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Rediscovery of the Patagonian mushroom *Austroomphaliaster nahuelbutensis* 41 years after the type collection

Redescubrimiento del hongo patagónico *Austroomphaliaster nahuelbutensis* 41 años después de la colección tipo

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Abstract

Erected by Garrido in 1988, the genus *Austroomphaliaster* contains a single species, *A. nahuelbutensis*, which has not been cited again since its original description. Despite numerous expeditions across the *Nothofagus* forests, the species remains unlocated, and no morphological or molecular studies of the type have been published ever since. In 2023, an expedition led by the Fungi Foundation aimed to search for this lost species, resulting in the collection of two specimens consistent with the original description. One year later, mycologists from the University of Concepción found the same species a few kilometers from the type locality. A morphological revision of the reference materials, along

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with a phylogenetic study that included type ITS and LSU sequences, confirmed its identity. Our study places this putatively saprotrophic species within the family Fayodiaceae. *Austroomphaliaster nahuelbutensis* appears to have a very restricted distribution and should be included in conservation programs.

Keywords: Patagonia; Nahuelbuta; conservation; Fayodiaceae; Omphalinoid.

Resumen

Erigido por Garrido en 1988, el género *Austroomphaliaster* contiene una sola especie, *A. nahuelbutensis*, que no ha vuelto a citarse desde la descripción original. Numerosas campañas a lo largo de los bosques de *Nothofagus* no han podido volver a encontrarlo, y ningún estudio morfológico ni molecular del tipo se ha publicado desde entonces. En 2023, una campaña a la localidad tipo en Nahuelbuta fue liderada por la Fundación Fungi con el objetivo de buscar esta especie perdida, y resultó en el hallazgo de dos especímenes congruentes con la descripción original. Un año después, micólogos de la Universidad de Concepción encontraron la misma especie a algunos km de la localidad tipo. La revisión morfológica del material de referencia confirmó la identidad junto con el estudio filogenético que incluyó secuencias de ITS y LSU del tipo. Nuestro estudio ubica esta especie aparentemente saprotrófica en la familia Fayodiaceae. *Austroomphaliaster nahuelbutensis* parece tener una distribución muy limitada y debe ser incluido en programas de conservación.

Keywords: Patagonia; Nahuelbuta; conservación; Fayodiaceae; Ophalinoide.

INTRODUCTION

As a relatively young discipline, Conservation Biology has focused primarily on charismatic animal and tree species until recently, a strategy justified by the need to involve the population, especially the younger generations. In the last decades, however, the importance of preserving less conspicuous organisms has become evident, reaching even microorganisms due to their role in biogeochemical cycles and the innumerable metabolites of biomedical or industrial importance produced by them (Cockell & Jones, 2009).

For numerous reasons, fungi have been proposed as a target of much-needed conservation actions (e.g., Moore *et al.*, 2001). In recent years, the need for organized strategies led to including numerous species in the IUCN Fungal Redlist (Mueller *et al.*, 2022), an initiative that was particularly successful in South America (Hernandez Caffot *et al.*, 2023).

Using environmental DNA tools to survey the funga of particular environments resulted in the publication of invaluable contributions to fungal ecology (Truong *et al.*, 2017).

More recently, the information provided by the inventory of sporomes was recognized (Vašutová *et al*., 2023), and combined strategies were proposed to assess fungal communities (Truong *et al*., 2017). On the individual species level, detecting and studying rare taxa is paramount for establishing priorities in conservation and identifying landscapes to be protected (Molina, 2008).

The Nahuelbuta Mountain Range is part of the Chilean Coastal Cordillera, a mountain formation that runs parallel to the Andes Mountains along the Pacific coast. It hosts one of the most biodiverse temperate forests in the region, with numerous plant and animal endemisms. Still, a high degree of modification due to human activities (Wolodarsky-Franke & Herrera, 2011) indicates that this area needs to be studied, and actions must be undertaken to ensure its preservation. This range dates back to the Paleozoic, originating more than 500 million years ago and surpassing the Andes in age. Its coastal forests have survived successive glaciations intact, becoming a haven for biodiversity that, to this day, hosts highly endemic species but, at the same time, faces the greatest environmental disturbances and has scarce ecosystem protection (Wolodarsky-Franke & Herrera, 2011). Nahuelbuta's flora represents 55% of the endemic species present in continental Chile, including species that can reach over 1,500 years of age (Wolodarsky-Franke & Herrera, 2011). Habitat fragmentation, agricultural practices, fires, and replacing native forests with exotic tree plantations have led to the loss of approximately 70% of its vegetation. In addition to climate change, risk analyses conducted for this region show the most significant number of ecosystems classified as being at very high risk of impact and extinction (Pliscoff, 2022). Both nationally and internationally, the Nahuelbuta Mountain Range is considered a priority conservation area, making its study and ecosystem protection imperative.

