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Taxonomy of *Armillaria* in the Patagonian forests of Argentina

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Abstract: The taxonomy of *Armillaria* in southern South America has received little attention since the work of Singer and others. In this study we examine the morphological traits and cultural features for taxa representing the lineages revealed based on molecular phylogeny, and we link them to previously described taxa based on morphology. Lineages I–IV were identified as *Armillaria novae-zelandiae*, *A. montagnei*, *A. umbrinobrunnea* comb. nov. and *A. sparrei* respectively. They could be differentiated morphologically based on dimension, features of the epicutis, annulus, stipe, hymenophoral trama and flavor and characteristics in culture. Furthermore there was no evidence of host preference for the species recognized. This is the first study integrating the phylogeny and morphology of *Armillaria* species from Patagonia, and it provides a foundation for future research on these fungi in South America.

Key words: *Armillaria luteobubalina*, *Armillaria montagnei*, *Armillaria novae-zelandiae*, *Armillaria sparrei*, rhizomorphs, type studies

INTRODUCTION

Armillaria (Fr. : Fr.) Staude (Tricholomataceae, Agaricales, Basidiomycota) species are important components of forest ecosystems worldwide, where they survive as pathogens or saprotrophs. Some species are pathogens of forestry crops and others damage native forests (Hood et al. 1991, Kile et al. 1991). In temperate, native forests of the Patagonian Andes including Argentina and Chile *Armillaria* spp. have been reported from dead wood and stumps of *Nothofagus* Blume (Singer 1953, 1969; Horak 1979; Garrido 1988) and also have been reported causing root disease in plantations of several exotic *Pinus* species used for commercial timber production (Ramírez et al. 1990).

At least 37 species are recognized in *Armillaria* (Volk and Burdsall 1995, Lima et al. 2008). Of these 11 species have been reported from South America (TABLE I). While the taxonomy and systematics are relatively well elucidated for the species from the northern hemisphere and South Africa, Australia and New Zealand, little is known regarding the taxonomy of the South American taxa. In addition to the work of Spegazzini (1889) and Singer (1953, 1956, 1969, 1970, 1989) few reports pertain to the taxonomy of *Armillaria* species from this continent.

Armillaria is a genus easily recognized by its caespitose habit, annulus and honey-colored basidiocarps. However it is extremely difficult to identify some species due to the lack of morphological apomorphies (Watling et al. 1991, Pegler 2000). In addition basidiocarps often are not available to differentiate species, which further complicates the taxonomy of *Armillaria* (Harrington and Wingfield 1995). In this regard *Armillaria* provides a clear example of a genus where a phylogenetic approach can contribute significantly to its taxonomy.

Phylogenetic methods have made it possible to differentiate lineages of the genus in southern Argentina (Pildain et al. 2009). Lineages I and II grouped respectively with *A. novae-zelandiae* and *A. luteobubalina*. Lineages III and IV represented unique taxa that were closely related to *A. hinnulea* Kile & Watling, *Armillaria* 4th species from New Zealand (established by Coetzee et al. 2001) and *Armillaria* Group III from Kenya (Mwenje et al. 2006). Once the lineages had been determined we focused on the recognition of morphological characters to describe the taxa. The aim of this study consequently was to characterize the morphology of sporocarps linked to the four DNA-based phylogenetic lineages.

MATERIALS AND METHODS

Study area and isolates.—A total of 57 *Armillaria* specimens were collected in protected areas of native *Nothofagus*-dominated forests from continental Patagonia, Argentina, in Chubut, Río Negro and Neuquén provinces. A few additional collections were made in *Pseudotsuga menziesii* (Mir.) Franco and *Pinus radiata* D. Don plantations in the

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TABLE I. *Armillaria* species described and reported from South America (reference to *Armillaria* taxa as *A. mellea* not included)

Armillaria species/publication year	Reported locations in South America	Reported hosts in South America	References
Patagonian taxa			
A. montagnei (Singer) Herink/1956	ARGENTINA: Patagonian Andes, from Neuquén to Tierra del Fuego provinces CHILE: Southern part (Valdivia to Magallanes)	*Nothofagus dombeyi*, myrtaceous trees	Singer 1969, 1970; Horak 1979; Garrido 1988; Wright and Deschamps 1992; Valenzuela 1993
A. montagnei (Singer) Herink var. *umbrinobrunnea* Singer/1956	ARGENTINA: Patagonian Andes including provinces of Neuquén and Río Negro	*Nothofagus dombeyi*, myrtaceous trees	Singer 1969, 1970
A. sparrei (Singer) Herink/1956	ARGENTINA: Patagonian Andes, Neuquén Province. CHILE: Southern part (Valdivia to Magallanes)	*Aextoxicum* sp., *Drimys* sp., *Nothofagus* spp., *Saxegothaea* sp., *Pinus radiata*	Singer 1969, 1970; Garrido 1988; Valenzuela 1993
A. novae-zelandiae (G. Stev.) Herink/1964	ARGENTINA: Patagonian Andes (Neuquén) and Buenos Aires Province CHILE: Isla Grande de Chiloé	*Salix* sp., *Nothofagus* spp.	Singer 1969; Coetzee et al. 2003
A. limonea (G. Stev.) Boesew./1964	ARGENTINA: Tierra del Fuego. CHILE: Magallanes, Valdivia	*Nothofagus* spp.	Singer 1969; Horak 1979
A. sparrei (Singer) Herink var. *elaeodes* Singer/1969	ARGENTINA: Patagonian Andes including provinces of Río Negro, Neuquén, Chubut and Tierra del Fuego. CHILE: Juan Fernandez, Valdivia	*Aextoxicum* sp., *Drimys* sp., *Nothofagus* spp., *Nothomyrcia* sp., *Saxegothaea* sp.	Singer 1969, 1970.
A. griseomellea (Singer) Kile & Watling/1969	CHILE: Valdivia	*Aextoxicon* sp., *Cryptocarya alba*, *Persea lingue*	Garrido 1988
A. luteobubalina Watling & Kile/1978	ARGENTINA: Neuquén Province. CHILE: Temuco.	*Nothofagus* spp., *Pinus radiata*	Coetzee et al. 2003
Extra Patagonian taxa			
A. procera Speg./1889	ARGENTINA: Buenos Aires Province. BRASIL: São Pablo. CHILE: Santiago, Valparaiso	*Salix humboldtiana*	Singer 1970
A. puiggarii Speg./1889	ARGENTINA: Tucumán Province. BOLIVIA: La Paz. BRASIL: Rio Grande do Sul, São Paulo, Sao Leopoldo	*Sambucus* sp., *Alnus* sp., *Allophylus* sp.	Singer 1970; Wright and Albertó 2002
A. tigrensis (Singer) Volk & Burdsall/1970	ARGENTINA: Buenos Aires Province	*Salix humboldtiana*	Singer 1970; Raithelhuber 1983
A. yungensis (Singer) Herink/1970	ARGENTINA: Buenos Aires Province. BOLIVIA: La Paz	Dead dicotyledonous wood	Singer 1970; Raithelhuber 1983
A. paulensis Capelari/2008	BRASIL: São Paulo state	Undetermined angiosperm tree	Lima et al. 2008

