability from substrate, color in the fresh state, position, and substrate identity were recorded in the field.

Descriptions of fresh basidiomes were made following the method of Kõljalg[21] using a Zeiss Axio Imager.A2 light microscope (LM; Carl Zeiss, Oberkochen, Germany) and a Hitachi SU5000 Schottky field-emission scanning electron microscope (SEM) at the University of Florida Interdisciplinary Center for Biotechnology Research (ICBR) Electron Microscopy Core Facility. Basidiospores, including ornamentation, were measured in 3% KOH in frontal and lateral views. At least 20 elements were measured for each morphological feature. Collections are deposited in the Fungarium of the Florida Museum of Natural History in Florida, USA (FLAS), the Museo Nacional de Historia Natural de Chile in Santiago, Chile (SGO), and the Universidad Nacional de Córdoba, Argentina (CORD).

Small pieces of basidiomes were sampled inside a field laboratory using sterile forceps and placed into an extraction buffer from the Extract-N-Amp DNA extraction kit (Sigma-Aldrich, St. Louis, MO). Extraction procedures were performed according to the manufacturer's instructions. Polymerase chain reaction (PCR) of the ribosomal ITS region was performed using primers ITS1F and ITS4[22,23]. The PCR conditions were 94 °C for 5 min, followed by 35 cycles of 1 min at 94 °C, 1 min at 55 °C, and 2 min at 72 °C, and a final 7 min at 72 °C. Sanger sequencing was conducted at the ICBR, University of Florida. Sequences of other representatives of the genus were retrieved from GenBank, most of which correspond to the recent study by Song et al.[24], one environmental sequence was retrieved by BLAST search, and four sequences were generated for this study. Following Tedersoo et al.[25], no outgroup was used because sequences from closely related genera produced low-quality alignments with large gaps. Instead, the maximum likelihood (ML) tree was rooted at the same position as in Svantesson et al.[17] Sequence data are shown in Table 1. The dataset was aligned with the L-INS-i strategy in MAFFT 7.0[26] and analyzed after trimming the ends. Nucleotide substitution models were selected using jModelTest 2.1[27]. ML analyses were done using PHYML[28]. Bootstrap values for the highest-likelihood tree were calculated from 1,000 replicates, and Bayesian analyses were conducted using MrBayes[29] for 8,000,000 generations to estimate the Bayesian posterior probabilities (BPPs).

Table 1. GenBank accession numbers of the sequences of *Polyozellus* species used for the phylogenetic analyses.

Species	Voucher	Origin	ITS
P. abundilobus	OF110312	Norway	MK290731
P. alinae	FLAS-F-65464	Chile	PX132899
P. alinae	FLAS-F-65451	Chile	PX132898
P. alinae	FLAS-F-65350	Chile	PX132897
P. alinae	FLAS-F-65377	Chile	MH930334
P. alinae	Environmental	Argentina	KY687675
P. alnophilus	OF110313	Norway	MK290715
P. alobatus	OF110315	Norway	MK290695
P. alobatus	SSvantesson425	Sweden	MK290696
P. atrofuscus	ML7553	USA	MK290732
P. atrofuscus	1859RD	China	HQ850125
P. atrolazulinus	TU117559	Canada	MG214657
P. atrolazulinus	TU102998	USA	MF100819
P. flavovirens	KHL16310	Sweden	MK290723
P. griseopergamaceus	SSvantesson401	Sweden	MK290720
P. griseopergamaceus	T883	Norway	MK290721
P. humicola	SSvantesson345	Sweden	MK290724
P. mariae	TU117348	Canada	MF100831
P. mariae	TU117235	Canada	MF100826
P. marymargaretae	TU117347	USA	MF100841
P. medius	TU115609	Estonia	MK290714
P. medius	MBN021322	Canada	KC840631
P. mucidulus	T1155	Norway	MK290725
P. mucidulus	T1123	Norway	MK290726
P. multiplex	TU115322	Canada	MF100814
P. multiplex	TU117350	USA	MF100830
P. multiplex	TU115049	China	MF100812
P. niger	KHL16273	Finland	MK290718
P. niger	T838	Norway	MK290719
P. pinophilus	SSvantesson358	Sweden	MK290708
P. pinophilus	OF110328	Norway	MK290709
P. plurilobus	US4263	Finland	MK290698
P. plurilobus	SSvantesson439	Sweden	MK290699
P. purpureoniger	H7021198	Russia	MF100842
P. purpureoniger	TU103000	USA	MF100821
P. rhizopunctatus	SSvantesson129	Sweden	MK290717
P. rotundisporus	SSvantesson413	Sweden	MK290674
P. rotundisporus	SSvantesson394	Sweden	MK290728
P. sciastrus	OF110317	Norway	MK290684
P. sciastrus	OF110318	Norway	MK290688
P. tristis	SSvantesson193	Sweden	MK290679
P. tristis	OF110300	Norway	MK290676
P. tristoides	OF110306	Norway	MK290692
P. tristoides	R60p6	Czechia	GU327494
P. umbrinus	Ssvantesson 351	Sweden	MK290700
P. umbrinus	OF110268	Norway	MK290702
P. umbrinascens	Ssvantesson 355	Sweden	MK290697
P. umbrinascens	UE31	Italy	HM370480
P. vepallidosporus	5182-1201	Germany	HM146848

