Forest Pathology
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| Journal: | *Forest Pathology* |
| Manuscript ID | EFP-OA-2017-038.R2 |
| Manuscript Type: | Original Article |
| Date Submitted by the Author: | n/a |
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| Subject Area: | Eucalyptus < Host genus, Vitis vinifera, Stem decay < Disease type |
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# *Arambarria* the pathogen involved in canker-rot of *Eucalyptus*, native trees wood-rots and grapevine diseases in the Southern Hemisphere

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**Summary**

*Arambarria* (Hymenochaetales, Basidiomycota) is a monotypic genus recently described to accommodate specimens from the Patagonian forests of Argentina wrongly assigned in the past to *Inocutis jamaicensis*. On the basis of a wide sampling of strains and phylogenetic analysis inferred from combined sequences including the nuc rDNA ITS1-5.8-ITS2 region, 28S rDNA D1-D2 domains and partial sequences of translation elongation factor 1-a (*tef1-α*) we demonstrate that this genus is associated to an important canker-rot of eucalypt plantations in Uruguay, to wood-rots of many native and exotic hosts, and to 'hoja de malvón' and chlorotic leafroll of grapevines diseases in Central Chile, Central Argentina and Uruguay, formerly assigned to *I. jamaicensis* and/or *Fomitiporella* sp. The combined phylogenetic analysis showed the existence of three, closely related clades that corresponded to (1) the Pampas of Uruguay and Argentina ("uruguay" clade), (2) the Monte, Chaco Serrano and Yungas forests of Argentina ("cognata" clade), and (3) the Patagonian Andes forests and Chilean Province ("destruens" clade). Lack of morphological differences between taxa from the three clades, their occurrence in both native and exotic hosts, previous results showing interfertility between isolates from Uruguay and Argentina, and the lack of full support in the concatenated ITS + 28S + *tef1-α* analysis, prevents us to distinguish and describe three different taxa; the proper name of the taxon being *Arambarria*

*cognata* comb. nov. A fourth, distinctly separated clade corresponded to South African strains isolated from vineyards representing an undescribed taxon associated to Esca grapevine disease in that country. *Arambarria* is shown to be unrelated to *Inocutis*, with which it was confused in the past and, so far, remains restricted to the Northern Hemisphere in America (Mexico, Jamaica and the USA).

Short title: *Arambarria* a new pathogen for old diseases

**Introduction**

Hymenochaetaceae (Hymenochaetales, Basidiomycota) is a fungal family comprising species with a worldwide distribution and extensive host range, including cultivated and native trees, shrubs and herbaceous plants (Dai 2010; Zhou et al. 2016; Sharma 1995; among others). These fungi cause white heart rot and/or canker rot and are actively involved in the degradation of standing and fallen wood. Canker rots occurs when functional sapwood is killed by the heart rot fungus and that results in development of a stem canker (Vasaitis 2013). Another characteristic that defines this family is the controversy and confusion in the naming of taxa, a very important issue related their relevance as fungal pathogens and wood-rotters. Accurate species identification of the causal organism of plant disease is therefore crucial for disease control and prevention.

An important canker- and stem-rot disease of *Eucalyptus globulus* Labill. (Myrtaceae) has been extensively studied in plantations of this species in the last decade in Uruguay. The causal agent of the disease was reported as *Inocutis jamaicensis* (Murrill) A.M. Gottlieb, J.E. Wright & Moncalvo (syn.: *Inonotus jamaicensis* Murrill) (Hymenochaetales, Basidiomycota) (Martínez 2005; Speranza et al. 2006; Lupo et al. 2009). The fungus has been responsible for up to 15% incidence in southeastern Uruguay eucalypt plantations, causing important white fibrillar, stringy wood-rots in the hardwood, ridges of callus tissue and axially cracking of the bark, necessitating the search for tree species, clones and/or varieties for replacement (Oliver Sala et al. 2005). *Inocutis jamaicensis* was also found associated with vineyards in Uruguay (Pérez et al. 2008) and with several native tree species growing in the gallery forests of Parana and Uruguay rivers that belong, phytogeographically, to the Paranaense Province, Amazonic Domain (Cabrera 1971). Recorded hosts include *Dodonaea viscosa* (L.) Jacq. Chapulixtle (Sapindaceae), *Baccharis dracunculifolia* D. C. (Asteraceae), *Eupatorium buniifolium* Hook. ex Arn. (Asteraceae), *Heterothalamus alienus* (Spreng.) Kuntze (Asteraceae), *Daphnosis racemosa* Gris. (Timelaceae), *Lithraea brasiliensis* (L.) March. (Anacardiaceae), *Parkinsonia aculeata* L.

