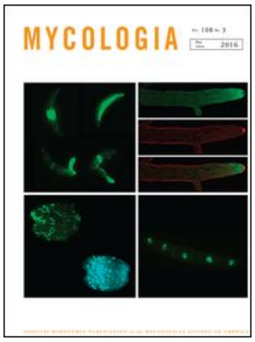

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Species and genera in Aleurodiscus sensu lato as viewed from the Southern Hemisphere

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ABSTRACT

Phylogenetic relationships of 12 species in *Aleurodiscus* sensu lato (Stereaceae, Russulales) described from the Patagonian forests of Chile and Argentina were investigated based on sequences of nuc rDNA internal transcribed spacer region ITS1-5.8S-ITS2 (ITS) and the D1–D2 domains of nuc 28S rDNA (28S). A new genus and a new species are presented, and 10 new combinations proposed. The genus *Gloeosoma* is shown to be phylogenetically well supported and morphologically circumscribed; it includes *G. vitellinum* (type species), *G. mirabile*, comb. nov., *G. zealandicum*, comb. nov., and *Gloeosoma decorticans*, sp. nov., which is newly described from Chile. The new genus *Stereodiscus* is proposed to accommodate a group of taxa characterized by an austral distribution and morphologically by smooth, thin-walled, amyloid basidiospores and a lack of gloeocystidia and acanthocystidia; three species develop *Stereum*-like basidiomata and two species present discoid ones. The new genus includes the species formerly known as *Aleurodiscus antarcticus, A. limonisporus, A. parmuliformis, A. patagonicus*, and *A. triviale*. Specimens of *Stereodiscus parmuliformis* (*A. parmuliformis*) from New Zealand (where it was originally described) and southern Chile are shown to be phylogenetically conspecific, which confirms its presence in Patagonia. *Gloeosoma* and *Stereodiscus* are shown to be distantly related to *Aleurodiscus* s. str. and other genera in Stereaceae. The new combinations *Aleurocystidiellum bernicchiae, Aleurocystidiellum hallenbergii*, and *Acanthobasidium quilae* are proposed based on morphology and phylogenetic analyses, and *Aleurodiscus cerussatus* is shown to be a cryptic species complex.

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INTRODUCTION

Aleurodiscus Rabenh. ex J. Shröt. (Stereaceae, Russulales), a corticioid genus of wood-rotting fungi, has been the focus of many studies that reported on its global diversity and phylogenetic relationships in recent years (Wu et al. 2010, 2019; Dai and He 2016; Dai et al. 2017a, 2017b; Phookamsak et al. 2019). The genus, in a broad sense, is rather easy to recognize morphologically (Núñez and Ryvarden 1997): amyloid basidiospores with thin to thick hyaline walls that are smooth, verruculose to aculeate; a mono- or dimitic hyphal system with simple-septate or clamped generative hyphae and skeletal hyphae; and the presence or lack of an array of cystidial types: gloeocystidia (sulfopositive or sulfo-negative) that may be club-shaped to moniliform, acanthocystidia, dendrophyses, botryophyses, and incrusted pseudocystidia. The high level of morphological variation displayed by *Aleurodiscus* s. lat. led, in the past, to several proposals to divide it into smaller genera: *Acanthobasidium* Oberw., *Acanthofungus* Sheng H. Wu, Boidin & C.Y. Chien, *Acanthophysellum* Parmasto, *Acanthophysium* (Pilát) G. Cunn., *Aleurobotrys* Boidin, *Aleurocystidiellum* P. A. Lemke, *Aleurodiscus* s. str., *Aleuromyces* Boidin & Gilles, *Gloeosoma* Bres., and *Neoaleurodiscus* Sheng H. Wu. Wu et al. (2001, 2010) summarized the main morphological differences between the different genera, and Boidin (1990), Boidin and Lanquetin (1984), and Boidin et al. (1986) presented the scant available knowledge regarding their cultural features,

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mating systems, and nuclear behavior. Phylogenetic studies supported the monophyly of only a small group of these names, which include *Aleurocystidiellum* and *Acanthobasidium*, whereas the others still require deeper analysis, since they were either intermixed with other taxa in the Stereaceae or possess or lack characters that intermingle with those present in other genera of the family. In the case of *Aleurocystidiellum*, it was shown that the genus corresponds to a family of its own (Larsson 2007) distantly related to the Stereaceae. Thus, the question remained whether to treat *Aleurodiscus* in a broad or a narrow sense (Wu et al. 2019). Gorjón (2020) summarized the proposed genera, their features, and their taxonomic and phylogenetic status and presented a key for their identification within the amyloid, spore-bearing corticioid fungi.

In Patagonia in southern South America, *Aleurodiscus* s. lat. has been investigated by several studies (Greslebin 2002; Gorjón and Hallenberg 2012; Gorjón et al. 2013; Phookamsak et al. 2019) that included specimens from Argentina and Chile. The forests of southern Argentina and Chile belong to a biome characterized by a historical relationship with Gondwanic landmasses and isolation from the rest of the Americas (Crisci et al. 1991; Sanmartín and Ronquist 2004; Moreira-Muñoz 2011). It is an area with numerous districts and forest types that represents a hot spot of species diversity and peculiarities reflected in its particular biota (Hueck 1978; Cabrera and Willink 1980; Donoso 1993; Morrone 2001). To date, 11 species of *Aleurodiscus* s. lat. have been accepted and/or described: *A. antarcticus* (Speg.) Ryvarden, *A. bernnichiae* Gorjón, Gresl. & Rajchenb., *A. cerussatus* (Bres.) Höhn. & Litsch., *A. corticola* Gorjón, Gresl. & Rajchenb., *A. hallenbergii* Gorjón, Gresl. & Rajchenb., *A. parmuliformis* G. Cunn., *A. patagonicus* Nogal et al., *A. quilae* Gorjón, Gresl. & Rajchenb., *A. stratosus* Gorjón, Gresl. & Rajchenb., *A. trivialis* (Speg.) Gresl., and *A. vitellinus* (Lév.) Pat. (TABLE 1).

During field work that aimed to collect russuloid fungi from central Chile (Bío Bío Province), we found an undescribed taxon of *Aleurodiscus*. This prompted the examination of morphologically related taxa, and the need to evaluate those already known within a phylogenetic framework, including the endemic *A. vitellinus*, which also serves as the type species of *Gloeosoma*. This was the first time *A. vitellinus* was included in this kind of research. In recent years, this species attracted increased attention due to its edibility (Toledo et al. 2014; Toledo and Barroetaveña 2017) and production of secondary metabolites that may be of medical importance (González-Ramírez et al. 2018). The aims of this study were to (i) analyze the Patagonian taxa of *Aleurodiscus* s. lat. from a phylogenetic perspective and (ii) discuss the validity of the several proposed genera segregated from *Aleurodiscus* s. lat.

MATERIALS AND METHODS

Studied areas.—Samples were collected in forested regions of Coronel, Bio Bio Province, southern Chile, in the Valdivian Rainforest, and the subtropical xerophytic and durifoliate forests of southern Chile, Subantarctic Province, Subantarctic Domain, Antarctic Region (Hueck 1978; Cabrera and Willink 1980; Donoso 1993). Specimens and cultures obtained in previous works were also incorporated into this study (see below).

