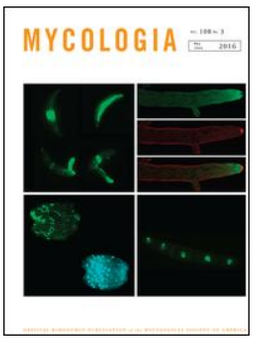

Mycologia

ISSN: 0027-5514 (Print) 1557-2536 (Online) Journal homepage: http://www.tandfonline.com/loi/umyc20

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To cite this article: Beatriz San-Fabian, Tuula Niskanen, Kare Liimatainen, Pepijn W. Kooij, Alija B. Mujic, Camille Truong, Ursula Peintner, Philipp Dresch, Eduardo Nouhra, P. Brandon Matheny & Matthew E. Smith (2018): New species of *Cortinarius* sect. *Austroamericani*, sect. nov., from South American Nothofagaceae forests, Mycologia, DOI: 10.1080/00275514.2018.1515449

To link to this article: https://doi.org/10.1080/00275514.2018.1515449

Published online: 29 Nov 2018.

MYCOLOGIA
https://doi.org/10.1080/00275514.2018.1515449

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New species of *Cortinarius* sect. *Austroamericani*, sect. nov., from South American Nothofagaceae forests

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ABSTRACT

In this study, we document and describe the new *Cortinarius* section *Austroamericani*. Our results reveal high species diversity within this clade, with a total of 12 recognized species. Of these, only *C. rufus* was previously documented. Seven species are described as new based on basidiomata collections. The four remaining species are only known from environmental sequences. All examined species form ectomycorrhizal associations with species of Nothofagaceae and are currently only known from Argentinean and Chilean Patagonia. The phylogenetic analysis based on the nuc rDNA internal transcriber spacer (ITS1-5.8S-ITS2 = ITS) and partial 28S gene (28S) sequences shows that this section is related to other taxa from the Southern Hemisphere. Species in this group do not belong to subg. *Telamonia*, where *C. rufus* was initially placed. *Cortinarius rufus* and the newly described *C. subrufus* form a basal clade within sect. *Austroamericani* that has a weakly supported relationship with the core clade. Because the two species are morphologically similar to species from the core clade and share their distribution and Nothofagaceae associations, we include them here as part of sect. *Austroamericani* sensu lato (s.l.) until more material is available to refine the delimitation.

ARTICLE HISTORY
Received 19 January 2018
Accepted 21 August 2018

KEYWORDS
Agaricales; diversity; DNA barcoding; ectomycorrhizal fungi; Patagonia; species delimitation; southern temperate forests; 8 new taxa

INTRODUCTION

The genus *Cortinarius* (Pers.) Gray is one of the most species-rich ectomycorrhizal (ECM) genera of *Agaricales*. *Cortinarius* species are ecologically important and critical for nutrient cycling in forests, especially at higher latitudes (Bödeker et al. 2014). They are also used as indicators of valuable forests (e.g., Vesterholt 1991). This genus is one of the most widely distributed ECM genera throughout the Northern and Southern Hemispheres (Kirk et al. 2008). However, *Cortinarius* diversity in the Southern Hemisphere remains insufficiently studied compared with the diversity in the Northern Hemisphere (Peintner et al. 2004; Garnica et al. 2005). *Cortinarius* is the most species-rich genus in southern South American Nothofagaceae forests, with approximately 250 species described from the region to date (Garnica et al. 2002, 2003; Romano and Lechner 2014). The earliest publications of South American *Cortinarius* species are from Spegazzini (1887a, 1887b), whereas the largest contribution was made by Moser and Horak (1975) and Horak (1980) from Andino-Patagonian forests. Singer and Moser (1965), Garrido (1988), Valenzuela and Esteve-Raventós (1994), and Garnica et al. (2002) were also involved in the discovery and description of *Cortinarius* species from South America. DNA sequencing of ECM roots subsequently revealed that *Cortinarius* are also highly abundant and speciose on the roots of Nothofagaceae host trees (Nouhra et al. 2013).

In southern South America, temperate Nothofagaceae forests host a high diversity of previously unknown *Cortinarius* species that have not been reported from other regions (Truong et al. 2017a). This suggests that there are probably many species and lineages that are endemic to the region but that these taxa have not been formally recognized in the past. It is critical to name these species and lineages so that the unique biodiversity of this region can be conserved. The extensive explorations and

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Published online 29 Nov 2018

mycological collections made by the authors in Argentinean and Chilean Patagonia will contribute to a better understanding of this hyperdiverse genus globally and in South America. In addition to potentially endemic lineages, the *Cortinarius* mycobiota of South America also has similarities to those of other Austral regions, i.e., Australia-Tasmania and New Zealand. For example, Peintner et al. (2004) and Garnica et al. (2005) previously showed that the *Pseudotriumphantes* clade is shared between South America and Oceania (Australia-Tasmania and New Zealand) and is only found in the Southern Hemisphere. Such "southern Gondwana" connections are probably explained by the presence of specific host plants in the Southern Hemisphere that are absent in other regions and vice versa (Tedersoo et al. 2010; Kuhar et al. 2017; Truong et al. 2017b). These Gondwanan hosts harbor unique ECM associations and some lineages not found in the Northern Hemisphere (Truong et al. 2017a). Some lineages of *Cortinarius* have representative species in both the Northern and Southern Hemispheres, including sections *Anomali, Delibuti*, and *Obtusi*, among others (Garnica et al. 2005). Generally, species from different geographic regions form distinct monophyletic subgroups within these sections (Garnica et al. 2005). They are also associated with different host plants in the Southern Hemisphere (i.e., *Nothofagus, Eucalyptus*) from those in the Northern Hemisphere (i.e., Fagaceae, Betulacea, Malvaceae, Salicaceae, or Pinaceae) (Niskanen et al. 2008).

The structure of ECM fungal communities depends strongly on their host associations (Tedersoo et al. 2008, 2012). Nouhra et al. (2012) studied forests dominated by the evergreen *N. dombeyi* and the deciduous *N. pumilio*, as well as how the community composition of hypogeous fungi is affected by whether the host is evergreen or deciduous. They found that the evergreen forests (*N. dombeyi*), occurring in warmer, wetter, more acidic, and lower altitude areas, showed a greater species richness and biomass production. A later study by Nouhra et al. (2013), however, did not reveal significant host preferences for different ectomycorrhizal fungi among different species of Nothofagaceae (*N. dombeyi* and the deciduous species *Lophozonia obliqua* and *L. alpina*) based on sampling of ectomycorrhizal root tips. Fungal community composition is also influenced by environmental factors such as elevation, precipitation, and temperature (Nouhra et al. 2012; Tedersoo et al. 2012).

The present study concentrates on Patagonian *Cortinarius* species that are morphologically similar to the telamonioid clades Obtusi Melot (known from both the Northern and Southern Hemispheres) and Fulvescentes/Laeti Melot (known only from the Northern Hemisphere). Using both morphological and molecular data, we studied the species limits and phylogenetic placement of Patagonian specimens collected in 2016 and 2017. The purpose of this paper is to (i) determine the number of species that belong to this group based on morphological and molecular data; (ii) describe the previously unknown species as new; (iii) provide the taxonomic placement of the studied specimens; and (iv) produce DNA barcodes for all of these species for the RefSeq (Schoch et al. 2014) and UNITE databases (Kõljalg et al. 2013).

MATERIALS AND METHODS

Material.—Sixteen collections made Mar–May 2016 and 2017 (Southern Hemisphere autumn) from Nothofagaceae forest sites in Patagonia (Argentina and Chile) were studied. Dried fungal material is deposited in the Museum Botánico of Córdoba (CORD) or Museo Nacional de Historia Natural de Chile (SGO), and the duplicates in Royal Botanic Gardens, Kew (K). We also examined the type specimen of *C. rufus* M.M. Moser (IB19630369) preserved in the mycological collection of the herbarium Innsbruck (IB). Herbarium acronyms follow Index Herbariorum (Thiers [continuously updated]). Collectors are represented by their initials: Camille Truong (CT), Matthew E. Smith (MES), Meinhard Moser (MM), and Tuula Niskanen (TN). Collections indicated with MES numbers were made by numerous collaborators associated with the University of Florida and University of Tennessee research team as part of National Science Foundation grant DEB-1354802 (see collection data for more details).

Morphological studies.—Macroscopic descriptions are based on observations of basidiomata at different stages of development when possible and made from notes and photographs of fresh material. The microscopic descriptions are made from exsiccatae. Color codes for exsiccatae were taken from Munsell (2009). Descriptions and measurements of the micromorphology of basidiospores, basidia, lamellae structures, and pileipellis were made from dried material mounted in Melzer's reagent (MLZ). The color of the spores was also recorded from material in 10% KOH. Twenty basidiospores were measured from one basidiome of each specimen, from the spore deposit on the pileipellis after examining the spore morphology on the lamellae to confirm that the spores belonged to that species. The length and width were measured from each spore, and their Q values (basidiospore length/width ratio) were calculated. Mean values are indicated by "av." When more than

one specimen was studied and the averages differ from one another, the range of averages is given. Two basidia were measured from each specimen, except in the species with only one collection where six basidia were measured. Pileipellis structure was studied from both radial freehand sections and scalps made from midway to the pileus center.

DNA extraction, PCR amplification, and sequencing.—Our data set included five published sequences of the nuc rDNA internal transcriber spacers (ITS1-5.8S-ITS2 = ITS) from Truong et al. (2017a) and six newly produced sequences. The full methods for DNA extraction, polymerase chain reaction (PCR) amplification, and sequencing for these specimens are detailed in the supporting information of Truong et al. (2017a).