ecotone between Andean forests and Patagonian steppe. Thirty-two isolates that were used in the phylogenetic study of Pildain et al. (2009) were included for reference purposes, and the previous study also provided a map of collection sites.

Study of materials.—Most specimens were photographed in situ or in the laboratory while fresh. Conspicuous macroscopic features (i.e. flavor, size of the structures, pileus color, texture, annulus features, stipe morphology and color, color and form of the gills) of the basidiomes were annotated and/or measured. Spore prints were obtained on glass or acetate slides and kept for measurement and statistical treatment of spore dimensions. Colors were characterized with the reference charts of Munsell (1990). Fifty-eight polyspore isolates were obtained from fresh spore prints and maintained on 2% MEA. Specimens were dried overnight and kept at the Pathology Herbarium, Centro Forestal CIEFAP, for microscopic examination. Representative specimens of each species also were deposited at BAFC. Reference material and type specimens were obtained from herbaria LIL, BAFC, K, DAR and PDD (acronyms following Holmgren et al. 1990) and examined. Specimens from FRI were not available for this study. Microscopic features, such as spore shape and size, anatomy of the gills trama, hyphal septation, cystidia and basidia, were measured.

Culture studies.—Two methods were used to characterize the culture morphology of the isolates growing in 90 mm diam Petri dishes. Isolates were grown on 3% MEA for 21 d at 23 C with a 24 h photoperiod provided by cool, white fluorescent tubes (Hood and Sandberg 1987). Isolates also were grown on dextrose (2%) malt (3%) peptone (0.5%) agar (1.9%) medium 15 d at 25 C in the dark (Shaw et al. 1981). After 3 wk the rhizomorphs were characterized based on morphology, including the aspect of the aerial mat, rhizomorph surface features, type of branching, presence and color of the mycelium, growth speed, anticlinal vs. periclinal ending of the tips and number of tips per quadrant in a Petri dish.

RESULTS

Basidiome morphology.—A number of morphological characters of the basidiomes were found that are diagnostic for the four phylogenetic lineages for *Armillaria* spp. from Argentina (TABLE II). The main features that distinguished Lineage I were the olivaceous pileus surfaces coupled with basidiospores shorter than 9 µm. The species representing Lineage II produced medium to large basidiocarps with incurved pilei and a thick annulus with squamules. Those of Lineage III had strongly astringent basidiomes with intensively squamulose pilei. The species representing Lineage IV was characterized by bulbose stipes and large basidiocarps with a viscid pileus surface.

Characteristics in culture.—Isolates representing the lineages could be distinguished from each other based on their growth, morphology of the mycelial mats, morphology and branching patterns of the rhizomorphs and growth rate (TABLE II). The preferred medium from culture observation was dextrose-malt-peptone-agar medium. The colonies of Lineage I isolates had a brown crustose mycelium at the center of inoculum plug, which was surrounded by fluffy white surface mycelium (FIG. 1A). Rhizomorphs were cylindrical, with dichotomous branches at their tips and smooth, narrow, mycelial sheaths, similar to characteristics described for *A. novae-zelandiae* (Shaw et al. 1981). Anticlinal aerial endings of the rhizomorphs were present. The isolates covered the Petri dishes in 4–5 wk (FIG. 1A).

Lineage II strains developed a cottony surface mycelium with abundant dark chestnut, crustaceous areas. Rhizomorphs were applanate in section, with a crêpe-like (accordion-like) morphology, similar to that described for *A. luteobubalina* (Podger et al. 1978). Branching of the rhizomorphs was irregular and distant, with a wide, surrounding mycelial sheath. An average of six rhizomorph tips per quadrant were recorded. Isolates in this lineage grew fastest, covering the surface of a Petri dish in 3 wk (FIG. 1B).

The culture morphology of isolates belonging to Lineage III was similar to that of isolates in Lineage II but with smaller amounts of brown crustose mycelium. Rhizomorphs were cylindrical or applanate, smooth, branched but not strictly dichotomous, and had a narrow mycelial sheath. Anticlinal aerial endings of rhizomorphs were present, and 15 rhizomorph tips per quadrant were recorded. Mycelial growth covered the Petri dish in 4–5 wk (FIG. 1C).

Lineage IV strains developed a mat-like morphology similar to those in Lineage II but with brown liquid droplets on the surface. Rhizomorphs were applanate, smooth, heavily branched, and they had a narrow and unabundant mycelial sheath. Nineteen rhizomorph tips per quadrant were recorded. Lineage IV strains had the slowest growth, covering 50% of the Petri dish in 4 wk (FIG. 1D).

For strains belonging to lineages I and II, taxa having culturally consistent features were available (see above). However for strains in lineages III and IV, which corresponded to taxa restricted to Patagonia (see below), no references and no other literature from the southern hemisphere was available with which they could be compared.

