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ABSTRACT

In the Patagonian region, Cortinarius is the most diverse and abundant genus of ectomycorrhizal fungi with at least 250 species. Sequestrate forms were until recently documented within the genus Thaxterogaster, a genus now known to be polyphyletic, and many were consequently transferred to Cortinarius. Original descriptions were mostly available in German and Spanish and interpretations of morphological structures outdated. Despite recent advances in Cortinarius systematics, the current classification, diversity, and ecology of sequestrate "cortinarioid" fungi in Patagonia remain unclear. The objective of this study was to provide an update on sequestrate Cortinarius of southern South America. We documented each species with morphological descriptions, photographs, basidiospore scanning electron microscopy (SEM) images, and molecular characterization using nuc rDNA internal transcribed spacer region ITS1-5.8S-ITS2 (ITS) and nuc 28S rDNA (28S) sequence data. Original descriptions of taxa were also translated to English and revised based on fresh collections. We documented 24 species from Patagonia based on molecular data and conducted morphological and phylogenetic analysis for 18 previously described species based on type and reference specimens. In addition, we formally described two new species. Four additional taxa were provisionally determined as new but require further study. New ITS sequence data were produced from eight type specimens. We also provide a new name, Cortinarius gloioides, nom. nov., for the taxon previously described as Thaxterogaster gliocyclus. In addition to the species treated in detail, we provided additional reference information and discussion on six described species that remained incompletely known or for which no recent collections were found. Of the 24 taxa documented from Patagonia, 15 species were assigned to 12 current sections in the genus Cortinarius. Analysis of spore ultrastructure showed that sequestrate forms of Patagonian Cortinarius lack a true perisporium.

INTRODUCTION

The diversity of secotioid and sequestrate Cortinarius (Pers.) Gray species from Nothofagaceae forests of Patagonia has repeatedly drawn attention during the last century. Cortinarius is one of the largest and most taxonomically diverse genera in the Agaricales, accounting for at least 2700 described species worldwide (Peintner et al. 2001, 2004; Garnica et al. 2005; Frøslev et al. 2007; Danks et al. 2010; Soop et al. 2019). Cortinarius is also considered the largest and most species-rich genus of ectomycorrhizal (ECM) fungi in the Patagonian region of Argentina and Chile (Garrido 1988; Garnica et al. 2002; Romano and Lechner 2014; Truong et al. 2017). The forests of Patagonia are dominated by Nothofagaceae (Nothofagus

and Lophozonia), and these trees serve as the main ECM host plants in the region (Garnica et al. 2003). Nothofagaceae forests contain more than 250 species of Cortinarius (Romano and Lechner 2014; Truong et al. 2017), including several recently described species of hypogeous (Pastor et al. 2019) and epigeous (San-Fabian et al. 2018; Liimatainen et al. 2020) forms.

The enormous diversity of Cortinarius includes numerous sequestrate forms that were until recently treated in the genus Thaxterogaster Singer (Peintner et al. 2001, 2004) or less often in Hymenogaster Vittad. and Protoglossum Massee (Dodge and Zeller 1934; May 1995). This has resulted in a confusing infrageneric classification system, as samples of these genera were

found to be nested within *Cortinarius* (Peintner et al. 2001, 2004; Frøslev et al. 2005; Garnica et al. 2005; Danks et al. 2010). As a result, the genus *Thaxterogaster* was synonymized with *Cortinarius* (Peintner et al. 2002).

Sequestrate taxa were first collected in Patagonia in 1905–1906 when Roland Thaxter visited South America (Halling 1981). Some of the specimens from Thaxter's collections were later described by Dodge and Zeller (1934). Others, such as Singer (1951, 1960), Singer and Smith (1963), Horak and Moser (1965), and Horak (1979), described 21 additional sequestrate Patagonian species in *Thaxterogaster*. However, most of these descriptions and taxonomic keys to the genus *Thaxterogaster* were originally published in German and a few in Spanish. These constitute useful resources but are challenging to interpret because German is not widely used in South America where these taxa are endemic. Most of the studies cited above included detailed morphological descriptions, as well as black and white drawings of basidiomata and spores. These drawings depicted a wide range in the size of spore ornamentation for some species (Horak and Moser 1965; Horak 1979). Spore ornamentation in *Thaxterogaster* species varies from reduced to quite developed (Horak and Moser 1965), but the ornamentation was always illustrated as rounded warts. In a few cases, drawings and photographs of *Thaxterogaster* spores were depicted with an episporium (e.g., Horak 1979; Halling 1981), despite the fact that sequestrate *Cortinarius* do not appear to have episporium (Kuhar et al. 2017). In Patagonia, true episporia have only been identified in species of sequestrate *Descolea*, which are also common in the region (Kuhar et al. 2017). More recently, studies on new sequestrate *Cortinarius* species from South America (Pastor et al. 2019) and Australia (Danks et al. 2010) have shown the diagnostic and predictive value of spore shape and ornamentation when spores are viewed with scanning electron microscope (SEM). These recent studies also suggested a transition to larger and more irregular spore ornamentation in sequestrate species when compared with agaricoid species, presumably due to the transition from ballistospory to statismospory.

Despite recent advances in the systematics of *Cortinarius*, the classification, diversity, and ecology of these fungi in southern South America remains unclear. The objectives of this study are to (i) update descriptions of previously described sequestrate *Cortinarius* species, (ii) describe new and recently discovered species, (iii) identify diagnostic characters useful for species-level identification and provide a key to sequestrate *Cortinarius* in the region, and (iv) document the diversity of this group using high-resolution macromorphological photos of basidiomata and SEM images of spores, as well as nuc rDNA internal transcribed spacer region ITS1-5.8S-ITS2 (ITS) and partial nuc 28S rDNA (28S) sequence data.

MATERIALS AND METHODS

Field sampling and morphological analysis.—We refer here to sequestrate fungi in general terms following definitions provided by Kendrick (1992), Peintner et al. (2001), and Kirk et al. (2008). This treatment includes all *Cortinarius* species with a loculated, unexposed or partially exposed gleba that is enclosed by a peridium. Gasteroid taxa included here have a highly reduced stipe or a small sterile basal attachment and a hypogeous to subhypogeous habit. The secotioid taxa tend to have a well-developed stipe, but the margin of the pileus usually does not break free from the stipe, the lamellae are convoluted and anastomosed, and the basidiospores are statimosporic rather than ballistosporic. Kendrick (1992) suggests how these fungal fruiting bodies evolved from ancestors with exposed hymenia and forcibly discharged spores to an enclosed and sometimes hypogeous habit in which the spores are retained in the fruiting body until it decays or is eaten by an animal vector. Specimens were collected in spring and autumn 2005–2019 of the Southern Hemisphere in various localities throughout Patagonia of Argentina and Chile. The region of Patagonia is generally defined as the southern end of South America. However, as a geological unit, Patagonia has its northern limit at the Huincul Fault, a fault zone that is oriented east-west, and is roughly delimited as the area south of the Río Colorado in Argentina and the Río Biobío in Chile (Ramos et al. 2004). For a complete list of studied specimens and locations, see SUPPLEMENTARY TABLE 1 and the section "Specimens examined" included for each species. Specimens were photographed when fresh and then dried on a forced air drier or with silica gel. Additional specimens were obtained from the following herbaria: Herbario del Museo Botánico de Córdoba (CORD), Museo de La Plata Herbarium (LP), Fundación Miguel Lillo (LIL), Florida Museum of Natural History (FLAS), Herbarium Turicense (ZT+T), the New York Botanical Garden Herbarium (NY), Munich Herbarium (M), and the Farlow Herbarium at Harvard University (FH). Herbarium codes follow Thiers (continuously updated). New collections were deposited at FLAS and CORD, with additional splits of some taxa also deposited at FH and the Museo Nacional de Historia Natural de Chile (SGO). Note that several collections by Smith and Caiafa from April and May 2019 were photographed and their tissues were sampled for DNA, but they were subsequently stolen and destroyed during a field expedition. These collections are designed by their original MES collection numbers and the herbarium code FLAS but with no accession number. Sequences for these collections are available on GenBank and photographs are available at

the University of Florida, despite the fact that the specimens no longer exist. These records were retained and cited below because they expand the known geographic and/or host range of many species treated here. Sections of dried material were rehydrated and mounted in water, 3% KOH, Melzer's reagent, or lactophenol cotton blue. Basidiospores were measured in KOH, and their shape described following Largent et al. (1977). Spore measurements included the apiculus but not spore ornamentation. At least 20 different measurements were made per individual, and the average length-to-width ratio (Qr) value was recorded. Variation in the pileipellis (the exterior layer of the peridium) was also observed and characterized by examining thin cross-sections from multiple specimens of each species. For new species, pileus coloration is given in general terms followed by formal color designations in parentheses that are capitalized following Ridgway (1912). Microscopic characters were observed with a Nikon light microscope (LM) (Tokyo, Japan) at 400–1000X magnification. Scanning electron microscopy (SEM) photographs were captured using a Zeiss LEO 1450VP microscope (Oberkochen, Germany) in order to observe and describe spore ornamentation, including the type (ranging from minute warts to coarse warts), structure (ranging from isolated or grouped warts to connected ridges and reticulate structures), and apiculus (from small apiculi in most secotioid taxa to broader apiculi in gasteroid taxa). Morphological descriptions of known species are brief, but new species are described in greater detail, including morphological analyses of the pileipellis structure.

DNA extraction, PCR, and sequencing.—DNA was extracted from basidiomata following a modified cetyltrimethylammonium bromide (CTAB) method (Gardes and Bruns 1993) or using the Extract-N-Amp DNA extraction kit (Sigma-Aldrich, St. Louis, Missouri). Polymerase chain reaction (PCR) of ITS was performed with primers ITS1F and ITS4 or ITS4B (White et al. 1990; Gardes and Bruns 1993). The 28S fragment was amplified using primers LR0R and LR5 (Vilgalys and Hester 1990). PCR conditions were 94 C for 5 min, followed by 35 cycles of 1 min at 94 C, 1 min at 55 C, and 2 min at 72 C, followed by 7 min at 72 C. The most variable region of the second largest subunit of RNA polymerase II (*rpb2*) was amplified and sequenced using primers b6f and b7R (Matheny 2005). For PCR of the *rpb2* region, we used Phusion Hot Start II DNA polymerase (Thermo Fisher Scientific, Waltham, Massachusetts) and thermal cycling parameters as follows: initial denaturation at 98 C for 30 s; 35 cycles at 98

C for 10 s, 60 C for 30 s, and 72 C for 30 s; and final extension at 72 C for 7 min. PCR products were visualized on 1.5% agarose gels with SYBR Green I (Molecular Probes, Eugene, Oregon) and purified with EXO (exonuclease I) and SAP (shrimp alkaline phosphatase) enzymes (Werle et al. 1994). For type specimens and other reference collections that were not easily amplified by PCR, or that produced low-quality sequences, the ITS1 and ITS2 regions where amplified separately and sequenced using the same PCR conditions but with primer pairs ITS1F/ITS2 (ITS1 region) and ITS3/ITS4B (ITS2 region). Sanger sequencing was conducted at the Interdisciplinary Center for Biotechnology Research at the University of Florida or at Macrogen (Seoul, Korea). Sequencher 4.1 (Gene Codes, Ann Arbor, Michigan) was used to edit sequence chromatograms and build accurate consensus sequences for each specimen. For the final data set, we used representative ITS sequences of Patagonian specimens and also included the 28S fragment of the new species and those recently described by Pastor et al. (2019) (SUPPLEMENTARY TABLE 1).

Taxon sampling and phylogenetic analyses.—We completed the taxon sampling with ITS and 28S sequences representing all sections within *Cortinarius* assessed by Soop et al. (2019) and San-Fabian et al. (2018) (SUPPLEMENTARY TABLE 2). Sequences of the clade Australienses were discarded, since they failed to align well and introduced long gaps in the final alignment matrix. A sequence of *Crassisporium funariophilum* (MT703796) containing both ITS and 28S was used as the outgroup due to the likely position of this genus as sister clade of *Cortinarius* inferred from genomic data (Grigoriev et al. 2014). The alignment was assembled in MAFFT (Katoh et al. 2019) using the L-INS-i strategy for ITS, whereas the 28S fragment was aligned using the G-INS-i strategy. The concatenated data set alignment was analyzed with maximum likelihood (ML) and Bayesian inference (BI). The data set was analyzed in two partitions (ITS and 28S) with the nucleotide substitution models inferred using fast model selection (Kalyaanamoorthy et al. 2017). ML was run on the IQ-Tree server (Chernomor et al. 2016; Trifinopoulos et al. 2016) with 1000 bootstrap iterations under models TVM+F+R4 for the ITS region and TN+F+R6 for the 28S region. BI was run using MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) using the GTR+I+G model (nst = 6) for both partitions, as suggested by the IQ-Tree model selection inference, after restricting the model to the options available in MrBayes using the "-mset mrbayes" option. Ten million generations were run

with a sampling frequency of 1000, with the first 25% of samples discarded as the burn-in. Run convergence, stationarity, and effective sample size were verified in Tracer 1.6 (Rambaut et al. 2014). Resulting phylogenetic trees for both ML and BI analyses were visualized in FigTree 1.4.3 (Rambaut 2009). Nodes were considered strongly supported when ML bootstrap values were ≥70% and Bayesian posterior probabilities (PPs) were ≥0.95.

RESULTS

Below we have provided a taxonomic overview of 16 of the 24 sequestrate Cortinarius for which molecular data were available, including two new species based on morphology and sequence analyses. New images and notes were provided for four additional species recently described by Pastor et al. (2019). In addition, *C. glabriceps* Peintner and *C. subalbidus* (A.H. Sm.) Peintner & M.M. Moser were treated in this study based on previous references and included in the taxonomic key. However, we were unable to collect recent specimens, so these species were not included in the phylogenetic data set. We also included anatomical information and other aspects that we considered relevant to clarify confusing features of the species included in this study. For each taxon, we provided a morphological description, SEM photographs of the basidiospores (FIGS. 1–9), and other details of the studied specimens. For the newly described species, we provided additional images of various anatomical structures. The taxonomy of four taxa provisionally identified as new are not discussed.

Phylogenetic results.—Our data set comprised 223 sequences, including sequestrate *Cortinarius* as well as epigeous *Cortinarius* from Patagonia, sequestrate *Cortinarius* from Australasia, and ECM root tip sequences. Our final alignment, excluding ambiguously aligned sequences, included 1829 sites. The backbone nodes of our phylogeny were generally not supported, but both ML and BI analyses provided support for each of the 24 sequestrate *Cortinarius* taxa, including the two newly described species, *Cortinarius galbus*, sp. nov., and *C. quadrisporus*, sp. nov., and the four recently described hypogeous taxa from Patagonia (Pastor et al. 2019). In addition, four additional undescribed taxa (*Cortinarius* sp. 1, sp. 2, sp. 3, and sp. 4) were also detected (FIG. 10). We were able to place 15 sequestrate species within the taxonomic framework of *Cortinarius* provided by Soop et al. (2019). The sequestrate taxa from Patagonia were dispersed among the following 12 sections of *Cortinarius: Alboaggregati, Archeriani, Crassi,* *Cycnei, Laquelli, Luteini, Majestatici, Purpurascentes, Subcastanelli, Thaumasti, Turmales,* and *Verniciori.* Only those clades representing sections *Archeriani, Thaumasti,* and *Turmales* received significant ML bootstrap and Bayesian PP support (FIG. 10A, B). Details on taxonomic placement are discussed under the "Notes" section of each species. Although some sequestrate species were apparently overrepresented in particular sections of *Cortinarius* (e.g., section *Turmales*), agaricoid representatives of all sections of *Cortinarius* and a well-resolved phylogeny would be necessary to rule out the random versus phylogenetically structured occurrence of sequestration within *Cortinarius*.

TAXONOMY

Cortinarius albocanus (E. Horak & M.M. Moser) Peintner & M.M. Moser, Mycotaxon 81:178. 2002.　　　FIG. 1A–B
　≡ *Thaxterogaster albocanus* E. Horak & M.M. Moser, Nova Hedwigia 10:234. 1965.
　= *Thaxterogaster subulatus* E. Horak, Nova Hedwigia 10:233. 1965.
　Additional description: Horak (1979).
　Basidiomata 12–39 × 7–32 mm high, secotioid (FIG. 1A). Pileus white to light lilac, subglobose to depressed in the center; margin incurved, detached from stipe at maturity, entire or split with age exposing the hymenophore in age remnants of partial veil present; surface smooth to fibrillose, dry, waxy, KOH negative. Lamellae anastomosed, exposed at maturity; ochraceous to rusty brown when mature. Stipe 16–35 × 4–10 mm, mostly cylindrical to clavate or bulbous at the base, sometimes curved; white, dry but waxy in appearance; whitish fibrillose veil present. Odor pleasant, taste not recorded. No staining upon bruising.

　Basidiospores 8–11 × 5–6 μm (Qr = 1.67), ovate (egg-shaped) to elliptical, wall covered by short warts (less than 0.3 μm), warts more crowded toward the apex, apiculus present under LM; warts usually connected by irregular low ridges (FIG. 1B) under SEM. Basidia 20–30 × 6–8 μm, 4-spored. Cystidia absent. Pileipellis of cylindrical hyphae 2–8 μm wide, encrusted with brownish pigment in KOH. Clamp connections present.