In our preliminary analysis, 3 of these 11 sequences were unique and represented three putative species. From those collections, a different basidiome was sequenced to verify the quality and identity of the sequence. DNA was extracted from dried material (pieces of lamellae) using the Phire Plant Direct PCR kit (F130WH; Thermo Scientific; Waltham, Massachusetts) following the manufacturer's instructions. Amplification of ITS was conducted with primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990). PCR amplification and sequencing followed Liimatainen et al. (2014).

In addition, eight ITS sequences and eight nuc rDNA partial 28S gene (28S) sequences were produced from six additional collections and two previously sequenced collections following Ivanova et al. (2006) with the modifications suggested by Dentinger et al. (2010). The ITS region was amplified using the primers ITS1F and ITS4, and the 28S region using the primers LR0R (Bunyard et al. 1994) and LR5 (Vilgalys and Hester 1990). PCR reactions were prepared in 10 µL final volume with 5 µL DreamTaq Green PCR Master Mix (2×) (K1081; Thermo Scientific), 2 µL TBT-PAR (5×), 0.2 µL each of forward and reverse primers, 1.6 µL double-distilled water (ddH_2O), and 1 µL of undiluted DNA, and the PCR conditions were 4 min initial denaturing at 94 C, followed by 36 cycles of 30 s at 94 C, 45 s at 53 C, 1.5 min at 72 C, and 10 min final extension at 72 C. PCR products were verified by electrophoresis on 1% agarose gel and purified using exonuclease I and alkaline phosphatase (Thermo Scientific). Purified products were sequenced bidirectionally using the same PCR primers on an ABI PRISM 3730 automated DNA sequencer (Applied Biosystems, Foster City, California) at Royal Botanic Gardens, Kew.

Data analyses.—A total of 18 ITS sequences and eight 28S sequences were newly generated (GenBank numbers are indicated in Taxonomy, after corresponding specimens) and, together with the five published sequences from Truong et al. (2017a), were assembled and edited with Sequencher 4.1 (Gene Codes, Ann Arbor, Michigan). The sequences were then compared with those in GenBank (https://www.ncbi.nlm.nih.gov/) and UNITE (Abarenkov et al. 2010) databases through BLAST searches to obtain published sequences that are similar or identical to the target sequences in our data set. The sequence of the type specimen of *C. rufus* only included the ITS2 region and was excluded from the phylogenetic analysis. We also incorporated in our phylogenetic analysis sequences of other selected *Cortinarius* species that represent different lineages of stipitocarpic *Cortinarii*, mainly from other traditional subgenera except *Phlegmacium*, to resolve the relationships of our target sequences (stipitocarpic is when the stipe lengthens first and then the pileus opens, in contrast to pileocarpic wherein the pileus opens first and then the stipe lengthens). Sequences were mostly obtained from Garnica et al. (2005), Harrower et al. (2011), and Stensrud et al. (2014). Sequences from section *Phlegmacioides* were selected as the outgroup based on Stensrud et al. (2014).

A total of 87 ITS and 70 28S sequences were aligned separately for both regions using MAFFT 7 (Katoh and Standley 2013) with the G-ING-i algorithm (Katoh et al. 2005). The alignments were then manually improved in SeaView (Galtier et al. 1996). Two alignments of the more variable ITS region were created with and without ambiguously aligned regions. The phylogenetically informative indels in the ITS and 28S regions were coded as characters (Simmons and Ochoterena 2000) with FastGap 1.2 (Borchsenius 2009). Alignments were concatenated in Mesquite 3.2 (Maddison and Maddison 2017). Finally, three different data sets were created for the phylogenetic analyses: (i) ITS and 28S regions with gap coding included; (ii) ITS and 28S regions excluding gap coding; and (iii) ITS and 28S regions without gap coding and excluding ambiguously aligned regions. Three phylogenetic trees were generated using maximum likelihood (ML) analyses with 1000 bootstrap replicates under the GTRGAMMA model in RAxML 8 (Stamatakis 2014). Analyses including and excluding gap coding showed that including the gaps improved the phylogeny. Incorrectly aligned regions may have an effect on the phylogeny, but removing ambiguously aligned regions also leads to the loss of informative characters. Therefore, to retain as much information as possible but also to test the sensitivity of our data set to these

regions, we performed analyses with and without these ambiguously aligned regions.

Genetic differences within and between species were calculated for paired sequences by dividing the number of indels and/or substitution found in the ITS1+5.8S+ITS2 regions by the length of the shortest sequence in the pair.

RESULTS

Phylogenetic analysis.—The phylogenetic tree resulting from the first analysis, ITS and 28S regions including gap coding, is shown in FIG. 1. The final ITS +28S alignment under FastGap treatment is composed of 1634 nucleotides (including gaps and gap coding) and is available at TreeBASE (http://www.treebase.org/treebase-web/home.html) under study no. S21331. The topologies of the phylogenies resulting from the different analysis were largely congruent for the clades that were significantly supported (bootstrap support [BS] >70). The support values of the different analyses are reported on or below the branches in the FIG. 1 as follows: (i) BS value from our indel coding analysis; (ii) BS value from our analysis without indel coding; and (iii) BS value from our analysis excluding ambiguous sites and indel coding.

Our target species formed a monophyletic clade within the stipitocarpic *Cortinarii*. The clade is further split into two main entities. The core group received a BS value of 71% in analysis (i), whereas in analyses (ii) and (iii) the group was present but without statistical support. This group is also supported morphologically and does not represent a sister relationship with other morphologically similar clades, i.e., sect. *Obtusi*, sect. *Fulvescentes*, or subg. *Telamonia*. Thus, we propose this clade as sect. *Austroamericani* (see Taxonomy). The smaller sister clade was well supported in all analyses (BS 93/84/73), but the relationship with the core group was not supported, and in analyses (ii) and (iii) it constituted a separate clade. However, because it is morphologically similar with the core species of sect. *Austroamericani* and shares the same distribution and associations with Nothofagaceae spp., we here treat it as part of sect. *Austroamericani* and refer to it as sect. *Austroamericani* s.l.

Based on the phylogenetic analysis, sect. *Austroamericani* s.l. includes 12 species. Four are only known from environmental sequences derived from ectomycorrhizal root tips. The remaining eight species are known from basidiomata collections, and two of these species are also known from ectomycorrhizal root tips. Seven of the species represented by basidiomata received high bootstrap support in all three of our analysis (BS value >90): *Cortinarius patagoniensis* (99/97/97), *C. austroamericanus* (100/96/95), *C. morenense* (100/100/99), *C. rufoides* (100/100/100), *C. mascardiensis* (100/98/99), *C. rufosimilis* (96/99/96), and *C. subrufus* (92/84/73). The eighth species, *C. rufus*, was only represented by one full-length ITS sequence in our analysis.

The species in this new section can also be delimited based on their morphological characters (see Taxonomy). In addition, the intraspecific variation in the ITS region in most species is <0.3%, whereas the interspecific variation is >1.6%. The only exceptions are the *C. patagoniensis* clade and the two species from *Austroamericani* s.l. The two clades in *Austroamericani* s.l. are treated here as separate but closely related species, *C. rufus* and *C. subrufus*. Their interspecific variation is <0.7% (five substitutions and indels), but the division into two distinct lineages is supported by multiple sequences (six in *C. subrufus*, two in *C. rufus*; although the second sequence of *C. rufus* only includes the ITS2 region, this region is 100% identical with the first sequence). These species can also be differentiated based on both morphological and ecological associations. In *C. patagoniensis*, one specimen (here referred as *C.* aff. *patagoniensis*) differs from the others in the ITS region by 0.7% (four substitutions). These two taxa can be separated based on their host associations. However, considering that no morphological differences have been found and that *C.* aff. *patagoniensis* is based on a single specimen, we conclude that further sampling is required to support its formal recognition as a distinct taxon.

TAXONOMY

Cortinarius* sect. *Austroamericani San-Fabian, Niskanen & Liimat., sect. nov. FIGS. 2–4

Index Fungorum IF554566

Typification: Cortinarius austroamericanus San-Fabian, Niskanen & Liimat., sp. nov.

Description: Basidiomata small, pileus 1–5.7 cm in diam, stipe apex 0.2–0.9 cm wide. Pileus brown, yellowish brown to reddish brown, predominantly convex to low convex, umbonate, surface smooth, margin entire, hygrophanous. Lamellae adnate, medium-spaced to distant, moderately broad, in most species yellowish brown. Stipe usually cylindrical, whitish silky fibrillose, becoming brown with handling and age. Universal veil white to buff, sparse, often forming a thin, sock-like sheath on the lower part of the stipe. Context brown, yellowish brown to brownish yellow; usually darker in the pileus and at the base of the stipe. Odor in lamellae and base of the stipe usually indistinct, in some species raphanoid in lamellae. Exsiccatae with brown to dark brown pileus and lamellae, and white to dark brown stipe.