Specimens and strains studied.—Herbarium specimens and cultures pertaining to *Aleurodiscus* s. lat. described from Patagonia (both Argentina and Chile) were used to perform morphological and phylogenetic analyses (Gorjón et al. 2013) (TABLE 2). Specimens were gathered and oven dried overnight at 45 C. Fresh portions of basidiomata were separated in order to obtain cultures from either contextual tissue or spore prints, which were then grown on 2% malt extract agar. Specimens and strains were deposited at HCFC and with the culture collection CIEFAPcc. Specimen duplicates were deposited at CONC-F. Morphological description of basidiomata followed standardized methods (Gorjón et al. 2013; Wu et al. 2019). Herbarium codes follow Thiers (continuously update; accessed Aug 2020).

Morphological studies.—Basidiome morphology was examined using a Zeiss Stemi 508 stereo microscope (Göttingen, Germany) and a Leica DM2500 Led compound microscope (Weltzlar, Germany) with a Leica DFC7000T camera attached. Microscopic structures were studied by mounting tissue sections of dried basidiomes in 3% KOH supplemented with 1% phloxine and Melzer's reagent (IKI− = nonamyloid, IKI+ = amyloid), the latter prepared according to Kirk et al. (2008). The aldehyde reaction in cystidia was checked with sulfovanillin prepared according to Hjortstam et al. (1987). Thirty measurements were performed of each structure. Basidiospore measurements were made in Melzer's reagent and expressed as L × W (L = mean basidiospore length as the arithmetic average of all basidiospores ± SD, W = mean spore width as the arithmetic average of all basidiospores ± SD) and n/s = number of basidiospores measured from a given number of specimens.

Table 1. Species of *Aleurodiscus* s. lat. from the Patagonian Andean forests of Argentina and Chile, with their associated names (basionym and synonyms), hosts (as found in Patagonia), and distribution.

Species	Name of taxon accepted here (see text)	Hosts (in Patagonia)	Distribution
Aleurodiscus antarcticus ≡ *Corticium antarcticum* Speg. = *Stereum antarcticum* (Speg.) Rajchenb. = *Stereum magellanicum* Hjortstam & Ryvarden	*Stereodiscus antarcticus*, comb. nov.	*Nothofagus betuloidesNothofagus dombeyi* *Nothofagus pumilio*	Endemic to Patagonia (Argentina and Chile)
Aleurodiscus bernicchiae	*Aleurocystidiellum bernicchiae*, comb. nov.	*Fitzroya cupressoidesPilgerodendron uviferum* *Podocarpus salignus*Saxegothaea conspicua*	Endemic to Patagonia (Argentina and Chile)
Aleurodiscus cerussatus ≡ *Corticium cerussatum* Bres. = *Acanthophysellum cerussatum* (Bres.) Parmasto	*Aleurodiscus cerussatus*	*Austrocedrus chilensisChusquea culeouEmbothrium coccineum* *Lomatia hirsutaNothofagus antarctica* *Nothofagus dombeyiNothofagus pumilio*	Cosmopolitan (numerous hosts)
Aleurodiscus corticola	*Aleurodiscus corticola*	*Nothofagus betuloidesNothofagus dombeyi* *Nothofagus pumilio*	Endemic to Patagonia (Argentina)
Aleurodiscus hallenbergii	*Aleurocystidiellum hallenbergii*, comb. nov.	*Austrocedrus chilensisFitzroya cupressoides* *Pilgerodendron uviferum*	Endemic to Patagonia (Argentina)
Aleurodiscus parmuliformis = *Aleurodiscus pateriformis* G. Cunn.	*Stereodiscus parmuliformis*, comb. nov.	*Nothofagus dombeyi*	Known from Patagonia (Chile) and New Zealand (numerous hosts)
Aleurodiscus patagonicus	*Stereodiscus patagonicus*, comb. nov.	Undetermined host(s)	Endemic to Patagonia (Chile)
Aleurodiscus quilae	*Acanthobasidium quilae*, comb. nov.	*Chusquea quila*	Endemic to Patagonia (Chile)
Aleurodiscus stratosus	*Aleurodiscus stratosus*	*Saxegothaea conspicua*	Endemic to Patagonia (Argentina)
Aleurodiscus trivialis ≡ *Corticium triviale* Speg. = *Aleurodiscus fuegianus* Núñez & Ryvarden	*Stereodiscus trivialis*, comb. nov.	*Nothofagus antarcticaNothofagus betuloides* *Nothofagus dombeyiNothofagus pumilio*	Endemic to Patagonia (Argentina)
Aleurodiscus vitellinus ≡ *Exidia vitellina* Lév. = *Gloeosoma vitellinum* (Lév.) Bres.	*Gloeosoma vitellinum*	*Nothofagus dombeyiNothofagus pumilio* *Nothofagus* sp.	Endemic to Patagonia (Argentina and Chile)

*New host determined from newly found specimens (see TABLE 2).

Table 2. Strains and herbarium specimens studied, with their new GenBank sequence numbers.