　Ecology and distribution: Epigeous to subepigeous on soil, in Nothofagaceae forests under *Nothofagus betuloides, N. dombeyi, N. glauca, N. pumilio,* and *Fuscospora alessandrii,* Argentina and Chile (Patagonia), Mar to May.
　Specimens examined: ARGENTINA. TIERRA DEL FUEGO: Ushuaia, Martial glacier valley, Asensi, under Nothofagaceae, 11 Mar 1963, *E. Horak* (**holotype** ZT 64/4); Tierra Mayor, under Nothofagaceae, 2 Mar 1974, *E. Horak LPS 37972*; RÍO NEGRO: Nahuel Huapi
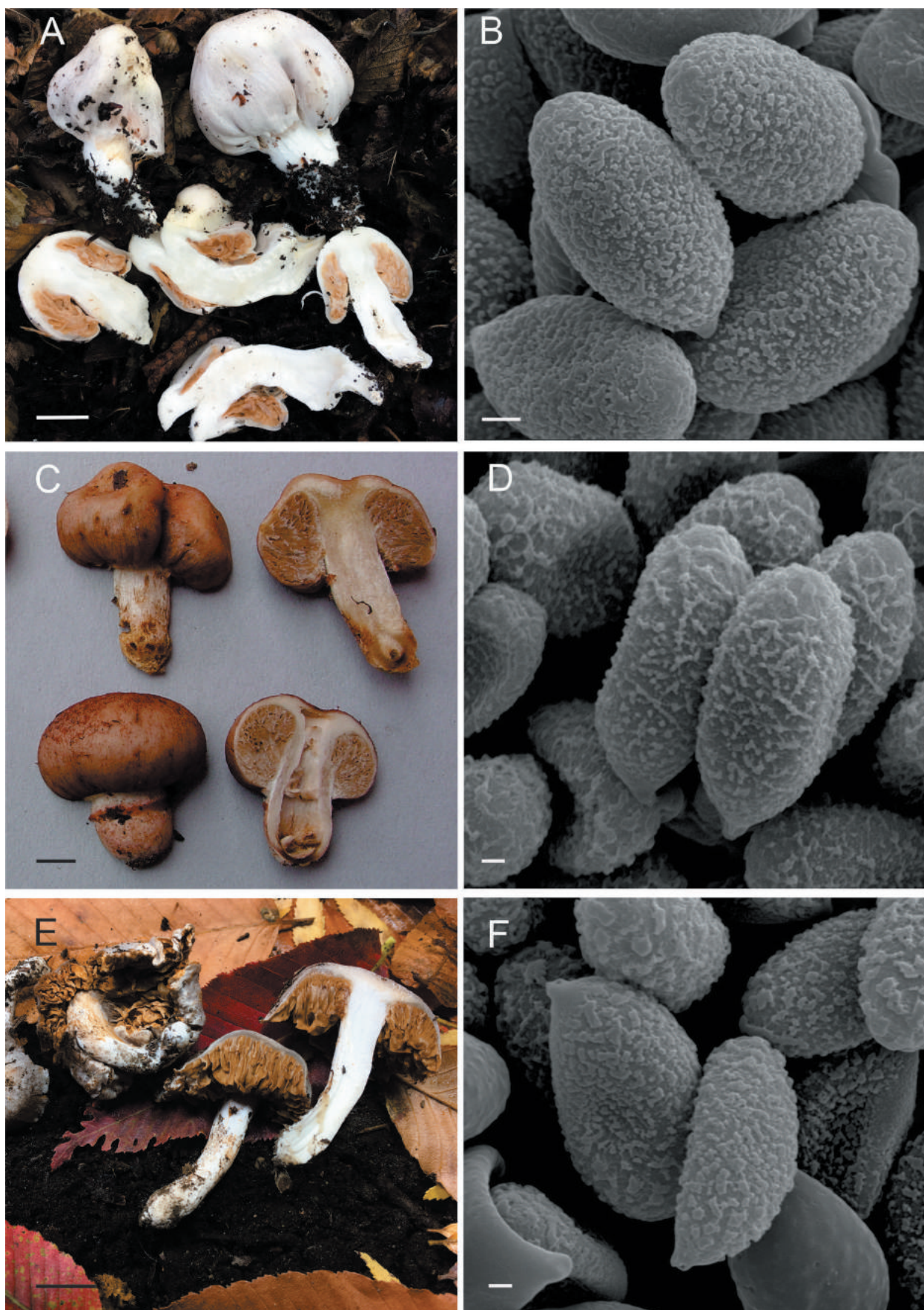
Figure 1. Sequestrate *Cortinarius* from Patagonia. A. *Cortinarius albocanus* basidiomata. B. *Cortinarius albocanus* basidiospores under SEM. C. *Cortinarius carneoroseus* basidiomata. D. *Cortinarius carneoroseus* basidiospores under SEM. E. *Cortinarius cretaceous* basidiomata. F. *Cortinarius cretaceus* basidiospores under SEM. Bars: A, C, E = 1 cm; B, D = 2 μm; F = 1 μm.
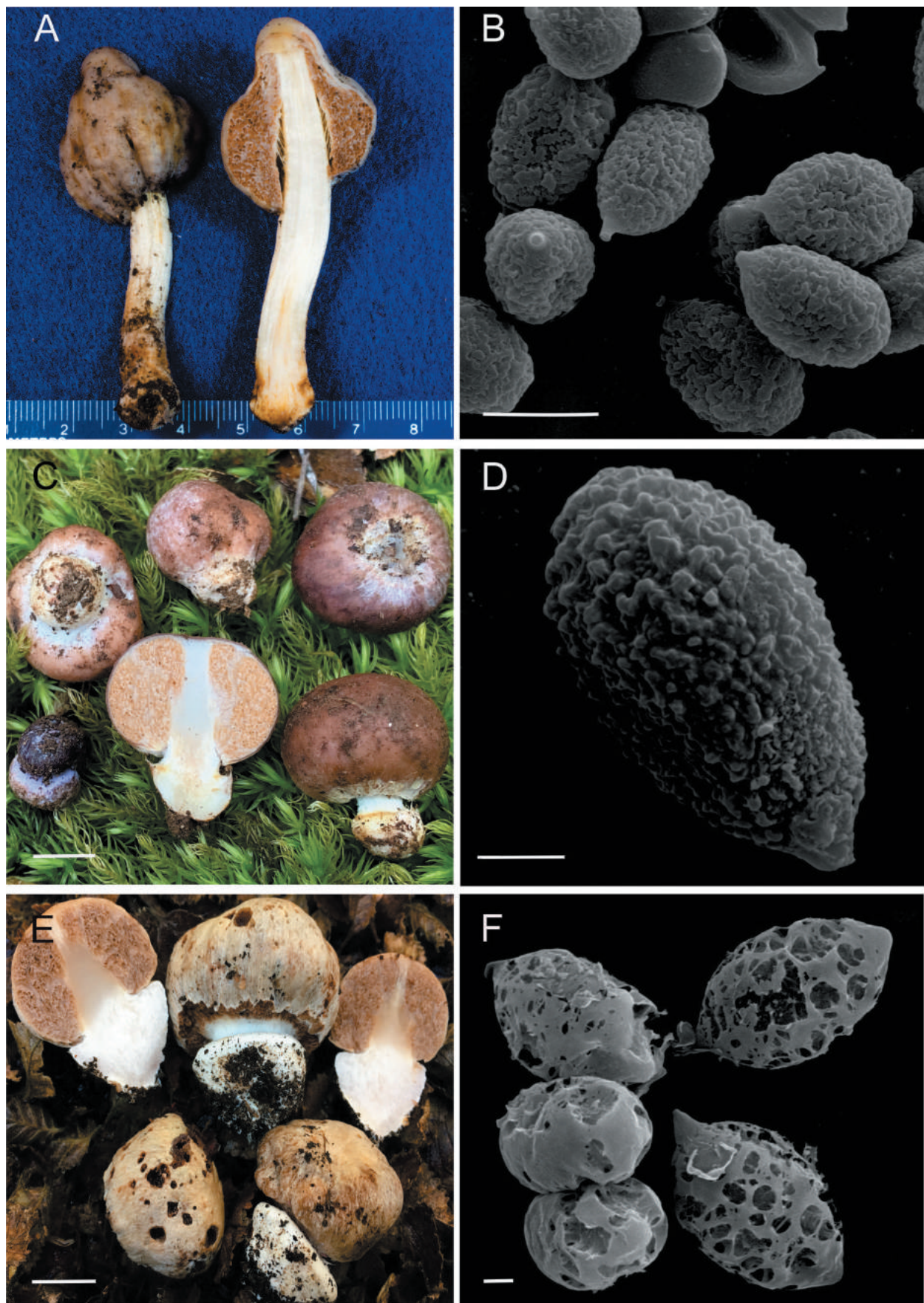
Figure 2. Sequestrate *Cortinarius* from Patagonia, continued. A. *Cortinarius dibaphoides* basidiomata. B. *Cortinarius dibaphoides* basidiospores under SEM. C. *Cortinarius dombeyi* basidiomata. D. *Cortinarius dombeyi* basidiospores under SEM. E. *Cortinarius fragilis* basidiomata. F. *Cortinarius fragilis* basidiospores under SEM. Bars: A, E = 1 cm; B = 10 µm; C = 1.5 cm; D = 3 µm; F = 2 µm.
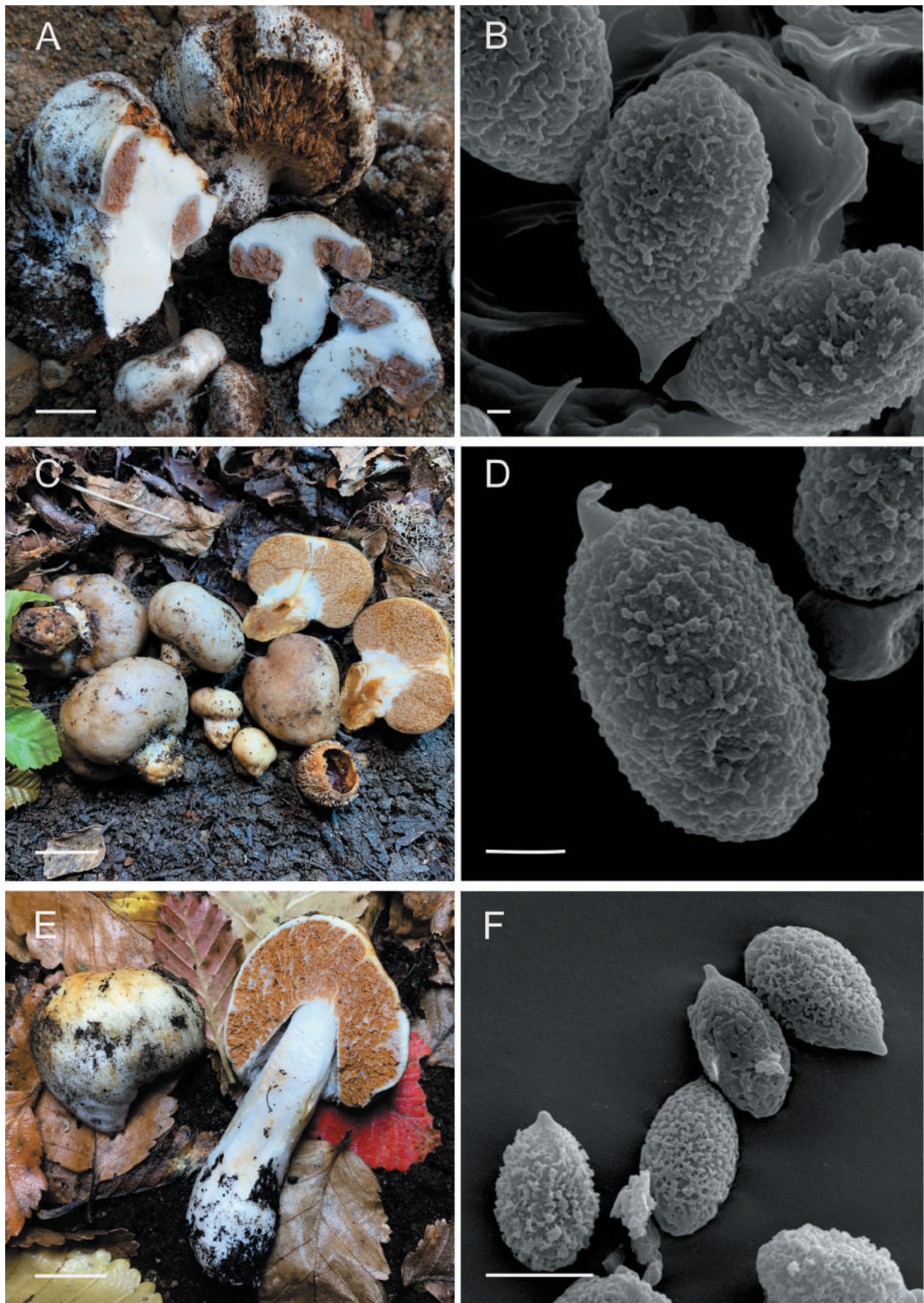
Figure 3. Sequestrate *Cortinarius* from Patagonia, continued. A. *Cortinarius fuegianus* basidiomata. B. *Cortinarius fuegianus* basidiospores under SEM (specimen LSD2380). C. *Cortinarius gloiodes* basidiomata. D. *Cortinarius gloiodes* basidiospores under SEM. E. *Cortinarius glutinopallens* basidiomata. F. *Cortinarius glutinopallens* basidiospores under SEM. Bars: A, E = 1 cm; B = 1 μm; C = 2 cm; D = 3 μm; F = 10 μm.

Figure 4. Sequestrate *Cortinarius* from Patagonia, continued. A–F. *Cortinarius galbus*, sp. nov. A. Basidiomata. B. Basidiospores under SEM. C. Peridium in cross-section showing two layers. D. Mediopellis of short isodiametric segments. E. Subpellis. F. Hymenial trama and spores. Bars: A = 1 cm; B = 2 μm; C = 100 μm; D, E = 2.5 μm; F = 5 μm.
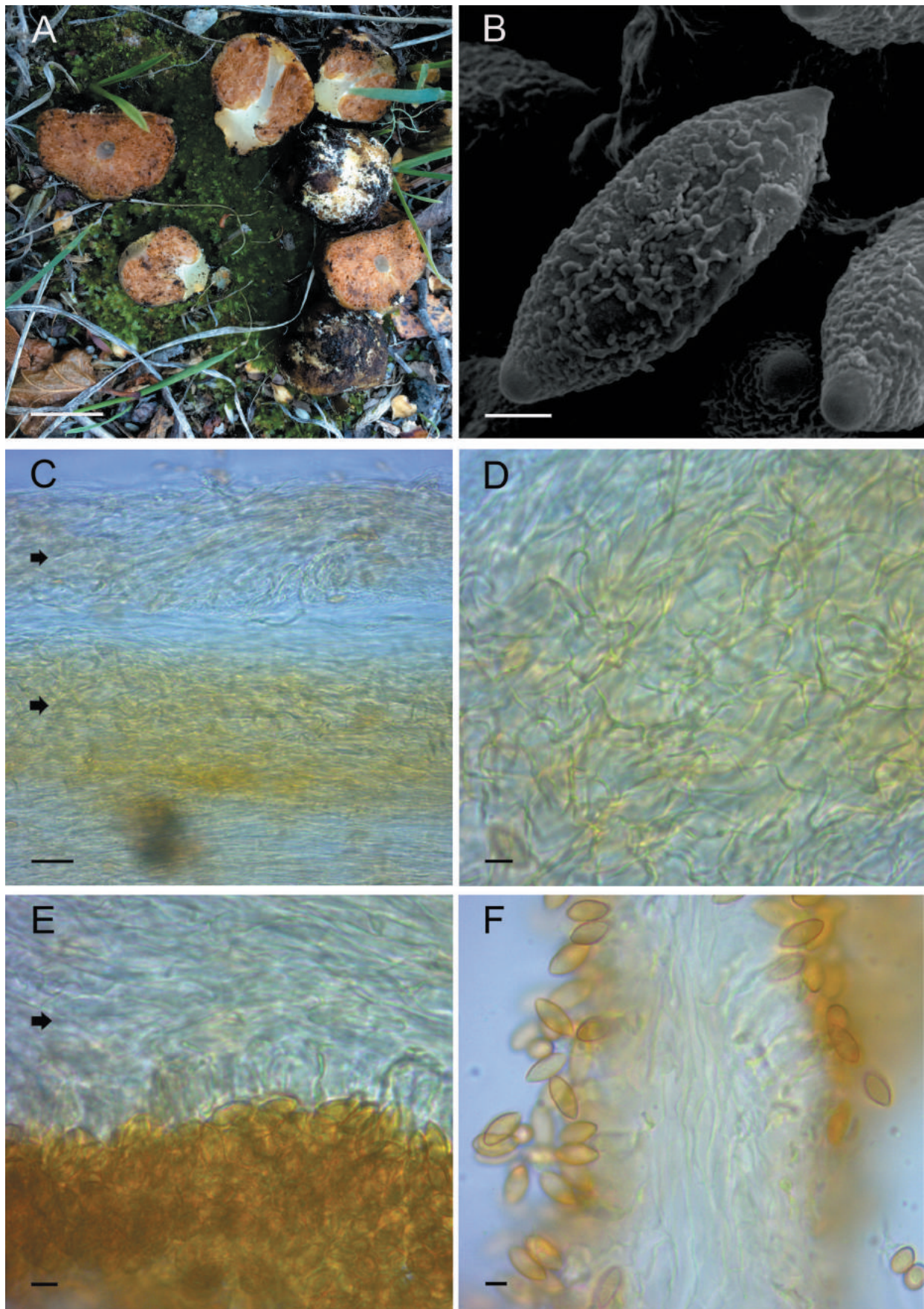
Figure 5. Sequestrate *Cortinarius* from Patagonia, continued. A. *Cortinarius holojanthinus* basidiomata. B. *Cortinarius holojanthinus* basidiospores under SEM. C. *Cortinarius janthinocaulis* basidiomata. D. *Cortinarius janthinocaulis* basidiospores under SEM. E. *Cortinarius mustella* basidiomata. F. *Cortinarius mustella* basidiospores under SEM. Bars: A, E = 1.5 cm; B, F = 3 μm; C = 2 cm; D = 2 μm.