Basidiospores 7–12(–14) × 4.5–7 µm, av. = 7.6–10.8 × 5.1–6.0 µm, Q = 1.35–2.2(–2.4), Q av. = 1.47–2.0, amygdaloid-ellipsoidal, less commonly obovoid,

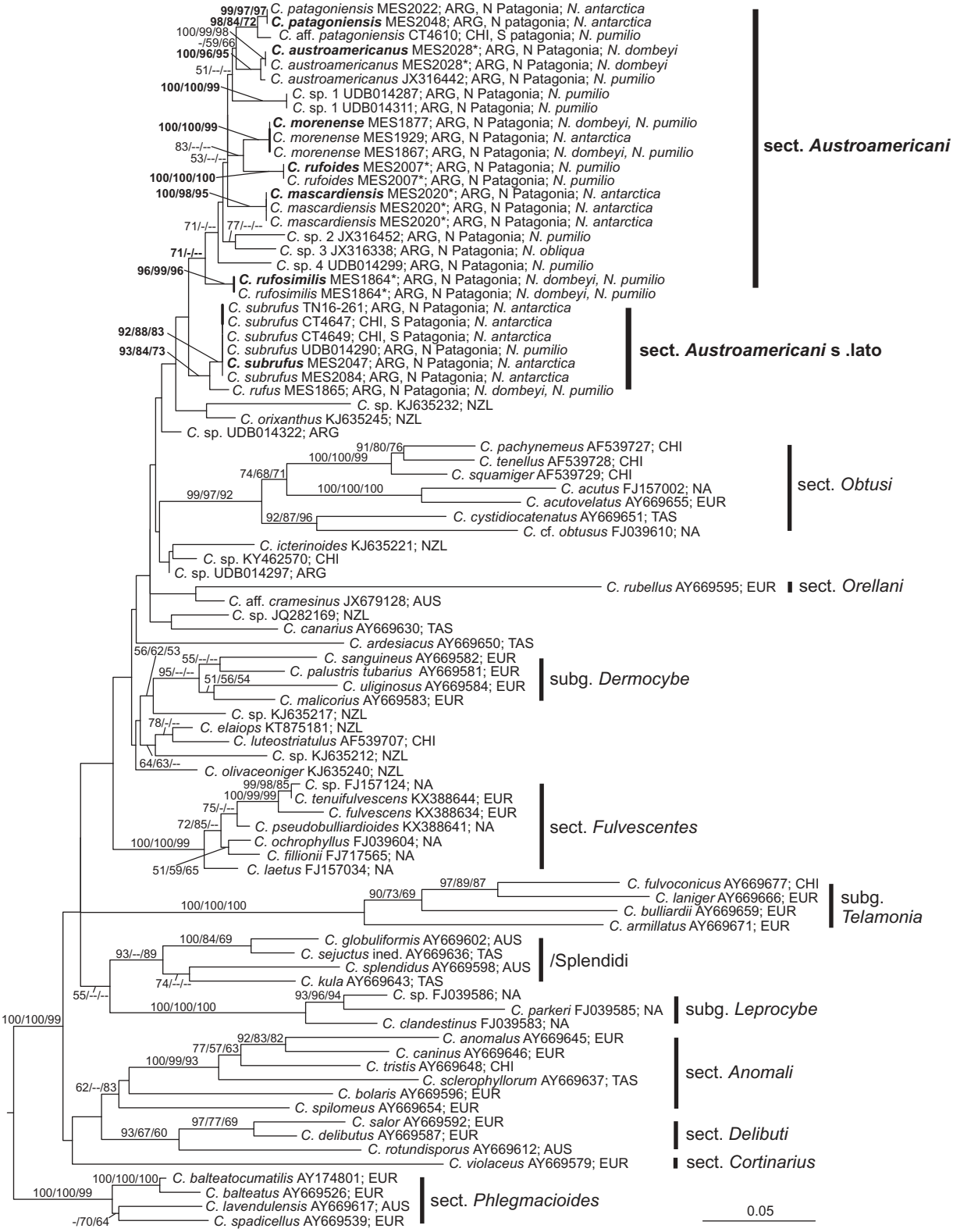

Figure 1. Maximum likelihood phylogeny based on ITS and 28S (D1–D2) sequences. Topology based on analyses under indel coding treatment. Three bootstrap values of different analyses are shown as follows: BS value from indel coding analysis/BS value from analysis without indel coding/BS value from analysis without indel coding and excluding ambiguous sites. Bootstrap values ≥50% are indicated above branches. "-" indicates <50% bootstrap value; "–" indicates nonexistent topology; "*" indicates sequences generated from different basidiomata of the same collection. Species names of newly described type specimens and sections are in boldface. Bootstrap values of sect. *Austroamericani* s.s. and s.l. as well as of the species within the section are in boldface. ARG = Argentina; CHI = Chile; NZL = New Zealand; AUS = Australia; TAS = Tasmania; NA = North America; EUR = Europe.

Figure 2. Basidiomata of the species of *Cortinarius* sect. *Austroamericani*. A. *C. austroamericanus* (K(M)235066, isotype). B. *C. mascardiensis* (K(M)235045, isotype). C. *C. morenense* (K(M)234989, isotype). D. *C. patagoniensis* (K(M)235070, isotype). E. *C. rufoides* (K(M)235037, isotype). F. *C. rufosimilis* (K(M)234988, isotype). G. *C. rufus* (K(M)234990). H. *C. subrufus* (K(M)235584). Photographs: A–G. R. Healy, M. E. Smith, and T. Niskanen; H. T. Niskanen and C. Truong. Bar = 10 mm.

broadly ellipsoidal in *C. mascardiensis*; finely to strongly ornamented, more strongly ornamented at the apex, somewhat to strongly dextrinoid. Lamellar trama hyphae yellowish brown, finely to zebra-striped encrusted in MLZ. Lamellar edge mainly sterile, with undifferentiated sterile cells and a very few basidia, no cystidia or differentiated marginal cells observed. Basidia four-spored, clavate, yellowish, with a granulose content. Pileipellis duplex: epicutis thin, hyphae up to 23 µm wide, yellowish brown, finely to zebra-striped encrusted, less commonly smooth, with refracting granules. Hypoderm distinct, smooth to finely encrusted and somewhat pigmented. Clamp connections present.

Ecology and distribution: Associated with evergreen (*Nothofagus dombeyi*) or deciduous (*N. pumilio* and *N. antarctica*) species of *Nothofagus*. Currently only known from Patagonia, South America.

Notes: The species of *Cortinarius* sect. *Austroamericani* are reminiscent of the species of *C.* sect. *Fulvescentes*/*Laeti* and *Obtusi*. The members of these sections, however, do not have refracting granules in their epicutis. In addition, the members of sections *Fulvescentes* and *Laeti* are currently only known from the Northern Hemisphere and have a colored universal veil (yellow, ochraceous, pink to vinaceous) in contrast to the white to buff veil of the species of sect. *Austroamericani*. The species of sect. *Obtusi* occur both in the Northern and Southern Hemispheres but have a smell of iodoform at the base of the stipe when slightly dried, and some species have lamellar trama with ellipsoidal inflated hyphae ending in balloon-shaped cystidia.

Cortinarius austroamericanus San-Fabian, Niskanen & Liimat., sp. nov. FIGS. 2A, 3A, 4
Index Fungorum IF554559

Etymology: The epithet refers to the distribution of the species in South America.

Typification: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, road to Tronador, after Pampa Linda, at the base of the hill, in *N. dombeyi* forest, 14 May 2016, *T. Niskanen 16-235/MES2028* (**holotype** CORDC00005643). **Isotype** K(M)235066. GenBank: MF568549 (ITS) and KY462644 (ITS), generated from two different basidiomes of the isotype.

Description: Pileus 2.7–3.6 cm, at first somewhat conical, then low convex to almost plane with a very low umbo, margin entire, in older basidiomata becoming slightly undulating, surface smooth, somewhat waxy-looking, medium brown, hygrophanous. Lamellae medium-spaced to distant, adnate, moderately broad, yellow brown. Stipe 5.9–8.5 cm long, 0.3–0.6 cm thick at apex, 0.5–0.9 cm at base, cylindrical, at the very base slightly bulbous, surface whitish silky fibrillose, with age and handling the fibrousness is lost and the stipe becomes more concolorous with the context but

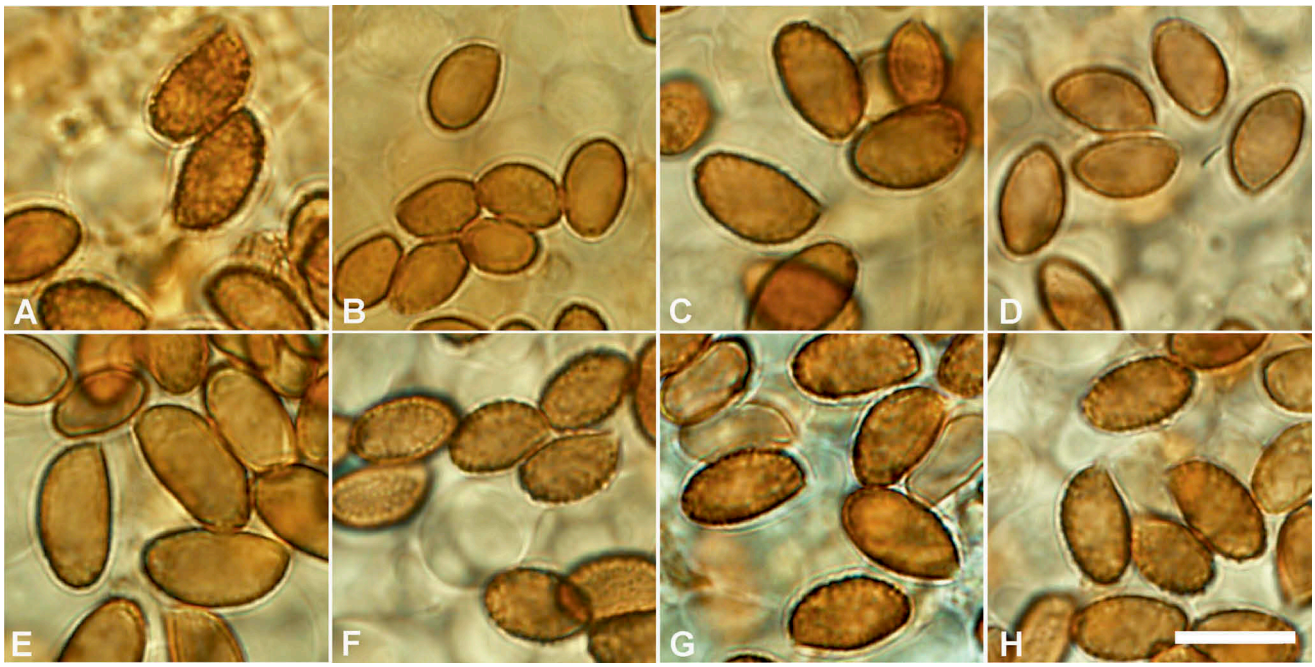

Figure 3. Basidiospores of the species of *Cortinarius* sect. *Austroamericani*. A. *C. austroamericanus* (K(M)235066, isotype). B. *C. mascardiensis* (K(M)235045, isotype). C. *C. morenense* (K(M)234989, isotype). D. *C. patagoniensis* (K(M)235070, isotype). E. *C. rufoides* (K(M)235037, isotype). F. *C. rufosimilis* (K(M)234988, isotype). G. *C. rufus* (K(M)234990). H. *C. subrufus* (K(M)235069, isotype). Photographs: B. San-Fabian. Bar = 10 µm.