Results

ML analysis of the ITS rDNA (Fig. 1) confirmed that the new *Polyozellus* collections from Patagonia represent a well-supported monophyletic group (95% ML bootstrap and 0.96 BPP). This genetic evidence, combined with their distinct morphological features and unique occurrence in the Nothofagaceae forests of Patagonia, indicates that these specimens represent a new species, which we

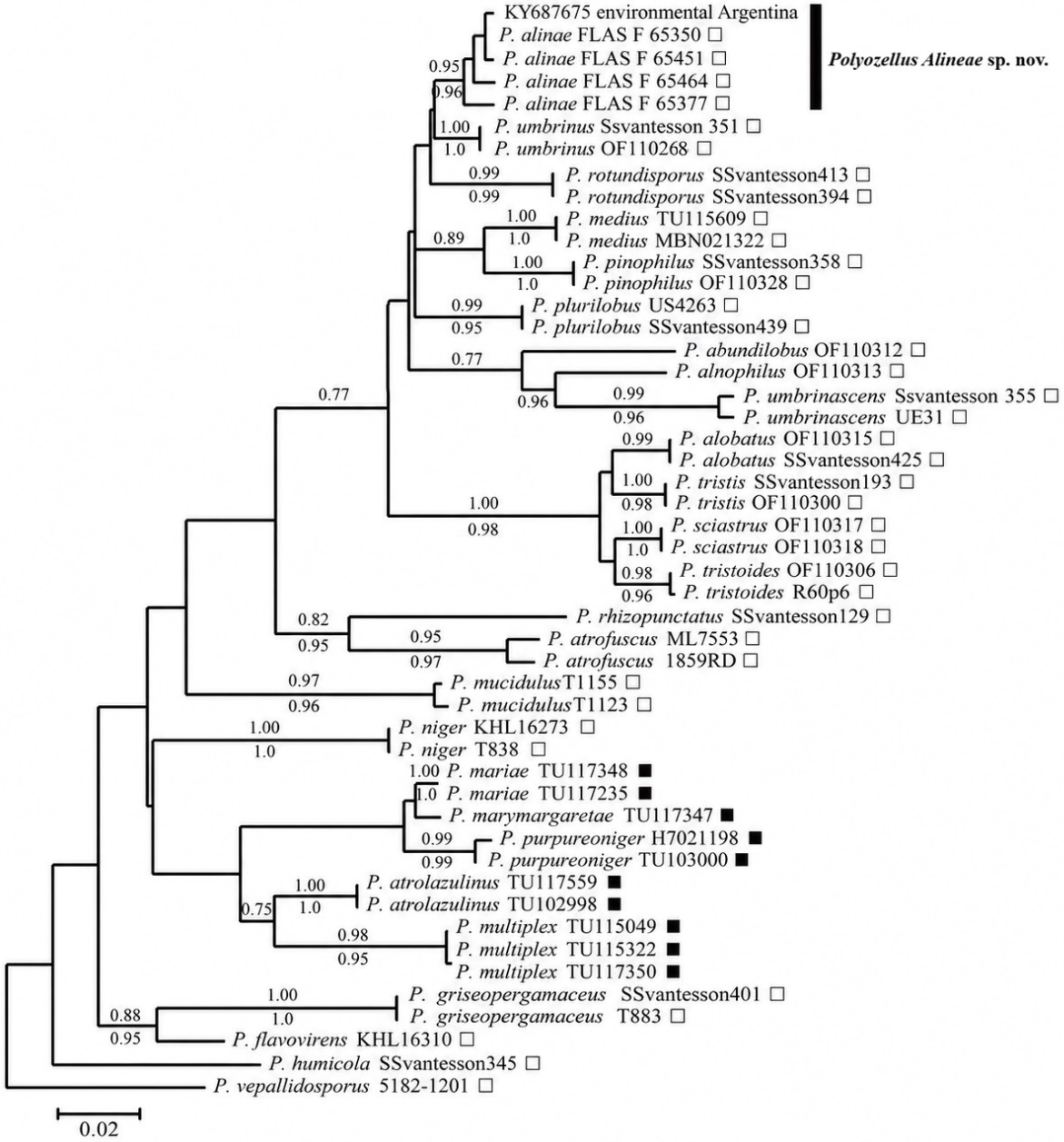

Fig. 1 Maximum likelihood phylogeny of the ITS ribosomal DNA showing the monophyly of *Polyozellus alinae* sp. nov. within the genus. The white squares after the labels indicate resupinate basidiomes, and the black squares indicate pileate basidiomes. Significant clade support is indicated by the bootstrap values (> 75% ML) above the branches and BPP values (> 0.95) below the branches.

describe here as *Polyozellus alinae* sp. nov. Deeper nodes and relationships cannot be inferred from these analyses because the ITS dataset achieved a low resolution; however, the clade containing the pileate forms was recovered in the topology.

Taxonomy

***Polyozellus alinae* sp. nov.** Kuhar, Figs. 2,3, and 4.

MycoBank #MB861149

Diagnosis — Basidiomes dimitic with simple septate generative hyphae and unbranched skeletal hyphae regularly bending at angles of swollen vertices of reduced cell lumen.