Figure 6. Sequestrate *Cortinarius* from Patagonia, continued. A–F. *Cortinarius quadrisporus*, sp. nov. A. Basidiomata. B. Basidiospores under SEM. C. Pileipellis in cross-section showing three layers. D. Suprapellis. E. Subpellis plectenquima (arrow) and oleiferous hyphae (arrow). F. Basidia, immature and mature spores (arrow), and subhymenium (arrow). Bars: A = 1 cm; B = 2 μm; C = 100 μm; D–F = 10 μm.
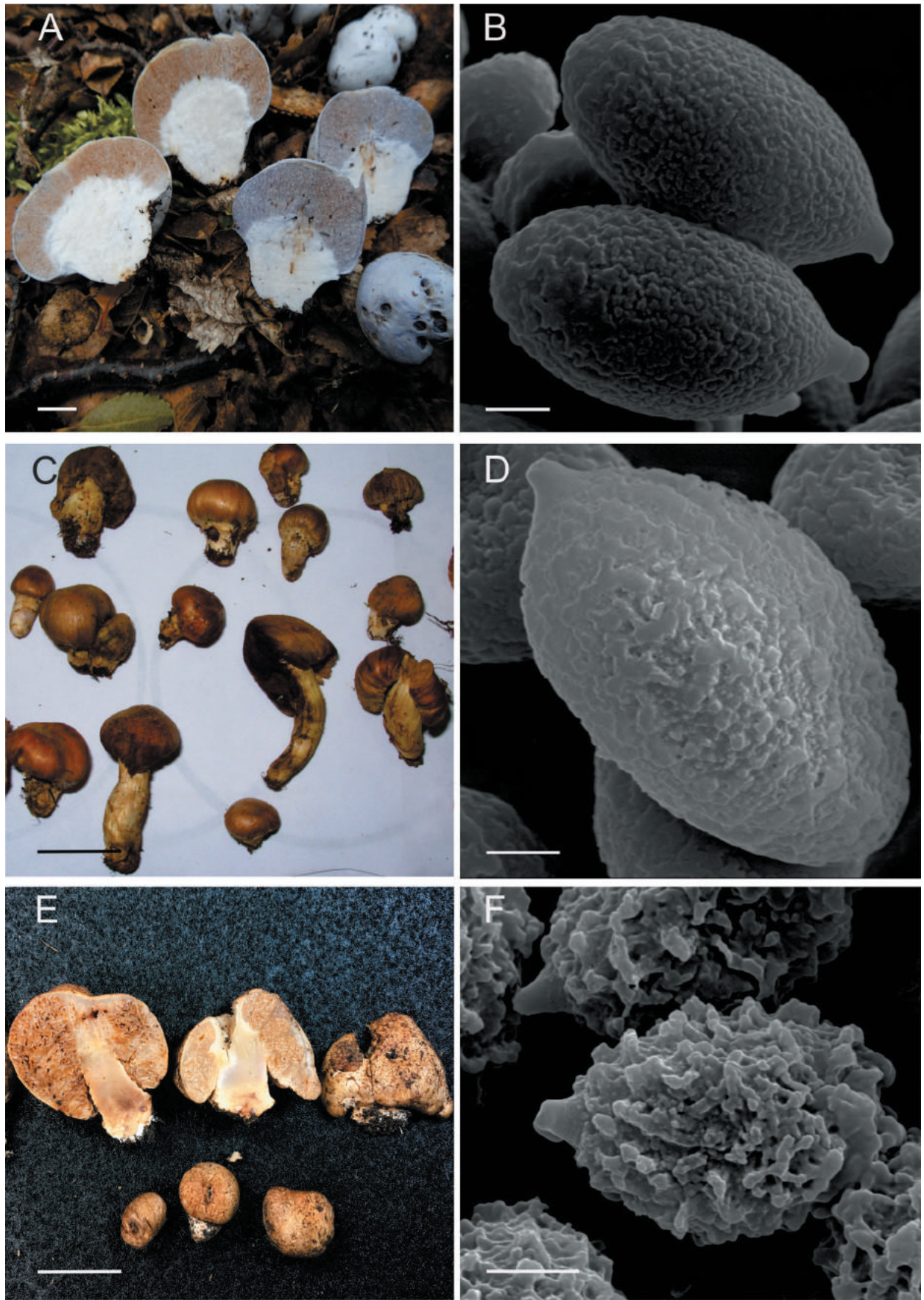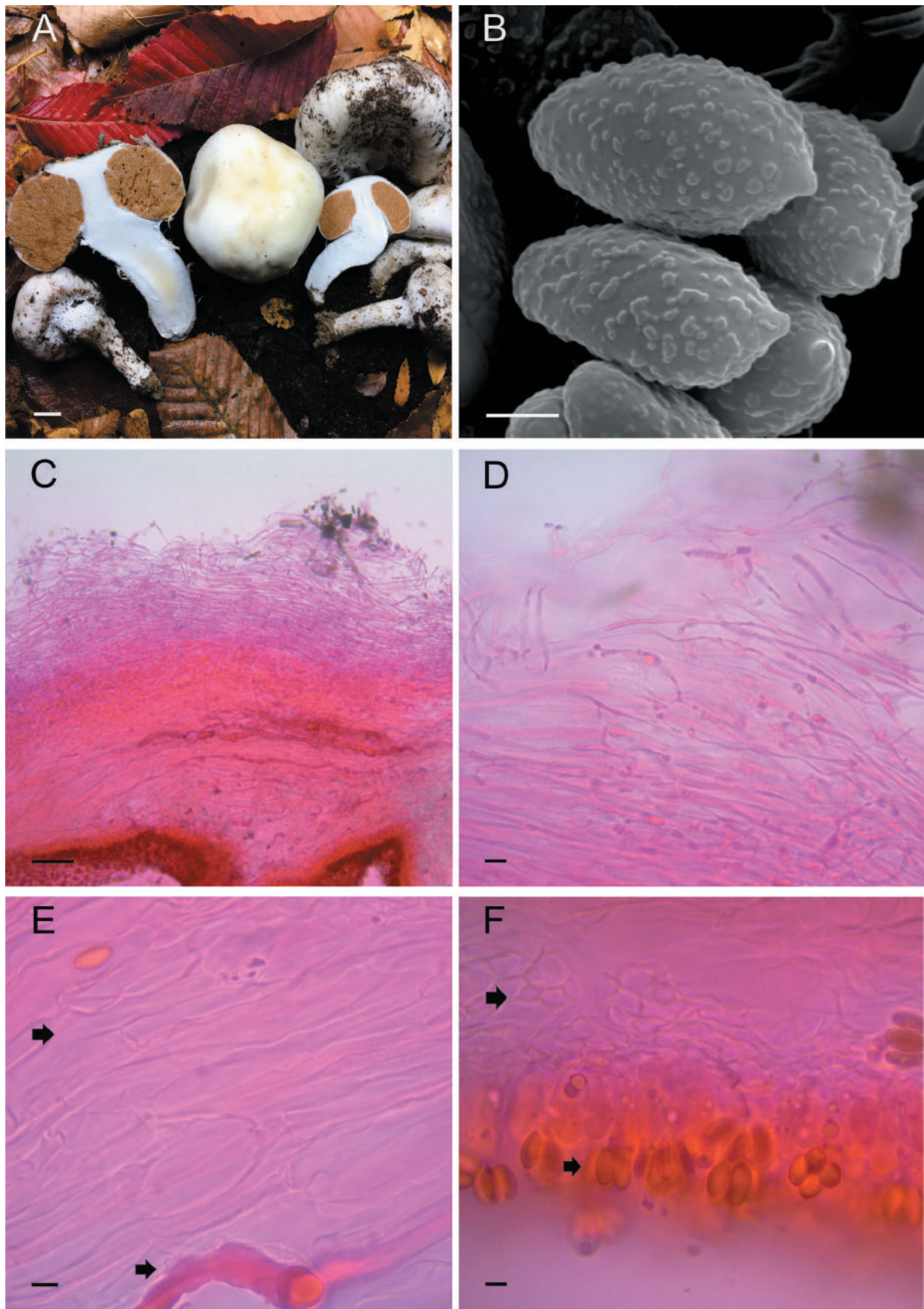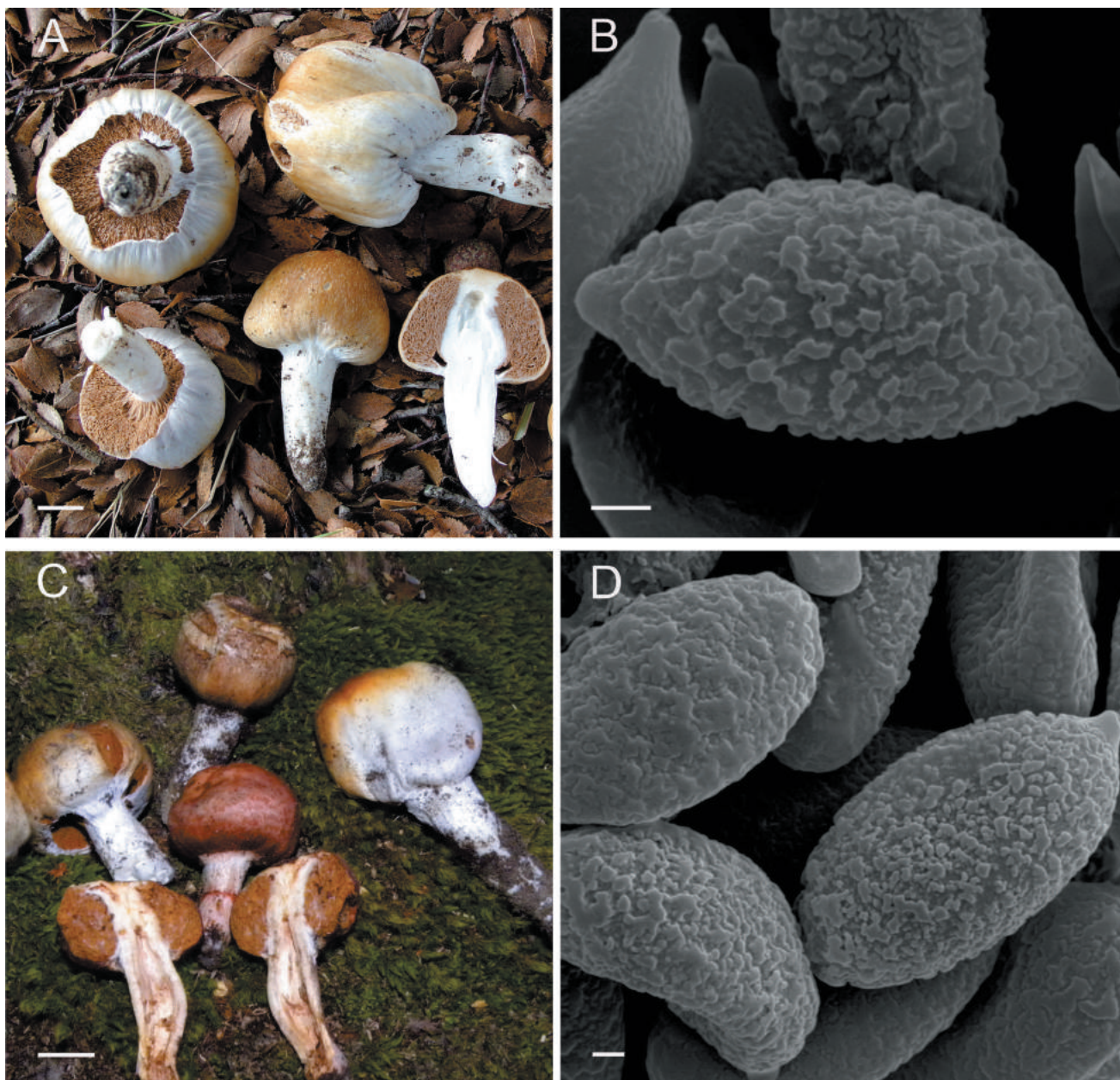
Figure 7. Sequestrate *Cortinarius* from Patagonia, continued. A. *Cortinarius sphaerocephalus* basidiomata. B. *Cortinarius sphaerocephalus* basidiospores under SEM. C. *Cortinarius tympanicus* basidiomata (the basidiome in the center is *C. carneoroseus*). D. *Cortinarius tympanicus* basidiospores under SEM. Bars: A = 1 cm; B, D = 1 μm; C = 3 cm.

National Park, Cerro Chall Huaco, under *N. pumilio*, 7 May 2005, *E. Nouhra EN23* (CORDC00006497); Nahuel Huapi National Park, Laguna Los Moscos, sector Mascardi, under *N. dombeyi*, 5 May 2005, *C. Urcelay EN31* (CORDC00006511); ibid., *E. Nouhra EN25* (CORDC00006496); ibid., *E. Nouhra EN27* (CORDC00006499); ibid., *E. Nouhra EN24* (CORDC00006512); ibid., *E. Nouhra EN29* (CORDC00006513); Nahuel Huapi National Park, Laguna Frías, Paso de las Nubes 10 Apr 1962, *E. Horak LPS 38214* holotype of *T. subulatum*);

CHUBUT: Cañadón Huemules (−42.781011, −71.470039), under *N. pumilio*, 10 Apr 2014, *F. Kuhar & E. Nouhra FK14007* (CORDC00006081). CHILE. REGIÓN MAGALLANES: Magallanes Forest Reserve, on Sendero de Chile across the street from the parking lot above the park guard station (−53.145556, −71.006972), under *Nothofagus pumilio* forest with *N. betuloides* at forest edges, 6 Apr 2017, *A. Mujic MES-2409* (FLAS-F-64235); near the park guard station (−53.141811, −71.006260), under *N. pumilio*, 6 Apr 2017, *M. E. Smith MES-2519* (FLAS-F-64242); near
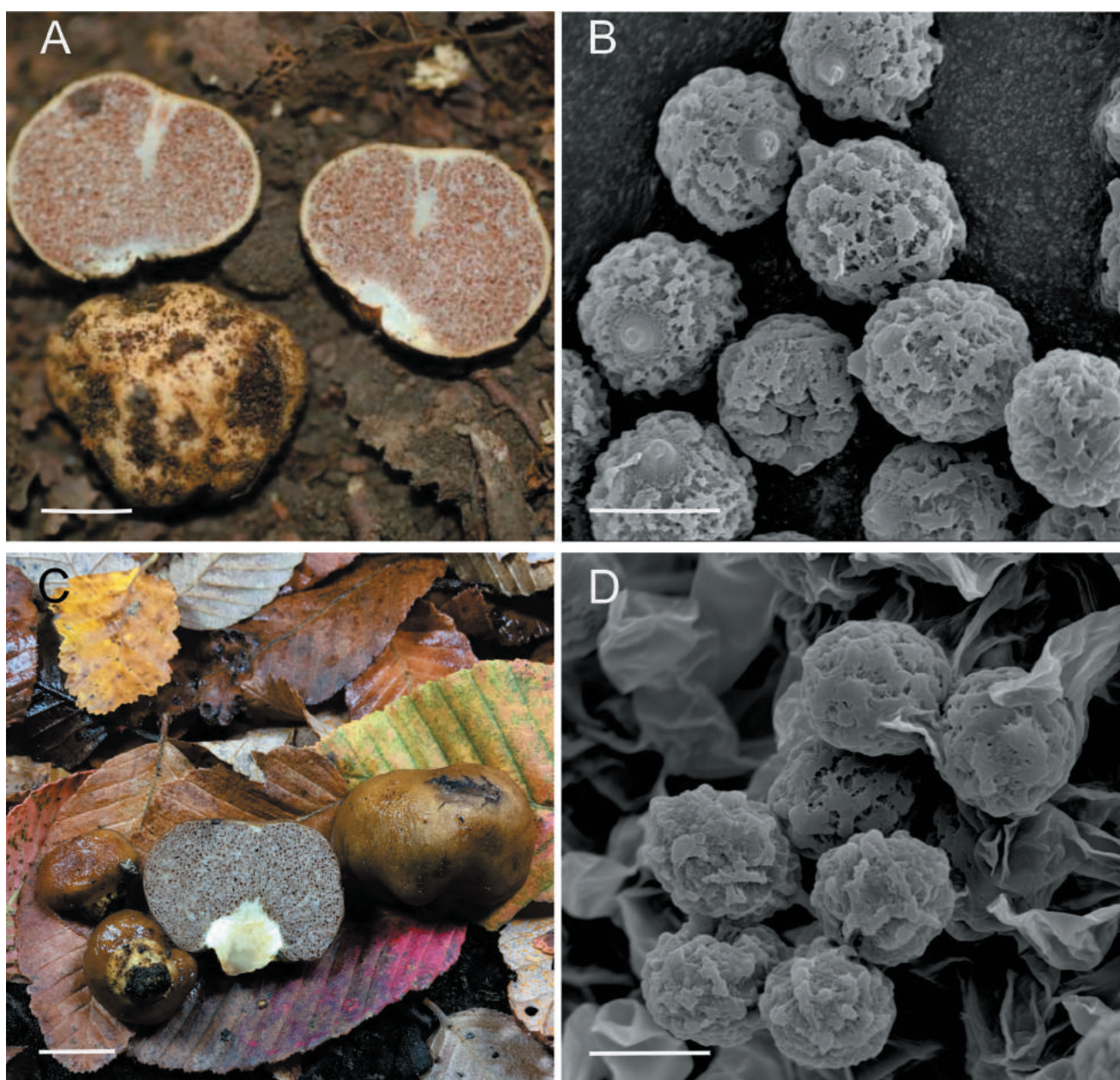
Figure 8. Sequestrate *Cortinarius* from Patagonia, continued. A. *Cortinarius flavopurpureus* basidiomata. B. *Cortinarius flavopurpureus* basidiospores under SEM. C. *Cortinarius infrequens* basidiomata. D. *Cortinarius infrequens* basidiospores under SEM. Bars: A = 1 cm; B = 10 μm; C = 2 cm; D = 10 μm.

the park guard station (−53.142861, −71.006083), in *Nothofagus pumilio* forest, 7 Apr 2017, *A. Mujic MES-2539* (FLAS-F-64247); ibid., *C Truong MES-2538* (FLAS-F-64246); trail to Mirador (−53.144139, −71.003333), in mixed *Nothofagus pumilio* and *N. betuloides* forest, *C. Truong MES-2536* (FLAS-F-64245); REGIÓN DEL MAULE: Cauquenes Province, Los Ruiles National Reserve (−35.841861, −72.420378), in mixed forest with *N. glauca, N. dombeyi*, and *Fuscospora alessandrii*, 27 May 2019, *M. Caiafa MVC752* (FLAS-F-64290).

Notes: The synonymy proposed by Horak (1979) between *Cortinarius albocanus* (as *Thaxterogaster albocanus*) and *Thaxterogaster subulatus* was missed by other researchers (Peintner et al. 2002). However, no analyses or discussion are available to reject this synonymy, so we accept *C. albocanus* and *Th. subulatus* as heterotypic synonyms. We retain this species as *C. albocanus*, the epithet chosen by Horak (1979), given the fact that both species were published in the same article (Horak and Moser 1965). In our analysis, *C. albocanus* was nested
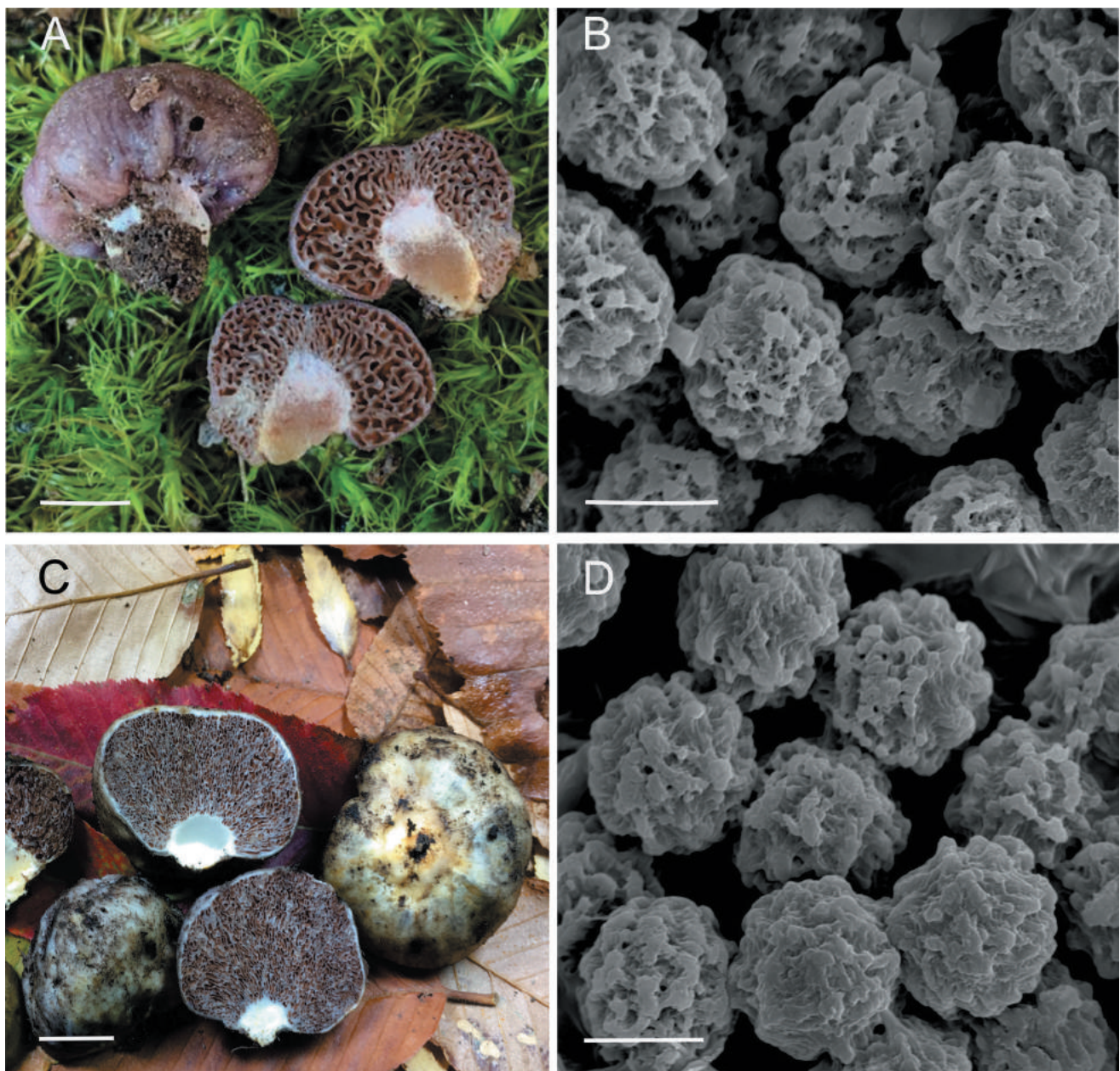
Figure 9. Sequestrate *Cortinarius* from Patagonia, continued. A. *Cortinarius nahuelhuapensis* basidiomata. B. *Cortinarius nahuelhuapensis* basidiospores under SEM. C. *Cortinarius translucidus* basidiomata. D. *Cortinarius translucidus* basidiospores under SEM. Bars: A = 5 mm; B, D = 10 μm; C = 2 cm.

with sequences of the section *Verniciori* (FIG. 10A) sensu Soop (2019). This austral clade includes *C. verniciorum* from New Zealand as well as other species that are associated with Nothofagaceae.

Cortinarius carneoroseus (E. Horak) Peintner & M.M. Moser, Mycotaxon 81:179. 2002.   FIG. 1C–D
   ≡ *Thaxterogaster carneoroseus* E. Horak, Nova Hedwigia 10:229. 1965.