Norberto Garrido was the first mycologist to undertake significant surveys of the funga of the Nahuelbuta range during the 1980s (Garrido, 1988). He collected a considerable number of basidiomycetes new to science, some of which are thought to be endemic in the coastal mountains of southern Chile.

Among the most interesting newly described taxa by Garrido is *Austroomphaliaster nahuelbutensis* Garrido, representing a new and so far monotypic genus.

According to Garrido this blackish brown, omphaloid mushroom resembles *Hygroaster* Singer (Hygrophoraceae) due to its thick gills and long basidia. Its ornamented spores point towards a relation with *Rhodocybe* Maire (Entolomataceae) or *Omphaliaster* Lamoure (incertae sedis), from which the new taxon derives its generic name. The subgenus *Heterosporula* Singer within *Fayodia* Kühner, now a synonym of *Gamundia* Raithelhuber, is also mentioned in the comments on *Austroomphaliaster* Garrido as a possible relative due to the dark basidiomes, the occurrence of clamp connections and the presence of cheilocystidia.

However, the unique combination of the above-mentioned attributes together with finely aculeate spore ornamentation and diverticulate hyphae of the pileipellis justifies a genus of its own. Due to its association with *Nothofagus* forests, Garrido proposed an ectomycorrhizal role for *A. nahuelbutensis*.

Although more mycological studies and field campaigns were conducted in the same area and habitat, some of which yielded taxonomical and chemical novelties (Lam *et al*., 2019, 2024), no further record of *A. nahuelbutensis* had been registered since the original collection made by Garrido.

In May 2023, the Fungi Foundation led an expedition to the type locality to find this species again based on Garrido's original description (1988) as part of the Search for Lost Species campaign by the conservation organization Re:wild. Basidiomes matching the diagnosis were found. One year later, another specimen of the species was detected close to Nahuelbuta National Park by students from Concepción University.

Based on the gathered material, this work aims to report the successful re-encounter of this fascinating mushroom and to assess its phylogenetic position and putative ecological role based on the DNA sequencing of the reference material, obtained for the first time for this species.

MATERIALS AND METHODS

Specimens matching the original description were collected in autumn 2023 and 2024, photographed, and dried on a forced air drier at 45°C. Reference material was accessed at the M Herbarium (Bavarian State Collection for Botany, Munich) and samples for DNA extraction were taken. The new collections were deposited in FFCL (Fungi Foundation Fungarium, Santiago) and CONCF (Fungarium Concepción University). Light microscopy of diagnostic features was performed by mounting the material in water, 3 % KOH, Melzer's reagent, and cotton blue. Spores were measured in 3 % KOH (n = 20).

DNA was extracted from dried gill tissue using the NZY Tissue gDNA Isolation kit (NZYTECH, Portugal) and amplified by Polymerase Chain Reaction (PCR) of the nuclear rDNA ITS1-5.8S-ITS2 region (ITS) with the forward primer ITS1F and reverse primer ITS4 (White et al. 1990) and NZYTaq II DNA polymerase the manufacturer's protocol (NZYTECH, Portugal). PCR of the nuclear large RNA subunit (28S) was performed using the same protocol with forward primer LR0R (Hopple & Vilgalys, 1994) and reverse primer LR5 (Tedersoo *et al*., 2008).

PCR products were visualized on 1.5% agarose gels stained with the NZYDNA loading dye. Amplicons were sequenced at Macrogen (South Korea). Sequences were then edited manually.

Table 1. GenBank accession numbers and vouchers of the sequences used in the phylogenetic analyses.

Tabla 1. Números de acceso de GenBank y materiales de referencia de las secuencias utilizadas en los análisis filogenéticos.