The gross morphological characteristics of the basidiomes and those of the cultures for these fungi reflect four distinct taxa in *Armillaria* that are consistent with the four phylogenetic lineages emerging from DNA sequence comparisons. These four species are *A. novae-zelandiae*, *A. montagnei*, *A.*

TABLE II. Morphological differences among *Armillaria* lineages from Patagonia

	Lineage I	Lineage II	Lineage III	Lineage IV
Basidioma size	S, M (2–6 cm)	M, L (4–8 cm)	S, M (1.5–5 cm)	M, L (3.5 – up to 10 cm)
Flavor of context	Mild	Sharp and acidic	Strongly sharp and acidic	Very slightly acidic
Pileus	Olivaceous-gray. Incurve margins	Beige-light brown and dark brown in the center, with seriate margins. Umbonate, margins remarkable incurve	Beige-light brown, squamules conspicuous in all surfaces. Slightly incurve margins	Beige-light brown, pubescent in the center. Convex, flattened
Epicutis	Not viscid	Not viscid	Not viscid	Viscid
Annulus	Simple, membranaceous; when dried torn up/vestigial. Without squamules underneath	Prominent, thick and persistent, with brown squamules underneath	Simple, membranaceous; when dried torn up/ vestigial. With brown squamules underneath	Simple, membranaceous; when dried torn up/vestigial. With brown squamules underneath
Stipe	Cylindrical, robust, someone with bulbose base	Cylindrical, robust	Cylindrical	Bulbose stipe thinning upward, long and stylized
Spores	Small, ≤ 9 μm. (6)7–8.5(10) × (4.5)5–6.5(7) μm	Long, ≥ 9 μm. (8)9.5–11(12) × (5)5.5–7(8.5) μm	Long, ≥ 9 μm. (7)9–11(13) × (5)5–6.5 (7) μm	Long, ≥ 9 μm. (7)8.5–11(12) × (4)5–6.5(7) μm
Q = L − W	≤ 2	≥ 3	≤ 2	≤ 2
Spore print	Pure white	Pure white	Pure white	Pure white
Hymenophoral trama	Divergent/subdivergent	Regular, 'lacunar'	Regular, 'lacunar'	Divergent/subdivergent
Growth on malt-peptone	Mycelium cottony; rhizomorphs cilindrical, with dichotomous branches in the tips, smooth, surrounding mycelial sheath narrow; anticlinal aerial endings of rhizomorphs; average of tips per quadrant = 7	Fast growth; mycelium cottony with dark-chestnut crustaceous areas; rhizomorphs applanate in section, with crèpe-like, irregular surface; irregularly branched, branches distant; average of tips per quadrant = 6; surrounding mycelial sheath wide.	Rhizomorphs cylindrical or applanate, smooth, branched but not strictly dichotomous, surrounding mycelial sheath narrow; anticlinal aerial endings of rhizomorphs; average of tips per quadrant = 15	Slow growth; aerial mycelium present and cottony, with dark chestnut crustose area; rhizomorphs applanate, smooth, intensely branched, mycelial sheath narrow and scarce; average of tips per quadrant = 19

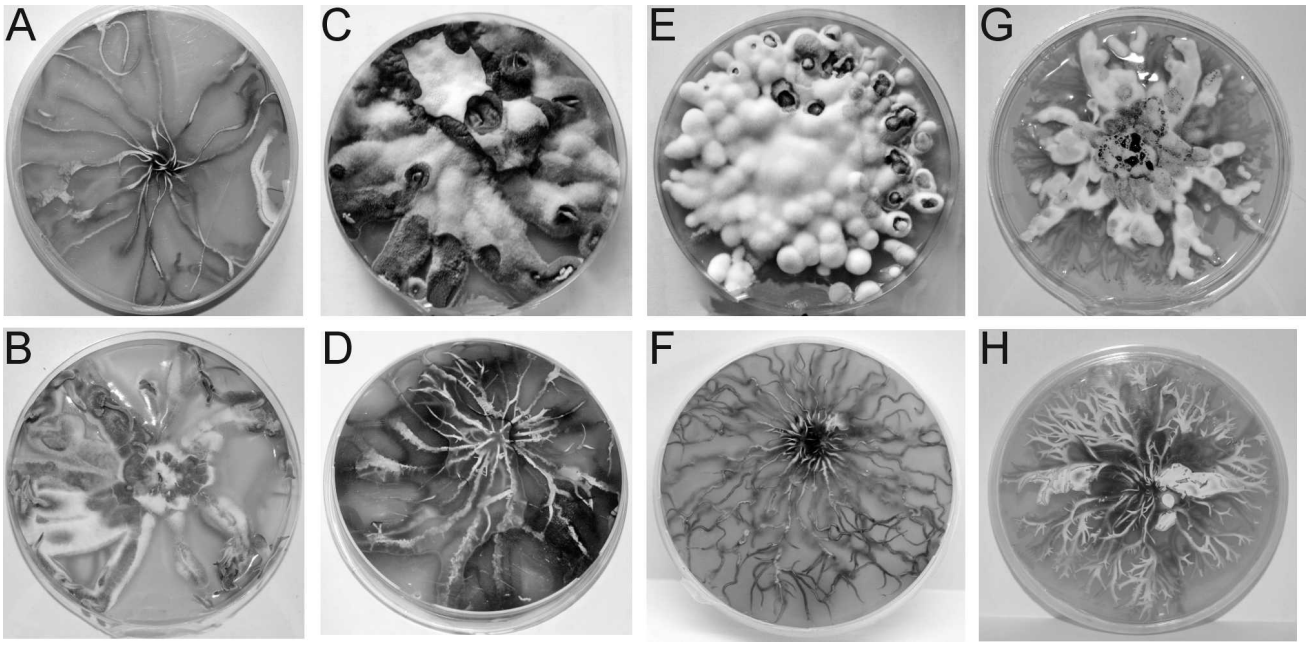

FIG. 1. Culture morphology of isolates representing *Armillaria* Lineages I–IV and species from Patagonia, Argentina, after 5–6 wk growth. A, B. Lineage I (*Armillaria novae-zelandiae*, strain 57). C, D. Lineage II (*A. montagnei*, strain 309). E, F. Lineage III (*A. umbrinnobrunnea*, strain 29). G, H. Lineage IV (*A. sparrei*, strain 40). B, C, E, G show cultures seen from the top, and A, D, F, H represent the same cultures viewed from the bottom of Petri dishes.

umbrinobrunnea and *A. sparrei*, representing respectively lineages I–IV. The next section provides detailed morphological characteristics of the species from Patagonia as well as information regarding the collections and a key to the species.

TAXONOMY

Armillaria novae-zelandiae Stevenson, Kew Bull. 19:14, 1964 (K!) FIG. 2A, B

= *Armillariella sparrei* Singer var. *elaeodes* Singer, Mycoflora australis pg. 45, 1969 (LIL!).