Figure 4. Epicutis hyphae of *Cortinarius austroamericanus* (K(M) 235066, isotype) with refracting granules. Photographs: T. Niskanen. Bar = 10 µm.

remains slightly paler, pale brown. Universal veil white, sparse, often forming a thin sheath on the basal part of the stipe. Context medium brown in pileus and stipe. Odor in lamellae and base of the stipe indistinct. Exsiccatae: pileus dark brown (7.5YR 3/3), lamellae dark brown (7.5YR 3/3), stipe dark brown to white (7.5YR 3/2; 10YR 8/1).

Basidiospores (8.5–)9.5–10(–11.5) × (5–)5.5–6.0(–6.5) µm, av. = 9.9 × 5.8 µm, Q = (1.47–)1.52–1.82(–2.04), Q av. = 1.70, narrowly amygdaloid to ellipsoidal, less commonly obovoid, strongly and fairly coarsely verrucose, strongest ornamentation at the apex, moderately to strongly dextrinoid, brown in 10% KOH. Lamellar edge mainly sterile, with undifferentiated sterile cells and a very few basidia, no cystidia or differentiated marginal cells observed. Basidia four-spored, 25.5–30.5 × 8–9.5 µm, clavate, yellowish, with a granulose content. Pileipellis duplex: epicutis thin, hyphae 3–18.5 µm wide, yellowish brown, finely to zebra-striped encrusted, less commonly smooth, with 0.5–4 µm wide refracting granules in the upper most layer. Hypoderm distinct, elements 24.5–94 × 16.5–39 µm, finely encrusted, less commonly smooth, and somewhat brownish pigmented. Clamp connections present.

ITS region: In this region, *C. austroamericanus* (GenBank MF568549, isotype) differs from other known members of sect. *Austroamericani* as follows: *C. mascardiensis* (GenBank MF568550, isotype) by 2.0% (12 substitutions and indels), *C. patagoniensis* (GenBank MF568555, isotype) by 2.1% (13 substitutions and indels), and *C. rufosimilis* (GenBank KY462600, isotype) by 2.3% (14 substitutions and indels).

Ecology and distribution: In temperate Andino-Patagonian forests of *N. dombeyi* and *N. pumilio*. Currently known from Northern Patagonia, Nahuel Huapi National Park, Argentina. Basidiomata thus far found only in May.

Specimen details of a downloaded sequence: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, San Carlos de Bariloche, ectomycorrhizal root tip from *N. pumilio*, clone OTT01, UNITE UDB008440, GenBank JX316442 (ITS+28S).

Notes: Cortinarius austroamericanus is most easily identified by the intermediate to large spores that have the strongest ornamentation and the strongest dextrinoid reaction of any species in the section. The species is also characterized by a medium brown pileus and context and by the presence of abundant refracting granules in the upper layer of the epicutis. *Cortinarius morenense, C. rufoides, C. rufus*, and *C. subrufus* have similar-sized spores. *Cortinarius morenense*, however, has finely to moderately ornamented spores that have a smaller average length/width ratio (Q av. = 1.63–1.64), and the pileus and the context in the upper part of the stipe are distinctly more yellow brown. *Cortinarius rufoides* can be differentiated by its characteristic large and relatively narrower spores (av. = 10.8 × 5.9 µm, Q av. = 1.84) that are finely ornamented and almost indextrinoid. *Cortinarius rufus* and *C. subrufus* can be distinguished by their moderately ornamented spores; in addition, the average length/width ratio of the spores of *C. rufus* is somewhat bigger (Q = 1.79–2.2) than that of *C. austroamericanus*.

Cortinarius mascardiensis San-Fabian, Niskanen & Liimat., sp. nov. FIGS. 2B, 3B
Index Fungorum IF554560

Etymology: The epithet refers to the Mascardi region, where the species was found.

Typification: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, road to Tronador, at the end of Lake Mascardi before Pampa Linda, in *N. antarctica* forest, 14 May 2016, *T. Niskanen 16-217/MES2020* (**holotype** CORDC00005658). **Isotype** K(M)235045. GenBank: MF568550 (ITS), MF568551 (ITS), MF568552 (ITS), and MF489803 (28S), generated from two different basidiomes of the isotype.

Description: Pileus 3.5–5.2 cm, somewhat hemispherical at first, then low convex, rarely with a low and broad umbo, margin entire, becoming wavy in more mature basidiomata, surface smooth, somewhat matt-looking, brown to almost dark brown, hygrophanous. Lamellae medium spaced, adnate, moderately broad,

rather dark brown. Stipe 2–6 cm long, 0.7–0.9 cm thick at apex, 0.6–0.8 cm at base, rooting, surface whitish fibrillose. Universal veil white, sparse. Context in pileus brown, in stipe pale brown. Odor in lamellae indistinct. Exsiccatae: pileus very dark brown (7.5YR 2.5/3); lamellae very dark brown (7.5YR 2.5/3); stipe white to very pale brown (10YR 8/1; 8/2) with some brown and black (7.5YR 2.5/1; 4/4).

Basidiospores (6.5–)7–8.5 × (4–)5–6 µm, av. = 7.6 × 5.2 µm, Q = (1.30–)1.35–1.54(–1.70), Q av. = 1.47, mainly broadly amygdaloid, less commonly broadly ellipsoidal to somewhat obovoid, finely verrucose, moderately and more strongly ornamented at the apex, moderately dextrinoid, brown in 10% KOH. Lamellar trama hyphae yellowish brown, finely to zebra-striped encrusted. Lamellar edge mainly sterile, with undifferentiated sterile cells and very few basidia, no cystidia or differentiated marginal cells observed. Basidia four-spored, 24.5–37 × 7–9 µm, clavate, yellowish, with a granulose content. Pileipellis duplex: epicutis thin, hyphae 3.1–13.7 µm wide, yellowish brown, finely to zebra-striped encrusted, less commonly smooth, rarely with refracting granules 0.3–3.1 µm wide in the upper most layer. Hypoderm distinct, elements 12.5–52 × 8–34 µm, finely encrusted, less commonly smooth, and somewhat pigmented. Clamp connections present.

ITS region: The sequence of *C. mascardiensis* (GenBank MF568550, isotype) differs from the other known members of sect. *Austroamericani* as follows: *C. rufosimilis* (GenBank KY462600, isotype) by 1.6% (10 substitutions and indels), *C. morenense* (GenBank KY462604, isotype), *C. patagoniensis* (GenBank MF568555, holotype), and *C. rufus* (GenBank MF568565) by 1.8% (11 substitutions and indels), *C. austroamericanus* (GenBank MF568549, isotype) and *C. subrufus* (GenBank KY462648, isotype) both by 2.0% (12 substitutions and indels), and *C. rufoides* (GenBank MF568557, isotype) by 2.5% (15 substitutions and indels).

Ecology and distribution: In temperate Andino-Patagonian forests of *N. antarctica*. Currently known from Northern Patagonia, Nahuel Huapi National Park, Argentina. Basidiomata thus far found only in May.

Notes: Basidiomata of *C. mascardiensis* are distinctly stouter than in the other species of the section, and together with its characteristic finely ornamented amygdaloid-subglobose basidiospores, the smallest and relatively broadest (Q av. = 1.5) of this group, this species can be easily differentiated from the other members of the section. The other seven species included in this study all have larger spores with higher average length/width ratios (Q av. >1.6).

Cortinarius morenense San-Fabian, Niskanen & Liimat., sp. nov. FIGS. 2C, 3C

Index Fungorum IF554561

Etymology: The epithet refers to the lake Perito Moreno, which is close to the place where the species was found.

Typification: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, Arroyo Goye near Colonia Suiza, nearby the Perito Moreno Lake, in mixed *N. dombeyi* and *N. pumilio* forest, 12 May 2016, *T. Niskanen 16-162/MES1877* (**holotype** CORDC00005599). **Isotype** K(M) 234989. GenBank: KY462604 (ITS) from the isotype.