Species	Voucher	LSU	ITS
Austroomphaliaster nahuelbutensis	FFCL1934	PV362215	PV350692
Austroomphaliaster nahuelbutensis	FFCL1933	PV362215	PV350691
Austroomphaliaster nahuelbutensis	M-0307482	PV362217	PV350693
Caulorhiza hygrophoroides	DAOM172075	AF042640	-
Conchomyces bursaeformis	RV95 302	AF042603	-
Conchomyces bursaeformis	RV95 695	AF261376	-
Conchomyces bursiformis	15830	MF784865	-
Fayodia bisphaerigera	OW241 19	OR863499	OR863429
Fayodia gracilipes	DAOM187531	AF261377	AF261377
Fayodia gracilipes	TUB 011585	AF261377	-
Fayodia gracilipes	T 850	KC176299	KC176299
Gamundia leucophylla	DAOM192749	EU669382	EU669382
Gamundia leucophylla	p672L	EU669424	EU669424
Gamundia striatula	CBS 479 50	MH856713	MH856713
Gamundia striatula	F-3654	PQ639143	PQ639143
Gamundia striatula	F-1098	PQ653137	PQ653137
Gamundia striatula	JL45 18	OR863431	OR863431
Leucopaxillus giganteus	AMB 18857	OR863493	OR863423
Myxomphalia maura	DAOM187839	AF261378	-
Myxomphalia maura	377644	MT735143	MT735143
Omphalina pyxidata	AMB:19294	OR863534	OR863467

All available high-quality sequences were retrieved using BLAST (Zhang *et al.*, 2000) from the GenBank NCBI database (Clark *et al.*, 2015) and listed in Table 1, and sequences corresponding to *Leucopaxillus giganteus* (Sowerby) Singer and *Omphalina pyxidata* (Bull.) Quél. were used as an outgroup in light of the results of Vizzini *et al.* (2024). ITS and LSU sequences were separately aligned with the L-INS-i strategy as implemented in MAFFT 7.0 (Katoh & Standley, 2014), and the concatenated alignment was partitioned after verifying that no incongruences occurred among single-gene phylogenies. The final dataset consisted of 1576 characters. The credibility of evolutionary models for each partition was estimated independently by JModel Test 2.1.6 (Darriba *et al.*, 2012), and the GTR + G + I model was selected for both partitions. The final concatenated alignment was analyzed with Maximum likelihood (ML) performed in PHYML as implemented on the Montpellier Bioinformatics Platform, France (http://www.atgc-montpellier.fr/phyml/), following Guindon *et al.* (2010), and Bayesian inference was conducted with MrBayes (Huelsenbeck & Ronquist, 2001) with 10,000,000 generations starting with a random tree and four parallel chains and sampling every 1000 trees. The first 100,000 generations were discarded as burn-in. TRACER1 ensured stationarity after the first 100,000 generations (http://evolve.zoo.ox.ac.uk/software.html/tracer/).

Convergence, stationarity, and sample size were checked in Tracer v1.6 (Rambaut *et al*., 2014), and the final trees from each run were merged to generate a maximum credibility tree in MrBayes 3.2.6.

For scanning electron microscopy of basidiospores, small pieces of dehydrated lamellae were fixed on SEM mounts with patches of double-sided adhesive tape, metalized with gold and observed in a JSM-6380LV scanning electron microscope (JEOL, Tokyo, Japan) at the Microscopy Laboratory of Concepción University.

RESULTS

Phylogeny

Two selected specimens of the new collections of *Austroomphaliaster nahuelbutensis* grouped together with the sequences from the type material with a high percent ITS (99.5%) and LSU similarity (99.9%), good bootstrap (93%) and posterior BP (0.95) support (Fig. 1). Sequences representing the genera *Fayodia* Kühner, *Gamundia* Raithelh., *Myxomphalia* Hora, *Conchomyces* Overeem, and *Austroomphaliaster* grouped in well-supported, separate clades within the family Fayodiaceae. One reference sequence (AF042640) of a specimen identified as *Caulorhiza hygrophoroides* (Peck) Halling (Moncalvo *et al*., 2000) shows a high percent identity (> 99.5%) with four sequences of *Gamundia* spp., suggesting that its identity needs to be revised. More profound affinities among genera cannot be inferred from our dataset due to the lack of bootstrap or posterior BP support.