In Patagonia this species is characterized by small to medium size basidiomes, 20–60 mm diam., with cylindrical and robust stipes and mild flavor when fresh (FIG. 2A, B). The pileus surface is dry, light olivaceous-gray (5Y6/2) at the center and olive brown (2.5Y4/3) at the margin, with abundant to scarce pubescence. The annulus is inconspicuous, membranaceous and when dried torn up and vestigial, without forming squamules below the surface. Lamellae are subdecurrent, with lines running down in the apex of the stipe, white to pallid, with lamellulae. Basidia are 2–4-spored, 35.5–39(–46) × 8–9(–10) µm; cheilocystidia are predominantly clavate; basidiospores (6–)7–8.5(–10) × (4.5–)5–6.5(–7) µm. The trama is made up of divergent to subdivergent hyphae.

Specimens examined. ARGENTINA. CHUBUT: *Nothofagus dombeyi* (Mirb) Blume, 10 May 1996, leg. *R. Petersen RP8306* (TENN054984). NEUQUÉN: Villa la Angostura, Bahía Manzano, *Nothofagus dombeyi*, 18 May 1952, leg. *R. Singer M741*, (HOLOTYPE of *Armillaria sparrei* var. *elaeodes*, LIL); Villa la Angostura, Nahuel Huapí National Park, Península Quetrihué, *Nothofagus dombeyi*, 18 May 1952, leg. *R. Singer M514*, (LIL, duplic. BAFC 22385; specimen recorded as *Armillaria sparrei* by Singer [1956] and as *Armillaria novae-zelandiae* by Singer [1969]); Nahuel Huapí National Park, Península Quetrihué, *Nothofagus* sp., 14 May 1996, leg. *R. Petersen RP8367*, (TENN055039); Lanín National Park, Chachin Waterfall Walk, *Nothofagus dombeyi*, 17 May 2007, *M.B. Pildain* and *M. Rajchenberg* Arg49 (BAFC51701); Lanín National Park, Chachin Waterfall Walk, *Nothofagus alpina* (Poepp. et Endl.) Oerst., 17 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg52* (BAFC51660); Lanín National Park, Quechuquina farm, *Pseudotsuga menziesii*, 17 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg53* (BAFC51702); Lanín National Park, Quillén lake coast, *Nothofagus obliqua* (Mirb) Blume, 18 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg55* (BAFC51703); Lanín National Park, Quillén Lake shore, *Nothofagus obliqua*, 18 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg56* (BAFC51659); Lanín National Park, Quechuquina farm, *Pseudotsuga menziesii*, 19 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg57* (BAFC51704). RÍO NEGRO: Nahuel Huapí National Park, Isla Victoria, *Pinus radiata*, 10 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg46* (BAFC51705). AUSTRALIA. TASMANIA: Lyrebird Nature Walk, Mount Field National Park, on wood, 30 Apr 2002, leg. *G. Gates*, *D. Ratkowsky* and *B. Gasparini 0645*; nr. Collinsvale, Myrtle Forest Creek, on wood, 6 Mar 2003, leg. *G. Gates* and *D. Ratkowsky 0644*; nr. Collinsvale, Myrtle Forest Creek, on wood, 1 Jul 2003, leg. *G.*

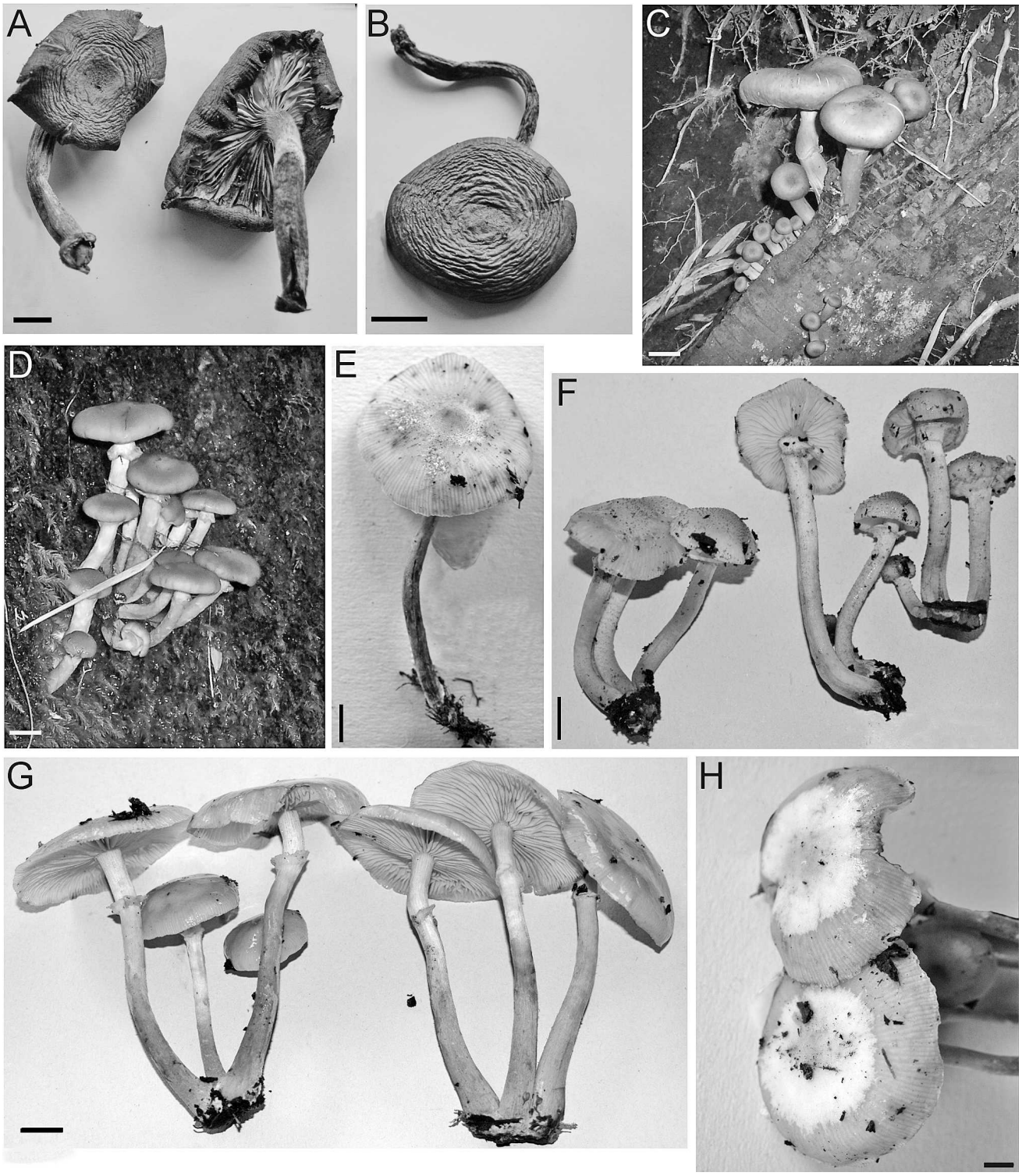

FIG. 2. Basidiocarp morphology of lineages I–IV and species from Patagonia. A, B. Lineage I (*Armillaria novae-zelandiae*, strain 57). C, D. Lineage II (*A. montagnei*, strain 309). E, F. Lineage III (*A. umbrinnobrunnea*, strain 29). G, H. Lineage IV (*A. sparrei*, strain 40). Bars = 1 cm.