Etymology — Dedicated to our friend and colleague Alina Greslebin for her invaluable work researching the corticioid fungi of Patagonia.

Holotype — CHILE, Los Lagos, Vicente Perez Rosales National Park, on the road to the ski area just above Mirador el Bosque: 41°08'20.6" S 72°32'14.8" W. 17 April 2017, on the rotten bark of *Nothofagus* sp., Francisco Kuhar, FLAS-F-65464 (MES-2909).

Basidiomes annual, resupinate, membranaceous, of irregular margins, reaching 13 cm in diameter, velvety and compact. Immature sectors in discontinuous patches, relatively thin and cottony, showing thread-like hyphal aggregates at the margins. True rhizomorphs not observed. Hymenophore smooth, with irregular and rounded undulations, brown when fresh and dark purple-gray when dried. Subiculum developed but not extending beyond the edge of the hymenophore. Hyphal system dimitic, with simple septate generative hyphae of 3–6 μm diameter. KOH negative, branching at straight angles, hyaline in the subhymenium and brown in the subiculum, and smooth skeletal hyphae of 4–5.5 μm

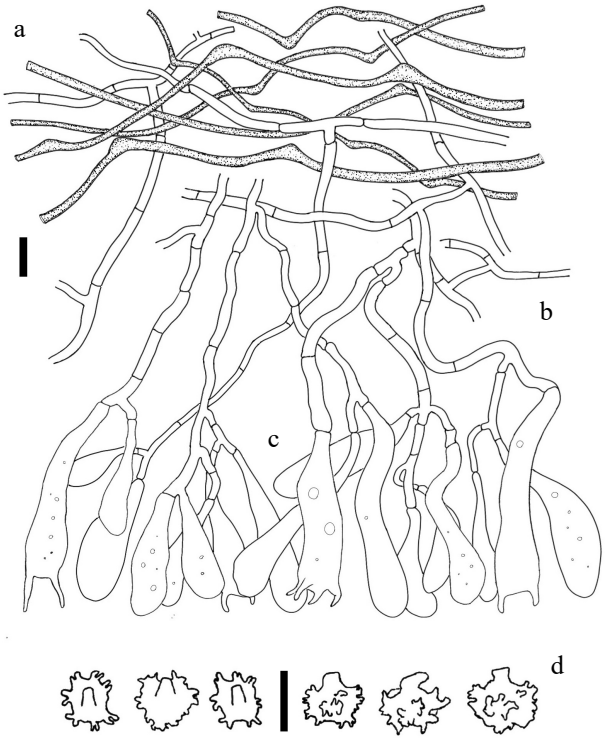

Fig. 2 *Polyozellus alinae* sp. nov. FLAS-F-65464: (a) subiculum; (b) subhymenium; (c) hymenium; (d) basidiospores. Reference bar = 10 μm.