Description: Pileus 2.7–5.7 cm, at first somewhat conical, then low convex to almost plane with uplifted margins and with a medium-sized and broad umbo, margin entire, in older basidiomata becoming slightly undulate, surface matt, yellowish brown to brown, hygrophanous. Lamellae medium-spaced, adnate, moderately broad, yellow brown. Stipe 3.7–5 cm long, 0.3–0.7 cm thick at apex, 0.3–0.5 cm at base, cylindrical, the very base slightly bulbous, surface whitish silky fibrillose, with age and handling the fibrousness is lost and the stipe becomes more concolorous with the context but is slightly paler, pale yellowish brown. Universal veil white, sparse, often forming a thin sheath on the basal part of the stipe. Context of pileus and base of the stipe medium brown, stipe brownish yellow. Odor in lamellae raphanoid. Exsiccatae: pileus vivid brown (7.5YR 4/6; 5/8) to brown (7.5YR 4/4); lamellae vivid brown (7.5YR 5/8); stipe brown (7.5YR 4/4; 5/4) to dark brown (7.5YR 3/4) to very pale brown (10YR 8/3; 8/4), with some gray (7.5YR 5/1).

Basidiospores (8.5–)9–11(–12) × (4.5–)5.5–7 µm, av. = 9.7–9.9 × 5.9–6.0 µm, Q = (1.46–)1.53–1.76(–1.87), Q av. = 1.63–1.64, mainly amygdaloid, less commonly narrowly amygdaloid or ellipsoidal, finely to moderately verrucose, more strongly ornamented at the apex, moderately dextrinoid, brown in 10% KOH. Lamellar trama hyphae yellowish brown, finely to zebra-striped encrusted. Lamellar edge mainly sterile, with undifferentiated sterile cells and a very few basidia, no cystidia or differentiated marginal cells observed. Basidia four-spored, 34–37 × 7–9 µm, clavate, yellowish, with a granulose content. Pileipellis duplex: epicutis thin, hyphae 3–23.5 µm wide, yellowish brown, finely to zebra-striped encrusted, less commonly smooth, with 0.5–6 µm wide refracting granules in the upper most layer. Hypoderm distinct, elements 15.5–58 × 12.5–28 µm, smooth to finely encrusted and somewhat pigmented. Clamp connections present.

ITS region: The sequence of *C. morenense* (GenBank KY462604, holotype) differs from other known members of sect. *Austroamericani* as follows: *C.*

mascardiensis (GenBank MF568550, isotype) by 1.8% (11 substitutions and indels), *C. rufoides* (GenBank MF568557, isotype) by 2.3% (14 substitutions and indels), and *C. rufosimilis* (GenBank KY462600, isotype) by 2.5% (15 substitutions and indels).

Ecology and distribution: In mixed, temperate Andino-Patagonian forests of *N. dombeyi* and *N. pumilio*, and in *N. antarctica* forests. Currently known from Northern Patagonia, Nahuel Huapi National Park, Argentina. Basidiomata thus far found only in May.

Other specimens examined: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, Los Rapidos, in *N. antarctica* forest, 13 May 2016, *T. Niskanen 16-191/MES1929* (K(M)235018), GenBank: MF568553 (ITS); Arroyo Goye near Colonia Suiza, in mixed *N. dombeyi* and *N. pumilio* forest, 12 May 2016, *T. Niskanen et al. 16-166/MES1867* (K(M)234993), GenBank: MF568554 (ITS) and MF489804 (28S).

Notes: Cortinarius morenense has large, finely to moderately verrucose, and moderately dextrinoid spores. This species is further recognized by the yellowish brown to brown pileus, yellowish context, and a raphanoid odor. Other large-spored species of the section, *C. austroamericanus, C. rufoides, C. rufus*, and *C. subrufus*, have at least somewhat bigger average length/width ratios of the spores (Q av. = 1.68–2.2). In addition, *C. austroamericanus* has strongly ornamented spores, *C. rufoides* has finely ornamented and almost indextrinoid spores, and *C. rufus* and *C. subrufus* have strongly to moderately ornamented spores. Macroscopic examinations of *C. austroamericanus, C. rufoides, C. rufus*, and *C. subrufus* also revealed that these species differ in the color of the pileus and context; all of them are more brown to reddish brown than *C. morenense*.

Cortinarius patagoniensis San-Fabian, Niskanen & Liimat., sp. nov. FIGS. 2D, 3D

Index Fungorum IF554562

Etymology: The epithet refers to the distribution of the species in Patagonia, South America.

Typification: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, road to Tronador, after Pampa Linda, at the base of the hill, in *N. antarctica* forest, 14 May 2016, *T. Niskanen 16-239/MES2048* (**holotype** CORDC00005611). **Isotype** K(M)235070). GenBank: MF568555 (ITS) from the isotype.

Description: Pileus 1.7–4.3 cm, at first conical to somewhat convex with a medium and broad umbo, remaining conical with age, margin entire, cracking radially in older basidiomata, surface smooth, slightly waxy-looking, yellowish brown to medium brown, hygrophanous. Lamellae medium-spaced to distant, adnate, moderately broad, yellow brown. Stipe 4.5–8.3 cm long, 0.2–0.6 cm thick at apex, 0.3–0.6 cm at base, cylindrical, the very base slightly bulbous, surface whitish silky fibrillose, with age and handling the fibrousness is lost and the stipe becomes more concolorous with the context but is still slightly paler, pale yellowish brown. Universal veil white, sparse, often forming a thin sheath on the basal part of the stipe. Context in pileus brown, in stipe yellowish brown. Odor in lamellae indistinct. Exsiccatae: pileus brown (7.5YR 4/4); vivid brown lamellae (7.5YR 5/8); stipe dark brown to very pale brown (7.5YR 3/4; 10YR 8/2).

Basidiospores (7.5–)8–10 × 4.5–6 µm, av. = 8.4–8.7 × 5.1–5.3 µm, Q = (1.38–)1.43–1.76(–1.92), Q av. = 1.63–1.65, mainly amygdaloid, less commonly ellipsoidal and obovoid, finely verrucose, moderately and more strongly ornamented at the apex, moderately dextrinoid, brown in 10% KOH. Lamellar trama hyphae yellowish brown, zebra-striped encrusted, less commonly finely encrusted in MLZ. Lamellar edge mainly sterile, with undifferentiated sterile cells and a very few basidia, no cystidia or differentiated marginal cells observed. Basidia four-spored, 25.5–39 × 7–9 µm, clavate, yellowish, with a granulose content. Pileipellis duplex: epicutis thin, hyphae 3–17 µm wide, yellowish brown, finely to zebra-striped encrusted, less commonly smooth, with 0.5–2.5 µm wide refracting granules in the upper most layer. Hypoderm distinct, elements 31–115 × 14–50 µm, smooth, less commonly finely encrusted, and somewhat pigmented. Clamp connections present.

ITS region: The sequence of *C. patagoniensis* (GenBank MF568555, isotype) differs from other known members of sect. *Austroamericani* as follows: *C. mascardiensis* (GenBank MF568550, isotype) by 1.8% (11 substitutions and indels), *C. austroamericanus* (GenBank MF568549, isotype) by 2.1% (13 substitutions and indels), and *C. rufosimilis* (GenBank KY462600, isotype) by 2.5% (15 substitutions and indels).

Ecology and distribution: In temperate Andino-Patagonian forests of *N. antarctica* and *N. pumilio*. Currently known from Southern and Northern Patagonia, Nahuel Huapi National Park, Argentina, and Karunkinka Reserve, Chile. Basidiomata thus far found only in March in Southern Patagonia and May in Northern Patagonia.

Other specimens examined: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, road to Tronador, at the end of Lake Mascardi before Pampa Linda, in *N. antarctica* forest, 14 May 2016, *T. Niskanen 16-216/MES2022* (K(M)235044), GenBank: KY462640 (ITS). CHILE. MAGALLANES: Karukinka Reserve, around Vicuña station, 54°08.31′S, 68°42.68′W, alt. 172 m above sea level (a.s.l.), in *N. pumilio* forest, close to the edge with *N. antarctica*, in an open area

grazed by horses with dense understory, 26 Mar 2017, *T. Niskanen & C. Truong CT4610*, (K(M)235581). GenBank: MF568556 (ITS) and MF489804 (28S).

Notes: This small and slender species looks like those in sect. *Obtusi*. This is the only species known from sect. *Austroamericani* with a conical yellowish brown to medium brown pileus. The basidiospores are of intermediate size, finely verrucose, and almost indextrinoid. The spores of *C. rufosimilis* are of similar size and shape but they are moderately ornamented and moderately dextrinoid and the pileus is convex and reddish brown. Based on molecular data, *C. patagoniensis* is composed of two taxa, *C. patagoniensis* and *C.* aff. *patagoniensis*, because our specimen CT4610 differs from the type of *C. patagoniensis* by four substitutions. To date, *C. patagoniensis* has only been found in forests of *N. antarctica* and *C.* aff. *patagoniensis* in forests of *N. pumilio*. However, considering that no morphological differences have been found, we treat all of the collections mentioned here as *C. patagoniensis* s.l. Further studies with additional specimens are needed to determine the species limits in this group.

Cortinarius rufoides San-Fabian, Niskanen & Liimat., sp. nov. FIGS. 2E, 3E

Index Fungorum IF554563.

Etymology: The epithet indicates that the color of the basidiomata resembles that of *C. rufus*.

Typification: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, road to Tronador, just before the mountain base, in *N. pumilio* forest, 14 May 2016, *T. Niskanen 16-209/MES2007* (**holotype** CORDC00005552). **Isotype** K(M)235037. GenBank: MF568557 (ITS) and MF568558 (ITS), generated from two different basidiomes of the isotype.