Gates and *D. Ratkowsky* WR046. NEW ZEALAND. EASTBOURNE: Wellington, fallen timber, 4 May 1949, leg. *Stevenson 629* (HOLOTYPE of *Armillaria novae-*zelandiae, K).

Commentary. The combination of an olivaceous-gray pileus, which persists after drying, and spores smaller than 9 µm long are diagnostic for this taxon vis-à-vis other *Armillaria* specimens found in Patagonia. The holotype from New Zealand differs from the Patagonian collections in having a distinct bulbose and darkened base, but this feature seems variable because it was not found in all specimens studied (except Arg57), including the reference material (see above).

Armillariella sparrei var. *elaeodes* was found to be morphologically similar to *A. novae-zelandiae*, and we consider the species as synonyms. The former species was referred to *Armillaria* sp. A by Singer (1970) who grouped it with *A. novaezelandiae*. Strains of *A. novae-zelandiae* from Patagonia were included in the ''*novae-zelandiae clade*'' by Pildain et al. (2009) as Lineage I. This clade had substructure with four subclades, each corresponding to geographically different areas. Strains from Patagonia grouped together and apart from those of other geographic regions in a well supported clade, suggesting the possibility that they represent a distinct taxon. However, based on morphology (olivaceous-gray pileus, spores smaller than 9 µm long), they are similar to specimens from New Zealand and additional evidence is necessary before describing new species in this group.

Armillaria montagnei (Singer) Herink, Sympozium o Václavce Obecné *Armillaria mellea* (Vahl ex Fr.) Kumm. (Brno): 41 (1973) FIG. 2C, D

Armillariella montagnei Singer, Lloydia 19:182, 1956.

=? *Armillaria luteobubalina* Watling & Kile, Trans. Br. Mycol. Soc. 71:79, 1978.

Basidiocarps astringent, medium to large, 40–81 mm diam, with an umbonate pileus and a cylindrical and robust stipe. Pileus surface dry, nonviscid, dark brown to olive melleous (7.5YR4/4–10YR4/6), with a lime zone in the middle (10YR7/4), pileus covered with abundant, small squamules, becoming smooth with age with fewer squamules, beige toward the margin, which is striated (FIG. 2C, D). Annulus thick, persistent, developing brown squamules underneath. Lamellae subdecurrent with lines running down from the apex of the stipe, white to pallid, with lamellulae. Basidia 2–4-spored, 37–41(–46) × 6–7(–8) µm; cheilocystidia clavate; basidiospores (8–)9.5–11(–12) × (5–)5.5–7(–8.5) µm, with a Q (L − W) ≥ 3. Dissepiments are regular, with a lacunar appearance.

Specimens examined. ARGENTINA. CHUBUT: Los Alerces National Park, east shore of Menendez lake, *Nothofagus* sp., 7 Sep 1997, leg. *R. Petersen RP8329*, (TENN055003); Futaleufú, La 106 Farm, *Nothofagus antarctica* (G. Forst) Oerst., 23 Apr1999, leg. *M. Rajchenberg 143* (BAFC51706); Futaleufú, Baggilt Provintial Reserve, Baggilt Lake shore, *Nothofagus pumilio* (Poepp. & Endl.) Krasser, 23 Apr1999, leg. *M. Rajchenberg 270* (BAFC51662). NEUQUÉN: Nahuel Huapí National Park, Península Quetrihué, *Nothofagus dombeyi*, 31 Mar1980, leg. *I. Gamundi* and *E. Horak* (LPS); Lanín National Park, Lácar Lake shore, *Nothofagus obliqua*, 31 Mar1980, leg. *I. Gamundi* and *E. Horak* (LPS); Villa la Angostura, *Nothofagus dombeyi*, 16 May1996, leg. *R. Petersen RP8377* (TENN055049); Nahuel Huapí National Park, Puerto Blest, track to Los Cántaros, *Nothofagus dombeyi*, 6 May 1999, leg. *M. Rajchenberg 272* (BAFC51707); Lanín National Park, Lácar Lake shore, *Nothofagus obliqua*, 19 May 1999, leg. *M. Rajchenberg 281* (BAFC51661). RÍO NEGRO: Bariloche, Lla Llao Hotel, north end of Municipal Park track, *Nothofagus* sp., 15 May 1999, leg. *R. Petersen RP8371* (TENN055043); Nahuel Huapí National Park, Nahuel Huapí Lake shore, *Nothofagus dombeyi*, May 2005, leg. *M. Rajchenberg 309* (BAFC51708); Nahuel Huapí National Park, Nahuel Huapí Lake shore, *Nothofagus dombeyi*, leg. *M. Rajchenberg 311* (BAFC51709), 5.2005. Tierra del Fuego, Lapataia, *Nothofagus pumilio*, 14 Mar 1975, leg. *E. Horak* (LPS). CHILE. MAGALLANES: Puerto Natales, Río Rubens, *Nothofagus pumilio*, 23 Mar 1963, leg. *E. Horak* (LPS). NEW ZEALAND. WELLINGTON: Butterfly, *Nothofagus* sp. 2 Jun 1949, leg. *Stevenson 552* (HOLOTYPE of *Armillaria limonea*, K). AUSTRALIA. VICTORIA: Traralgon, *Eucalyptus regnans*, leg. *G.A. Kile* (ISOTYPE of *A. luteobubalina*, DAR). TASMANIA: between Orford and Copping, Wielangta Long Walk, on wood, 29 May 1999, leg. et det. *G. Gates* and *D. Ratkowsky* (G. Gates pers herbarium); nr. Longford, Woolmers Estate, on *Cupressus macrocarpa* Hartw., 18 May 2006, leg. *N. Tapson W186* (G. Gates pers herbarium).