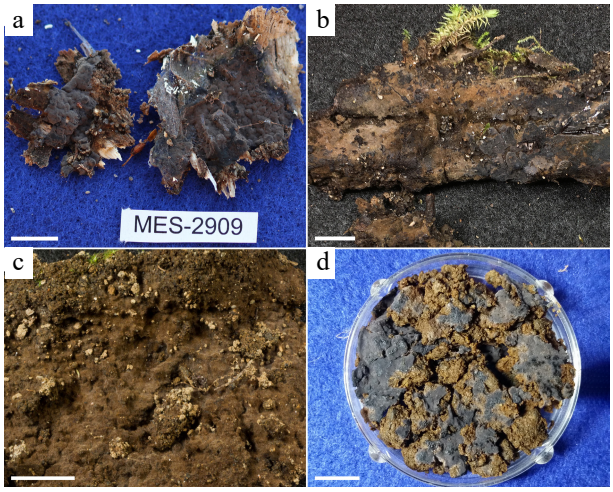

Fig. 3 Fresh specimens of *Polyozellus alinae* in different substrates and developmental stages. (a) FLAS-F-65264 (MES-2909) on *N. dombeyii* bark; (b) FLAS-F-65451 (MES-2895) on *N. dombeyii* wood; (c) FLAS-F-65337 (MES-2813) on soil; (d) FLAS-F-65538 (MES-2673) on soil. Reference bar = 1 cm.

diameter, thickened walls, seldom branching but regularly bending at angles with the lumen, almost occluded by the cell walls at the swollen vertices, brown in both KOH and water. Basidia 50–70 (90) x 10–13 (15) μm with two or four slightly curved sterigmata; clavate, narrowly clavate, or clavopedunculate, thin-walled, and frequently showing a slight constriction and greenish granular content in KOH. Sterigmata 9.5–11.5 μm long, curved. Basidioles present, of similar size to the basidia. Cystidia lacking. Basidiospores 6.5–7.5 (12) (length) x 6.5–7.5 (10) (width) x 4–5.5 (7) μm (height), subcircular and angular to nodulose in frontal view, covered in ornamentations di- or trichotomously branched, reaching 0.5 μm in length, ellipsoid

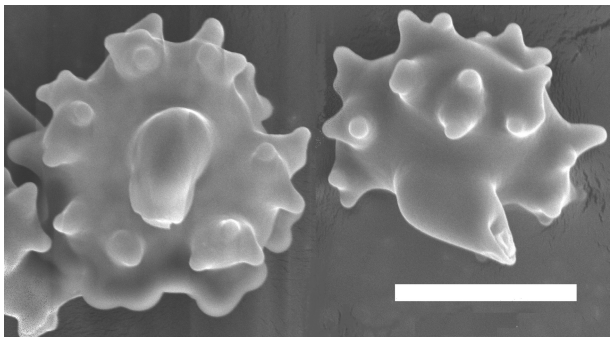

Fig. 4 Basidiospores of *Polyozellus alinae* in both basal and lateral views. Reference bar = 5 μm.

in lateral view, with rounded edges, pale brown to brown in KOH, inamyloid, with a notably developed apiculum, 2–3 μm long. No chlamydospores observed.

Additional materials studied — CHILE, Los Lagos, Salto de Petrohué, near the Sendero Solitario: 41°10'50.5" S 72°27'42.1" W, 16 April 2017 on soil and wood of *Nothofagus dombeyi*, Matthew E. Smith, FLAS-F-65451 (MES-2895). Puyehue National Park, big flat area near Antillanca, 16 April 2017, on the stream embankment, associated with *Nothofagus pumilio*, 40°46'48.4" S 72°12'31.5" W, Francisco Kuhar, FLAS-F-65350 (MES-2778). Puyehue National Park, Sendero los Derrumbes, close to Anticura: 40°39'25" S 72°10'21" W on soil, Francisco Kuhar 13 April 2017 FLAS-F-65377 (MES-2813).

Habitat — On soil or highly decayed wood in forests dominated by *Nothofagaceae* in Argentina and Chile.