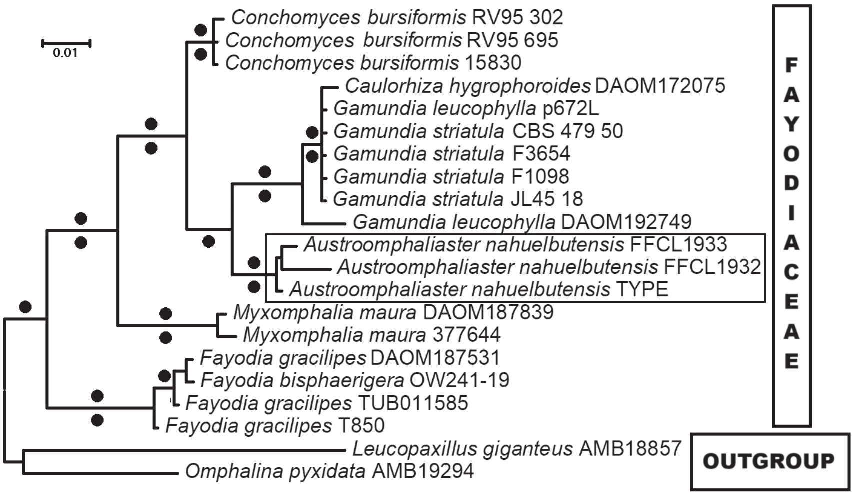

Fig. 1. Maximum Likelihood tree based on two loci (ITS and LSU). Significant support values of ML bootstrap (>75%) and Bayesian PS (>0.95) are indicated with black dots (above and below the branches, respectively).

Fig. 1. Arbol de Máxima Verosimilitud basado en dos loci (ITS y LSU). Valores significativos de soporte de ML (>75%) y probabilidad posterior (>0.95) se indican con círculos negros por encima y debajo de las ramas respectivamente.

Taxonomy

Austroomphaliaster nahuelbutensis Garrido,
Bibl. Mycol. 120: 199 (1988). Figs. 2, 3, and 4

Pileus 16–38 mm diam. hemispheric-depressed to umbilicate, dry, with a waxy texture when moist and a thin context, olive grey to dark grey becoming clear towards the margin. **Gills** broadly attached, emarginate to almost decurrent, thick, numerous, relatively distant, greyish white. **Stipe** 53–85 x 4–8 mm, cylindrical or somewhat thickened towards the base, centrally attached, frequently hollow, concolorous with the pileus, finely striate on the surface, rarely with isolated fibrils but without veil. **Taste and smell** mildly raphanoid. Not reacting to KOH. Spore print white. **Spores** 5.5–6-5 x 4.5–5.5 μm, subglobose to broadly elliptic, spinulose, inamyloid, cyanophilous, hyaline. **Basidia** 39–51 X 9–10 μm, tetrasporic, hyaline. **Cheilocystidia** 35–42 x 9–10 μm, clavate to cylindrical, rarely with short projections at the tip, hyaline. **Pileipellis** of cylindrical hyphae, 3–8 μm in diam., sometimes with simple to coralloid excrescences and greyish-brown pigmentation. **Stipitipellis** of cylindrical, in part diverticulate hyphae, 3–7 μm in diam. **Hymenophoral trama** of interwoven hyphae of 3–5 μm and oleiferous hyphae of 4–8 μm diam. **Clamp connections** present.

Fig. 2. Basidiomes of *A. nahuelbutensis* in situ (FFCL 1933).

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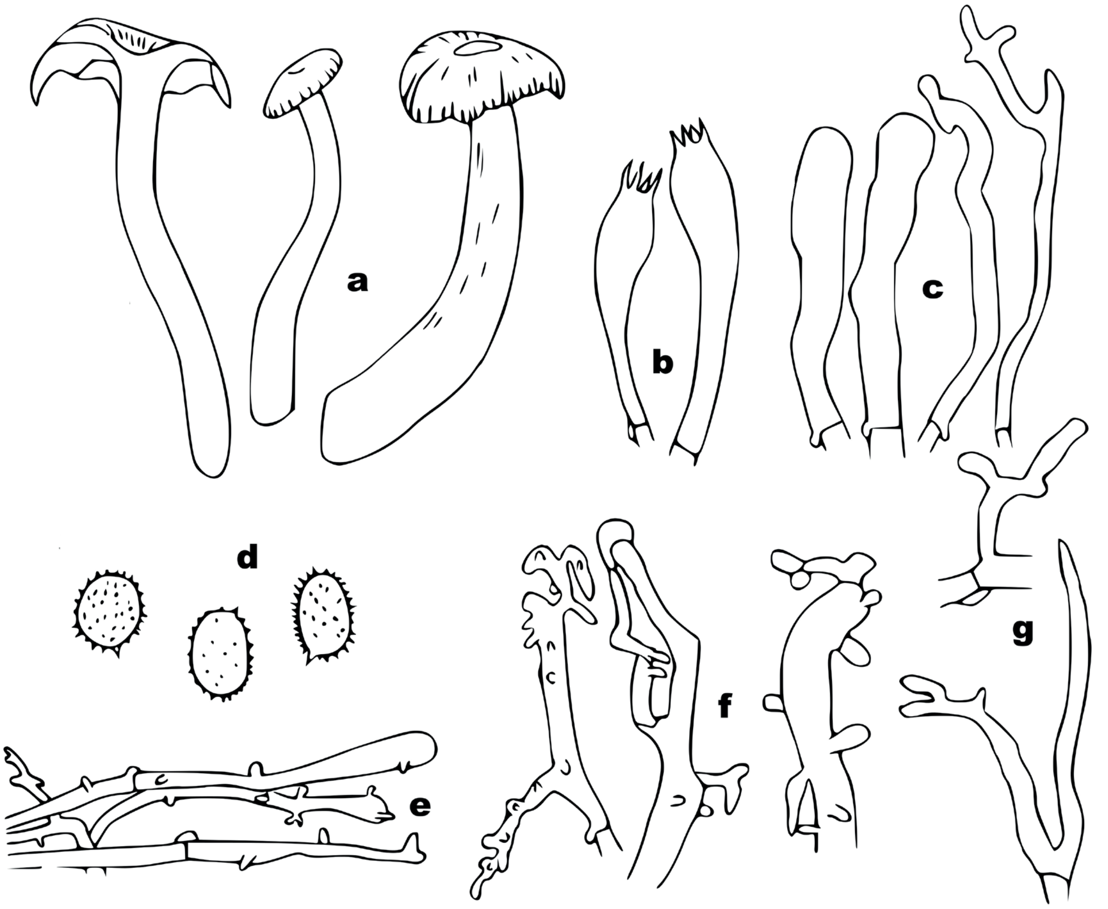