Commentary. This species is characterized by astringent basidiomes, with pilei heavily covered with squamules and the thick annulus covered by squamules, different from those of other taxa from the area. The spores' Q value is higher than that of the other species from Patagonia. The specimens studied were similar to those of the original description (Singer 1956) and those reported by Wright and Deschamps (1972), Horak (1979), Valenzuela (1993) and Garrido (1988). The type material at LIL appears to have been lost, and a neotype for this species must be selected. We herein designate specimen BAFC51662 as the neotype for *A. montagnei*; other than presenting the typical morphological features of the species, its culture is kept in the CIEFAP and CMW culture collection and its ITS and LSU rDNA regions were incorporated in phylogenetic studies (Pildain et al. 2009). Specimens of *A. luteobubalina* from New Zealand and Australia (Podger et al. 1978) differed from *A. montagnei* in this study by having smaller spores, 6.5–7.5 × 4.5–5.5 µm (*A. montagnei*: 9.5–11 × 5.5–7 µm).

Strains of *A. montagnei* were treated in the ''*luteobubalina* clade'' by Pildain et al. (2009) as Lineage II. This clade had a substructure with two clades that corresponded to geographically different areas, one from Australia the other from southern Argentina. Both subclades are well supported, suggesting that they represent different taxa. We support the distinction of two taxa based on the correlation between phylogenetic and morphological data, principally differences in spore size. Also field observations and unpublished experimental data have shown that the Patagonian *A. montagnei* is not typically recovered from hosts showing severe symptoms of root disease as is known for *A. luteobubalina* (Podger et al. 1978). It is relevant that the description of *A. montagnei* predates that of *A. luteobubalina*; *A. montagnei* thus would have priority if all isolates in the clade were to be treated as a single species (Singer 1956, Podger et al. 1978).

Armillaria umbrinobrunnea (Singer) Pildain & Rajchenb. stat. et comb. nov. FIG. 2E, F

Basionym: *Armillariella montagnei* Singer var. *umbrinobrunnea* Singer, Lloydia 19:183, 1956 (LIL!).

Basidiome flavor strongly sharp and acidic, small to medium size, 15–50 mm diam. Pileus surface beige to light brown (10YR8/3–4) when fresh, and with a dark (10YR3/4), umbrinous (7.5YR4/3) center, characterized by the presence of abundant, relatively large and dense squamules that are homogeneously scattered in the pileus, lacking any pubescence; margin striate. Stipes cylindrical, subbulbose at the base, with a well formed annulus that is membranaceous and becomes vestigial after drying, but with brown squamules underneath (FIG. 2E, F). Lamellae subdecurrent with lines running down the apex of the stipe, white to pallid, with lamellulae. Basidia 38–42(–47) × 7.5–8(–9) μm, cheilocystidia clavate, basidiospores (7–)9–11(–13) × (5–)5–6.5(–7) μm, with a $Q \leq 2$. Trama regular, lacunar (barrel-shape cells) in the middle and eventually hyphal (but never divergent) toward the subhymenium. Squamules formed by hyphae up to 20 μm diam.

Specimens examined. ARGENTINA. CHUBUT: Futaleufú, Baggilt Provintial Reserve, Baggilt Lake shore, *Nothofagus pumilio*, 23 Apr 1999, leg. *M. Rajchenberg 269* (BAFC51664); Los Alerces National Park, Torrecillas Glacier, *Nothofagus dombeyi*, 2 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg21* (BAFC51710); Los Alerces National Park, Sagrario Harbor, *Nothofagus dombeyi*, 2 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg25* (BAFC51711); Los Alerces National Park, Menéndez Lake shore, *Nothofagus dombeyi*, 2 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg29* (BAFC51663). NEUQUÉN: Nahuel Huapí National Park, Península Quetrihué, 14 May 1952, leg. *Singer M596* (HOLOTYPE of *Armillaria montagnei* var. *umbrinobrunnea*, LIL; ISOTYPE at BAFC); Nahuel Huapí National Park, Puerto Blest, track to Los Cántaros, *Nothofagus dombeyi*, 6 May 1999, leg. *M. Rajchenberg 271* (BAFC51712). CHILE. VALDIVIA: Cordillera Pelada, 6 May 1965, leg. *Singer M5553* (BAFC).

Commentary. This is a well characterized taxon within the *Armillaria* complex in southern Argentina, characterized by the abundance and persistence of squamules on the pileus surface. It corresponds morphologically to variety ''*umbrinobrunnea*'' described by Singer (1956); it is a name that has not been reconsidered since its description (cf. Volk and Burdsall 1995). Specimens in this study were identical to the holotype at LIL, and the species corresponds to Lineage III in Pildain et al. (2009). The synonymy of *A. montagnei* var. *umbrinobrunnea* with *A. ostoyae* (Romagnesi) Herink proposed by Garrido (1985) and Watling et al. (1991, under *umbrinolutea*) appears not to be based on the proper study of types and/or reference material. Also the phylogenetic studies did not show any relationship among *A. umbrinobrunnea* isolates and taxa from the northern hemisphere.

Armillaria sparrei (Singer) Herink, Sympozium o Václavce Obecné *Armillaria mellea* (Vahl ex Fr.) Kumm. (Brno): 43 (1973) FIG. 2G, H

= *Armillariella sparrei* Singer, Lloydia 19:183, 1956.

Basidiocarps mild when fresh, becoming sharp and acidic with time, of variable size from medium to large, 35–100 mm diam, rarely smaller. Pileus surface beige to light brown (10YR8/3–4) at the center to reddish-light brown at the margin (5YR5/4–7.5YR6/3), viscid, with few to many squamules at the center, but never abundant, that disappear with age. Stipe long and stylized, distinctly bulbose at the base; annulus poorly developed, membranaceous, becoming turned up or vestigial after drying, not developing squamules in its lower face (FIG. 2G, H). Basidia 38–43(–55) × 8–9(–10) μm; cheilocystidia clavate; basidiospores (7–)8.5–11(–12) × (4–)5–6.5(–7) μm, with a $Q \leq 2$. The trama is hyphal, divergent to subdivergent.