Additional description: Horak (1979).

Basidiomata 16–36 × 12–36 mm high, secotioid (FIG. 1C). Pileus reddish brown, subglobose to depressed; margin incurved, entire to wrinkled, lobed; at times hymenophore exposed at maturity; surface smooth to fibrillose, dry to slightly glutinous (greasy), devoid of scales, KOH negative. Hymenophore composed of elongated chambers more or less radially arranged and attached to the stipe; pale yellowish brown to rusty brown when mature
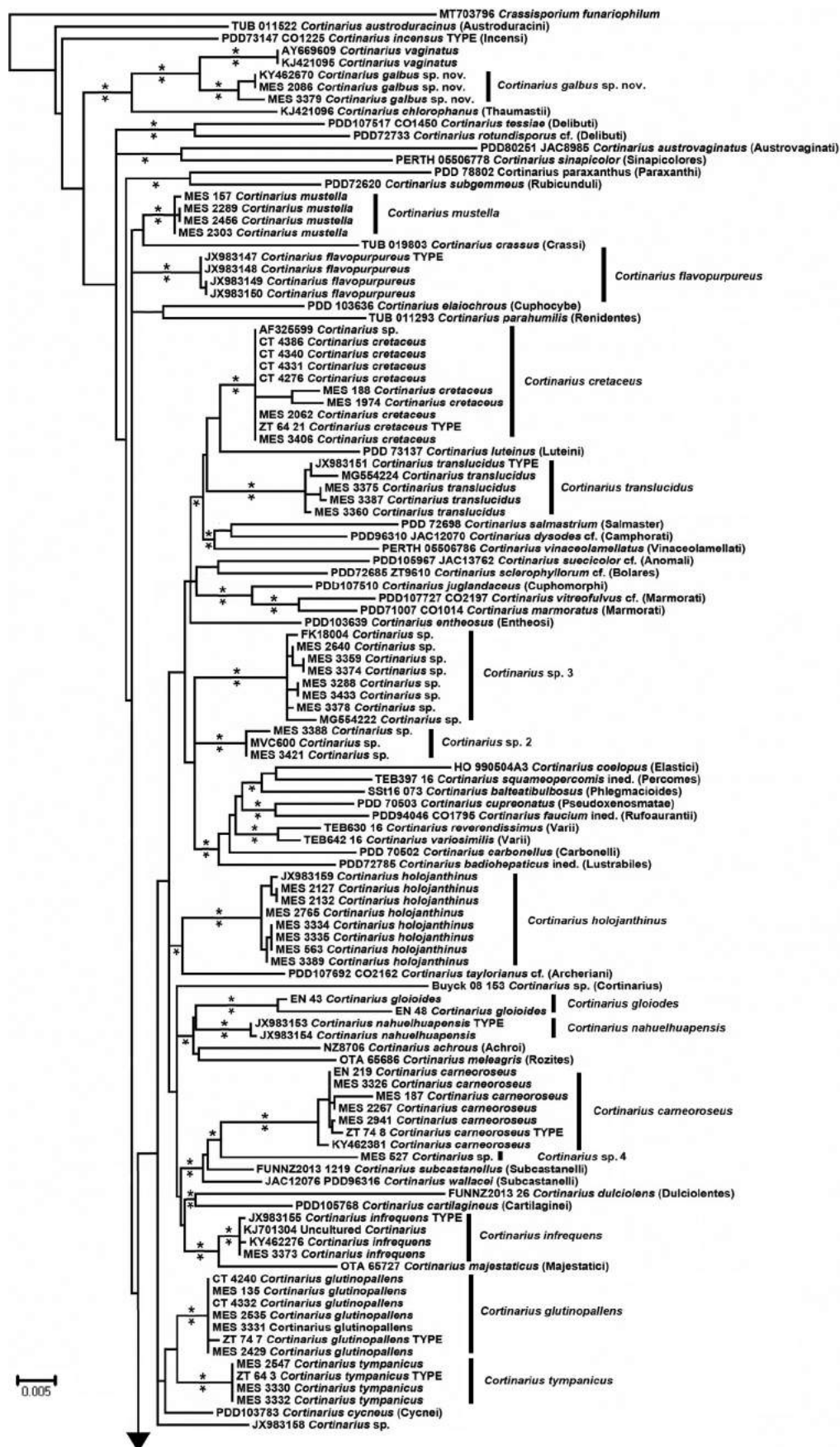
Figure 10. Maximum likelihood (ML) phylogeny of *Cortinarius* with an emphasis on sequestrate species from Patagonia based on ITS and 28S sequences from voucher specimens and ECM root tip samples. Significant ML bootstrap support (≥70%) and BI PPs (≥0.95) are indicated with asterisks above and below the branches, respectively.
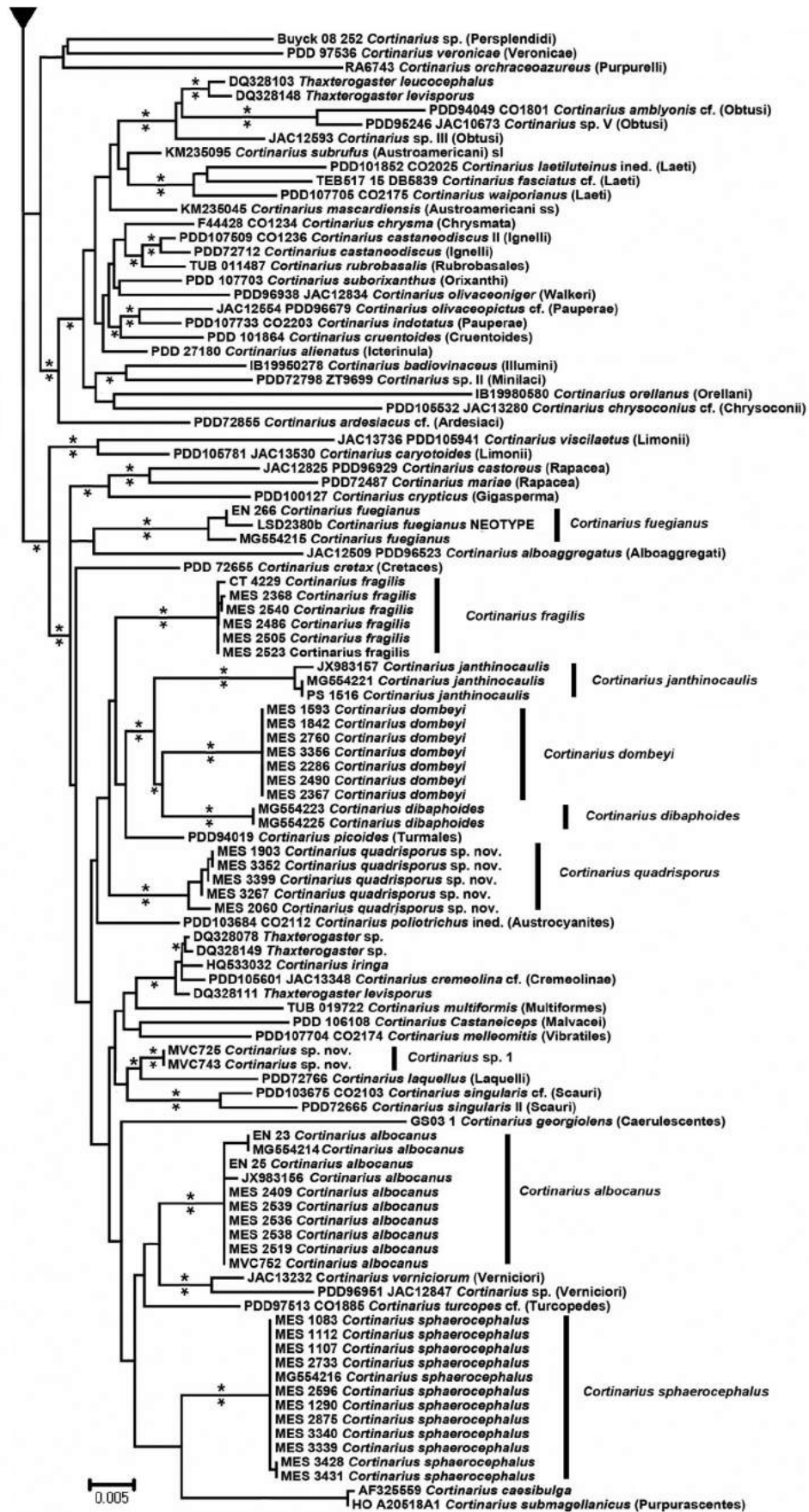
Figure 10. (Continued).

(FIG. 1C). Stipe 16–35 × 4–10 mm, well developed, mostly cylindrical to clavate; surface dry, with a tight whitish to light pink cortina attached to the pileus margin at first, leaving a visible and usually notable reddish brown ring on the stipe below the attachment point; cream to pinkish, slightly emarginate in some specimens. Odor not distinctive. Not staining upon bruising.

Basidiospores 11–12.5 × 6.5–8 µm (Qr = 1.63), elliptical to amygdaliform (almond-shaped), wall covered by small and irregularly shaped warts, apiculus present under LM; warts barely connected by ridges under SEM (FIG. 1D). Basidia 30–40 × 6–10 µm, 4-spored. Cystidia absent. Pileipellis of cylindrical gelatinized hyphae, 2–8 µm wide, encrusted with brownish pigment when viewed in KOH. Clamp connections present.

Ecology and distribution: Epigeous to subepigeous on soil, in Nothofagaceae forests under *Nothofagus betuloides, N. dombeyi*, and *N. pumilio*, Argentina and Chile (Patagonia), Mar to May.

Specimens examined: ARGENTINA. RÍO NEGRO: Nahuel Huapi National Park, Río Manso, near Mascardi Lake (−41.346619, −71.581558), under *N. dombeyi*, 18 May 2010, *E. Nouhra EN219* (CORDC00006498). CHILE. REGIÓN DE MAGALLANES: Puerto Natales, Monte Alto, 23 Mar 1963, *E. Horak* (holotype ZT 64/8); Punta Arenas Club Andino ski area entrance (−53.159778, −71.023333), under *N. betuloides* and *N. pumilio* soil, 31 Mar 2017, *A. Mujic MES-2267* (FLAS-F-64229); REGIÓN LOS LAGOS: Volcán Osorno, tourist turnout site, Pérez Rosales National Park, near Ensenada, under *N. dombeyi*, 27 Mar 2008, *M.E. Smith MES-187* (FLAS-F-64219); REGIÓN DE ARAUCANÍA: Villarrica National Park, Parque Accesso Coñaripe, Quetrupillán, Mirador Los Volcanes, forest dominated by *N. pumilio*, 13 May 2019, *M.E. Smith MES-3326* (FLAS); REGIÓN DE AYSÉN: Queulat National Park, road to Ventisquero Colgante, with *N. dombeyi*, 9 May 2016, *C. Truong CT-4473* (FLAS-F-63539).

Notes: Cortinarius carneoroseus is relatively easy to identify based on the reddish pileus coloration and presence of a pink to reddish cortina that is initially attached to the stipe and then later leaves a reddish brown ring on the stipe. In our analysis, *C. carneoroseus* was nested within section *Subcastanelli* (FIG. 10) as defined by Soop et al. (2019). This austral clade known from New Zealand is characterized by glutinous, red-brown to dark yellow-brown basidiomata, cinnamon to yellow-brown or brownish pink lamellae, a cylindrical stipe with thick girdles, often with a striate, membranous collar, among other characters that are also present in *C. carneoroseus*. Species in this group are found under Nothofagaceae.

Cortinarius cretaceus (E. Horak) E. Horak, in Fl Criptog Tierra del Fuego 11:464. 1980 [1979]. FIG. 1E–F

≡ *Thaxterogaster cretaceus* E. Horak, Nova Hedwigia 10:236. 1965.

Basidiomata 10–38 ×12–40 mm high, secotioid with a superficially agaricoid appearance in the field (FIG. 1E). Pileus whitish to pale brown (beige in the original description) to vinaceous, slightly translucent, subglobose to flat, depressed in the center; margin incurved with silvery fibrillose veil remnants, irregular and torn, soon exposing the hymenophore; surface smooth to fibrillose, dry to slightly glutinous, KOH negative. Lamellae adnate, anastomosed, forming irregular chambers, pale brown to ferruginous brown. Stipe 10–35 × 50–13 mm, well developed, cylindrical to clavate or bent to tortuous; surface dry; whitish to pale brown fibrillose veil present, composed of long and scarce fibrils when young, fibrillose ring not persistent. Odor sweet, fragrant, or somewhat fruity. Not staining upon bruising.

Basidiospores 9–11 × 5.5–6.5 µm (Qr = 1.57), elliptical to amygdaliform, apiculus present, wall covered by notable warts under LM; warts coarsely irregular at the apex and mostly unconnected by ridges under SEM (FIG. 1F). Basidia 20–24 × 6–8 µm, 4-spored. Cystidia absent. Pileipellis of cylindrical hyphae 2–7 µm wide, without encrusting pigment in KOH. Clamp connections present.

Ecology and distribution: Often epigeous but sometimes hypogeous on soil, in Nothofagaceae forests under *Nothofagus pumilio, N. dombeyi, N. antarctica*, and *Lophozonia obliqua*, Argentina and Chile (Patagonia), Mar to May.

Specimens examined: ARGENTINA. TIERRA DEL FUEGO: Martial glacier valley, close to Ushuaia, under Nothofagaceae, 2 Mar 1963, *E. Horak* (**holotype** ZT 64/22); Tierra Mayor, road to Cerro Bonete, with *Nothofagus pumilio*, 10 Apr 2016, *C. Truong CT-4386* (FLAS-F-63458); Estancia Ushuaia, with *Nothofagus pumilio*, 23 Apr 2016, *C. Truong CT-4276* (FLAS-F-63372); RÍO NEGRO: Nahuel Huapi National Park, road to Tronador near Pampa Linda, under *N. antarctica*, 14 May 2016, *E. Nouhra MES-1974* (FLAS-F-64222, CORDC00006518); Nahuel Huapi National Park, Arroyo Goye near Colonia Suiza, under mixed *N. dombeyi* and *N. pumilio*, 12 May 2016, *E. Nouhra MES-1869* (FLAS-F-64330, CORDC00006519); Nahuel Huapi National Park, Los Rapidos, in *N. dombeyi* forest, 16 May 2016, *R. Healy MES-2062* (FLAS-F-64224); Nahuel Huapi National Park, Lago Mascardi, 4 km before the mirador area, under *Nothofagus dombeyi*, 11 May 2015, *E. Nouhra MES-1191* (FLAS-F-63162). CHILE. REGIÓN LOS LAGOS: Osorno near Ensenada, Pérez Rosales National Park, near Ensenada (−41.202350, −72.525768), under mixed Nothofagaceae forest, 27 Mar 2008, *M.E. Smith & D. Pfister MES-188* (FLAS-F-64220, CORDC00006546); REGIÓN DE MAGALLANES: Parque Karukinka, La Paciencia valley, under

N. pumilio, 8 Mar 2016, *C. Truong CT-4340* (FLAS-F-63417, CORDC00006514); ibid., 8 Mar 2016, *C. Truong CT-4331* (FLAS-F-63409, CORDC00006515); Torres del Paine National Park, under *N. pumilio*, 25 Feb 2013, *L. Domínguez LSD2390* (CORDC00006516); Fuerte Bulnes, near the reserve entrance, 27 Feb 2013, *L. Domínguez LSD2394* (CORDC00006517); REGIÓN DE ARAUCANÍA: Villarrica National Park, Sendero Avutardas, under *N. dombeyi*, 18 May 2019, *M.E. Smith & M. Caiafa MES-3353* (FLAS-F-64331); Fundo Rucalemu, Cordillera de Nahuelbuta, 20 km west of Angol (−37.769781, −72.851425), with *Lophozonia obliqua* and non-ECM trees, *M. E. Smith MES-3406* (FLAS-F-64274).

Notes: Cortinarius cretaceus was transferred to *Cortinarius* by Moser and Horak (1965) before the other *Thaxterogaster* species were synonymized with *Cortinarius*. This species is superficially quite similar to *C. albocanus*. However, *C. albocanus* is typically whiter, has a pileus with a waxy appearance, and has basidiomata that are usually more elongated. *Cortinarius cretaceus* has a pileus that is typically more open, a stipe that is not always contorted, and lamellae that are sometimes only slightly anastomosed, making it less obviously secotioid upon first glance. Spores of the two species are similar in size. Although these two species can be difficult to distinguish, they are clearly separated by ITS data. *Cortinarius cretaceus* has a sweet fragrant odor that is strong and obvious when fresh. In our analysis, *C. cretaceus* was nested with *C. luteinus* of section *Luteini* (FIG. 10) as defined by Soop et al. (2019), which includes agaricoid species associated with Nothofagaceae in New Zealand.

Cortinarius dibaphoides (E. Horak) Peintner & M.M. Moser, Mycotaxon 81:179. 2002.   FIG. 2A–B
 ≡ *Thaxterogaster dibaphoides* E. Horak, Fl Criptog Tierra del Fuego 11:33. 1980 [1979].

Basidiomata 15–25 × 25–45 mm high, secotioid (FIG. 2A). Pileus subglobose, typically umbonate to slightly umbonate and relatively elongated, ovoid to convex at maturity; pale brown to yellow-brown, reddish brown when mature; margin incurved, slightly vinaceous, bearing fibrillose remnants of the partial veil, usually exposing the hymenophore at maturity; surface smooth to fibrillose, dry. Hymenophore lacunose, with irregular chambers that are more or less radially arranged, pale brown to ferruginous brown. Stipe 20–40 × 3–5(–7) mm, well developed, mostly cylindrical or gradually tapered at the base; with a persistent fibrillose, whitish, irregular ring; white to pale brown; context KOH negative. Odor not distinctive, taste not recorded. Not staining upon bruising.

Basidiospores 12–15 × 8–10 μm (Qr = 1.51), mostly ovate, almost bilaterally symmetrical; apiculus present; wall covered by coarse warts regularly distributed, when viewed under LM; warts mostly connected and forming ridges under SEM (FIG. 2B). Basidia 20–25 × 7–8 μm, 4-spored. Cystidia absent. Pileipellis of cylindrical, narrow, gelatinized hyphae 2–7 μm wide, encrusted with yellowish pigment in KOH. Clamp connections present.

Ecology and distribution: Subepigeous to epigeous on soil, under *Nothofagus pumilio*, apparently rare, Argentina and Chile (Patagonia), Dec to May.

Specimens examined: ARGENTINA. TIERRA DEL FUEGO: Departamento Ushuaia, Tierra Mayor, 25 Feb 1974, *E. Horak* (**isotype** ZT 72/84); RÍO NEGRO: Nahuel Huapi National Park, near Cerro Tronador, 300 m past the Ventisquero Negro glacier area (−41.198959, −71.827917), under *N. pumilio*, 8 May 2006, *E. Nouhra EN167* (CORDC00006048); ibid., 3 Dec 2005, *E. Nouhra EN44* (CORDC00006521); ibid., *E. Nouhra EN47* (CORDC00006522); ibid., 3 Dec 2005, *E. Nouhra EN50* (CORDC00006034). CHILE. REGIÓN MAGALLANES: Magallanes Forest Reserve, near the park guard station (−53.141811, −71.006260), under *N. pumilio*, 7 Apr 2017, *M.E. Smith MES-2549* (FLAS-F-64251).

Notes: Cortinarius dibaphoides typically has a well-developed and relatively long stipe and umbonate pileus. These features, along with the apparent affinity for *N. pumilio*, make the species fairly easy to recognize. The holotype specimen (LPS 37847) is lost. In our analysis, *C. dibaphoides* grouped with good support with other sequestrate Patagonian species (e.g., *C. dombeyi* and *C. janthinocaulis*), as well as with the agaricoid *C. picoides* of section *Turmales* (FIG. 10) as defined by Soop et al. (2019). This group includes species associated with Nothofagaceae in New Zealand and with *Picea* in the Northern Hemisphere.