Species	Strain CIEFAPcc or specimen HCFC no.	Location	Host	Collector	Number	Date	GenBank accession nos.	
							ITS	28S
Aleurodiscus antarcticus	227cc	Argentina, Chubut, Futaleufú, P.N. Los Alerces, L. Rivadavia, A. Coligual	*Nothofagus dombeyi*	M. Rajchenberg	11265	11 Jun 1997	MT831048	MT831028
	302cc	Argentina, Chubut, P.N. Los Alerces, Lago Futalaufquen, Cascada Irigoyen	*Nothofagus dombeyi*	M. Rajchenberg	12098	4 May 2002	MT831044	MT831024
	HCFC 1308	Argentina, Chubut, P.N. Los Alerces, Lago Rivadavia	*Nothofagus dombeyi*	S.P. Gorjón	3313	6 May 2011	MT831046	MT831026
	HCFC 1309	Argentina, Tierra del Fuego, Paso Garibaldi	*Nothofagus* sp.	M. Rajchenberg	11857	10 Nov 1998	MT831049	MT831029
A. bernicchiae	HCFC 1310	Chile, Bío Bío, Chillán, Los Lleuques	*Podocarpus salignus*	M. Rajchenberg	12636	1 Sep 2018	—	MT831017
	HCFC 1311	Argentina, Río Negro, P.N. Nahuel Huapi, Puerto Blest	*Saxegothaea conspicua*	S.P. Gorjón	3217	12 Apr 2011	MT831037	MT831016
	HCFC 1312	Chile, Los Lagos, Chiloé, Reserva Sendero Darwin	*Podocarpaceae*	M. Rajchenberg	12675	3 Oct 2019	MT831038	MT831018
A. cerussatus	HCFC 1313	Argentina, Chubut, P.N. Los Alerces, Lago Futalaufquen, Arroyo Irigoyen	*Aristotelia chilensis*	M. Rajchenberg	s.n.	4 Jan 1998	MT831055	MT831036
	HCFC 1314	Argentina, Chubut, Futaleufú, Los Cipreses	*Austrocedrus chilensis*	S.P. Gorjón	3004	15 Oct 2010	MT831058	—
	HCFC 1315	Argentina, Chubut, P.N. Lanín, Lago Quillén	*Nothofagus obliqua*	S.P. Gorjón	3353	11 May 2011	MT831053	MT831034
	HCFC 1316	Argentina, Chubut, P.N. Los Alerces, Sector La Balsa	*Austrocedrus chilensis*	S.P. Gorjón	3031	4 Mar 2011	MT831054	MT831035
A. mirabilis	405cc	Brazil, Rio Grande do Sul, Campo Bom	—	J.M. Baltazar	JMB2152	23 Sep 2010	MT568513	—
A. parmuliformis	HCFC 1317	Chile, X Región, Ventisquero Yelcho	—	S.P. Gorjón	3104	4 Apr 2011	MT831051	MT831031
A. quilae	HCFC 1318	Chile, X Región, Ventisquero Yelcho,	*Chusquea quila*	S.P. Gorjón	3088	4 Apr 2011	MT831059	—
A. stratosus	HCFC 1319	Argentina, Río Negro, P.N. Nahuel Huapi, Puerto Blest	*Saxegothaea conspicua*	S.P. Gorjón	3219	12Apr 2011	MT831052	MT831033
A. trivialis	232cc	Argentina, Neuquén, P.N. Nahuel Huapi, paso fronterizo C. Samoré	*Nothofagus pumilio*	M. Rajchenberg	AG 1141	30 Oct 1997	MT831043	MT831023
	228cc	Argentina, Chubut, Futaleufú, P.N. Los Alerces, L. Rivadavia, A. Coligual,	*Nothofagus dombeyi*	M. Rajchenberg	11264	11 Jun 1997	MT831047	MT831027
	HCFC 1320	Argentina, Chubut, P.N. Los Alerces, río Rivadavia	*Nothofagus dombeyi*	S.P. Gorjón & M. Rajchenberg	3308	6 May 2011	MT831050	MT831030
	HCFC 1321	Argentina, Tierra del Fuego, Ushuaia, Estancia El Valdéz	*Nothofagus sp.*	A. Greslebin	747	2–4 Nov 1996	MT831056	—
	HCFC 1322	Argentina, Neuquén, Los Lagos, San Martín de los Andes, Laguna Rosales	*Nothofagus pumilio*	M. Rajchenberg	11721	17 Aug 1998	MT831045	—
Gloeosoma decorticans	HCFC 1307	Chile, Bío Bío, Concepción, Coronel, Fundo Escuadrón	*Eucryphia cordifolia*	M. Rajchenberg	12665	1 May 2019	MT831042	MT831022
	HCFC 1306	Chile, Bío Bío, Concepción, Coronel, Fundo Escuadrón	*Eucryphia cordifolia*	M. Rajchenberg	12666	1 May 2019	MT831041	MT831021
G. vitellinum	259cc	Argentina, Chubut, P.N. Los Alerces, rio Rivadavia	*Nothofagus dombeyi*	S.P. Gorjón	2743	6 May 2010	MT831040	MT831020
	646cc	Argentina, Chubut, P.N. Los Alerces, Lago Futalaufquen, Arroyo Centinela	*Nothofagus dombeyi*	J. Monges & G. González	s.n.	6 Jun 2019	MT831039	MT831019

Note. P.N. = Parque Nacional

DNA extraction and sequencing.—The nuc rDNA internal transcribed spacer region (ITS) and portions of the 28S gene region were amplified from cultures or dried herbarium specimens using the UltraClean Microbial DNA Isolation Kit (MoBio Laboratories, Carlsbad, California) per the manufacturer's instructions. DNA was amplified with primers ITS4 and ITS5 for ITS (White et al. 1990) and LR0R and LR7 for 28S (Vilgalys and Hester 1990; Cubeta et al. 1991). Polymerase chain reaction (PCR) protocols followed Dai and He (2016). Amplified fragments were sequenced at the DNA Synthesis and Sequencing Facility, Macrogen (Seoul, South Korea). Sequences were assembled and edited with BioEdit 7.0.9.0 (Hall 1999). Newly generated sequences were submitted to GenBank (TABLE 2).

Phylogenetic analyses.—A molecular phylogeny was inferred from the combined data set of ITS and 28S. The ITS and 28S sequences from our *Aleurodiscus* s. lat. collections were compared with those in the National Center for Biotechnology Information (NCBI) database using the BLASTn tool (Altschul et al. 1990). For phylogenetic analyses, the Patagonian sequences were placed in an alignment of ITS and 28S sequences of Stereaceae and allied fungi, including *Aleurocystidiellum*, as previously generated by Wu et al. (2001) and Phookamsak et al. (2019) (TABLE 2). *Gloeodontia discolor* and *G. pyramidata* were chosen as outgroups based on the results of Tian et al. (2018) and Phookamsak et al. (2019). Sequences were aligned with MAFFT 7.470 (using the –auto flag) (Katoh and Standley 2013), and the final alignment was deposited at TreeBase (S26696).

The concatenated data set was partitioned by gene region and analyzed with maximum likelihood (ML) and Bayesian inference (BI). ML was run via RAxML 8.2.10 (Stamatakis 2014) with 1000 bootstrap iterations and a GTRGAMMA model under the default parameters (Stamatakis 2014). BI analyses were performed using MrBayes 3.2.7a (Ronquist et al. 2012). Evolutionary models for both partitions were estimated independently using the Akaike information criterion (AIC; Akaike 1974) implemented in jModelTest (Posada 2008; http://darwin.uvigo.es). The GTR+G and GTR+I+G models were selected for ITS and 28S, respectively. Eight million generations were performed in BI analyses using four chains and other default parameters, sampling trees and other parameters every 1000 generations. Trees sampled from the first 25% of the generations were discarded, by which point the average standard deviation of split frequencies had reached <0.01 and potential scale reduction factors (PSRFs) approximated 1.0 for all parameters. Bayesian posterior probabilities (PPs) were then calculated. Alignment of the data set was submitted to TreeBASE (S26008).

RESULTS

Phylogenetic analyses.—Twenty-five ITS and 28S sequences were generated for this study. The combined data set contained 74 ITS and 89 28S sequences from 104 samples representing 102 ingroup taxa and two outgroups. The data set had an aligned length of 1565 sites (ITS: 673; 28S: 892). The topologies of trees obtained from ML and BI were almost the same. FIG. 1 shows only the BI tree, with maximum likelihood bootstraps (MLB) ≥70% and Bayesian posterior probabilities (BPPs) ≥0.95 labeled along the branches.

Most Patagonian collections were nested within the Stereaceae (FIG. 2), but several also clustered within the distantly related genus *Aleurocystidiellum*. Those embedded in the Stereaceae clustered within *Acanthobasidium, Aleurodiscus* s. str., the newly proposed genus *Stereodiscus*, and *Gloeosoma*, all with significant measures of clade support. *Stereodiscus* and *Gloeosoma* formed a strongly supported sister group. None of the Patagonian species recovered in our analyses were included in *Aleurodiscus* s. str.

The species *A. bernicchiae, A. stratosus, A. quilae, A. antarcticus, A. trivialis*, and *A. vitellinus* were sequenced for the first time, whereas new collections of *A. mirabilis* and *A. cerussatus* were also sequenced. The Patagonian collections of *A. bernicchiae* nested in *Aleurocystidiellum*. Five Patagonian samples (two different lineages of *A. cerussatus* and one of *A. stratosus*) clustered in a diverse group of taxa without a definite phylogenetic relationship between them. By contrast, *A. quilae* clustered within *Acanthobasidium* with strong support.