Specimens examined. The holotype at LIL probably was lost. We examined other materials originally included in the description, as indicated below with LIL!. ARGENTINA. CHUBUT: Los Alerces National Park, Puerto Café, *Nothofagus dombeyi*, 18 Apr 2007, *M.B. Pildain* and *M. Rajchenberg Arg5* (BAFC51713); Los Alerces National Park, Menéndez Lake shore, *Nothofagus dombeyi*, 18 Apr 2007, *M.B. Pildain* and *M. Rajchenberg Arg7* (BAFC51714); Los Alerces National Park, Arrayanes River shore, *Nothofagus dombeyi*, 18 Apr 2007, *M.B. Pildain* and *M. Rajchenberg Arg11* (BAFC51715); Los Alerces National Park, Menéndez Lake shore, *Nothofagus dombeyi*, 27 Apr 2007, *M.B. Pildain* and *M. Rajchenberg*

Arg12 (BAFC51716); Los Alerces National Park, Menéndez Lake shore, *Nothofagus dombeyi*, 27 Apr 2007, *M.B. Pildain* and *M. Rajchenberg Arg17* (BAFC51717); Los Alerces National Park, Puerto Sagrario, *Nothofagus dombeyi*, 2 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg26* (BAFC51718); Los Alerces National Park, Puerto Sagrario, *Nothofagus dombeyi*, 2 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg28* (BAFC51719); Los Alerces National Park, Puerto Toro, *Nothofagus dombeyi*, 2 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg30* (BAFC51720). NEUQUÉN: Nahuel Huapí National Park, Península Quetrihué, 13 May 1952, leg. *Singer M514* (LIL!, BAFC) (recorded as *Armillaria sparrei* by Singer [1956] but later as *Armillaria novae-zelandiae* by Singer [1969]); Nahuel Huapí National Park, Península Quetrihué, 14 May 1952, leg. *Singer M577* (LIL!); Villa la Angostura, Puerto Manzano, 22 Mar 1963, leg. *Singer* (BAFC); Lanín National Park, Lácar Lake shore, *Nothofagus dombeyi*, 1995, leg. *M. Rajchenberg 142* (BAFC51721); Nahuel Huapí National Park, Puerto Blest, track to Los Cántaros, *Nothofagus dombeyi*, 7 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg32* (BAFC51722); Nahuel Huapí National Park, Correntoso lake coast, *Nothofagus dombeyi*, 18 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg48* (BAFC51666). RÍO NEGRO: Nahuel Huapí National Park, Puerto Blest, Frías Lake, *Nothofagus dombeyi*, 8 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg40* (BAFC51665); Nahuel Huapí National Park, Puerto Blest, Frías Lake, *Nothofagus dombeyi*, 8 May 2007, leg. *M.B. Pildain* and *M. Rajchenberg Arg44* (BAFC51723); Nahuel Huapí National Park, Puerto Blest, Frías Lake, *Fitzroya cupressoides*, 8 May 2007, *M.B. Pildain* and *M. Rajchenberg Arg45* (BAFC51667). CHILE. VALDIVIA: Cordillera Pelada, 29 Mar 1963, leg. and det. *Singer M3228* (BAFC). Representative specimens of *A. hinnulea* studied: AUSTRALIA. TASMANIA: nr. Dover, Duckhole Lake, on wood, 3 Jul 2003, leg. and det. *G. Gates* WR056; Warra Long-Term Ecological Research Site, Bird Track, old growth plot, subplot D1, on wood, 21 Nov 2006, leg. and det. *G. Gates*. HOLOTYPE of *A. hinnulea* at FRI was not available for study.

Commentary. Both Singer (1956) and Valenzuela (1993) described the pileus surface as of variable color, including olive in some cases, but we could not confirm the latter characteristic. *A. sparrei* was the most widely distributed *Armillaria* species in Patagonia. Although the type specimen has seemingly been lost, the species concept applied here is consistent with other authenticated material collected by Singer. We herein designate specimen M514 (LIL) as neotype of the species, this collection being among the paratypes designated by Singer (1956) and presenting the morphological features of the species. Among the more recently collected specimens BAFC 51665 and BAFC 51666 provide acceptable representatives of the taxon; cultures have been maintained in CIEFAP and CMW culture collections. In addition the ITS and LSU rDNA sequence data were incorporated in phylogenetic studies (Pildain et al. 2009).

Armillaria sparrei was the name applied to Lineage IV in the phylogenetic study by Pildain et al. (2009). Isolates clustered within a group of taxa that included *A. hinnulea* from Australia and New Zealand, *Armillaria* sp. III from Kenya and *Armillaria* 4th species from New Zealand. *Armillaria hinnulea* is distinguished from *A. sparrei* based on the fact that it is an astringent, nonviscid species that has clamped hyphae in the subhymenium, is generally pink with violaceous-pink hues and a strongly bulbose stipe.

KEY TO *ARMILLARIA* SPECIES FROM PATAGONIA

1a. Basidiocarps astringent, unpleasant odor; hymenophoral trama regular with lacunar, barrel shape cells . . . 2
1b. Basidiocarps mild or slightly sharp and acidic; hymenophoral trama divergent/subdivergent, with hyphal cells . . . 3
  2a. Pileus convex, flattened with conspicuous, beige to light brown squamules on all surfaces; basidiomata small to medium; annulus simple, membranaceous, with brown squamules underneath; spores length ≥ 9 µm with Q (L/W) ≤ 2 . . . *A. umbrinobrunnea*
  2b. Pileus umbonate with few, beige, light brown to dark brown squamules present only in the center, margins incurved and striate; basidiomata large to medium; annulus prominent, thick and persistent, with brown squamules underneath; spores length ≥ 9 µm with Q (L/W) ≥ 3 . . . *A. montagnei*
3a. Epicutis viscid; pileus beige to light brown, pubescent in the centre, convex to flattened; stipe bulbose, thinning upwards, long and stylized; annulus simple, membranaceous, with brown squamules underneath; spores length ≥ 9 µm with Q (L/W) ≤ 2 . . . *A. sparrei*
3b. Epicutis not viscid; pileus olivaceous-gray with incurved margins; stipe cylindrical, robust, exceptionally with a bulbose base; annulus simple, membranaceous, without brown squamules underneath; spores length ≤ 9 µm with Q (L/W) ≤ 2 . . . *A. novae-zelandiae*

DISCUSSION

Results of this study revealed the morphological characteristics and confirmed the identity of four phylogenetic lineages (Pildain et al. 2009) of *Armillaria* from continental Patagonia forests and timber plantations. Through the study of types, morphology of the basidiomes and characters of the fungi in culture, it was possible to link phenotypic characters of the species involved to the phylogenetic lineages. Morphological evidence was consistent with the phylogenetic lineages, confirming that lineages I–IV represent *A. novae-zelandiae*, *A. montagnei*, *A. umbrinobrunnea* and *A. sparrei* respectively.