Description: Pileus 2–2.8 cm, at first somewhat conical, then convex with a low and broad umbo, margin entire, surface smooth, slightly waxy-looking, not viscid, medium red brown, center often dark brown, sometimes yellow brown toward the margin, hygrophanous. Lamellae medium-spaced, adnate, moderately broad, yellow brown. Stipe 3.1–4 cm long, 0.3–0.5 cm thick at apex, 0.4–0.5 cm at base, cylindrical, surface whitish silky fibrillose, with age and handling the fibrousness is lost and the stipe becomes more concolorous with the context but is slightly paler, pale yellowish brown. Universal veil white, sparse, often forming a thin sheath on the basal part of the stipe. Context in pileus reddish brown, in stipe yellowish brown. Odor in lamellae indistinct. Exsiccatae: pileus dark brown to vivid brown (7.5YR 3/4; 4/6); lamellae brown (7.5YR 4/4); stipe dark brown to very dark brown (7.5YR 2.5/2; 3/4).

Basidiospores (8.5–)10–12(–12.5) × (4.5–)5.5–6.5 µm, av. = 10.8 × 5.9 µm, Q = (1.72–)1.74–1.94(–2.13), Q av. = 1.84, narrowly amygdaloid-ellipsoidal, less commonly obovoid, finely verrucose, moderately ornamented at the apex, somewhat dextrinoid, brown in 10% KOH. Lamellar trama hyphae yellowish brown, zebra-striped encrusted, less commonly finely encrusted in MLZ. Lamellar edge mainly sterile, with undifferentiated sterile cells and a very few basidia, no cystidia or differentiated marginal cells observed. Basidia four-spored, 30.5–41 × 7–10 µm, clavate, yellowish, with a granulose content. Pileipellis duplex: epicutis thin, hyphae 4.5–19 µm wide, yellowish brown, finely to zebra-striped encrusted, less commonly smooth, with 0.5–5.5 µm wide refracting granules in the upper most layer. Hypoderm distinct, elements 19–86 × 15.5–47 µm, finely encrusted, less commonly smooth, and somewhat pigmented. Clamp connections present.

ITS region: The sequence of *C. rufoides* (GenBank MF568557, isotype) deviates from the other known members of sect. *Austroamericani* by at least 2.3% (14 substitutions and indels).

Ecology and distribution: In temperate Andino-Patagonian forests of *N. pumilio*. Currently known from Northern Patagonia, Nahuel Huapi National Park, Argentina. Basidiomata thus far found only in May.

Notes: Cortinarius rufoides has among the largest and relatively narrowest spores of the section, and they are finely ornamented and almost indextrinoid. The pileus is medium red brown and often with a dark brown center. The sister species *C. morenense* has slightly more ornamented and more dextrinoid spores with a smaller average length/width ratio (Q av. = 1.63–1.64). *Cortinarius rufosimilis, C. rufus*, and *C. subrufus* are macroscopically rather similar to *C. rufoides* but often have somewhat darker, more reddish brown pileus and can be distinguished from *C. rufoides* by their moderately verrucose and moderately dextrinoid spores. The spores of *C. rufus* and *C. subrufus* are similar in size to those of *C. rufoides*, but the spores of *C. rufosimilis* are smaller and relatively broader (Q av. = 1.65).

Cortinarius rufosimilis San-Fabian, Niskanen & Liimat., sp. nov. FIGS. 2F, 3F

Index Fungorum IF554564

Etymology: The epithet refers to the similarity in the color of the basidiomata of this species to *C. rufus*.

Typification: ARGENTINA. RIO NEGRO: Huapi National Park, Arroyo Goye near Colonia Suiza, in mixed *N. dombeyi* and *N. pumilio* forest, 12 May 2016, *T. Niskanen 16-161/MES1864* (**holotype** CORDC00005566). **Isotype** K(M)234988. GenBank: KY462600 (ITS),

MF568559 (ITS), and MF489802 (28S), generated from two different basidiomes of the isotype.

Description: Pileus 2.5–3.2 cm, at first somewhat conical, then convex umbonate with a medium and broad umbo, margin entire, becoming slightly undulate in more mature basidiomata, surface smooth, slightly waxy-looking, vivid reddish brown to dark reddish brown often with a darker center, hygrophanous. Lamellae medium-spaced, adnate, moderately broad, yellow brown. Stipe 5–5.4 cm long, 0.3–0.4 cm thick at apex, 0.5–0.7 cm at base, cylindrical, the very base slightly bulbous, surface whitish silky fibrillose, with age and handling the fibrousness is lost and the stipe becomes more concolorous with the context but is slightly paler, pale brown. Universal veil white to buff, sparse, often forming a thin sheath on the basal part of the stipe. Context in pileus and in base of the stipe stronger brown, in stipe yellowish brown. Odor in lamellae faintly raphanoid. Exsiccatae: pileus dark brown (7.5YR 3/4); lamellae dark brown (7.5YR 3/4); stipe dark brown to very pale brown (7.5YR 3/2; 10YR 8/2).

Basidiospores 8–9.5(–10) × 5–6 µm, av. = 8.7 × 5.3 µm, Q = 1.49–1.78(–1.83), Q av. = 1.65, mainly amygdaloid, less commonly ellipsoidal and obovoid, moderately to strongly verrucose, strongest ornamented at the apex, moderately dextrinoid, brown in 10% KOH. Lamellar trama hyphae yellowish brown, finely but distinctly encrusted. Lamellar edge mainly sterile, with undifferentiated sterile cells and a very few basidia, no cystidia or differentiated marginal cells observed. Basidia four-spored, 21.5–33 × 7–9 µm, clavate, yellowish, with a granulose content. Pileipellis duplex: epicutis thin, hyphae 3–19 µm wide, yellowish brown, finely to zebra-striped encrusted, less commonly smooth, with 0.5–4 µm wide refracting granules in the upper most layer. Hypoderm distinct, elements 23.5–83 × 15.5–37 µm, finely encrusted or with more distinctive encrustations, less commonly smooth, and somewhat pigmented. Clamp connections present.

ITS region: The sequence of *C. rufosimilis* (GenBank KY462600, isotype) differs from other known members of sect. *Austroamericani* as follows: *C. mascardiensis* (GenBank MF568550, isotype) and *C. subrufus* (GenBank KY462648, isotype) both by 1.6% (10 substitutions and indels), *C. rufus* (GenBank MF568565) by 1.8% (11 substitutions and indels), *C. austroamericanus* (GenBank MF568549, isotype) by 2.3% (14 substitutions and indels), and *C. morenense* (GenBank KY462604, isotype) and *C. patagoniensis* (GenBank MF568555, isotype) both by 2.4% (15 substitutions and indels).

Ecology and distribution: In mixed Andino-Patagonian forests of *N. dombeyi* and *N. pumilio*. Currently known from Northern Patagonia, Nahuel Huapi National Park, Argentina. Basidiomata thus far found only in May.

Notes: Cortinarius rufosimilis is characterized by a vivid reddish brown to dark reddish brown pileus, a slightly raphanoid odor in the lamellae, and intermediate-sized, moderately to strongly verrucose spores. The spores of *C. patagoniensis* are of similar size but are finely ornamented and almost indextrinoid. In addition, the pileus is more conical and yellowish brown. *Cortinarius rufoides, C. rufus*, and *C. subrufus* could be macroscopically confused with *C. rufosimilis* because of the similar color and shape of the basidiomata. However, their spores are larger and the average Q value is typically somewhat larger (Q av. = 1.68–2.2) than in *C. rufosimilis*.

***Cortinarius* sect. *Austroamericani* s.l.**—The two species listed below form a well-supported basal clade that is separated from the core sect. *Austroamericani*. This clade is treated as *Austroamericani* s.l. because the relationship with *Austroamericani* s.s. is not statistically supported. Additional taxon sampling and genetic studies with other loci are needed to resolve the delimitation of this section.

Cortinarius rufus M.M. Moser, Beihefte zur Nova Hedwigia 52:335. 1975. FIGS. 2G, 3G

Typification: ARGENTINA. NEUQUÉN: Cerro Cortinario, Puerto Manzano, in *N. pumilio* forest, 18 Apr 1963, *M. Moser 1963/0369* (**holotype** IB19630369). GenBank: MF568564 (ITS2).

Description: Pileus up to 2 cm wide, at first somewhat conical, then convex umbonate, margin entire, surface smooth to radially fibrillose, reddish brown to somewhat dark brown, hygrophanous. Lamellae medium-spaced to distant, adnate, moderately broad, vividly cinnamon brown. Stipe 2.5–3 cm long, 0.3–0.4 cm thick at apex, up to 0.5 cm at base, cylindrical, the very base slightly bulbous, surface at first whitish silky fibrillose, with age and handling the fibrousness is lost and the stipe becomes more concolorous with the context. Universal veil white, sparse, forming a thin sheath on the basal part of the stipe. Context in pileus and stipe dark brown. Odor in lamellae indistinct. Exsiccatae: pileus dark brown (7.5YR 3/3); lamellae dark brown (7.5YR 3/3); stipe dark brown (7.5YR 3/4) to white (10YR 8/1).

Basidiospores (9.5–)10–12(–13.5) × 5–6(–6.5) µm, av. = 10.1–11.1 × 5.6 µm, Q = (1.61–)1.7–2.2(–2.4), Q av. = 1.79–2.0, narrowly amygdaloid to ellipsoidal, often with a

suprahilar depression, moderately to strongly verrucose, strongest ornamented at the apex, moderately to almost strongly dextrinoid, brown in 10% KOH. Lamellar trama hyphae yellowish brown, finely to zebra-striped encrusted. Lamellar edge mainly sterile, with undifferentiated sterile cells and a very few basidia, no cystidia or differentiated marginal cells observed. Basidia four-spored, 31.5–37 × 8–9 µm, clavate, yellowish, with a granulose content. Pileipellis duplex: epicutis thin, hyphae 4.7–19 µm wide, yellowish brown, finely to zebra-striped encrusted, less commonly smooth, with some refracting granules 0.3–1 µm wide in the upper most layer. Hypoderm distinct, elements 33–100 × 23–37 µm, smooth to finely encrusted and somewhat pigmented. Clamp connections present.