Cortinarius dombeyi (Singer) Peintner & M.M. Moser, Mycotaxon 81:179. 2002.   FIG. 2C–D
 ≡ *Thaxterogaster dombeyi* Singer, Persoonia 1:385. 1960.

Basidiomata 13–25 mm × 28–35 mm high, secotioid, subglobose at maturity, compressed (FIG. 2C). Pileus reddish brown to dark purplish brown when mature, with violet tones that are particularly notable in young specimens; surface smooth, dry to waxy, shiny when dry; margin attached to the stipe by a white veil, at maturity detached exposing the hymenophore; KOH reaction not recorded. Hymenophore lacunose, formed by irregular small chambers up to 1 mm diam; initially white and becoming yellowish brown to ocher with translucent veins, darker brown at maturity. Stipe 15–20 ×

30–40 mm, well developed and thick, light violet fading to whitish or pale brown; context whitish violet when fresh; submarginate base; veil fibrillose and usually persistent. Odor fruity when fresh but fishy when dried, taste not recorded. Singer (1960) claims that the species becomes "bleached to white in age," but we did not note this or other color changes in our collections.

Basidiospores 13–15.5 × 8.2–9.7 μm (Qr = 1.59), mostly ovate to elliptical, bilaterally symmetrical; wall covered by coarse warts, regularly distributed across the surface of the spores (FIG. 2D), apiculus present. Basidia 37 × 9–10 μm, 4-spored. Cystidia absent. Pileipellis of oppressed, cylindrical, nongelatinized hyphae. Clamp connections present.

Ecology and distribution: Epigeous to subepigeous on soil or occasionally hypogeous, in Nothofagaceae forests, Argentina and Chile (Patagonia), Mar to May.

Specimens examined: ARGENTINA. RÍO NEGRO: Nahuel Huapi National Park, Arroyo Blest, 17 Mar 1959, *Singer* (holotype LIL-M1861). CHILE. REGIÓN DE LOS LAGOS: Puyehue National Park, foothills of Volcan Puyehue, up the road past El Caulle north of Río Golgol, under *Nothofagus dombeyi*, 4 Mar 2016, *R. Healy MES-1593* (FLAS-F-64216); near Aguas Calientes, mixed *N. dombeyi* and *Lophozonia obliqua* forest, 8 May 2016, *A. Mujic MES-1842* (FLAS-F-64218); Antillanca, under bamboo and *N. dombeyi*, 12 Apr 2017, *R. Healy MES-2760* (FLAS-F-64254); REGIÓN DE ARAUCANÍA: Villarrica National Park, near Curarrehue Avutardas Trail, near the park guard station (−39.553763, −71.628430), with *N. dombeyi, L. alpina*, and *L. obliqua*, 18 May 2019, *M. E. Smith MES-3356* (FLAS-F-64259); Fundo Rucalemu, Cordillera de Nahuelbuta, 20 km west of Angol (−37.769781, −72.851425), with *L. obliqua* and non-ECM trees, 8 Oct 2019, *M. E. Smith & M. Caiafa MES-3543* (FLAS-F-64332); MAGALLANES REGION: Río Santa Maria, just south of San Juan and Fuerte Bulnes Reserve (−53.676490, −70.977820), under *N. betuloides*, 1 Apr 2017, *M. E. Smith MES-2286* (FLAS-F-64230); Magallanes National Reserve (−53.145631, −71.004920), under *N. pumilio*, 3 Apr 2017, *A. Mujic MES-2367* (FLAS-F-64233); mirador Las Minas (−53.140717, −71.055550), 6 Apr 2017, *C. Truong MES-2490* (FLAS-F-64239).

Notes: We examined the type specimen of *Thaxterogaster dombeyi* (LIL-M1861) that was deposited by Singer at the Miguel Lillo Foundation in Tucumán, Argentina (LIL). The holotype was collected in Valdivian rainforest under *Nothofagus dombeyi*. Recent collections are from Araucanía, Los Lagos, and Magallanes provinces in Chile in similar wet forests with *N. dombeyi, N. betuloides, Lophozonia obliqua, L. alpina*, and

N. pumilio. We have not found this species in the more seasonal and drier *Nothofagus* forests on the eastern slopes of the Andes, but the species is common in coastal Chilean forests, some of which experience periods of marked drought. Young basidiomata almost always have a notable, dry, lavender universal veil. The odor of fresh, mature specimens is like apples or pears. In our analysis, *C. dombeyi* grouped with various species of section *Turmales*.

Cortinarius fragilis (Zeller & C.W. Dodge) Peintner & M.M. Moser, Mycotaxon 81:180. 2002. FIG. 2E–F
  ≡ *Hymenogaster fragilis* Zeller & C.W. Dodge, Ann Mo Bot Gdn 21:646. 1934.
  ≡ *Setchelliogaster fragilis* (Zeller & C.W. Dodge) E. Horak, Fl criptog Tierra del Fuego 11:19. 1980 [1979].
  ≡ *Thaxterogaster fragilis* (Zeller & C.W. Dodge) A.H. Sm., Bol Soc Argent Bot 10:64. 1962.
  = *Thaxterogaster fragilis* var. *cortinariopsis* Singer, Beih Nova Hedwigia 29:364. 1969.
  = *Cortinarius sclerospermus* Peintner & M.M. Moser [as "*sclerosperma*"], Mycotaxon 81:182. 2002.
  = *Setchelliogaster tetrasporus* Singer [as "tetrasporum"], Evol High Basidiomyc 467. 1971.
  = *Thaxterogaster verrucisporus* E. Horak 1965, Nova Hedwigia 10:226.

Basidiomata 16–36 mm × 22–37 mm high, secotioid (FIG. 2E); subglobose in shape, somewhat compressed in the apical portion. Pileus surface whitish to pale grayish, fibrillose; margin incurved and attached to the stipe, usually exposing the hymenophore at maturity; KOH negative. Hymenophore lacunose, formed by chambers 1–3 mm wide, irregularly arranged and exposed in mature specimens; pale brown to clay color when young but becoming ferruginous dark brown at maturity. Stipe 15–30 × 8–15 mm, white to cream colored, well developed, clavate to bulbous marginated base, solid, the upper portion completely or partially translucent and running as a continuous band of tissue through the middle of the hymenophore; fibrillose cortina present. Odor not evident, taste not recorded. Not staining upon bruising.

Basidiospores 12–15 × 7–8 μm (Qr = 1.80), symmetrical, mostly lemoniform (lemon-shaped), with a well-developed rostrum (a beak-like projection on the distal portion of the spore); apiculus present; warts regularly distributed under LM; wall covered by irregularly coarse warts coalescing at the apical portion into an outer incomplete membrane under SEM (FIG. 2F). Basidia 22–27 × 8–9 μm, 4-spored. Cystidia absent. Pileipellis of cylindrical hyphae, 5–15 μm wide. Clamp connections present.

Ecology and distribution: Hypogeous to subhypogeous on soil, in Nothofagaceae forests under *N. antarctica* and *N. pumilio* in Tierra del Fuego and Magallanes, Argentina and Chile (Patagonia), Feb to Apr.

Specimens examined: ARGENTINA. TIERRA DEL FUEGO: Valle Andorra, Ushuaia (−54.750680, −68.325212), under *N. antarctica* and *N. pumilio*, 16 Feb 2015, *C. Truong CT-4229* (FLAS-F-63330, CORDC00006523); Martial Glacier, 9 Mar 1963, *E. Horak 64/5* (LPS 38212). CHILE. REGIÓN MAGALLANES: Punta Arenas, Feb & Mar 1906, *B. Thaxter* (**holotype** Farlow 111-1906); Parque Karukinka, Valle La Paciencia (−54.365694, −68.793528), under *N. pumilio*, 7 Mar 2016, *C. Truong CT-4330* (FLAS-F-63408, CORDC00006524); Casa Escondida, 9 km north of Punta Arenas, under *Nothofagus* sp., 22 Mar 2008, *M. E. Smith & D. Pfister MES-166* (FLAS-F-64333); Magallanes Forest Reserve, near the guard station (−53.142861, −71.006083), under *Nothofagus pumilio*, 7 Apr 2017, *M. E. Smith MES-2540* (FLAS-F-64248); group camping site B (−53.143028, −71.030806), in *N. pumilio* forest soil, 3 Apr 2017, *A. Mujic MES-2368* (FLAS-F-64234); group camping site A (−53.142111, −71.028944), in *Nothofagus pumilio* forest soil, 6 Apr 2017, *M. E. Smith MES-2523* (FLAS-F-64243); ibid., *A. Mujic MES-2505* (FLAS-F-64241); ibid., *A. Mujic MES-2501* (FLAS-F-64240); ibid., *C. Truong MES-2486* (FLAS-F-64238).

Notes: The far southern distribution of *Cortinarius fragilis*, along with the unusual form of the spore ornamentation, makes it relatively easy to recognize. Dodge and Zeller (1934) described *Hymenogaster fragilis* based on specimens collected by R. Thaxter in southern Chile in 1906. The species was transferred to *Thaxterogaster* by Singer and Smith (1963). Horak (1979) later treated *Setchelliogaster tetrasporum* and *Thaxterogaster verrucisporus* as synonyms of this species under the name *Setchelliogaster fragilis*. This species was formally transferred to *Cortinarius* as *C. fragilis* by Peintner et al. (2002). Horak's synonymy of *C. fragilis* with *Th. verrucisporus* was not taken into account by Peintner et al. (2002); therefore, *Th. verrucisporus* was subsequently transferred to *Cortinarius* as *C. sclerospermus*. After carefully studying the type materials of *H. fragilis, S. tetrasporum*, and *Th. verrucisporus*, we consider Horak's synonymy correct and the three taxa conspecific. We treat all of these taxa under the name *C. fragilis*.

New sequences from fresh material demonstrate that *C. fragilis* is not related to the Australian voucher of "*Thaxterogaster fragilis*" used by Peintner et al. (2001) (Trappe 18313; AF325559), which is nested within section *Purpurascentes*. In our analysis, *C. fragilis* grouped within section *Turmales* (Soop et al. 2019). The members of section *Turmales* occur in both the Northern and Southern Hemispheres, but taxa in the Southern Hemisphere are often associated with Nothofagaceae hosts. After the Peintner et al. (2001) publication, the Trappe 18313 voucher specimen was subsequently used as the holotype specimen for the new species *Cortinarius caesibulga* Vernes, Danks & T. Lebel (Danks et al. 2010). We included this sequence in our analysis under this new name.

Cortinarius fuegianus Peintner & M.M. Moser, Mycotaxon 81:180. 2002. FIG. 3A–B
MycoBank MBT390649

≡ *Thaxterogaster magellanicus* Singer [as "*magellanicum*"] Mycologia 43:219. 1951.

Additional description: Horak 1979 [1979].

Neotypification: ARGENTINA. TIERRA DEL FUEGO: Ushuaia, los Humedales (−54.745321, −68.325605), under Nothofagaceae, 16 Feb 2015, *L. Domínguez LSD2380b* (**neotype designated here** CORDC00006504). GenBank: ITS = MN855076.

Basidiomata 10–35 mm × 22–37 mm high, secotioid (FIG. 3A). Pileus lilac to violaceus, later whitish to pale cream to yellowish brown, ovoid to subglobose; surface dry to slightly viscid, fibrillose; pileus margin incurved and attached to the stipe, usually exposing remnants of cortina around the margin; KOH negative. Hymenophore lacunose, formed by irregular chambers 1–2 mm wide, irregularly arranged and exposed in mature specimens; pale lilac when young but becoming ferruginous brown at maturity. Stipe 15–60 × 15–30 mm, well developed, solid, cylindrical to subclaviform, usually marginate; lilac to white; fibrillose cortina present, often with cortina-like remnants around the stipe base. Odor and taste tangy and aromatic. Not staining upon bruising.

Basidiospores 12.5–17.5 × 7–9.5 μm (Qr = 1.82), ovate to elliptical, mostly symmetrical, apiculus present, yellowish to rusty brown; wall covered by irregularly coarse warts under LM; coalescing at the apical portion under SEM (FIG. 3B). Basidia 30–50 × 8–10 μm, 4-spored. Cystidia absent. Pileipellis of cylindrical hyphae 2–5 μm wide, strongly gelatinized. Clamp connections present.

Ecology and distribution: Usually epigeous on soil, in Nothofagaceae forests under *Nothofagus antarctica, N. dombeyi*, and *Lophozonia alpina*, Argentina and Chile, spring (Nov), summer (Feb), and autumn (Mar to May).

Other specimens examined: ARGENTINA. TIERRA DEL FUEGO: Estancia Nueva Argentina, under *N. antarctica*, 22 Feb 1950, *Singer* (LIL-M423); RÍO NEGRO: Nahuel Huapi National Park, Arroyo Los Notros, Colonia Suiza, under *N. dombeyi*, 18 Mar 2012,

E. Nouhra EN266 (CORDC00006503); Cerro Tronador close to Ventisquero Negro glacier, under *N. pumilio*, 8 May 2006, *E. Nouhra EN139* (CORDC00006525); NEUQUÉN: Quetrihué, under *Nothofagus dombeyi*, 7 Mar 1959, *Singer* (M1702) (M-0307481); Villa Traful, under Nothofagaceae, 22 Apr 2001, *M. Castellano, Trappe 26146* (CORDC00006526); Lanin National Park, road to cascada Chachin, under *N. dombeyi* and *L. alpina*, 26 Nov. 2008, *E. Nouhra EN165* (CORDC00006493); CHUBUT: Lago Puelo, road from Los Hitos to Prefectura, under *N. dombeyi*, 12 Apr 2014, *F. Kuhar FK14001* (CORD00006080). CHILE. REGIÓN DE MAGALLANES: Punta Arenas, 7 Feb 1906, *Thaxter 8* (FH4572).

Notes: Inspired by material collected by Thaxter (Thaxter 4572), Singer (1951) established the genus *Thaxterogaster* as a "link" between "gasteromycetes" and "agaricales." This specimen was provisionally given the name "*Secotium magellanicum*" by Thaxter, but this name was never published. Singer (1951) named this species *Thaxterogaster magellanicus* and designated this species as type of the genus *Thaxterogaster* (Singer 1951; Halling 1981). Although the species was inspired by Thaxter's collection 4572, Singer (1951) described the species based on his own collection and he designated this collection (LIL-M515) as the holotype. However, Horak (1979) erroneously indicated Thaxter's collection as the holotype of *Th. magellanicus* instead. The true holotype (LIL-M515) is now lost according to the curatorial team at LIL.

Singer (1951) described *Th. magellanicum* as similar to *Th. violaceum*. However, he pointed out that *Th. magellanicum* had a well-developed stipe, lacked violaceous tones, and the peridium separated from the stipe at maturity to reveal the gleba. By contrast, *Th. violaceum* had a less well-developed stipe, obvious violaceous tones, and the peridium typically remained attached to the stipe. Horak and Moser (1965), Horak (1979), and Gamundi and Horak (1993), among other authors, also employed a species concept that changed over time and was notably different from the original description of Singer (1951) and later the description of Singer and Smith (1958).

Horak and Moser (1965) noted the differences in the magnitude and distribution of the spore ornamentation among collections at IB, but they nonetheless concluded that these specimens all belonged to the same species, *Th. magellanicus*. Horak (1979) synonymized *Thaxterogaster magellanicus* with both *Th. dombeyi* Singer and *Th. subalbidus* A.H. Sm. However, Halling (1981) pointed out that *Th. subalbidus* and *T. magellanicus* could be distinguished based on differences in spore ornamentation.

After careful reexamination of reference specimens and our new collections, we treat *C. fuegianus, C. subalbidus*, and *C. dombeyi* as three distinct species. Considering that the holotype specimen is lost, we designate a neotype to stabilize the name *Cortinarius fuegianus*. We have selected a neotype collected near the type locality. The neotype is also consistent with the type description and matches well in morphology and ITS sequence with our other specimens of this species. In our analysis, *C. fuegianus* grouped with *C. alboaggregatus* from New Zealand within section *Alboaggregati* as defined by Soop et al. (2019). This section also includes the epigeous species *C. pseudotriumphans* from Nothofagaceae forests in South America.

In the field, *C. fuegianus* can be confused with *C. albocanus*, which also has white and sometimes lilac coloration on the pileus. However, *C. albocanus* is frequently pure white and has a unique waxy or silky appearance. *Cortinarius albocanus* can also be differentiated from *C. fuegianus* by the presence of anastomosed lamellae, as opposed to the lacunose hymenophore in *C. fuegianus*. In addition, *C. albocanus* has much smaller spores than *C. fuegianus*. *Cortinarius tympanicus* can also be confused with *C. fuegianus* due to similarities in the coloration and overall morphology. However, *C. tympanicus* has a noticeably glutinous pileus with more yellowish brown tones at maturity. The spores of *C. tympanicus* are also smaller than those of *C. fuegianus*.

Cortinarius galbus Kuhar & Nouhra, sp. nov. FIG. 4A–F
MycoBank MB829673

Typification: CHILE. REGIÓN DE LA ARAUCANÍA: Villarrica National Park, near Currarehue Avutardas Trail, near the park guard station (−39.553763, −71.628430), under *N. dombeyi, L. alpina, L. obliqua*, 19 May 2019, *M. E. Smith MES-3379* (**holotype** FLAS-F-64267). GenBank: ITS = MN855009; 28S = MT893322; *rpb*2 = MW456522.

Etymology: galbus (Latin), referring to the presence of yellow pigments on the cuticle.

Diagnosis: Basidiomata sequestrate, gasteroid, globose; yellow to olive brown, covered by a white to translucent universal veil. Hymenophore enclosed, lacunose, reddish brown. Stipe highly reduced and percurrent into the fertile tissue; context white to translucent. Basidiospores fusiform and highly elongated, finely verrucose and with smooth umbos at both apices. The white to translucent universal veil, in addition to the translucent short stipe and the shape of the spores, distinguishes this species from other sequestrate taxa in Patagonia. Occurring under the litter layer beneath trees of the Nothofagaceae in Argentina and Chile.

Description: Basidiomata 5–16 × 5–17 mm high, gasteroid, hypogeous, subglobose to slightly flattened (FIG. 4A); universal veil tissue white, membranaceous, usually rubbing off easily upon collection. Pileus yellowish (Reed Yellow), bruising olive yellow (Olive Yellow to Light Yellowish Olive); entirely or partially covered by a white to translucent universal veil, viscid with adhering soil particles. Pileus enclosing the fertile tissue; margins convoluted and attached to a broadened sterile base; KOH reaction on the surface not recorded. Hymenophore uniformly lacunose, formed by elongated minute chambers 70–150 μm diam; light brown to dull brown. Odor mild, taste not recorded.

Stipe 3–8 × 3–5 mm, reduced to a bulbose stub, appearing truncate at the base (FIG. 4A); solid, cylindrical, percurrent into the hymenophoral tissue; white in cross-section, becoming translucent in the apical portion and at the base.

Basidiospores 8.5–10.5 × 4–5 μm (Qr = 2.12), fusiform, symmetrical, apiculus present, finely warted under LM; warts distributed evenly across the surface but with a smooth umbo at the spore apex when observed under SEM (FIG. 4B). Basidia 15–20 × 3–7 μm, 4-spored, cylindrical to slightly capitate with cyanophilic contents; sterigmata short, up to 2 μm long. Hymenial trama parallel, 45–65 μm thick. Pileipellis 250–700 μm thick, three-layered (FIG. 4C), irregularly covered by a universal veil 100–390 μm thick and continuous with the sterile base, consisting of hyaline, weakly encrusted hyphae 4–7 μm wide when viewed in KOH; suprapellis 150–320 μm thick, consisting of slightly gelatinized and loosely arranged cylindrical hyphae, 1–3 μm thick; mediopellis a more compact layer, 110–380 μm of thick, dark yellow, pigmented hyphae formed by short isodiametric segments 4–12 μm wide with intense golden incrustations (FIG. 4D); subpellis 100–130 μm thick, composed of tightly compacted hyaline subcylindrical hyphae 2–7 μm wide (FIG. 4E). Clamp connections present.