Armillaria novae-zelandiae represented by phylogenetic Lineage I had gray-olivaceous pilei and small spores, while Lineage II representing *A. montagnei* mainly produced large basidiocarps with viscid pileus surfaces and a thick annulus with squamules. *A. umbrinobrunnea* represented by Lineage III had intensely squamulose pilei that had strongly sharp and acidic flavor and *A. sparrei* (Lineage IV) had bulbose stipes. Overall our results presented a clear example of agreement between molecular and morphological approaches to the identification of *Armillaria* spp. This was despite the scarce morphological characters that are typically informative for species in this genus. Culture characteristics for the four *Armillaria* species treated in this study showed distinct differences between the taxa. These were sufficient to differentiate clearly between the species with characteristics constant and consistent for each lineage. This offers a simple technique that could be incorporated in a polyphasic taxonomic study of *Armillaria*.

In the study area *A. novae-zelandiae* comprised specimens only from NW continental Patagonia (Lanín National Park, Neuquén Province), while the rest of the lineages represented isolates from all three provinces surveyed. Likewise *A. novae-zelandiae* was collected from more host species than the other three *Armillaria* species identified in Patagonia. *A. novae-zelandiae* was found on the native trees *Nothofagus dombeyi* and *N. alpina* and on the exotics *Pseudotsuga menziesii* and *P radiata*. These results are consistent with the view of Gregory et al. (1991) and Ota et al. (1998) that differences in host range and geographical distributions sometimes become more apparent after morphological studies of *Armillaria* specimens have been completed.

Results of the phylogenetic study by Pildain et al. (2009) suggested two possible taxonomic treatments for lineages I and II. Each of these thus could be treated either as a species complex or as a single species showing a strong biogeographical isolation. Within Lineage I, and despite the strong support provided by molecular data, we considered the differences in morphology between specimens from Australia, New Zealand, Tasmania and Argentina as insufficient to recognize more than one species. For this reason we chose to reduce *Armillariella sparrei* var. *elaeodes* to synonymy with *A. novae-zelandiae*. The former species was described by Singer (1969), who distinguished it from *A. sparrei* var. *sparrei* based on its olivaceous-gray pileus as well as small spores and basidiocarps. All these morphological features were found to be shared with *A. novae-zelandiae*, a species from Argentina (Singer 1970, Coetzee et al. 2003), thus justifying the treatment of *A sparrei* var. *elaeodes* here as its synonym. Examination of the type of *A. novae-zelandiae* in this study showed that the Argentinean species are distinguishable only by their nonbulbose-swollen stipes, which also is a diagnostic characteristic described for the species (Stevenson 1964, Kile and Watling 1983). The fact that several other specimens of *A. novae-zelandiae* also did not show this diagnostic feature and that there were exceptions for some collections from Argentina lends support to our view that *A. novae-zelandiae* is an appropriate designation for the Argentina specimens.

Lineage II comprised isolates of *A. luteobubalina* from Australia and isolates from Argentina and Chile, including one originally identified as *A. montagnei* var. *montagnei* on the basis of basidiome morphology. In this particular case, due to the strong support for the two sublineages (Pildain et al. 2009) and due to the presence of morphological differences between *A. luteobubalina* and the Argentinean collections, we chose to retain *A. montagnei* var. *montagnei* as separate from *A. luteobubalina*. Although *A montagnei* and *A. luteobubalina* share pileus features and an unpleasant flavor (Singer 1956, Podger et al. 1978), *Armillaria montagnei* var. *montagnei* has pilei with an olive tinge, larger spores and a more conspicuous annulus than those found in *A. luteobubalina*. These features together with the lack of rhizomorphs in nature, a diagnostic characteristic for *A. luteobubalina* (Podger et al. 1978), warrant their separation.

Lineages III and IV represent respectively species *A. umbrinobrunnea* and *A. sparrei*. *Armillaria umbrinobrunnea* is a new combination derived from *A. montagnei* var. *umbrinobrunnea*. The type material (M596LIL) and our specimens reflect the diagnostic characteristics of a densely squamulose and beige-dark pileus, a membranaceous annulus and sharp and acidic flavor. In contrast *A. montagnei* var. *montagnei* has pilei with olive tinges that are squamulose when young, and presents a thick and double annulus (Singer 1956, Singer 1970). Specimens representing Lineage IV have the same morphology as the specimens used by Singer (1956) in the original description of *A. sparrei* (M514LIL, M577LIL). *Armillaria sparrei* specimens were different from those of the other taxa having larger basidiomes, viscid pilei and a bulbose stipe that becomes narrower toward the apex (Singer 1956, Singer 1970).

This study failed to reveal specimens or strains of *A. limonea*, a taxon that was recorded from the study area in southern Tierra del Fuego (Singer 1969, Horak 1979, Godeas et al. 1993). Future collections in that region to evaluate its presence in Patagonia are clearly warranted.

The delineation of *Armillaria* species from South America stems from the last treatment of the genus

based on morphological characters (Singer 1970). Results of this study of collections from Patagonia have shown that the placement of some southern hemisphere *Armillaria* taxa might be questioned. Species native to Patagonia, such as the recognized *A. novae-zelandiae* and *A. luteobubalina*, can act as saprophytes but may become virulent pathogens when the native forest is replaced by introduced crops such as *Pinus*, *Eucalyptus* and vineyards, as has occurred in Chile (Artigas 1984, Ramírez 1990, Ramírez et al. 1992). It therefore is important to have a clear understanding of the species that are present to prevent the development of undesireable pathogen outbreaks. Further studies of *Armillaria* in South America need to progressively incorporate fresh specimens and strains from other areas, notably from the Neotropics, including the revision of type specimens, morphological, cultural, pathological and compatibility studies, as well as DNA sequence comparisons. Such studies will contribute to further resolving the relationships and taxonomy of *Armillaria* spp. in South America.

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