The newly proposed genus *Stereodiscus* had a good structure and included five well-supported species: *A. patagonicus, A. limonisporus, A. parmuliformis, A. antarcticus*, and *A. trivialis*. The latter two were sister species with strong support and clustered more inclusively with *A. parmuliformis and A. limonisporus* with strong support (FIG. 3).

Within *Gloeosoma*, four species were included: *A. vitellinus, A. mirabilis, A. zealandicus*, and the newly described *Gloeosoma decorticans. Aleurodiscus mirabilis* clustered with *A. zealandicus* and *G. decorticans* with significant measures of support.

TAXONOMY

Gloeosoma Bres., Ann Mycol 18:51. 1920.

Type: Gloeosoma vitellinum (Lév.) Bres.

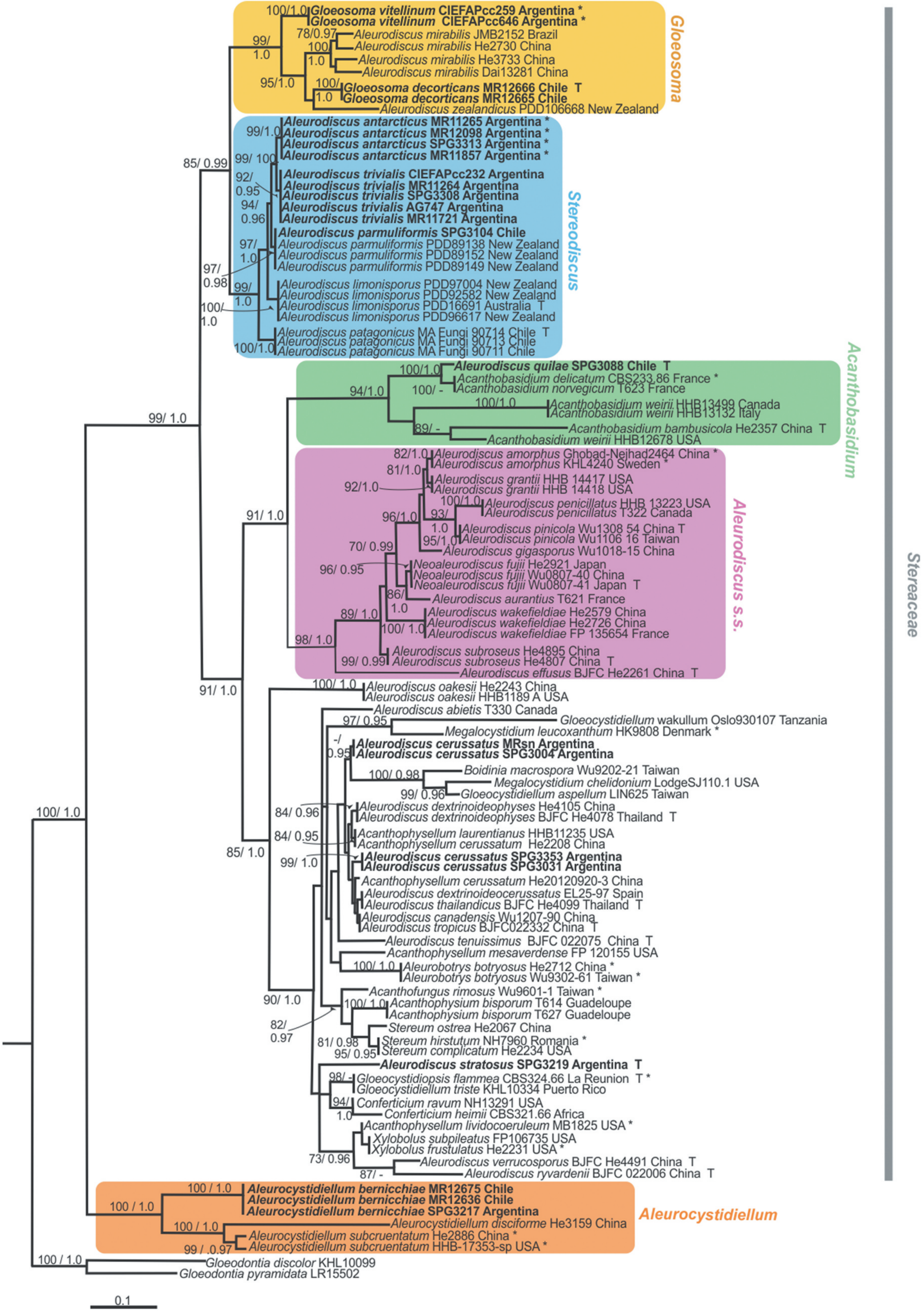

Figure 1. BI phylogram of Russulales based on data set ITS + 28S. PPs ≥0.95 and bootstrap values ≥70% are shown. Names in bold indicate newly sequenced specimens. T = sequence from the type specimen. * = generic type species.