Ecology and distribution: Hypogeous to subhypogeous in soil, in Nothofagaceae forests under *Nothofagus antarctica, N. dombeyi, Lophozonia alpina*, and *L. obliqua*, Argentina and Chile (Patagonia), May.

Other specimens examined: ARGENTINA. RÍO NEGRO: Nahuel Huapi National Park, Mascardi, 1 km north of Lago Hess, under *N. antarctica* (−41.373353, −71.746673), 16 May 2016, *A. Mujic MES-2086* (FLAS-F-64225, CORDC00006509); near Lago Hess, under *N. antarctica*, 18 May 2016, *E. Nouhra MES-2150* (FLAS-F-64328, CORDC00006510); Nahuel Huapi National Park, by the road near Lago Hess, under *N. antarctica*, 16 May 2016, *E. Nouhra MES-2098* (CORDC00006508, FLAS-F-64226). CHILE. REGIÓN DE LOS LAGOS: Osorno, Puyehue National Park, near Aguas Calientes, in mixed *N. dombeyi* and *L. obliqua* forest, 8 May 2016, *A. Mujic MES-1844* (FLAS-F-64329).

Notes: The long fusiform spores, along with the yellowish coloration of the basidiomata and distinctive universal veil, make *C. galbus* easy to distinguish from any other known taxa of sequestrate *Cortinarius*. In our analysis, *C. galbus* was placed in section *Thaumasti*, a well-supported clade including *C. vaginatus* and *C. chlorophanus*, two agaricoid species that also occur in Patagonia (FIG. 10; Soop et al. 2019; Liimatainen et al. 2020). The intense yellow pigmentation as well as the well-developed universal veil that forms a volva (or an exoperidium in sequestrate species such as *C. galbus*) is a morphological feature that confirms the close phylogenetic relationship of the species in this group. In addition, species of section *Thaumasti* are associated with Nothofagaceae in both New Zealand and Patagonia. Note that data from a portion of the second largest subunit of RNA polymerase II (*rpb2*) are provided for this species to facilitate future multigene phylogenetic analyses of *Cortinarius* in Patagonia.

Cortinarius gloiodes Kuhar, Nouhra & M.E. Sm., nom. nov.   FIG. 3C–D
MycoBank MB836570

Basionym: *Thaxterogaster gliocyclus* E. Horak, Nova Hedwigia 10:221. 1965 (non *Cortinarius gliocyclus* E. Horak 1975).

Etymology: gloiodes from the Greek γλοιώδης, glutinous.

Basidiomata 15–40 × 20–50 mm high, secotioid (FIG. 3C). Pileus yellowish brown to reddish brown; ovoid to subglobose, glutinous and slightly translucent when moist but fibrillose when dry; surface brownish with KOH; margin incurved and attached to the stipe when immature, leaving remnants of a slimy whitish veil at the edge when detached from the stipe and exposing the lacunose hymenophore. Hymenophore compact when young, formed by irregular chambers up to 2.5 mm wide; pale ochraceous brown becoming dark brown at maturity. Stipe 10–45 (usually shorter than 45) × 8–15 mm, viscid, highly variable in length among different collections, cylindrical to subclavate and exposing remains of the veil; whitish when young to pale brownish at maturity. Odor and taste acidic. Not staining upon bruising.

Basidiospores 12–15 × 8–9 μm (Qr = 1.59), ovate to elliptical almost bilaterally symmetrical, apiculus present, wall covered with interconnected warts, mostly conical to irregular in shape, uniformly distributed across the spore surface (FIG. 3D). Basidia 35–45 × 7–9 μm, 4-spored. Cystidia absent. Pileipellis of cylindrical hyphae 2–8 μm wide, gelatinized, encrusted with brownish pigment. Clamp connections present.

Ecology and distribution: Subhypogeous to epigeous on soil, in Nothofagaceae forests under *Nothofagus* and *Lophozonia*, Argentina and Chile (Patagonia), spring (Oct to Dec) and summer (Feb to Mar).

Specimens examined: ARGENTINA. RÍO NEGRO: Nahuel Huapi National Park, Cerro Tronador close to Ventisquero Negro glacier (−41.196692, −71.831222), under *N. pumilio*, 3 Dec 2005, *E. Nouhra EN43* (CORDC00006502); ibid., *E. Nouhra EN48* (CORDC00006501); TIERRA DEL FUEGO: Ushuaia Department, south of Paso Garibaldi (−54.725000, −67.823611), under Nothofagaceae, 29 Feb 1988, *R. Halling REH5790* (NYBG); 3.2 km before Lago Escondido (−54.702916, −67.836672), under Nothofagaceae, 1 Mar 2013, *L. Domínguez LSD2406* (CORDC00006527). CHILE. REGIÓN DE MAGALLANES: Puerto Natales, Monte Alto, 26 Mar 1963, *E. Horak* (**holotype** "of *Thaxterogaster gliocyclus*" ZT 64/9); REGIÓN DE ARAUCANÍA: Fundo Rucalemu, Cordillera de Nahuelbuta, 20 km west of Angol (−37.769781, −72.851425), under *Lophozonia obliqua*, 4 Oct 2019, *M. E. Smith & M. Caiafa MES-3504* (FLAS-F-64280); ibid., *M. E. Smith & M. Caiafa MES-3509* (FLAS-F-64281); ibid., 6 Oct 2019, *M. E. Smith & M. Caiafa MES-3517* (FLAS-F-64282).

Notes: *Thaxterogaster gliocyclus* E. Horak has not been previously transferred to *Cortinarius*. However, since the name *Cortinarius gliocyclus* E. Horak (non *Th. gliocyclus*) is already occupied (Moser and Horak 1975), a new epithet is required. We propose here the new name *Cortinarius gloioides* to accommodate the species originally named as *Th. gliocyclus*. *Cortinarius gloioides* is similar to *C. glabriceps*, which was originally described as *Thaxterogaster lubricum* by Horak and Moser (1965). The anatomy and coloration of the pileus, the glutinous surface, and the stipe features are similar in both species, and the spore size and ornamentation fall into a similar size range. We have not been able to find specimens of *C. glabriceps*, nor have we been able to locate and examine the type. It is possible that the two species are synonymous, but both need to be compared in detail once the holotype of *C. glabriceps* can be located.

We also noted that our collections of *C. gloioides* showed a wide variation in stipe prominence and length. Recent collections from the coast range in Chile had highly reduced stipes (approximately 10 mm high), whereas the original description by Horak and Moser (1965) from Magallanes and our collections from the Andes tend to have longer and more well-developed stipes. Given ITS rDNA sequence diversity among the specimens in this group (FIG. 10), it is possible that there is cryptic species-level diversity hidden within this taxon.

Cortinarius glutinopallens (E. Horak) Peintner & M.M. Moser, Mycotaxon 81:180. 2002. FIG. 3E–F

≡ *Thaxterogaster glutinopallens* E. Horak & Moser, Nova Hedwigia 10:220. 1965.

Additional description: Horak (1979).

Basidiomata 10–25 × 15–37 mm high, secotioid (FIG. 3E). Pileus ranging from white to pale brown and darker in age, ovoid to subglobose; cuticle thick and highly viscid to glutinous, KOH negative; margin usually uniform, exposing the hymenophore at maturity, when immature the glutinous layer of the pileus margin extends toward the stipe base. Hymenophore lacunose, compact when young, formed by irregular chambers <5 mm wide, irregularly arranged; pale brown, becoming vinaceous to dark brown at maturity. Stipe 15–30 × 5–15 mm, solid, claviform, viscid, fibrillose; base submarginate with a volva-like structure at maturity, the upper portion continuous within the pileus; white, yellowish, to pale brown. Odor and taste not discernible. Darkening upon bruising.

Basidiospores 12–15 × 8–9.5 μm (Qr = 1.54), almost bilaterally symmetrical, apiculus present, ovate to elliptical, covered by warts under LM; warts irregular, appearing anastomosed more frequently toward the apex under SEM (FIG. 3F). Basidia 25–43 × 8–11μm, 4-spored. Cystidia absent. Pileipellis of cylindrical hyphae 2–4 μm wide, strongly gelatinized, not pigmented. Clamp connections present.

Ecology and distribution: Subhypogeous on soil, in Nothofagaceae forests under *Nothofagus pumilio*, *N. antartica*, and *N. betuloides*, Argentina and Chile (Patagonia), Feb to May.

Specimens examined: ARGENTINA. TIERRA DEL FUEGO: Ushuaia, Martial glacier valley, 11 Mar 1963, *E. Horak* (**holotype** ZT 64/7, **isotype** LPS 38206); Ushuaia, Valle Andorra (−54.766, −68.32727), under *N. antarctica*, 16 Feb 2015, *C. Truong CT-4228* (FLAS-F-63329, CORDC00006505); RÍO NEGRO: Nahuel Huapi National Park, Cerro Otto, near the cable car parking lot (−41.144808, −71.369993), under *Nothofagus pumilio*, 4 May 2005, *E. Nouhra EN36* (CORDC00006529). CHILE. REGIÓN DE MAGALLANES: Magallanes National Reserve, Las Minas summit area, under *Nothofagus* spp., 21 Mar 2008, *M.E. Smith & D.H. Pfister MES-153* (FLAS-F-64214); Magallanes Forest Reserve, on Sendero de Chile (−53.141390, −71.003102), under *N. pumilio*, 4 Apr 2017, *M.E. Smith MES-2429* (FLAS-F-64236); trail to Mirador (−53.144139, −71.003333), under mixed *Nothofagus pumilio/betuloides* forest, 4 Apr 2017, *C Truong MES-2535* (FLAS-F-64244); Karukinka Park, Valle La Paciencia (−54.3657, −68.79352), 7 Mar 2016, under *N. pumilio, C. Truong*

CT-4332 (FLAS-F-63410, CORDC00006530); Casa Escondida, 9 km from Punta Arenas, under Nothofagaceae, 18 Mar 2008, *M. E. Smith & D. Pfister MES-135* (FLAS-F-64212); REGIÓN DE ARAUCANÍA: Villarrica National Park, entrance to Park Coñaripe, Quetrupillán, Mirador Los Volcanes, forest dominated by *N. pumilio*, 13 May 2019, *M. E. Smith MES-3331* (FLAS).

Notes: Cortinarius glutinopallens was initially described from Tierra del Fuego. However, recent specimens were collected in the continental regions of Patagonia in Argentina and Chile. This species is superficially similar to *C. sphaerocephalus*, but *C. glutinopallens* is usually whiter, with fewer brownish tones on the cap, and the spores of *C. glutinopallens* are notably larger. In our analysis, *C. glutinopallens* and *C. tympanicus* are nested together with *C. cycneus* in section *Cycnei* as defined by Soop et al. (2019) but without significant support (FIG. 10). This group contains myxacioid taxa that are confined to the Southern Hemisphere (Soop et al. 2019).

Cortinarius holojanthinus Peintner & M.M. Moser, Mycotaxon 81:180. 2002.   FIG. 5A–B

≡ *Thaxterogaster violaceus* Singer, Mycologia 43:216. 1951.

= *Cortinarius holojanthinus* var. *citrisporus* (M.M. Moser) Peintner & M.M. Moser, Mycotaxon 81:180. 2002.

= *Cortinarius holojanthinus* var. *holojanthinus* Peintner & M.M. Moser, Mycotaxon 81:180. 2002.

= *Thaxterogaster violaceus* var. *citrisporus* M.M. Moser, Nova Hedwigia 10:223. 1965.

= *Cortinarius olorinus* (E. Horak) Peintner & M.M. Moser, Mycotaxon 81:181. 2002.

= *Thaxterogaster olorinum* E. Horak, Nova Hedwigia 10:218. 1965.

Basidiomata 20–55 × 15–50 mm high, gasteroid (FIG. 5A). Pileus whitish lilac to light grayish white; subglobose to irregular, almost completely enclosed, somewhat compressed, dry and smooth to fibrillose; margin attached to a turbinate sterile base or reduced stipe by a whitish partial veil, usually not exposing the fertile tissue at maturity; KOH negative. Hymenophore lacunose, formed by small chambers 1–1.5 mm wide, tightly arranged; bright violet when young but changing to light brown and later ferruginous brown at maturity. Stipe 10–50 × 18–20 mm, poorly developed and typically reduced to a turbinate base; white to lilac; fibrillose veil present. Odor of fermented fruit that becomes stronger with maturity, taste not recorded. Not staining upon bruising.

Basidiospores 13–20 × 8–10 μm (Qr = 1.51), mostly ovate to elliptical, apiculus present, wall covered by irregular minute blunt warts visible under LM; warts coalescing at the apical portion (FIG. 5B) under SEM. Basidia 35–55 × 7–10 μm, 4-spored. Cystidia absent. Pileipellis of cylindrical, slightly gelatinized, cylindrical hyphae, 2–10 μm wide. Clamp connections present.

Ecology and distribution: Hypogeous to subhypogeous on soil, in Nothofagaceae forests under a wide range of hosts including *Nothofagus dombeyi*, *N. antarctica, N. betuloides, N. pumilio*, and *Lophozonia alpina*, over a wide geographic area including Neuquén, Río Negro, Chubut, and Tierra del Fuego in Argentina and Araucanía and Magallanes in Chile (Patagonia), Feb to May.

Specimens examined: ARGENTINA. TIERRA DEL FUEGO: Lago Fagnano, 19 Feb 1950, *Singer M362* (**holotype** LIL); Estancia Moat (−54.9021, −67.0997), under *N. betuloides*, 6 Feb 2015, *C. Truong CT-4213* (FLAS-F-63316, CORDC00006531); Valle Andorra (−54.7523, −68.3248), under *N. antarctica and N. pumilio*, 6 Feb 2015, *C. Truong CT-4230* (FLAS-F-63331, CORDC00006532); Tierra Mayor, road to Cerro Bonete, under *Nothofagus pumilio*, 10 Apr 2016, *C. Truong CT-4387* (FLAS-F-63459); RÍO NEGRO: Nahuel Huapi National Park, Mascardi, Laguna Los Moscos (−41.347779, −71.602231), under *N. dombeyi*, 8 May 2006, *E. Nouhra EN195* (CORDC00006533); Mascardi, 2 km outside Río Manso by the road near the lakeshore (−41.347480, −71.581673), *E. Nouhra EN312* (CORDC00006051); Mascardi, Cerro Tronador area near Ventisquero Negro glacier (−41.196316, −71.829742), under *N. pumilio* forests, 8 May 2006, *E. Nouhra EN166* (CORDC00006534); Mascardi, 1 km outside Lago Hess, under *N. antarctica* and *N. dombeyi*, 18 May 2016, *F. Kuhar MES-2132* (FLAS-F-64228); ibid., *E. Nouhra MES-2127* (FLAS-F-64227); CHUBUT: Huemules, 20 Apr 2014, *F. Kuhar FK14037* (CORDC00006535). CHILE. REGIÓN LOS LAGOS: Puyehue National Park, Antillanca ski area, in *N. pumilio* forest soil, 12 Apr 2017, *F. Kuhar MES-2765* (FLAS-F-64255); Antillanca on the edge of the road, under *N. dombeyi*, 6 May 2015, *M. E. Smith MES-1077* (FLAS-F-63097, CORDC00005171); REGIÓN ARAUCANÍA: Villarrica National Park, Park entrance from Coñaripe, Quetrupillán, Mirador Los Volcanes, high-elevation forest dominated by *N. pumilio*, 13 May 2019, *M. E. Smith MES-3334* (FLAS); ibid., *M. E. Smith MES-3335* (FLAS); ibid., *M. E. Smith MES-3336* (FLAS); Nahuelbuta National Park, trail to Piedra de Águila, under *N. dombeyi* and *L. obliqua*, 21 May 2019, *M. E. Smith MES-3389* (FLAS-F-64271); ibid., *M. E. Smith MES-3393* (FLAS-F-64272); Fundo Rucalemu, Cordillera de Nahuelbuta, 20 km west of Angol (−37.769781, −72.851425), under *Lophozonia obliqua* and non-ECM trees, 23 May 2019, *M. E. Smith MES-3420* (FLAS-F-64275); REGIÓN MAGALLANES: Magallanes Forest Reserve near the guard station

(−53.142861, −71.006083), in *Nothofagus pumilio* forest, 7 Apr 2017, *A Mujic MES-2542* (FLAS-F-64249); Magallanes National Reserve, Las Minas, picnic area, under Nothofagaceae, 19 Mar 2008, *M. E. Smith & D. Pfister MES-145* (FLAS-F-64213); REGIÓN AYSEN: Cerro Huemules Reserve, trail to waterfall, under *Nothofagus pumilio* and *N. dombeyi*, 1 May 2016, *C Truong CT-4411* (FLAS-F-63481).

Notes: Horak (1979) synonymized *Thaxterogaster olorinum* with *Cortinarius holojanthinus* (as *Thaxterogaster violaceus*). However, this synonymization was not taken into account by Peintner et al. (2002), and *Thaxterogaster olorinum* was transferred to *Cortinarius* as *C. olorinus*. We accept the synonymy of Horak (1979) and treat both species under the name *Cortinarius holojanthinus*. This species is easily recognizable by the combination of the subglobose, sequestrate, mostly enclosed basidiomata, and the distinctive white to lilac to light grayish white cuticle and lilac gleba when young. In our analysis, *C. holojanthinus* was resolved with support (FIG. 10) as a member of section *Archeriani* (Moser and Horak 1975), a small group of glutinous agaricoid and sequestrate taxa with violaceus and whitish colors known primarily from Australasia (Soop et al. 2019).

Cortinarius janthinocaulis Peintner & M.M. Moser, Mycotaxon 81:180 2002.   FIG. 5C–D

≡ *Thaxterogaster violeipes* M.M. Moser, Nova Hedwigia 10:230. 1965.

Basidiomata 20–50 × 15–45(–50) mm high, secotioid (FIG. 5C). Pileus yellowish to olive brown to reddish brown, hemispheric to subglobose, sometimes dorsoventrally compressed; margin strongly incurved toward the stipe and cracked at maturity showing ochre veil remnants; surface smooth, somewhat viscid, opaque when dry; KOH reaction not recorded. Hymenophore lacunose, formed by irregular chambers that are more or less irregularly arranged; brown to ferruginous brown, exposed at maturity. Stipe 15–40 × 4–8 mm, well developed, cylindrical, fibrous, tapering from the mid-section toward the glebal interior; white to lilac when young, becoming creamy white and staining brown at the base; fibrillose veil present, remaining as fibrils at maturity. Odor of fermented fruit, taste not recorded. Staining brown upon bruising.

Basidiospores (9–)11–15(–15.8) × 7–7.5(–8.5) µm (Qr = 1.51), elliptical to amygdaliform, bilaterally symmetrical, apiculus present, moderately to strongly warted under LM; warts blunt, coarser at the apical portion under SEM (FIG. 5D). Basidia 30–32 × 9 µm, 4(–3)-spored with sterigmata 3–4 µm long. Cystidia absent. Pileipellis of cylindrical hyphae 4–5(–7) µm wide, slightly gelatinized. Clamp connections present.

Ecology and distribution: Subhypogeous, on soil under *Nothofagus pumilio*, Argentina and Chile (Patagonia), Nov to Mar.