Remarks — This species morphologically resembles *Polyozellus umbrinus*, a species with a holarctic distribution and a wide host range, but has a more intense purplish tinge in the dark gray patches of the basidiomes. Another diagnostic characteristic of *P. alinae* is the notable bending angle of the skeletal subicular hyphae, where the lumen is almost occluded by the cell walls at the swollen vertices. *P. alinae* is restricted to hosts in the genus *Nothofagus* and is often found on highly decayed wood, but can also be found fruiting directly on soil aggregates, a feature that is relatively rare among other Thelephoraceae in Patagonia, such as *Tomentellopsis* or *Tomentella*. These characteristics, along with the presence of both bisporic and tetrasporic basidia, clearly differentiate this new species from others in the genus. Exceptionally large spores were observed in some microscopic mounts, which might correspond to the spores produced on bisporic basidia.

Discussion

All available specimens of *P. alinae* were collected from the Los Lagos Region of Chile, on the western side of the Andes, where the species appears to be relatively abundant and produces conspicuous basidiomes on soil, leaf litter, and rotten woody debris. Despite extensive collecting expeditions in other areas, basidiomes of *P. alinae* were not located elsewhere in Andean Patagonia. However, a soil DNA sequence from GenBank (KY687675; Fig. 1) from the Argentinean side of the Andes and short DNA sequences of bird fecal samples from Araucanía and the Nahuelbuta coastal range in Chile (OTU6807, OTU3858[30], corresponding to *P. alinae*) suggest that this species has a much wider distribution. It is possible that *P. alinae* is rare in other areas or that it produces basidiomes at other times of the year.

As inferred from previous studies, distributions confined to the western slope of the Andes in Chile are usually considered to be related to high humidity requirements for fungal species in general; however, more restricted distributions, such as the one recently reported for the rare *Austroomphaliaster nahuelbutensis*[31], need further research to assess their relevance in conservation frameworks. Studies aimed at modeling the distributions of fungal species[32] have shown a high diversity of habitat suitabilities, by mainly depending on the annual precipitation and temperature as predictive variables, particularly in the case of infrequently occurring and inconspicuous corticioids[33]. The results of these studies suggest that basidiomes are more prolific and easier to locate in the western slope of the Andes and may help to explain why *P. alinae* was regularly found in the wet sites of Chile, but was found only based on environmental sequences in a wider range of sites. Geographically restricted corologies are among the factors considered by the International Union for Conservation of Nature (under criterion B) in assessing the conservation status of species in the Fungal Red Lists[34]. In this case, the assessment would be particularly well justified by the region's long-standing conservation issues, such as frequent fire events and timber exploitation[35]. However, more expeditions are needed to confirm whether the lack of sexually mature specimens is due to the low sampling effort in other areas. Also, further research is needed to evaluate the viability of potential biomedical applications, such as those reported for other representatives of the genus *Polyozellus*, e.g., antiviral[36] or anti-angiogenic[37] activities.

The fact that the genus *Polyozellus* has not been reported before in the Southern Hemisphere[17] (as is the case with the aforementioned *Tomentellopsis rosannae*) also underscores the immense value of Andean Patagonia for the study of the historical biogeography of the Thelephorales. This group shows its greatest biodiversity in the temperate forests of the Northern Hemisphere, and the biogeographical processes underlying the observed ecology have not been studied in depth. Further reports from the neotropics and Australia would help complete the datasets required to disentangle the history of this interesting group and verify the origins of unusual taxa such as *P. alinae*. The fact that this species has no known relatives in the Southern Hemisphere suggests that the origin of this taxon may be in the Northern Hemisphere; its spread to the southern South America may be attributed to the connectivity provided by the Panama land bridge approximately 3–6 million years ago[38]. However, further studies are required, focusing on poorly studied habitats and hosts, to better understand the global biogeography of *Polyozellus*.

Author contributions

The authors confirm their contributions to the paper as follows: study conception and design: Kuhar F, Smith ME, Nouhra E; data collection: Kuhar F, Nouhra E, Smith ME, Sandoval-Leiva P, Furci G, Caiafa MV; analysis and interpretation of the results: Kuhar F, Smith ME, Nouhra E; draft manuscript preparation: Kuhar F, Nouhra E, Smith ME. All authors reviewed the results and approved the final version of the manuscript.

Data availability

All the data used are included in the article. The sequences are cited by their accession numbers and are available from GenBank.

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Conflict of interest

The authors declare that they have no conflict of interest.

Dates

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