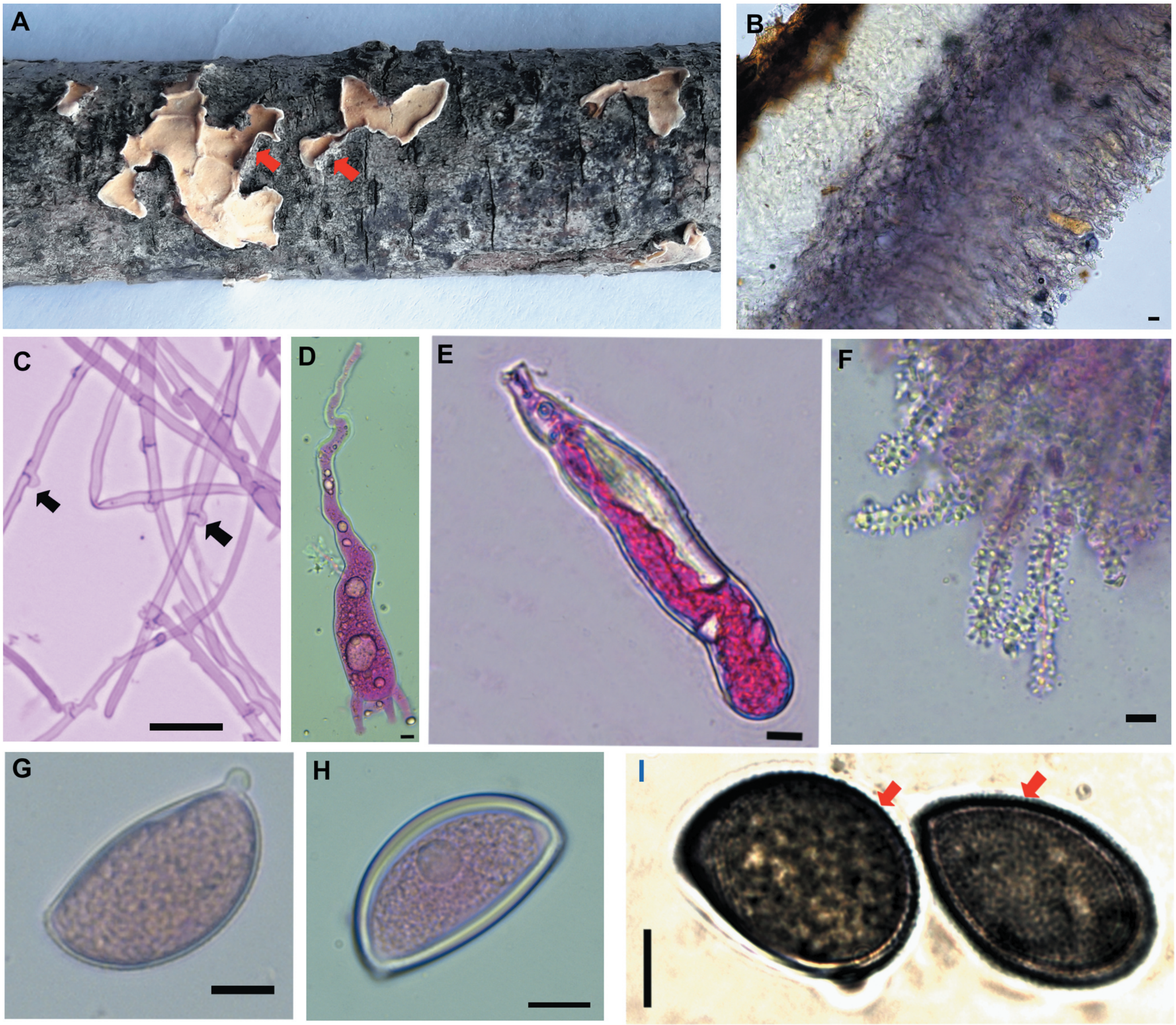

Figure 2. *Gloeosoma decorticans*, sp. nov., morphological features (holotype HCFC 1306). A. Basidioma; arrows show areas of decortication. B. Section of basidioma. C. Generative hyphae. D. Basidia. E. Basidiole. F. Acanthocystidia. G–H. Basidiospores in 3% KOH. I. Basidiospores in Melzer's reagent; arrows show ornamentation. Bars: A = 2 mm; B–I = 10 µm.

Basidiomata discoid, cupulate to large and auricularioid, gelatinous to fleshy, becoming cartilaginous to hard when dry; hymenial surface pink to salmon-colored, hyphal system monomitic with clamped generative hyphae, acanthocystidia always present, gloeocystidia present in some species, basidia clavate with four sterigmata; basidiospores large, more than 20 µm long, aculeate to echinulate, thick-walled, amyloid. Spore print pink to salmon pink.

Distribution: Four species known, most from the Southern Hemisphere with exception of *G. mirabile*, which occurs in the tropics.

Remarks: Gloeosoma was defined as a taxon growing on dead branches of Nothofagaceae in Patagonia and remained monotypic over the years. A lack of information on *G. vitellinum* in phylogenetic studies precluded any conclusion regarding its taxonomic status. It was a matter of personal decision whether to accept the genus or consider it a synonym of *Aleurodiscus*, as the microscopic features were quite typical of the latter in a broad sense. Our study includes sequences of *G. vitellinum* for the first time and shows that together with *G. zealandicum, G. mirabile*, and *Gloeosoma decorticans*, sp. nov. (described below), they form a well-defined group of species with strong phylogenetic support. This group clustered in the Stereaceae clade but was distant from *A. amorphus* (Pers.) J. Schröt., the type species of *Aleurodiscus*. The latter differs from *Gloeosma* morphologically by the simple-septate generative hyphae.

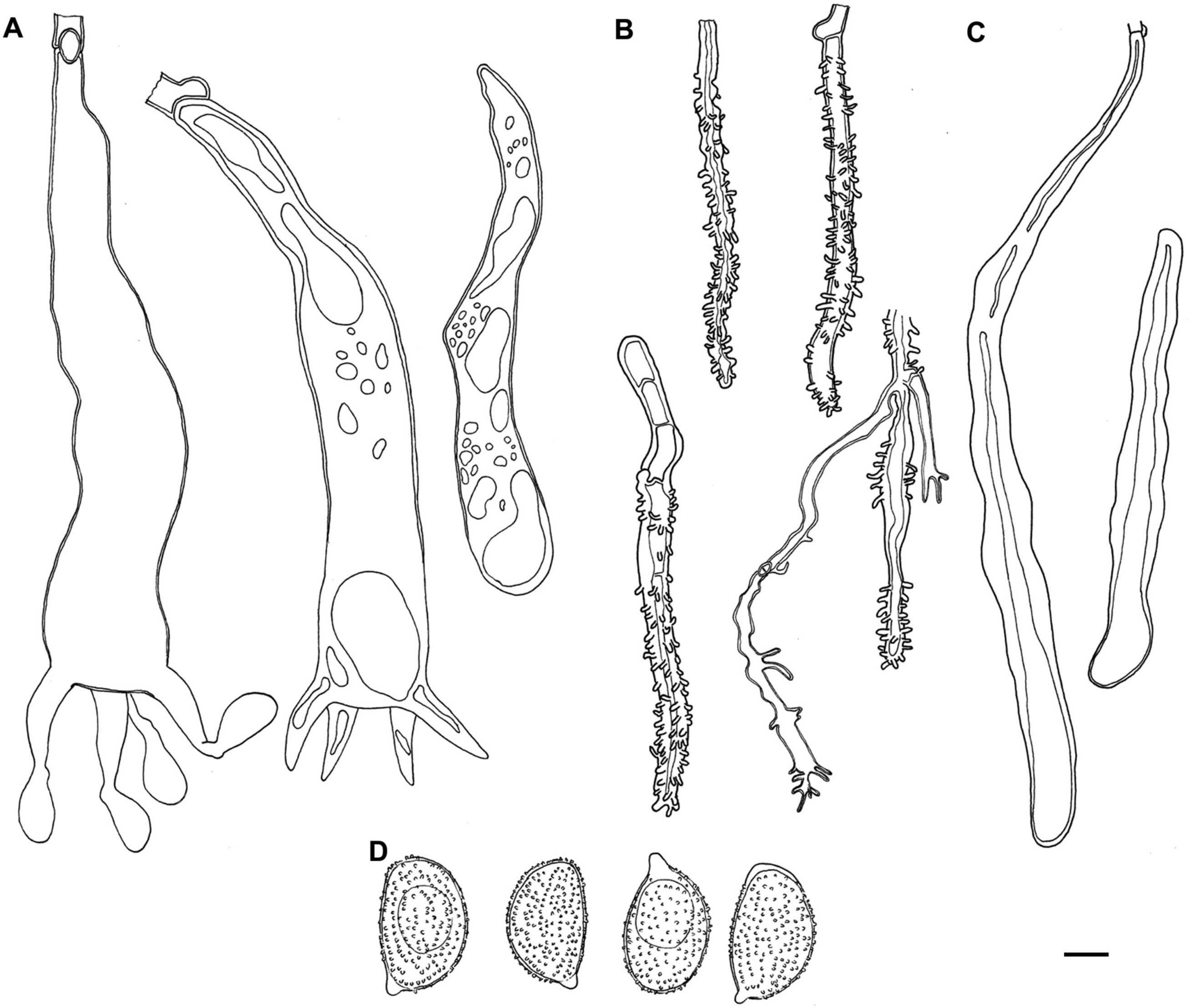

Figure 3. *Gloeosoma decorticans*, sp. nov., morphological features (holotype HCFC 1306). A. Basidia and basidioles. B. Acanthocystidia. C. Lamprocystidia. D. Basidiospores. Bar = 10 µm.