Specimens examined: ARGENTINA. RÍO NEGRO: Nahuel Huapi National Park, by the road to the Cerro Tronador base lodge (−41.195119, −71.830803), under *N. pumilio* on rocky soil and leaf litter near the river basin, 27 Nov 2006, *E. Nouhra EN90* (CORDC00006036); ibid., *E. Nouhra EN76* (CORDC00006494). CHILE. REGIÓN DE AYSÉN: Puerto Aysén, near Río Blanco, 1152 m above sea level (a.s.l.) (−45.707620, −72.628215), in soil among bryophytes in *N. pumilio* forest, 28 Jan 2008, *P. Sandoval Leiva PS1516* (CORD00006506).

Notes: This species is not frequently encountered. It was recently collected three times under *N. pumilio*. The collections occurred in spring (Río Negro, Argentina) and summer (Aysén, Chile) instead of autumn. We were not able to locate and study the holotype material (Moser 63/70), which also was collected under *N. pumilio*. In the field, this species looks similar to *C. gloioides* based on the similar pileus coloration. However, the pileus of *C. gloioides* is usually translucent and glutinous, whereas *C. janthinocaulis* is often opaque and drier. *Cortinarius janthinocaulis* also typically has a well-developed and fibrous stipe that is usually less developed in *C. gloioides*. In our study, *C. janthinocaulis* was phylogenetically placed among other species in section *Turmales*, as mentioned under the "Notes" section of *C. dibaphoides*.

Cortinarius mustella (M.M. Moser) Peintner & M.M. Moser, Mycotaxon 81:181. 2002.   FIG. 5E–F

≡ *Thaxterogaster mustella* M.M. Moser, in Horak & Moser, Nova Hedwigia 10:227. 1965.

Basidiomata 35–40 × 15–50 mm high, secotioid (FIG. 5E). Pileus light brown to chestnut brown, whitish in the depressions; irregularly globose, mostly enclosed; surface smooth to slightly granulose, dry; margin convoluted, with ochre veil remnants, usually with cracked edges; dark brown to black with KOH. Hymenophore lacunose, formed by irregular and compacted chambers, irregularly arranged, exposed at maturity; chestnut to ocher brown with thick translucent veins. Stipe 20–35 × 5–10 mm, clavate with a marginate and bulbous base; concolorous, context whitish brown to ochraceous, translucent and wet in appearance. Odor fruity and sweet, taste not recorded. Not staining upon bruising.

Basidiospores 10.5–14 × 8.5–9.5 µm (Qr = 1.36), lacrymoid, apiculus present, wall covered by irregular coarse pointy warts (spines) under LM; the warts distributed along the spore length, sometimes irregularly connected and coalescing into groups and almost forming a reticulum under SEM (FIG. 5F). Basidia 28–34 × 7–10.5 µm, 4(–2)-spored with sterigmata 3–5 µm long.

Cystidia absent. Pileipellis of cylindrical hyphae 7–16 μm wide. Clamp connections present.

Ecology and distribution: Hypogeous to subhypogeous on soil, in Nothofagaceae forests under Nothofagus *pumilio* and *N. betuloides*, mostly occurring in southern Patagonia in Argentina and Chile, Mar to Apr.

Specimens examined: CHILE. REGIÓN DE MAGALLANES: Santa Maria River, just south of San Juan and Fuerte Bulnes Reserve (−53.665384, −70.989184), in forest dominated by *N. betuloides* with some *N. pumilio*, 1 Apr 2017, *M. E. Smith & C. Truong MES-2303* (FLAS-F-64232); ibid., 1 Apr 2017, *R. Swenie MES-2288* (FLAS-F-64334); ibid., 1 Apr 2017, *M. E. Smith MES-2289* (FLAS-F-64231); ibid., 5 Apr 2017, *A. Mujic MES-2456* (FLAS-F-64237, CORDC00006541); Magallanes National Reserve, Las Minas summit area, under Nothofagaceae, 21 Mar 2008, *M. E. Smith & D. Pfister MES-157* (FLAS-F-64215).

Notes: Cortinarius mustella has been most commonly documented in southern Patagonia. We were unable to locate and examine the holotype specimen from Argentina, collected under *Nothofagus pumilio* (NEUQUEN: Cerro Cortinario, Puerto Manzano, 24 Apr 1963, *Moser 63/396*). However, the uniform coloration of the cuticle, gleba and stipe, in addition to the irregular and prominent spines on the spores, makes this species easily recognizable. In our analysis, *C. mustella* and *C. crassus* were nested with poor support in section *Crassi* (FIG. 10) as defined by Soop et al. (2019).

Cortinarius quadrisporus Nouhra & Kuhar, sp. nov.

FIG. 6A–F

MycoBank MB829674

Typification: CHILE. REGIÓN DE LA ARAUCANÍA: Nahuelbuta National Park, trail to Piedra de Águila, under *N. dombeyi* and *L. obliqua*, 21 May 2019, *M. E. Smith & M. Caiafa MES-3399* (**holotype** FLAS-F-64273). GenBank: ITS = MN855004; 28S = MT893323; *rpb2* = MW456520.

Etymology: quadrisporus (Latin), referring to the presence of basidiospores released in tetrads.

Diagnosis: Basidiomata secotioid, pileus globose. Cuticle mostly white to slightly olivaceous or yellowish brown. Margin attached by a fibrillose white cortina. Hymenophore composed of lacunose chambers, dull brown to cinnamon brown. Stipe white, well developed, solid, subcylindrical to slightly bulbous at the base. Basidiospores elliptical, warts minute and isolated, released in tetrads. No other sequestrate *Cortinarius* shares this last character in South America. Occurring under *Nothofagus dombeyi* and *N. pumilio* in northern Patagonia. Known from Argentina and Chile.

Description: Basidiomata 25–50 × 25–90 mm high, secotioid (FIG. 6A). Pileus white, silvery white, ivory white or olivaceous (Light Yellowish Olive), in exposed specimens the apical portion of the cap becoming darker (Honey Yellow); irregularly globose, sometimes compressed; surface viscid when young but becoming smooth and silky at maturity; margin convoluted, mostly attached to the stipe exposing the fertile tissue at maturity; KOH reaction not recorded. Hymenophore lacunose, formed by irregular elongated quadrangular chambers 1–6 mm wide (FIG. 6A); dull brown to cinnamon brown (Cinnamon). Stipe up to 90 × 5–25 mm, well developed; solid, subcylindrical or having a slightly bulbous base when immature; surface and context white, becoming dirty white at the base; cortina white and fibrillose. Odor not distinctive, taste not recorded. Not staining upon bruising.

Basidiospores 7–9(–11) × 4–4.5 μm (Qr = 2.01), mostly elliptical, apiculus present, wall covered by minute warts, warts small, less than 0.5 μm high, wall appearing almost smooth when viewed under LM (FIG. 6F); warts mostly isolated and regularly distributed, not coalescing into groups when observed under SEM (FIG. 6B). Spores frequently observed in tetrads, even after becoming detached. Basidia 18–28 × 5–8 μm, cylindrical to slightly claviform, 4-spored. Cystidia not observed. Pileipellis 650–1000 μm thick, three-layered (FIG. 6C); suprapellis of hyaline, loosely arranged, gelatinized, cylindrical, collapsed, clamped hyphae 2–5 μm wide, the outer hyphal tips with rounded ends and cell walls slightly amyloid; mediopellis layer formed by a discontinuous pseudoparenchyma, composed of isodiametric to rectangular hyaline cells, 15–40 × 8–22 μm. Subpellis a tightly arranged plectenchyma, composed of large, cylindrical, hyaline, inflated hyphae 6–18 μm wide, among these are large tortuous, nonseptate, oleiferous hyphae 4–23 μm wide. Clamps present but infrequent.

Ecology and distribution: Hypogeous to subhypogeous on soil, in Nothofagaceae forests under *Nothofagus pumilio, N. dombeyi, Lophozonia alpina*, and *L. obliqua*, northern Patagonia in Argentina and Chile, May.

Other specimens examined: ARGENTINA. RÍO NEGRO: Nahuel Huapi National Park, Arroyo Goye near Colonia Suiza (−41.097655, −71.519071), mixed *N. dombeyi* and *N. pumilio* forest, 12 May 2016, *M. E. Smith MES-1903* (FLAS-F-64221); Nahuel Huapi National Park, Los Rápidos, Sector Mascardi, *N. dombeyi* forest, 16 May 2016, *R. Healy MES-2060* (CORDC0000650, FLAS-F-64223). CHILE. REGIÓN LOS RÍOS: San Pablo de Tregua Reserve (−39.614190, −72.067450), under

N. dombeyi, 7 May 2019, *M. E. Smith MES-3267* (FLAS); REGIÓN DE LA ARAUCANÍA: Villarrica National Park, near Currarehue Avutardas Trail, near the park guard station (−39.553763, −71.628430), with *N. dombeyi*, *L. alpina*, and *L. obliqua*, 18 May 2019, *M. E. Smith & M. Caiafa MES-3352* (FLAS-F-64258).

Notes: The frequent release of the basidiospores in tetrads is a characteristic feature of some Australasian sequestrate species of *Cortinarius* previously considered in the genus *Quadrispora* by Bougher and Castellano (1993). Taxonomic changes, including the rejection of paraphyletic and polyphyletic taxa based on homoplasies (e.g., Peintner et al. 2001), rendered *Quadrispora* obsolete (Gasparini et al. 2014). However, the convergence in this character is always associated with sequestration. To date, no species of quadrisporic *Cortinarius* have yet been described from the Americas. This new species has been found primarily with *N. dombeyi* but also occurs in mixed forests with *N. pumilio*, *L. alpina*, and *L. obliqua*. *Cortinarius quadrisporus* macroscopically resembles *C. sphaerocephalus*, but *C. sphaerocephalus* has spores that are shorter, wider, and more coarsely ornamented (8–10.5 × 5.5–7 μm) and not typically grouped in tetrads after release from basidia. *Cortinarius quadrisporus* also resembles *C. tympanicus*, but *C. tympanicus* is distinguished by the much larger spores (11.5–14 × 7–8 μm) not grouped in tetrads. Note that data for *rpb2* are provided for this species to facilitate future multigene phylogenetic analyses of *Cortinarius* in Patagonia (GenBank MW456520, MW456521).

Cortinarius sphaerocephalus (E. Horak & M.M. Moser) Peintner & M.M. Moser, Mycotaxon 81:182. 2002.   FIG. 7A–B

≡ *Thaxterogaster sphaerocephalus* E. Horak & M.M. Moser, Nova Hedwigia 10:232. 1965.

Basidiomata 15–50 × 25–65 mm high, secotioid (FIG. 7A). Pileus white to ivory to pale yellow to light grayish white, becoming brownish yellow when emerging from litter; globose to hemispheric; surface smooth and glutinous; margin convoluted and irregular, usually attached to the stipe and covered by white partial veil material; KOH reaction not recorded. Hymenophore lacunose, formed by irregular chambers that are more or less irregularly arranged; light brown to coffee brown, with translucent veins; exposed at maturity. Stipe up to 70 × 5–20 mm, well developed; cylindrical, turbinate or having a slightly bulbous base; whitish; context white, sometimes hollow in the upper section; veil fibrillose. Odor absent to slightly fruity, taste not recorded. Not staining upon bruising.

Basidiospores 8–10.5 × 5.5–7 μm (Qr = 1.42), mostly elliptical or amygdaliform, rarely sublemoniform, apiculus present, wall covered by irregular coarse warts under LM; warts sometimes connected and coalescing into groups at the apical portion under SEM (FIG. 7B). Basidia 22–26 × 8–9 μm, 4-spored, sterigmata 3–5 μm long. Cystidia absent. Pileipellis of cylindrical gelatinized hyphae 5–16 μm wide. Clamp connections present.

Ecology and distribution: Hypogeous to subhypogeous or sometimes completely emergent on soil, often in Nothofagaceae forests dominated by *Nothofagus dombeyi*, but also under *N. pumilio* and in mixed forests with *Lophozonia obliqua* and *L. alpina*, Argentina and Chile (Patagonia), Feb to May.

Specimens examined: ARGENTINA. RÍO NEGRO: Valle Frias between Frias Lake and Paso de Las Nubes, under *N. dombeyi* and *N. antartica*, 8 Apr 1962, *E. Horak* (**holotype** ZT 64/15); Nahuel Huapi National Park, Mascardi, 3 km outside Río Manso (−41.347868, −71.582611), under *N. dombeyi*, 21 Mar 2012, *E. Nouhra EN314* (CORDC00006536); Mascardi, Los Rápidos (−41.349663, −71.603095), under *N. dombeyi*, 8 May 2015, *M.E. Smith MES-1112* (FLAS-F-63109, CORDC00005172); 2 km outside Los Rapidos near Lago Mascardi shore, under *N. dombeyi*, 8 May 2015, *F. Kuhar MES-1107* (FLAS-F-63097, CORDC00005171); Bariloche, Arroyo Los Notros (−41.080261, −71.556588), under *N. dombeyi*, 20 Mar 2012, *E. Nouhra EN308* (CORDC00006537); ibid., under *N. dombeyi*, 20 Mar 2012, *E. Nouhra EN307* (CORDC00006538); NEUQUÉN: Lanin National Park, trail to Chachin waterfall, under *N. dombeyi*, 15 May 2015, *M. E. Smith & E. Nouhra MES-1290* (FLAS-F-64211, CORDC00006539); CHUBUT: Huemules (−42.767777, −71.45694), at the end of the trail, under *N. pumilio*, 20 Apr 2014, *F. Kuhar FK14036* (CORDC00006082); Depto Tehuelche, Los Niños Lake (−44.010000, −71.493900), under *N. pumilio*, 21 Feb 2013, *L Domínguez LSD2379* (CORDC00006540). CHILE. REGIÓN DE ARAUCANÍA: Villarrica National Park, Park entrance from Coñaripe, Quetrupillán, Mirador Los Volcanes, high-elevation forest dominated by *N. pumilio*, 13 May 2019, *M.E. Smith & M. Caiafa MES-3339* (FLAS); ibid., *M.E. Smith & M. Caiafa MES-3340* (FLAS); Fundo Rucalemu, Cordillera de Nahuelbuta, 20 km west of Angol (−37.769781, −72.851425), under *Lophozonia obliqua* and non-ECM trees, *M.E. Smith & M. Caiafa MES-3431* (FLAS-F-64278); ibid., *MES-3428* (FLAS-F-64277); REGIÓN DE LOS LAGOS: Osorno, Puyehue National Park, Refugio Antillanca (−40.7, −72.3), under *N. pumilio* and *Drimys andina* on volcanic ashes, 18 Mar 1995, *G. Palfner GP1204a* (M-0307480); REGIÓN LOS LAGOS: Puyehue National Park, Antillanca ski area, along the trail, in forest soil dominated by *Nothofagus pumilio*, 12 Apr 2017, *M. E. Smith MES-2733* (FLAS-F-65317); Pérez Rosales National Park, near

Lago Todos Los Santos, Petrohue, in Nothofagaceae-dominated forest, 25 Mar 2008, *M. E. Smith & D. Pfister MES-183* (FLAS-F-64217); Puyehue National Park, just below Antillanca ski area, in *N. pumilio* forest, 10 Apr 2017, *C. Truong MES-2596* (FLAS-F-64252).

Notes: A key feature to separate *Cortinarius sphaerocephalus* from *C. tympanicus* is the occurrence of sublimoniform spores in *C. sphaerocephalus*. This species has been collected mostly in northern Patagonia. Collection M-0307480 in Munich was labeled as *Thaxterogaster albocanus*, but it fits our concept of *C. sphaerocephalus*. In our analysis, *C. sphaerocephalus* is placed within section *Purpurascentes* (Moser) but with poor bootstrap support. This section contains numerous species from both the Northern and Southern Hemispheres (Soop et al. 2019).

Cortinarius tympanicus (E. Horak) Peintner & M.M. Moser, Mycotaxon 81:182. 2002.　　　FIG. 7C–D
　 ≡ *Thaxterogaster tympanicus* E. Horak, Nova Hedwigia 10:224. 1965.

Basidiomata 13–35 × 20–39 mm high, secotioid (FIG. 7C). Pileus whitish to grayish lilac, then pale brownish to pale brown near the top, pale lilac at the margin; claviform to globose; surface smooth and glutinous; margin incurved, attached to the stipe; KOH negative. Hymenophore lacunose, formed by irregular chambers and exposed at maturity; white or pale lilac, then cinnamon to rusty brown at maturity. Stipe 20–50 mm × 3–15 mm, cylindrical to claviform, tapered upward toward the pileus, slightly bulbous at the base; context whitish with lilac tints; cortina white and fibrillose. Odor slightly sweet, taste not recorded. Not staining upon bruising.

Basidiospores 11.5–14 × 7–8 μm (Qr = 1.67), mostly elliptical, apiculus present, wall covered by irregular warts evenly distributed under LM, some are fused and connected under SEM (FIG. 7D). Basidia 20–25 × 7–8 μm, 4-spored. Cystidia absent. Pileipellis of cylindrical gelatinized hyphae 3–7 μm wide. Clamp connections present.

Ecology and distribution: Hypogeous to subhypogeous on soil, in Nothofagaceae forests under *Nothofagus pumilio* and *N. betuloides*, Argentina and Chile (Patagonia), Dec to May.

Specimens examined: ARGENTINA. TIERRA DEL FUEGO: Departamento Ushuaia, Ushuaia, Martial glacier valley, 2 Mar 1963, *E. Horak* (**holotype** ZT 64/3); RÍO NEGRO: Nahuel Huapi National Park, Mascardi, Cerro Tronador area, near the river, in *N.pumilio* forest (−41.196316, −71.829742), 3 Dec 2005, *E. Nouhra EN39* (CORDC00006032); ibid., *E. Nouhra EN53* (CORDC00006542); ibid., *E. Nouhra EN42* (CORDC00006543); ibid., *E. Nouhra EN49* (CORDC00006544); ibid., *E. Nouhra EN86* (CORD C00006545). CHILE. REGIÓN DE MAGALLANES:

Magallanes Forest Reserve, near the park guard station (−53.138165, −71.003928), under mixed *N. pumilio* and *N. betuloides* forest, 7 Apr 2017, *C. Truong MES-2547* (FLAS-F-64250); REGIÓN DE ARAUCANÍA: Villarrica National Park, Park entrance from Coñaripe, Quetrupillán, Mirador Los Volcanes, high-elevation forest dominated by *N. pumilio*, 13 May 2019, *M. E. Smith MES-3330* (FLAS); ibid., *M. E. Smith MES-3332* (FLAS).

Notes: The original description of *Cortinarius tympanicus* was based on a specimen collected in Tierra del Fuego. The ITS sequence of the holotype (ZT 64/3) groups with recently collected specimens from *N. pumilio* forests collected at several sites in Chile. Additional specimens from high-altitude *N. pumilio* forests at the base of Cerro Tronador, in Río Negro Province, Argentina, were identified based on morphological analyses. This species is superficially similar to *C. sphaerocephalus* but can be separated based on spore characters (see comments above under *C. sphaerocephalus*). In our analysis, *C. tympanicus* grouped with *C. glutinopallens* and *C. cycneus* (FIG. 10) in section *Cycnei*, which is confined to the Southern Hemisphere (Soop et al. 2019). However, the clade was poorly supported. Several species in section *Cycnei* have been described from South America, including the well-known agaricoid species, *C. magellanicus*.

Notes on taxonomic placement of other recently described sequestrate Cortinarius from Patagonia.— We also provide additional images and notes on several recently described sequestrate *Cortinarius* species. This includes photos of fresh basidiomata, as well as SEM photos of spores, for *C. infrequens* and *C. flavopurpureus* (FIG. 8A–D) and *C. nahuelhuapensis* and *C. translucidus* (FIG. 9A–D). Complete descriptions are featured in Pastor et al. (2019).