Fig. 3. *Austroomphaliaster nahuelbutensis* Type specimen: a, basidiomes; b, basidia; c, cheilocystidia; d, basidiospores; e, pileipellis; f, cuticular hyphae in detail (X1000); g, sitpitipellis elements. Modified from Garrido (1988) with permission from Schweizerbart Science Publishers.

Fig. 3. Tipo de *Austroomphaliaster nahuelbutensis*: a, basidiomas; b, basidios; c, queilocistidios; d, basidiosporas; e, pileipelis; f, detalle de las hifas cuticulares (X1000); g, elementos de la stipitipellis. Modificado de Garrido (1988) con permiso de Schweizerbart Science Publishers.

Habitat: On soil under *Nothofagus obliqua*, *N. antarctica*, in small groups.

Distribution: The available verified collections are restricted to Angol.

Studied material: CHILE, Angol, Parque Nacional Nahuelbuta, 19 May 1982, Garrido 465, M-0307482 (ISOTYPE). Camino Cerro Anai, 37°47’66”S 73°00’19,05”W, 1292 m asl, 20 May 2023, FFCL1933. Ruta P-562 Cayucupil, acceso Cañete: 37°48’76”S 73°01’54,96”W, 1245 m asl, 20 May 2023, FFCL1934. Ruta 150-P, road from Angol to Nahuelbuta National Park, Chanleo, 37°46’38”S 72°49’48”W, 720 m asl, 25 May 2024, on soil and leaf litter under *Nothofagus obliqua, CONCF 2212.*