(Fabaceae) and *Scutia buxifolia* Reiss. (Rhamnaceae); and the cultivated *Acacia longifolia* Willd. and *A. melanoxylon* R. Br. (Fabaceae)(Martínez 2005; Pérez et al. 2008).

More recently, *I. jamaicensis* was demonstrated to be, in part, responsible for the grapevine trunk disease in vineyards of west Argentina (Mendoza and San Juan provinces), which is the main grape and wine productive area in that country (Lupo et al. 2006). The so named 'hoja de malvón' ('geranium-like leaf') disease is characterized by symptomatic curly chlorotic leaves formation, trunk discoloration and decay, and by the development of a white fibrillar wood-rot in the hardwood, that may also develop into sapwood tissues. It produces drying, necrosis and death of branches and trunks. Lupo et al. (2006) showed, based on mating compatibility tests and Internal transcribed spacer of nuclear ribosomal RNA gene (ITS) sequencing, that the basidiomycetous fungus responsible for the white fibrillar wood-rot on grapevine trunks in Mendoza and San Juan provinces was the same as the one attacking eucalypts in Uruguay. The disease has been related to Esca disease of vineyards in Europe, North America, Canada, California, New Zealand, Australia and other wine producing areas (Surico et al. 2008). As in those countries, 'hoja de malvón' is also associated with several ascomycetous genera such as *Botryodiplodia* (Sacc.) Sacc. and *Phaeoacremonium* W. Gams, Crous & M. Wingf. Gatica et al. (2000) demonstrated their role in experimental inoculation of vine plantlets, also so for the then named *Phellinus* species associated with the disease and responsible for the white fibrillar wood-rot in the hardwood. This basidiomycetous fungus was found to be the most frequent species in the complex of organisms associated with 'hoja de malvón' symptoms on the leaves and wood (César and Gatica 2001; Gatica et al. 2004). It was however not assignable to any of the basidiomycetes such as *Fomitiporia mediterranea* M. Fisch. in Europe (Fischer 2002) or *Fomitiporia australiensis* M. Fisch., J. Edwards, Cunningt. & Pascoe in Australia (Fischer et al. 2005), that were found being associated with Esca disease in those countries. In Chile, two successive works by Aguilera et al. (2002) and Auger et al. (2003) showed that the basidiomycetous fungus associated with Leaf Curl Chlorotic grapevine disease, belonged to either an *Inocutis* Fiasson & Niemelä or a *Fomitiporella* Murrill species. This taxon is different from species of *Fomitiporia* Murrill known to be associated to Esca disease in different vineyards regions of the world (Fischer 2002; Fischer et al. 2005; Cloete et al. 2014). In Argentina *I. jamaicensis* has been widely reported, apart from vineyard areas, from the southern *Nothofagus*–dominated forests of Patagonia (Subantarctic Province and Domain), Central and northwestern Argentina in the Yungas forests, and the subxerophytic Chaco and Monte regions (Gottlieb et al. 2002; Rajchenberg 2006; Robledo and Urcelay 2009; Urcelay et al. 2012). The species was recorded on a wide range

of native hosts such as *Lomatia hirsuta* (Lam.) Diels. (Proteaceae), *Diostea juncea* (Gillies & Hook. ex Hook.) Miers and *Durantia* L. (Verbenaceae), *Allophylus edulis* St. Hil.) Radlk. (Sapindaceae), *Cedrela* sp. P. Browne (Meliaceae), *Phoebe* (Griseb.) Mez (Lauraceae), *Celtis tala* Gillet ex Planchon (Ulmaceae), *Polylepis australis* Bitter (Rosaceae), *Eupatorium buniifolium* and *Heterothalamus alienus*, *Acacia caven* (Mol.) Mol. and *A. aroma* Hook. & Arn. (Fabaceae), *Ruprechtia apetala* Weed. (Polygonaceae) and *Salix humboldtiana* Willd. (Salicaceae). It was also found on exotic trees such as *Prunus* L. spp. and *Salix babylonica* L. It was also reported from several planted/ornamental exotics in the Pampas around Buenos Aires city such as *Eucalyptus* L'Hér., *Taxodium distichum* (L.) L. Rich. and *Fraxinus* Tourn. ex L. (Rajchenberg and Wright 1998). In all cases the fungus attacked stumps or standing trees producing white fibrilar heart-rots.