Gloeosoma capensis (Lloyd) Lloyd, originally described in *Aleurodiscus*, belongs to *Aleurocystis* Lloyd ex G. Cunn., a genus with nonamyloid spores that may be related to Corticiales (Larsson 2007). Thus, the species is excluded here.

Gloeosoma decorticans Rajchenb., Pildain & C. Riquelme, sp. nov. FIGS. 2–3

MycoBank MB836689

Typification: CHILE. BÍO BÍO: Concepción, Coronel, Fundo Escuadrón, Área de Alto Valor de Conservación Alto Escuadrón, Forestal Mininco S.A., 480 m above sea level (asl), on fallen branch of *Eucryphia cordifolia* in mixed forest of *Persea lingue, E. cordifolia, Nothofagus obliqua*, and *Aextoxicon punctatum*, 15 May 2019, *M. Rajchenberg & C. Riquelme, M. Rajchenberg 12666* (**holotype** HCFC 1306, **isotype** CONC-F 2017). Ex-type culture CIEFAPcc 647. GenBank: ITS = MT831041; 28S = MT831021.

Diagnosis: The new species is distinguished from others in the genus by the discoid to cupuliform basidiomata surrounded by decorticated bark of the host, a salmon-colored hymenial surface, clamped generative hyphae, abundant acanthocystidia, and ellipsoid, amyloid, ornamented basidiospores (28–32 × 17–20 µm).

Etymology: decorticans (L.), in reference to the basidiomata that peel off bark.

Description: Basidiomata discoid, adnate, fleshy when fresh, solitary or 2 to several coalescing laterally or continuously, individually small, 3 × 2 mm, but up to 23 × 5 mm when fusing and then more or less elongated, up to 500 µm thick; basidiomata raised and separating bark from wood; the bark encloses, delimits, and contains the basidiomata and may also protect or cover them partially. Hymenial surface furfuraceous, salmon pink, smooth except in the coalescing areas where it forms ridges where fused; margin cream to white, protruding from the bark in parts. Context up to 250 μm thick, consisting of a 200–220-μm-thick lower stratum that is fleshy when fresh but horny after drying, forming a waxy, hard layer against the substrate, and an upper, narrow, woody subhymenial layer.

Hymenial layer up to 250 μm thick. Hyphal system monomitic, generative hyphae clamped, 2–5(–7) μm in diam, with thin to thickened, hyaline walls and normal or donut-shaped clamps; relatively few hyphae in the lower context and immersed in a jelly-like substance, in the upper context densely interwoven. Basidia claviform, with 4 sterigmata up to 20 μm long, with thickened walls at the base, thinning out toward the apex, 160–180 × 22–27 μm, at times containing oil-like, sulfo-negative contents. Basidiospores amyloid, ellipsoid to broadly ellipsoid, very rarely D-shaped, 29–33.5 × 18.5–22.5 μm (31.1 ± 2.3 × 20.4 ± 1.9 μm) (n/s = 60/2), with thick walls mostly up to 1 μm thick, up to 2–3 μm thick at times, and then as if 1–2-layered; aculeate to echinulate with echinulae of variable length, up to 1 μm long, irregularly distributed on the spore surface, with a prominent hyaline apiculum that is IKI–, cytoplasm with 1 to several oily guttulae, many spores collapsed.

Gloeocystidia absent, but basidioles present with oil-like, sulfo-negative contents that may be confused with gloeocystidia; basidioles claviform, large, with hyaline, thickened walls, 180–230 × 20–25 μm. Acanthocystidia abundant, cylindric, slightly enlarged toward the apex, unbranched, up to 100 μm long and 5–7 μm diam, thick-walled, hyaline, diverticulae distributed along the cystidium or only in parts. Dendrohyphidia scattered in the hymenium and at times consisting of young developing acanthocystidia, slightly thick-walled, hyaline, with digitiform ramifications. Lamprocystidia cylindric to club-shaped, thick-walled, smooth, scant and may be overlooked, 85–180 × 10–12.5 μm.

Ecology and distribution: On fallen branches of *Eucryphia cordifolia* in mixed *Nothofagus* forest, associated with white wood rot, Patagonia, May.

Other specimen studied: CHILE. BÍO BÍO: Concepción, Coronel, Fundo Escuadrón, Área de Alto Valor de Conservación Alto Escuadrón, Forestal Mininco S.A., 480 m asl, on fallen branch of *E. cordifolia* in mixed forest of *Persea lingue, E. cordifolia, Nothofagus oblique*, and *Aextoxicon punctatum*, 15 May 2019, *M. Rajchenberg & C. Riquelme, M. Rajchenberg 12665* (HCFC 1307, CONC-F 2016). Ex-culture CIEFAPcc 649. GenBank: ITS = MT831042; 28S = MT831022.

Remarks: Gloeosoma decorticans is characterized by the adnate basidiomata that break up the cortical tissue, leaving the hymenial surface exposed; the basal context layer is gelatinous to osseous. Microscopically, the species features abundant acanthocystidia and, to a lesser extent, club-shaped lamprocystidia; gloeocystidia are lacking, but basidioles contain a large amount of an oil-like substance that may confuse the observer; however, the presence of this substance in well-formed basidia precludes this possibility. *Aleurodiscus zealandicus*, from New Zealand, is similar but differs by the cupulate to discoid basidiomata with free raised bodies and margins and a central attachment point resembling a discomycete, and lacks lamprocystidia (Cunningham 1963; Núñez and Ryvarden 1997).

Gloeosoma mirabile (Berk. & M.A. Curtis) Rajchenb., Pildain & C. Riquelme, comb. nov.

MycoBank MB836690

Basionym: Psilopezia mirabilis Berk. & M.A. Curtis, J Linn Soc Bot 10:364. 1868 [1869].

Remarks: For a description, see Núñez and Ryvarden (1997).

Gloeosoma vitellinum (Lév.) Bres., Ann Mycol 18:51. 1920.

≡ *Exidia vitellina* Lév., Ann Sci Nat Bot Sér 3 2:219. 1844.

Remarks: For descriptions, see Núñez and Ryvarden (1997) and Gorjón et al. (2013).

Gloeosoma zealandicum (Cooke & W. Phillips) Rajchenb., Pildain & C. Riquelme, comb. nov.

MycoBank MB836691

Basionym: Cyphella zealandica Cooke & W. Phillips, Grevillea 8(46):57. 1879.

Remarks: For descriptions, see Cunningham (1963) and Núñez and Ryvarden (1997).

Stereodiscus Rajchenb. & Pildain, gen. nov.

MycoBank MB836692

Typification: Stereodiscus antarcticus (Speg.) Rajchenb. & Pildain.

Diagnosis: Basidiomata resupinate to stereoid, hyphal system monomitic, generative hyphae simple-septate or clamped. Skeletocystidia present or not, other types of cystidia lacking. Basidiospores cylindric, broadly ellipsoid to citriform, thin-walled, smooth, amyloid. Spore print white to cream.