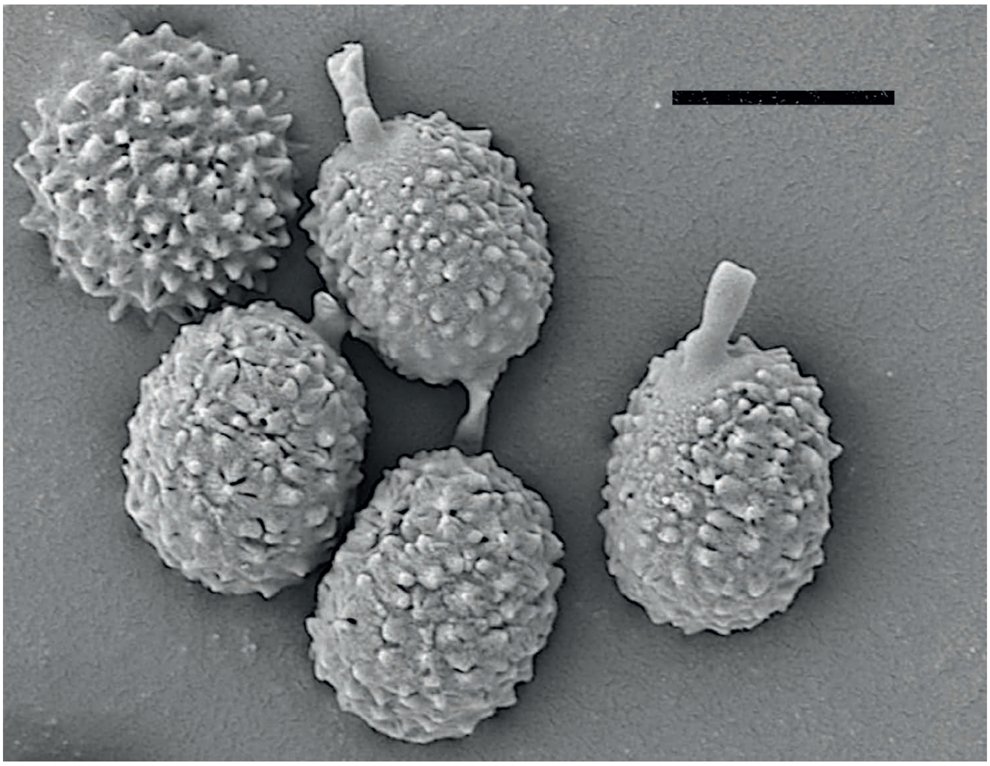

Fig. 4. SEM image of *A. nahuelbutensis* basidiospores (CONCF 2212). Bar = 5µm.

Fig. 4. Imágenes de microscopia electrónica de barrido de las basidiosporas de *A. nahuelbutensis* (CONCF 2212). Barra = 5µm.

DISCUSSION

The family Fayodiaceae was erected by Jülich (1981) to accommodate the omphalinoid genera *Fayodia* and *Myxomphalia.* However, features such as the spore wall ornamentation were variable in the group's original conformation. In a recent study, Vizzini *et al*. (2024) showed that *Fayodia bisphaerigera* and *Gamundia striatula* form an independent clade within the suborder Tricholomatineae and consequently applied the name Fayodiaceae to this clade. The same authors discuss the history and features of the family in depth, reaching conclusions supported by our present phylogenetic analyses. Under this concept, the family includes the genera *Myxomphalia*, *Conchomyces*, *Fayodia*, and *Gamundia*, all of them with verruculose basidiospore walls that, in the case of *Myxomphalia*, can only be observed under SEM. They also treat *Caulorhiza* as a probable member of this family following Moncalvo *et al*. (2000), who, in turn, based this conclusion on the sequence mentioned in the results, but in our view, no morphological affinities support this placement.

Our analyses show that from the phylogenetic point of view, the genus *Austroomphaliaster* is valid if we consider the genus separation accepted in modern literature (e.g., Antonin and Noordeloos, 2004 or more recently, Vizzini *et al*., 2024).

However, the group has not been exhaustively sampled in terms of DNA, and, given the complex morphological relations between the described genera, the internal relations and delimitations might need to be revised in the future if more materials are sequenced.

Regarding its ecological role, *A. nahuelbutensis* was originally understood to be an ectomycorrhizal species, probably because its occurrence coincides with *Nothofagus* spp. However, the database released by Põlme *et al*. (2020) listed it as saprotrophic. Although the particular reasons for this placement are not specified for each genus, two main aspects lead us to support the non-mycorrhizal interpretation. First, no root tip-associated DNA sequences are retrieved in public databases (UNITE, GenBank), and second, no ectomycorrhizal fungi seem to occur within the family as circumscribed by our analysis.

The narrow geographical area where all available collections of this species were found suggests a limited distribution. This assumption is supported by the numerous expeditions and deep sampling efforts in Andean Patagonia by expert mycologists since the beginning of the 20th century that did not report any species that could be associated with *A. nahuelbutensis*. A long history of monoculture forestry and cattle farming threatened the survival of endangered or declining species in this area (Aguayo *et al*., 2009). This, together with the high landscape fragmentation and the reduction of the native forest surface (Machuca Flores, 2023), suggests that closer supervision of the population of this species might be of high importance, not only for its preservation but also for the overall health of the delicate environment of the Nahuelbuta range. Also, science outreach actions like the ones implemented by the Fungi Foundation must be encouraged, supported, and replicated by governmental institutions. Furthermore, a deeper understanding of the chorology of this and other rare fungal species is paramount to designing strategic conservation policies and territorial planifications. Lastly, we suggest that *A. nahuelbutensis* be proposed to both the Chilean and Global Fungal Redlist initiatives for its threat of extinction to be determined and conservation actions be designed as an effort to ensure the species' survival.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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