ITS region: The sequence of *C. rufus* (GenBank MF568565) deviates from the other known members of sect. *Austroamericani* as follows: from the sister species *C. subrufus* (GenBank KY462648, isotype) by 0.7% (5 substitutions and indels), from *C. mascardiensis* (GenBank MF568550, isotype) and *C. rufosimilis* (GenBank KY462600, holotype) both by 1.8% (11 substitutions and indels), and from *C. rufoides* (GenBank MF568557, isotype) by 2.5% (15 substitutions and indels).

Ecology and distribution: In temperate Andino-Patagonian forests of *N. pumilio* and in forest mixed with *N. dombeyi*. Currently known from Northern Patagonia, Puerto Manzano, and Nahuel Huapi National Park, Argentina.

Specimen examined: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, Arroyo Goye near Colonia Suiza, in mixed *N. dombeyi* and *N. pumilio* forest, 12 May 2016, *T. Niskanen et al. 16-163/MES1865* (K(M)234990). GenBank: MF568565 (ITS) and MF489798 (28S).

Notes: Cortinarius rufus is notable for its large, moderately to strongly verrucose, and relatively narrow spores (Q av. = 1.8–2.0). This species is also defined by a rather small (up to 2 cm diam), reddish brown to brown pileus. The sister species C. *subrufus* is morphologically similar, but its spores are somewhat smaller (av. = 9.2–9.7 × 5.4–5.6 µm) and more ellipsoidal (Q av. = 1.68–1.70). *Cortinarius austroamericanus, C. morenense*, and *C. rufoides* are also large-spored species. However, the spores of *C. austroamericanus* are broader (Q av. = 1.7), *C. morenense* has broader and more finely ornamented spores (Q av. = 1.63–1.64), and *C. rufoides* has finely ornamented and almost indextrinoid spores. *Cortinarius morenense* and *C. rufoides* can also be differentiated by their slightly paler and more yellowish pilei and stipe context, especially in *C. morenense* where these features are more obvious.

Our observations of *Cortinarius rufus* fit with Moser's original description except that the pileus was described as radially fibrillose and the spores were described as warty and 10.5–13(–14) × 5.5–7 µm. We reexamined the spores of the type specimen and observed the following measurements: (10–)10.5–12(–13.5) × 5–6(–6.5) µm, av. = 11.1 × 5.6 µm, Q = (1.6–)1.8–2.2(–2.4), Q av. = 2.0. Observed values from the type are close to our measurements from recently collected material, (9.5–)10–10.5(–11.5) × 5–6 µm, av. = 10.1 × 5.6 µm, Q = (1.6–)1.7–1.9(–2.1), Q av. = 1.8. Furthermore, the shape, ornamentation, and dextrinoidity of the spores in our new collection are also similar to those of the type. The ITS2 sequence from the type specimen of *C. rufus* is identical to the sequence from MES1865. Our conclusion is that these two specimens represent the same species; thus, we provide an updated description of this species above.

Cortinarius subrufus San-Fabian, Niskanen & Liimat., sp. nov. FIGS. 2H, 3H

Index Fungorum IF554565.

Etymology: The epithet refers to the affinity to *C. rufus*.

Typification: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, road to Tronador, after Pampa Linda, at the base of the hill, in *N. antarctica* forest, 14 May 2016, *T. Niskanen 16-238/MES2047* (**holotype** CORDC00005558). **Isotype** K(M)235069. GenBank: KY462648 (ITS), generated from the isotype.

Description: Pileus 1.8–3.4 cm, at first somewhat conical, then convex umbonate with a medium to broad umbo, margin entire, becoming slightly undulate in more mature basidiomata, surface smooth, slightly waxy-looking, vivid reddish brown to dark reddish brown, hygrophanous. Lamellae medium-spaced to distant, adnate, moderately broad, yellow brown. Stipe 3.7–7.5 cm long, 0.3–0.5 cm thick at apex, 0.5–0.8 cm at base, cylindrical, the very base slightly bulbous, surface whitish silky fibrillose, rather stiff, with age and handling the fibrousness is lost and the stipe becomes more concolorous with the context but is slightly paler, pale brown. Universal veil white, sparse, forming a thin sheath on the basal part of the stipe. Context in pileus and base of the stipe dark brown, in stipe yellowish brown to pale brown. Odor in lamellae indistinct. Exsiccatae: pileus dark brown to brown (7.5YR 3/4; 4/4); vivid brown lamellae (7.5YR 4/6); stipe dark brown (7.5YR 3/3) to light gray and white (10YR 7/2; 8/1).

Basidiospores (8.5–)9–11 × 5–6.5 µm, av. = 9.2–9.7 × 5.4–5.6 µm, Q = (1.45–)1.50–1.88(–1.96), Q av. = 1.68–1.70, narrowly amygdaloid to ellipsoidal, less commonly obovoid; moderately to strongly verrucose, strongest ornamentation at the apex, moderately to almost strongly dextrinoid, brown in 10% KOH. Lamellar trama hyphae yellowish brown, finely to

zebra-striped encrusted. Lamellar edge mainly sterile, with a very few basidia, no cystidia or differentiated marginal cells observed. Basidia four-spored, 20.5–32 × 6.5–9 µm, clavate, yellowish, with a granulose content. Pileipellis duplex: epicutis thin, hyphae 6–20 µm wide, yellowish brown, finely to zebra-striped encrusted, less commonly smooth, with 0.5–3 µm wide refracting granules in the upper most layer. Hypoderm distinct, elements 18.5–89 × 14–42 µm, smooth to finely encrusted and somewhat pigmented. Clamp connections present.

ITS region: The sequence of *C. subrufus* (GenBank KY462648, isotype) differs from the other known members of sect. *Austroamericani* as follows: from its sister species *C. rufus* (GenBank MF568565) by 0.7% (5 substitutions and indels), from *C. rufosimilis* (GenBank KY462600, isotype) by 1.6% (10 substitutions and indels), and from *C. mascardiensis* (GenBank MF568550, isotype) by 2.0% (12 substitutions and indels).

Ecology and distribution: In temperate Andino-Patagonian forests of *N. antarctica* and *N. pumilio*. Currently known from both Southern and Northern Patagonia, Nahuel Huapi National Park, Argentina, and Karukinka Reserve, Chile. Basidiomata thus far found only in Mar in Southern Patagonia and May in Northern Patagonia.

Other specimens examined: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, Lago Hess, in *N. antarctica* forest, 17 May 2016, *T. Niskanen 16-259/MES2084* (K(M)235093), GenBank: MF568560 (ITS); loc. cit., 16 May 2016, *T. Niskanen 16-261* (K(M)235095), GenBank: MF568563 (ITS) and MF489801 (28S). CHILE. MAGALLANES: Karukinka Reserve, along the path to Laguna del Cura from Vicuña station, by the stream, 54°08′46.0″S, 68°43′40.2″W, alt. 252 m a.s.l., in *N. antarctica* forest, close by *N. pumilio* forest, by the creek, 26 Mar 2017, *T. Niskanen & C. Truong CT4647* (SGO; K(M)235584), GenBank: MF568562 (ITS) and MF489800 (28S); Karukinka Reserve, along the path to Laguna del Cura from Vicuña station, by the stream, 54°08′46.0″S, 68°43′40.2″W, alt. 252 m a.s.l., in *N. antarctica* forest, close by *N. pumilio* forest, by the creek, 26 Mar 2017, *T. Niskanen & C. Truong CT4649* (SGO; K(M)235583), GenBank: MF568561 (ITS) and MF489799 (28S).

Specimen details of a downloaded sequence: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, San Carlos de Bariloche, ectomycorrhizal root tip from *N. pumilio*, UNITE UDB014290 (ITS+28S).

Notes: Cortinarius subrufus is recognized by a vivid reddish brown to brown pileus and intermediate-sized to large-sized, moderately to strongly verrucose spores. Spores of the sister species *C. rufus* are somewhat larger (av. = 10.1–11.1 × 5.6 µm), and the average length/width ratio of the spores is higher (Q av. = 1.8–2.0). *Cortinarius austroamericanus* and *C. morenense* also have spores of similar sizes. The spores of *C. austroamericanus*, however, are strongly verrucose, and the spores of *C. morenense* finely ornamented and the average length/width ratio is smaller (Q av. = 1.63–1.64). *Cortinarius morenense* can also be differentiated by its notably more yellowish pileus and context. Based on macroscopic characters, *C. rufoides* and *C. rufosimilis* could be misidentified as *C. subrufus* because all three species have similar reddish brown pilei. However, the spores of *C. rufoides* are larger (av. = 10.8 × 5.9), more finely ornamented, narrower (Q av. = 1.84), and almost indextrinoid, whereas the spores of *C. rufosimilis* are smaller (av. = 8.7 × 5.3) and the average length/width ratio of the spores is higher (Q av. = 1.65).