Etymology: Stereo, due to its similarity to the genus *Stereum*, from Greek *Stereos*, which means solid, referring to the tough consistency of the basidiomata when dry; *discus*, from the Latin for disc, referring to the discoid shape of some basidiomata.

Description: Basidiomata stereoid, cupulate to discoid, also small and resupinate but coalescing in some species; hymenophore smooth to merulioid. Hyphal system monomitic; generative hyphae simple-septate or clamped, thin to thick-walled. Skeletocystidia present or not, other types of cystidia lacking. Basidiospores cylindric, broadly ellipsoid to citriform, thin-walled, smooth, amyloid, 12–25 µm long. Spore print white to cream. Species living on dead branches of angiosperms, associated with white rot.

Distribution: Five species are accepted, all known only from the Southern Hemisphere (Argentina, Chile, Australia, and New Zealand).

Remarks: Stereodiscus is characterized by smooth, thin-walled, cylindric, broadly ellipsoid to citriform basidiospores up to 25 µm long and absence of any of the typical cystidia in *Aleurodiscus* s. lat., i.e., acanthocystidia, acanthophyses, gloeocystidia, and dendrohyphidia, but with skeletocystidia present in three species (*S. antarcticus, S. parmuliformis*, and *S. trivialis*). The hyphal system is monomitic with simple-septate hyphae, except in the recently described *S. patagonicus* (as *Aleurodiscus*), which features scattered clamps on the hyphae and at the bases of basidia (Phookamsak et al. 2019). The latter is consistent with its phylogenetic position, as it is excluded from the main cluster of species (FIG. 1). Otherwise, the five species grouped with strong support.

Stereodiscus is most closely related to *Gloeosoma* (FIG. 1). Gorjón et al. (2013) suggested the cluster of *Aleurodiscus antarcticus, A. parmuliformis*, and *A. trivialis* warranted segregation at the genus level characterized by possession of simple-septate hyphae and presence of skeletocystidia and geographic distribution occurring only in the Southern Hemisphere. Our analyses show that two other taxa are included in this group, widening its morphological definition, and it indeed deserves generic rank.

Stereodiscus antarcticus (Speg.) Rajchenb. & Pildain, comb. nov.

MycoBank MB836693

Basionym: Corticium antarcticum Speg., Bol Acad Cienc Córdoba 11:170. 1887 [1888].

Remarks: For a description, see Gorjón et al. (2013).

Stereodiscus limonisporus (D.A. Reid) Rajchenb. & Pildain, comb. nov.

MycoBank MB836694

Basionym: Aleurodiscus limonisporus D.A. Reid, Kew Bull 10:631. 1955.

Remarks: For descriptions, see Cunningham (1963) and Núñez and Ryvarden (1997).

Stereodiscus parmuliformis (G. Cunn.) Rajchenb. & Pildain, comb. nov.

MycoBank MB836695

Basionym: Aleurodiscus parmuliformis G. Cunn., Trans R Soc N Z 84:244. 1956.

Remarks: For descriptions, see Gorjón et al. (2013) and Cunningham (1963).

Stereodiscus patagonicus (Nogal, Tellería, M. Dueñas & M. Martín) Rajchenb. & Pildain, comb. nov.

MycoBank MB836696

Basionym: Aleurodiscus patagonicus Nogal, Tellería, M. Dueñas & M. Martín, Fungal Divers 95:234. 2019.

Remarks: For a description, see Phookamsak et al. (2019).

Stereodiscus trivialis (Speg.) Rajchenb. & Pildain, comb. nov.

MycoBank MB836697

Basionym: Corticium triviale Speg., Bol Acad Cienc Córdoba 11:172. 1887 [1888].

Remarks: For a description, see Gorjón et al. (2013).

Acanthobasidium Oberw., Sydowia 19:45. 1966.

Type: Acanthobasidium delicatum (Wakef.) Oberw.

Basidiomata thin, delicate, adnate, white to cream-colored. Hyphal system monomitic with clamped generative hyphae. Gloeocystidia moniliform, SA−, present or not; acanthocystidia and/or acanthophyses present (in fact, they are young basidia; cf. Boidin et al. 1986) or absent. Acanthobasidia present; basidiospores finely warted to minutely and closely echinulate, less than 20 µm long (generally under 15 µm long). Spore print white.

Distribution: Species are known from temperate, boreal and austral regions, growing on Cyperaceae, Bambusoideae, Ericaceae, and conifers.

Remarks: Acanthobasidium is a well-circumscribed group of species displaying good phylogenetic support. The presence of acanthobasidia is not unique within *Aleurodiscus* s. lat. (Wu et al. 2019); however, it is a strong indication of relationship with the genus.

Acanthobasidium bambusicola L.D. Dai & S.H. He, Mycol Prog 15:720. 2016.

Remarks: For a description, see Dai and He (2016).

Acanthobasidium delicatum (Wakef.) Oberw., Sydowia 19:46. 1966.

≡ Aleurodiscus delicates Wakef., Trans Br Mycol Soc 35:44. 1952.

Remarks: For a description, see Núñez and Ryvarden (1997).

Acanthobasidium norvegicum (J. Erikss. & Ryvarden) Boidin, Lanq., Cand., Gilles & Hugueney, in Boidin et al., Bull Trimest Soc Mycol Fr 101:341. 1986.

≡ *Aleurodiscus norvegicum* J. Erikss. & Ryvarden, Norw J Bot 20:10. 1973

Remarks: For descriptions, see Eriksson and Ryvarden (1973), Boidin et al. (1986), and Núñez and Ryvarden (1997).

Acanthobasidium phragmitis Boidin, Lanq., Cand., Gilles & Hugueney, in Boidin et al., Bull Trimest Soc Mycol Fr 101:345. 1986.

Remarks: For a description, see Boidin et al. (1986).

Acanthobasidium quilae (Gorjón, Gresl. & Rajchenb.) Rajchenb. & Pildain, comb. nov.

MycoBank MB836698

Basionym: Aleurodiscus quilae Gorjón, Gresl. & Rajchenb., Mycol Prog 12:103. 2013.

Remarks: For a description, see Gorjón et al. (2013).

Acanthobasidium weirii (Burt) L.D. Dai & S.H. He, Mycol Prog 15:722. 2016.

≡ *Aleurodiscus weirii* Burt, Ann Mo Bot Gard 5:203. 1918.

Remarks: For a description, see Núñez and Ryvarden (1997).

Aleurocystidiellum P.A. Lemke, Can J Bot 42:277. 1964.

Type: Aleurocystidiellum subcruentatum (Berk. & M. A. Curtis) P.A. Lemke.

Basidiomata annual to perennial, resupinate, adnate to discoid, cupulate to subpileate and then attached to a central point. Hyphal system monomitic or dimitic, with clamped generative hyphae and skeletal hyphae. Incrusted cystidia or incrusted skeletocystidia (pseudocystidia) present. Gloeocystidia present or not. Basidiospores ovoid, broadly ellipsoid to globose, minutely verruculose to aculeate. Spore print white.