Notes: Cortinarius infrequens is well supported within the section *Majestatici*. This clade was previously recovered by Soop et al. (2019) and includes the type of the section, *C. majestaticus*, from New Zealand (FIG. 10). This is a small austral clade associated with Nothofagaceae forests in the South Pacific and South America. *Cortinarius flavopurpureus, C. nahuelhuapensis*, and *C. translucidus* were not phylogenetically placed within any of the previously defined sections.

Additional sequestrate Cortinarius reported from Patagonia.— The following two species of sequestrate *Cortinarius* from Patagonia are documented here and included in the key, but no new sequences, specimens, or photos are available. We provide descriptions and commentaries based on previous publications, including

Halling (1981), Horak and Moser (1965), and Singer and Smith (1963).

Cortinarius glabriceps Peintner, Mycotaxon 87:119. 2003.

≡ *Thaxterogaster lubricus* M.M. Moser, Nova Hedwigia 10:226. 1965.

≡ *Cortinarius lubricus* (M.M. Moser) Peintner & M. M. Moser, Mycotaxon 81:180. 2002 (non *Cortinarius lubricus* Poirier & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10:371. 2000).

Basidiomata 1–15 × 25–30 mm high, secotioid, sub-hypogeous. Pileus gray violaceous, becoming dark oli-vaceous; globose to hemispheric; surface smooth and glutinous; margin receding and slightly distant from the stipe, draped in a yellow-brown cortina; KOH response not recorded. Hymenophore lacunose, irre-gular, light brown to coffee brown. Stipe up to 44 × 17 mm, well developed, even and cylindrical or with a slightly bulbous base; surface slimy, yellowish blue in the upper section to grayish violet at the base; context white, staining dark olivaceous where bruised. Odor fruity and similar to unripe apples, taste not recorded. Basidiospores 14–16(–19.5) × 9–10.5(–11) μm, mostly ovate, bilaterally symmetrical, wall covered by coarse warts, warts larger toward the apical portion. Spores yellowish brown in KOH, apiculus present. Basidia 2-spored or 4-spored with sterigmata 4 – 5.5 μm long. Pileipellis hyphae 8–11(–17) μm wide, hyaline, with clamp connections. *Holotype*: ARGENTINA. NEUQUEN: On Cerro Cortinario, Puerto Manzano, under *N. pumilio*, 16 Mar 1963, *E. Horak* (IB 63/71).

Notes: The above description is modified from Horak and Moser (1965). *Cortinarius glabriceps* is known only from the type collected in northern Patagonia. We were unable to examine the type specimen and have found no recent collections that match the description of this species. *Cortinarius glabriceps* is apparently distinctive due to the glutinous surface and fruity smell of the fruiting bodies along with the bilaterally symmetrical spores.

Cortinarius subalbidus (A.H. Sm.) Peintner & M.M. Moser, Mycotaxon 81:182. 2002.

≡ *Thaxterogaster subalbidus* A.H. Sm., Madroño 17:24. 1963.

Basidiomata 10–20 × 10–15 mm high (based on dried material), secotioid. Pileus lavender white ("violet blue" based on Thaxter's field notes [Halling 1981]), becoming whitish when dry; surface smooth and silky; irregularly globose to convex; margin either connected to the stipe or free in places and exposing the fertile tissue. Hymenophore of minute chambers nearly filled with spores; dingy cinnamon brown. Stipe 10–15 × 5–7 mm, well developed, solid, percurrent; surface whitish, the interior slightly darker, extending well below the lower margin of the pileus. Odor and taste not recorded.

Basidiospores 10–13 × 6–8 μm, elliptical, with short sterigmata, very minutely warty, wrinkled to punctate-roughened, almost smooth, pale cinnamon in KOH. Basidia 28 –33 × 8–10 μm, 4-spored, hyaline in KOH. Cystidia absent. Pileipellis composed of appressed, hya-line, smooth, thin-walled hyphae that are 2–3 μm wide; context slightly yellowish in KOH. Clamp connections present.

Reference specimen: CHILE. PUNTA ARENAS: 5 Mar 1906, *R. Thaxter Fungi Hypogeus No. 4* (**holotype** FH4585).

Notes: The description above is modified from Singer and Smith (1963). Unlike most other secotioid *Cortinarius* from Patagonia, *C. subalbidus* is character-ized by the almost completely smooth spores. The only other species with spores that appear smooth when viewed under LM is the newly described taxon, *C. quadrisporus*. However, this species differs from *C. subalbidus* by the silvery white pileus (without lavender coloration) and the spores that are released from the basidia in tetrads. The holotype of *C. subalbidus* is a portion of "Fungi Hypogeus No. 4" that was collected by R. Thaxter and deposited at FH. This species was synonymized with *Thaxterogaster magellanicum* (*Cortinarius fuegianus*) by Horak (1979). However, Halling (1981) revised the Patagonian specimens col-lected by Thaxter and found obvious differences in spore ornamentation between *C. subalbidus* and *C. fuegianus*. Our analyses of *C. fuegianus* (EN165, EN266, FK14001, LSD2380) and *C. subalbidus* (FH4585) collections, in addition to Singer's analysis of *C. fuegianus* deposited at LIL (LIL-M423), confirm the differences between these species. Unfortunately, we have not located any new specimens of *C. subalbidus* among our recent collections.

Doubtful taxa

Cortinarius brachyspermus Peintner & M.M. Moser, Mycotaxon 81:178. 2002.

≡ *Thaxterogaster brevisporus* Singer, Persoonia 1:386. 1960.

Holotype: ARGENTINA. RIO NEGRO: Nahuel Huapi National Park, Los Cantaros, 15 Mar 1959, *Singer M1817* (LIL).

Notes: Thaxterogaster brevisporus was transfered to *Cortinarius* by Peintner et al. (2002) without any

morphological or molecular analysis. We analyzed the type specimen at LIL (M1817) and determined that Singer's type does not match the original description by Singer (1960). The original description and drawings by Singer (1960) depict spores with isolated and anastomosing warts forming short ridges and a narrow apiculus that is tightly fused to the sterigma and is only recognizable by the septum. However, our analysis of the type specimen revealed coarsely verrucose spores with columnar warts and a broadened apiculus characteristic of most fully sequestrate *Cortinarius*. Because the type material at LIL is in poor condition and does not match well with the original description, we are unable to interpret the identity of this taxon. It is possible that Singer accidentally accessioned the wrong specimen or there may have been an error during curation of the specimen. Regardless, due to the confusion regarding the type specimen, we must treat *Cortinarius brachyspermus* as a nomen dubidum. Accordingly, *Cortinarius brachyspermus* is not treated in the key below.

Excluded taxa.—Here, we provide brief comments on two species of sequestrate *Cortinarius* that were described by Raithelhuber (1983) as well as the agaricoid taxon *Cortinarius nothofagi* that was originally described as *Thaxterogaster nothofagi*. The publication by Raithelhuber (1983) is challenging to obtain and provides limited information on the morphology of the two sequestrate taxa. Unfortunately, we have been unable to locate the type specimens. However, we include comments about what is known about these species in hopes that the type specimens or fresh collections may become available for study in the future.

Cortinarius cabrinii (Raithelh.) Peintner & M.M. Moser, Mycotaxon 81:178. 2002.

≡ *Thaxterogaster cabrinii* Raithelh. Metrodiana, Sonderheft 2:21. 1983.

Holotype: ARGENTINA. RIO NEGRO: Bariloche, Cerro Otto, 2 Feb 1974, *J. Raithelhuber 42-49* (herbarium not cited).

Notes: Cortinarius cabrinii was originally described as *Thaxterogaster cabrinii* by Raithelhuber (1983), a secotioid species with a firm and well-developed white stipe, ochraceous pileus, white context, and amygdaliform spores 12.5–15 × 6–7.5 μm. Unfortunately, we were unable to locate the type specimen. Raithelhuber (1983) cites the type specimen in a brief Latin description without any supporting illustrations. The type specimen is presumably located with Raithelhuber's other collections in Switzerland or Germany (the type is cited as "in herb. Raith. conserv." but no institution was provided). *Cortinarius cabrinii* is very similar to, if not

conspecific with, *C. janthinocaulis* treated above. The spores of *C. janthinocaulis* are similar in size and shape to those described for *C. cabrinii* and both share a brown pileus and a notably lighter stipe color. Both type specimens were collected near Bariloche, Argentina. However, the spores of *C. cabrinii* are reported as smooth, whereas those of *C. janthinocaulis* are distinctly verrucose.

Cortinarius luteocarnosus (Raithelh.) Peintner & M.M. Moser, Mycotaxon 81:178. 2002.

≡ *Thaxterogaster luteocarnosus* Raithelh., Metrodiana, Sonderheft 2: 21. 1983 [as "*luteocarnosum*"].

Holotype: ARGENTINA. RIO NEGRO: Bariloche, Villa Tacul, 9 Feb 1974, *J. Raithelhuber 4260* (herbarium not cited).

Notes: Cortinarius luteocarnosus was originally described as *Thaxterogaster luteocarnosum* by Raithelhuber (1983), a secotioid species with a yellowish white stipe, dark olivaceous pileus, yellowish context, and elliptical spores 9–12 × 6–7.5 μm. Similar to *C. cabrinii* above, we were unable to locate the type specimen, and the species is difficult to interpret because of the brief description and lack of illustrations (Raithelhuber 1983). The superficial similarity of this species to the many other Patagonian secotioid *Cortinarius* makes it challenging to determine its identity without further morphological and potentially molecular analyses of the type specimen.

Cortinarius nothofagi (E. Horak) E. Horak, Fl Criptog Tierra del Fuego 11:452. 1980.

≡ *Thaxterogaster nothofagi* E. Horak, Nova Hedwigia 10:238. 1965.

Holotype: ARGENTINA. TIERRA DEL FUEGO: Depto. Ushuaia, Lapataia, 3 Mar 1963, *E. Horak* (ZT 64/20).

Notes: Cortinarius nothofagi was originally described as *Thaxterogaster nothofagi* by Horak and Moser (1965) due to the presence of partially anastomosed lamellae. However, the species is epigeous and distinct from the secotioid and fully gasteroid species that are presented above. Horak (1979) recognized the species was morphologically more similar to typical agaricoid forms of *Cortinarius* and therefore transferred the species to *Cortinarius*. We have not re-collected this taxon.

KEY TO SPECIES OF SEQUESTRATE *CORTINARIUS* FROM PATAGONIA

1. Hymenophore enclosed at all times, never exposed, stipe absent but in some cases with a small basal attachment; hypogeous... 2

1′. Hymenophore exposed at some stage of maturity, stipe well developed or slightly reduced, lamellae chambered or anastomosed; epigeous, slightly erumpent, or subhypogeous.................................... 5

2. Spores fusiform to lemoniform with low, connected warts but with smooth apices, 8.5–10.5 × 4–5 μm; with a prominent universal veil that often remains at maturity.................................... *C. galbus*, sp. nov.

2′. Spores globose to subglobose with conical warts usually blunt at the apex, >10 μm long; if present, the universal veil is not prominent and does not often remain at maturity.. 3

3. Pileus surface translucent in appearance, white to whitish yellow with lilac tints; spores 14.5–19.5 × 13–17 μm... *C. translucidus*

3′. Pileus surface opaque, pale yellow to bright yellowish brown or brownish orange, sometimes with lilac tints; spores smaller than above............................. 4

4. Pileus light yellow-brown, pileipellis of three distinct layers, spores 9.5–14.5 × 8–14.5 μm... *C. flavopurpureus*

4′. Pileus orange-brown, pileipellis a single layer of irregular to cylindrical hyphae, spores 11–17.5 × 9–13.5 μm... *C. infrequens*

5. Stipe reduced; hymenophore composed of chambers, mostly enclosed; typically subhypogeous.... 6

5′. Stipe typically well developed; hymenophore composed of chambers or anastomosed lamellae, exposed at maturity; typically epigeous 7

6. Pileus whitish lilac to light grayish white; spores ovate to elliptical, 13–20 × 8–10 μm .... *C. holojanthinus*

6′. Pileus brownish, purplish to vinaceous brown; spores globose to subglobose, 13–17.5 × 10–17.5 μm... *C. nahuelhuapensis*

7. Spore width typically 7 μm or less......................... 8

7′. Spore width typically greater than 7 μm 11

8. Hymenophore composed of anastomosed lamellae 9

8′. Hymenophore composed of chambers 10

9. Pileus not fully expanding; white to grayish white, silky to waxy; spores 8–11 × 5–6 μm .... *C. albocanus*

9′. Pileus completely expanding; clay brown with lilac tints, translucent; spores 9–11 × 5.5–6.5 μm... *C. cretaceus*

10. Spores mostly 7–9(–11) × 4–4.5 μm and weakly verrucose; mostly elliptical, grouped in tetrads.................................... *C. quadrisporus*, sp. nov.

10′. Spores mostly 8–10.5 × 5.5–7 μm and coarsely verrucose; elliptical or amygdaliform (some sublemoniform), not grouped in tetrads....... *C. sphaerocephalus*

11. Spores lemoniform with a well-developed rostrum (12–15 × 7–8 μm), with coarse coalescent verrucae fusing to resemble an episporium; known only from southern Patagonia......................... *C. fragilis*

11′. Spores not lemoniform or with a well-developed rostrum, spore ornaments not strongly fused to form an episporium; known from southern or northern Patagonia 12

12. Spores lacrymoid and highly ornamented with coarse pointy warts.. *C. mustella*

12′. Spores ovate, elliptical, or amygdaliform but not lacrymoid, spores may be ornamented but not with coarse pointy warts 13

13. Basidiomata notably reddish in color, often with a pink to reddish cortina that leaves a reddish brown ring on the stipe; spores elliptical to amygdaliform, ornamented with small warts .... *C. carneoroseus*

13′. Basidiomata not primarily red in color (but may have some reddish tones); spores not as above.. 14

14. Both pileus and stipe extremely glutinous or slimy when fresh 15

14′. Pileus dry to somewhat glutinous, stipe always dry.. 16

15. Basidiomata white; stipe claviform to bulbous.. *C. glutinopallens*

15′. Basidiomata yellowish when young; stipe highly variable, from reduced to cylindrical with a marginate base.. *C. gloiodes*

16. Pileus and basidiomata flesh primarily white in color with some lilac tones when young, stipe notably wide (at least 15 mm wide), spores up to 17.5 μm long; known only from southern Patagonia .... *C. fuegianus*

16′. Pileus not white at maturity stipe typically narrow (less than 15 mm wide), spores always less than 16 μm long; known from southern or northern Patagonia 17

17. Stipe equal or shorter than the height of the columella; smell fruity when fresh but fishy when dry.. *C. dombeyi*

17′. Stipe longer than the height of the columella...... 18

18. Pileus dry; mostly associated with *N. pumilio*.. *C. dibaphoides*

18′. Pileus viscid; may be associated with various species of Nothofagaceae 19

19. Partial veil white, any violet tones in the stipe restricted to the apical portion; widespread and locally common during summer (Dec) through fall (May), with various Nothofagaceae hosts.. *C. tympanicus*

19′. Partial veil ochre, lower half of the stipe violet when young; a rare species that has been recently collected in spring (Nov) and summer (Jan), primarily or exclusively with *Nothofagus pumilio* .... *C. janthinocaulis*

DISCUSSION

This study provides insight into the morphology and the phylogenetic affinities of 18 described species of sequestrate *Cortinarius*, as well as two newly described taxa, *C. galbus* and *C. quadrisporus*. We also identified four additional lineages that appear to constitute undescribed species (*Cortinarius* species 1–4 in FIG. 10; see below). In total, DNA sequences are provided for 24 sequestrate *Cortinarius* species from Patagonia. We also discuss six described species whose identities remain unclear or that have not been recently collected and that require further study in the future. Our ITS + 28S phylogeny allowed us to effectively differentiate species within *Cortinarius*, as previously shown by Garnica et al. (2016), San-Fabian et al. (2018), and others. Our phylogenetic analysis was also sufficient to illustrate the repeated convergent evolution of sequestrate *Cortinarius* species among the southern South America taxa.

The traditional taxonomic structure of *Cortinarius* was conceived mostly based on Northern Hemisphere taxa (Soop et al. 2019). Consequently, further molecular sampling of species from other regions is likely to profoundly change our vision of the evolutionary history of *Cortinarius*. The study by Soop et al. (2019) was based on a large number of globally sampled species and provided a useful framework to understand the taxonomy of *Cortinarius*, including newly defined subgenera, sections, and subsections. However, Patagonian taxa remain poorly integrated because the genus is extremely taxonomically diverse in the region, and verified sequence data outside of the ITS region are available for relatively few epigeous taxa (Truong et al. 2017). Nevertheless, 15 of the sequestrate taxa studied here were assigned to 12 of the sections of *Cortinarius* as defined by Soop et al. (2019). Liimatainen et al. (2020) described several additional new agaricoid taxa from Patagonia, another indication that more sampling is needed for *Cortinarius* in the Southern Hemisphere. Although a few sequestrate Patagonian species (e.g., *C. dombeyi, C. janthinocaulis*, and *C. dibaphoides*) formed a well-supported group, a much more comprehensive data set including numerous agaricoid *Cortinarius* from southern South America is needed to verify whether this group is a monophyletic sequestrate clade or not.

Unfortunately, six described species of sequestrate *Cortinarius* discussed above remain poorly known and will require additional taxonomic and phylogenetic treatment in the future to clarify their identities. Two species, *Cortinarius glabriceps* and *C. subalbidus*, were described with enough detail to include them in our taxonomic key, but we could not find recent collections, photos, or DNA sequences from these species. Another species, *Cortinarius nothofagi*, was described as a *Thaxterogaster* but is not sequestrate and has not been recently collected, so we excluded this species from our taxonomic key. Two additional species, *Cortinarius cabrinii* and *C. luteocarnosus*, are excluded from our analysis and taxonomic key because they are known only from their brief original descriptions that lack illustrations. The type specimens for these species have not yet been located, so their identities remain unclear. Lastly, we discuss *Cortinarius brachyspermus* as a problematic taxon because the type specimen does not match the morphology described by Singer (1960), leaving the identity of this species in doubt.

This study also revealed several putatively undescribed sequestrate taxa that will be treated in future taxonomic works when more material becomes available. These include specimens MVC743 and MVC725 (*Cortinarius* sp. 1), which are grouped together with samples of *Cortinarius* from New Zealand in sect. *Laquelli*. A second poorly known sequestrate species (*Cortinarius* sp. 2) was represented by vouchers MVC600, MES-3388, and MES-3421. Unfortunately, our analysis did not reveal any clear affinity with an existing section of *Cortinarius*, and more work will be needed to fully characterize this new taxon. A third undescribed sequestrate species (*Cortinarius* sp. 3) was represented by several samples (e.g., MES-2640, MES-3288, MES-3359, MES-3374, MES-3433). Sequences from these sporocarps matched ITS sequences derived from ECM root tips previously identified as the "*Nothofagirhiza vinicolor*" ECM morphotype that were identified from forests and nursery habitats by Palfner and Godoy (1996) and Palfner (2001). A final undescribed taxon (*Cortinarius* sp. 4) is known only from a single, brown-staining specimen (MES-527) collected at a remote site in southern Chile. More work is needed to fully characterize these putative new taxa and to ensure that they are novel species.

In Patagonia, consumption of fungi by animals and the ecological importance of this phenomenon for ECM associations in Nothofagaceae forests have been poorly studied. Mycophagy has been reported among native Patagonian rodents (Pérez Calvo et al. 1989), but detail on the dispersal of individual fungal species is rare or nonexistent. More recently, Skewes et al. (2007), Nuñez

et al. (2013), and Soteras et al. (2017) found that the introduced wild boar (*Sus scrofa*) regularly consumes both native and non-native sequestrate fungi in natural and disturbed habitats in Patagonia. However, the relationships among native hypogeous sequestrate fungi and their potential animal vectors in the region remain mostly unknown and deserve to be further studied, particularly given the high diversity of sequestrate fungi in the region.

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