KEY TO THE DESCRIBED SPECIES OF *CORTINARIUS* SECT. *AUSTROAMERICANI*

1. Basidiospores on average <9 µm long. 2
1′. Basidiospores larger, on average >9 µm long ... 4
2. Basidiospores on average <8 µm long; basidiomata comparatively stouter, apex of the stipe often ≥0.7 cm wide. ..... *C. mascardiensis*
2′. Basidiospores on average >8 µm long; basidiomata slender, apex of the stipe often ≤0.6 cm wide 3
3. Pileus yellow brown; basidiospores finely verrucose, almost indextrinoid ..... *C. patagoniensis*
3′. Pileus reddish brown; basidiospores moderately verrucose, moderately dextrinoid... *C. rufosimilis*
4. Q av. >1.75 5
4′. Q av. <1.75 6
5. Pileus medium red brown, center often dark brown, sometimes yellow brown toward the margin; context in the upper part of the stipe yellow brown; basidiospores finely verrucose, somewhat dextrinoid..... *C. rufoides*
5′. Pileus reddish brown to almost dark brown; context in the upper part of the stipe brown to dark brown; basidiospores moderately to strongly verrucose and dextrinoid..... *C. rufus*
6. Q av. <1.65, basidiospores finely to moderately verrucose, moderately dextrinoid... *C. morenense*
6′. Q av. >1.65, basidiospores moderately to strongly verrucose and dextrinoid. 7
7. Pileus medium brown; basidiospores on average 9.9 × 5.8 µm..... *C. austroamericanus*

7′. Pileus vivid reddish brown to dark reddish brown; basidiospores on average 9.2–9.7 × 5.4–5.6 µm..... ..... *C. subrufus*

DISCUSSION

Species delimitation and phylogenetic relationships.—Twelve species are recognized within the newly described sect. *Austroamericani*. All species have an intraspecific variation of less than 0.3% in the ITS region. The interspecific variation is greater than 1.6%, except in the species pair *C. rufus*/*C. subrufus* where variation between the species is also 0.7%. All species received high support in our phylogenetic analysis, and their delimitation is also supported by morphological data. This corresponds well with previous studies of *Cortinarius* that have shown that an ITS similarity threshold value of 99% is suitable for distinguishing species in the majority of lineages, although some morphologically distinguishable species may have even higher threshold values, probably indicating recent radiation events (Niskanen et al. 2011; Garnica et al. 2016). The barcodes of the species will be deposited in the RefSeq database (Schoch et al. 2014) and used to set reference sequences in UNITE (Kõljalg et al. 2013).

The species studied here formed a monophyletic clade consisting of two main entities, sect. *Austroamericani* s.s., which grouped together in all analyses, and sect. *Austroamericani* s.l., which formed a separate clade that is not statistically supported as sister to sect. *Austroamericani* s.s. However, we treat sect. *Austroamericani* s.l. as part of the section *Austroamericani* because the morphology, distribution, and host plant associations are consistent with sect. *Austroamericani* s.s. The *Austroamericani* s.l. clade is sister to *Austroamericani* s.s. in all analyses, suggesting that *C. rufus* and the closely related *C. subrufus* (the two species in the *Austroamericani* s.l. clade) may represent an ancestral clade within the section.

The only previously known species of the section, *C. rufus*, was originally placed in subg. *Telamonia* (Moser and Horak 1975). However, based on current knowledge, subg. *Telamonia* mainly includes representatives from the Northern Hemisphere (Peintner et al. 2004; Garnica et al. 2005). Our phylogenetic analysis revealed that *C. rufus* does not belong to subg. *Telamonia* and suggests that its closest relatives are Nothofagaceae-associated species from South America and New Zealand. The current classification for South American *Cortinarius* was proposed by Moser and Horak (1975) and is based on morphological characters. Recent studies have shown that traditional classifications are at least partly artificial and are in a need of revision based on molecular data (Peintner et al. 2001, 2004; Garnica et al. 2003, 2005). Our results show that sect. *Austroamericani* is not closely related to morphologically similar clades that have been described previously; we therefore propose it as a new section. Based on morphological and molecular features, this section belongs to the large and well-supported monophyletic lineage of stipitocarpic *Cortinarii* that includes subgenera *Cortinarius* and *Telamonia*, most of subg. *Myxacium*, and some phlegmacioid species (Stensrud et al. 2014). However, additional relationships within the lineage were not resolved in our current analysis.

The short branch leading to sect. *Austroamericani* suggests that it has undergone a rapid evolutionary diversification. In *Cortinarius*, Southern Hemisphere clades generally have shorter branch lengths than clades from the Northern Hemisphere or mixed clades that include species from both the Northern and Southern Hemispheres, i.e., *Obtusi, Fulvescentes*, and *Telamonia* (FIG. 1). This is not a feature derived from biased sampling because the same tree topology was also observed in analyses that included additional species from the Northern Hemisphere (T. Niskanen, unpubl. data). The recent radiation observed in sect. *Austroamericani* could be explained by an adaptive radiation during the process of speciation. We hypothesize that the species in sect. *Austroamericani* may have diversified in a relatively short time. Colonization of a new area may have led to rapid adaptation because of the availability of new niches. This phenomenon of short branches has not been reported so far in other studies of South American fungi; therefore, further studies of other *Cortinarius* groups are needed to verify this trend. Future directions include time-calibrated analyses to date lineage divergence events as well as phylogenies of Nothofagaceae and other plant associations, in order to understand coevolutionary processes. Moreover, dating the phylogeny could help to reveal how the occurrence of adaptive radiation is correlated with historical events (e.g., movement of landmasses or forest expansion). In addition, a biogeographic characterization could help to resolve the biogeographic history of Southern Hemispheric species, including the direction of colonization and characterization of ancestral clades.

Morphological characteristics.—We found several morphological characters that in combination can be used to recognize the members of sect. *Austroamericani*. All species form small basidiomata and have a more or less brown and hygrophanous pileus, white to buff universal veil, and brown to brownish yellow context in the stipe. The pileipellis is duplex, with a thin epicutis and a distinctive hypoderm. Zebra-striped encrusted hyphae are commonly found in

both the lamellae and epicutis, and refracting granules can be found in the epicutis. The refracting granules in the epicutis are not a common feature in telamonioid *Cortinarii* and may be a very useful character for distinguishing the members of this section from other morphologically similar species. However, morphological convergence exists with other clades such as subg. *Telamonia*, sect. *Fulvescentes*/*Laeti*, and sect. *Obtusi* (Peintner et al. 2004; Garnica et al. 2005; Niskanen 2008). Currently, because we are far from knowing all species and their characters in *Cortinarius*, sequence-based identification is generally needed for reliable section-level recognition.

For species-level identification within the section, the most important diagnostic characters are mainly spore size (length, width), shape (Q value), and ornamentation. The color and in some cases the shape of the pileus and the color of the context in the stipe are also useful for species identification when used together with additional significant diagnostic features.

Ecology and distribution.—The species of sect. *Austroamericani* s.l. are found in association with Nothofagaceae species, including *N. antarctica, N. dombeyi, N. pumilio*, and *Lophozonia obliqua* (Heenan and Smissen 2013). The ectomycorrhizal associations formed by species in sect. *Austroamericani* did not show any evident host specificity, as also previously suggested by Nouhra et al. (2013). This suggests that species are not strictly constrained to one host but may grow in association with different tree species from Nothofagaceae. However, most of our sampling was in forests in the southern part of Patagonia that were dominated by species of *Nothofagus*. We only rarely sampled in association with trees in the genus *Lophozonia*, and we were unable to visit endangered trees in the genus *Fuscospora*. Further sampling with these phylogenetically divergent hosts in the northern part of Patagonia may uncover additional new species that could belong to sect. *Austroamericani*.

All studied species of sect. *Austroamericani* have thus far been found only from Argentina and Chile, so we suggest that this section is likely endemic to South America. All collecting was done on the drier side of the Andes, and it is unknown whether these species also occur in more humid coastal areas. Most of the species are currently known only from a very limited area, with the exception of *C. patagoniensis* and *C. subrufus*, which have been found from both Southern and Northern Patagonia. The limited number of collections available does not permit us to draw further conclusions about the distribution of these species so far.

Conclusions.—This study contributes to the knowledge on Patagonian fungal diversity by formally recognizing the new section *Austroamericani*, represented by 12 species, of which 7 are described as new in this study. We have included *Cortinarius rufus* and *C. subrufus* as part of sect. *Austroamericani* s.l., although its relationship with the remaining species in the core sect. *Austroamericani* s.s. is not statistically supported by the phylogenetic analysis. However, we found that all the species are morphologically similar, form ECM associations with the trees from the family Nothofagaceae, and are endemic to southern South America. We therefore treat them all as part of the same section. Our study aims to encourage similar research in South America, a region that is largely understudied and with a presumably large fungal diversity yet to be described.

ACKNOWLEDGMENTS

We thank the Administracion de Parques Nacionales of Argentina for authorizing our collecting expeditions in Parque Nacional Nahuel Huapi and Parque Nacional Lanin under Projecto 2016/720 (to E. Nouhra). The Wildlife Conservation Society Chile in Parque Karukinka kindly authorized our investigation (C.T. and T.N.). We thank the staff at the CORD herbarium for helping to rapidly process loans to facilitate this work. We acknowledge critical logistical support and photography help during field collecting by R. Healy, F. Kuhar, G. Furci, N. Fernandez, and D. Pfister. We thank Ester Gaya for inspiring discussions on the evolution on South American Cortinarii during the preparation of the manuscript. Lastly, we would like to thank the editor and two anonymous reviewers who helped us to improve the manuscript.

FUNDING

This work was supported by the US National Science Foundation grant DEB 1354802 (to M.E.S. and P.B.M.), two Bentham-Moxon Trust grants in 2016 and 2017 for field work (to T.N.), an Advanced Postdoc Mobility Fellowship from the Swiss National Science Foundation (to C.T.), and the University of Florida Institute for Food and Agricultural Sciences (IFAS) (to M.E.S.).

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