Remarks: Well supported phylogenetically, not related to *Aleurodiscus* s. lat., and occupying an uncertain position within Russulales, *Aleurocystidiellum* corresponds to a family of its own (Larsson 2007; Zhou and Dai 2013). It is characterized by a combination of ornamented (minutely verruculose to aculeated), thick-walled basidiospores, a monomitic or dimitic hyphal system with clamped generative hyphae, and when dimitic, with skeletoid hyphae ending as cystidia-like, incrusted structures in the hymenium; gloeocystidia may be present (*A. disciformis*) or not (*A. subcruentatum*).

Aleurocystidiellum bernicchiae (Gorjón, Gresl. & Rajchenb.) Rajchenb. & Pildain, comb. nov.

MycoBank MB836699

Basionym: Aleurodiscus bernicchiae Gorjón, Gresl. & Rajchenb., Mycol Prog 12:98. 2013.

Remarks: For a description, see Gorjón et al. (2013). In our study, *Aleurodiscus bernicchiae* proved to pertain to this group. This taxon and the morphologically similar *A. hallenbergii* presented strongly amyloid, thick-walled, aculeate basidiospores, and a monomitic hyphal system with incrusted, thick-walled, hymenial cystidia.

Aleurocystidiellum disciforme (DC.) Boidin, Terra & Lanq., Bull Trimest Soc Mycol Fr 84:63. 1968.

≡ *Thelephora disciformis* DC., Fl franç, Edn 3 (Paris) 5/6:31. 1815.

Remarks: For descriptions, see Eriksson and Ryvarden (1973) and Núñez and Ryvarden (1997).

Aleurocystidiellum hallenbergii (Gorjón, Gresl. & Rajchenb.) Rajchenb. & Pildain, comb. nov.

MycoBank MB836700

Basionym: Aleurodiscus hallenbergii Gorjón, Gresl. & Rajchenb., Mycol Prog 12:102. 2013.

Remarks: For a description, see Gorjón et al. (2013). Although sequences of *A. hallenbergii* were not obtained, according to its morphological characters and similarity with *A. bernicchiae* (Gorjón et al. 2013), the species was also included in *Aleurocystidiellum*. Rajchenberg (2002) misidentified specimens of this taxon as *A. subcruentatum* (cf. Gorjón et al. 2013).

Aleurocystidiellum subcruentatum (Berk. & M.A.Curtis) P.A. Lemke, Can J Bot 42:278. 1964.

≡ *Stereum subcruentatum* Berk. & M.A. Curtis, Proc Am Acad Arts Sci 4:123. 1860.

Remarks: For a description, see Núñez and Ryvatden (1997).

Aleurocystidiellum tsugae (Yasuda) S.H. He & Y.C. Dai, Mycosphere 8:912. 2017.

≡ *Aleurodiscus tsugae* Yasuda, Mycol Writ (Cincinnati) 6(Letter 65):1066. 1920.

Remarks: For descriptions, see Núñez and Ryvarden (1997) and He and Dai (2017).

DISCUSSION

We investigated the phylogenetic disposition of *Aleurodiscus* s. lat. in southern South America, and based also on morphological characters, we propose several taxonomic solutions. These include description of a new genus and a new species, 10 new combinations, and molecular representation of six previously unsampled species for the first time.

Previous studies have circumscribed *Aleurodiscus* in a strict sense phylogenetically and confirmed that *Aleurodiscus* in the broad sense is paraphyletic (Wu et al. 2001, 2019; Phookamsak et al. 2019). Our phylogenetic results are consistent with these previous studies, but further information on the phylogeny and taxonomy of *Aleurodiscus* s. lat. is provided (FIG. 1).

This study also tested the phylogenetic position of most of the known species described in *Aleurodiscus* from southern Argentina and Chile in recent years, specifically from highly diverse Patagonian forests (Cabrera and Willink 1980; Donoso 1993; Moreira-Muñoz 2011). Our results reveal several well-supported clades, notably one including *Aleurodiscus vitellinus* (the type species of *Gloeosoma*), which has been phylogenetically enigmatic for many years and never studied until now. Wu et al. (2001, 2010) treated *A. penicillatus, A. mirabilis, A. oakesii*, and *A. wakefieldiae* in *Gloeosoma* but within a framework of relatively few species and without including the type species of the genus. Another clade included several taxa of austral distribution, here proposed as the new genus *Stereodiscus*. Based on basidiomata morphology, thin-walled basidiospores, and the presence of skeletocystidia, some species in this genus were previously considered to be related to *Stereum* Hill ex Pers., and some were described under that name in the past (cf. TABLE 1) (Núñez and Ryvarden 1997; Wu et al. 2001). Our study showed *Stereodiscus* to be distantly related to species of *Stereum*, showing features that could be synapomorphic within Stereaceae. Both *Gloeosoma* and *Stereodiscus* were shown to be phylogenetically related to each other, but distant from other clades in Stereaceae and from other genera segregated from *Aleurodiscus* s. lat.

Other taxa from Patagonia presented unsolved phylogenetic positions. *Aleurodiscus stratosus*, associated phylogenetically with a group of taxa in *Aleurodiscus* s. lat., currently remains there, awaiting further research and clarification. Specimens determined to be *A. cerussatus* from Patagonia grouped with other taxa determined to be such elsewhere, but their unstructured disposition reflects a cryptic species complex that requires further investigation as well. We were unable to obtain DNA material from specimens of *A. corticola* and *A. hallenbergii*. The latter was transferred to *Aleurocystidiellum*, given the morphological similarity to *A. bernicchiae* (Gorjón et al. 2013). *Aleurodiscus corticola* appears similar to *Aleurocystidiellum*, and specimens of this taxon were initially determined to be *Aleurocystidiellum* aff. *disciforme* by Greslebin (2002). This species features finely aculeate, thick-walled, amyloid basidiospores, clamped generative hyphae, and moniliform gloeocystidia; however, it lacks incrusted pseudocystidia or skeletal cystidia. We therefore recognize the species in *Aleurodiscus*.

The description of *Stereodiscus* and support for *Gloeosoma* were consistent with the recurrent demonstration of the existence of austral lineages at the genus level in the phylogeny of different fungal taxa (e.g., Peterson and Pfister 2010; Peterson et al. 2010; Rajchenberg et al. 2011; Ortiz-Santana et al. 2013; Pildain and Rajchenberg 2013; Kraisitudomsook et al. 2020). *Stereodiscus* and *Gloeosoma* proved to be sister clades, mostly composed of austral taxa, the only exception being the pantropic *Gloeosoma mirabile*. Crisci et al. (1991) demonstrated that southern South America as a landmass constitutes a monophyletic group together with Australia, Tasmania, New Guinea, New Caledonia, and New Zealand, which explains the existence of an austral biota with particular elements. Sanmartín and Ronquist (2004) provided evidence that interchanges between the southern and the tropical areas of South America were scant. However, the panbiogeography tracks analysis of the Chilean flora (Moreira-Muñoz 2011) showed a complex situation with the existence of several tracks different from the austral one: this might also be the case for fungi.

It was interesting to note that both *Stereodiscus* and *Gloeosoma* displayed morphological features that were also reflected, in different combinations, in the other genera and species complexes defined for other *Aleurodiscus* s. lat. (except, certainly, *Acanthobasidium*). That is, these features were already present in the origins of the Stereaceae family and have evolved in different combinations worldwide.

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