Rajchenberg et al. (2015) found that specimens from Patagonia, determined as *I. jamaicensis* on the basis of morphological studies, grouped separately from sequences of *I. jamaicensis* from the North Hemisphere and also from other *Inocutis* species. The study revealed, with the support of molecular phylogenetic studies and detailed morphological analyses, the existence of a new genus and species *Arambarria destruens* Rajchenb. & Pildain. Surprisingly, it clustered with a sequence from a Chilean strain isolated from grapevine wood decay that was determined as *Fomitiporella* sp. by Auger et al. (2003). This discovery triggered an interest to compare *I. jamaicensis* specimens of several origins and to properly establish their identity, given the fact that the name was repeatedly used in Argentina, Chile and Uruguay to name a fungus associated with different important forest and agricultural diseases. In this context, we studied the genus *Arambarria* from southern South America. Our aims were: (a) to determine its phylogenetic relationships within the Hymenochaetaceae, (b) to establish its hosts and distribution, and (c) to relate morphological features with molecular phylogeny.

**Materials and methods**

*Strains and herbarium specimens*.— Strains studied, with their voucher specimens, are deposited at the institutional culture collection (CIEFAPcc) and phytopathological herbarium (CIEFAP). For some but not all strains, duplicates were deposited at BAFC culture collection. Herbarium designations follow Thiers (2016), and culture collection designations follow that of the World Federation for Culture Collection website (http://www.wfcc.info).

*Morphology*.— Description of basidiomata and terminology followed Ryvarden and Melo (2014). Basidiospore measurements are expressed as L × W (L = mean basidiospore length as the arithmetic average of all

basidiospores ± SD, W = mean spore width as the arithmetic average of all basidiospores ± SD), Q as the mean variation in the L/W ratios between the specimens studied, and n/s = number of basidiospores measured from a given number of specimens.

*DNA extraction and PCR conditions*.— DNA was extracted from herbarium specimens or freshly collected mycelium from pure culture grown in liquid malt peptone broth consisting of 10% malt extract (Merck) (w/v) and 0.1% (w/v) Bacto peptone (Difco), in 15 mL tubes at 24 C in the dark. Approximately 50 mg of fungal tissue was sliced into small sections with a sterile blade, placed in 2mL collection tubes containing 300µl MicroBead solution (MO BIO Laboratories Inc., Solana Beach, California) and homogenized 30s at a velocity of 6m/s in a MP FastPrep 24 (MP Biomedicals) homogenizer. Extractions were carried out with the UltraCleanTM Microbial DNA Isolation Kit (MO BIO Laboratories Inc., Solana Beach, California), following the manufacturer's recommendations. DNA quantification was performed with ultraviolet spectroscopy. The primer pairs LROR-LR5 (Vilgalys and Hester 1990), ITS5-ITS4 (White et al 1990) and 983F-2218R (Rehner and Buckley 2005) were used to amplify, respectively, the partial 28S Large sub-unit of nuclear ribosomal RNA gene (LSU) that includes the variable D1/D2 domains), the full ITS region (i.e., ITS1, ITS2 and the intervening 5.8S RNA gene) and the fragment between exons 4 and 8 of the translation elongation factor 1-a (*tef1-α*) gene. Amplification and sequencing of 28S, ITS and *tef1-α* regions are described in Rajchenberg et al. (2015), Rehner and Buckley (2005) and Amalfi et al. (2010). The amplified fragments were purified and sequenced at the DNA Synthesis and Sequencing Facility, Macrogen (Seoul, Korea). Sequences generated in this study were submitted to GenBank (*tef1-α*: KY907685 - KY907703; ITS: KY907677 - KY907685; 28S: KY907686 - KY907703).

*Dataset selection*.— As a framework for taxon selection we used sequences of representative species from genera defined by Larsson et al. (2006), Parmasto et al. (2013), Zhou et al. (2012, 2014) and Drechsler-Santos et al. (2016) based on morphological and molecular characteristics, and accepted in the Hymenochateaceae. Whenever possible, sequences of the generic type species were included.

*Sequence and phylogenetic analyses*.— Three data sets were analyzed for this study: concatenated analyses of the ITS region and 28S gene were used to expand available sequences for *Arambarria* on GenBank with Chilean sequences deposited in the GenBank and to ascertain its phylogenetic relationships with related genera. Concatenated analyses of ITS, 28S and *tef1-α* was performed for *Arambarria* to solve the phylogenetic structure within the genus. Nucleotide sequences were initially edited with BioEdit 7.0.9.0 (Hall 1999), then aligned automatically with MAFFT (Katoh and Standley 2013) and manually adjusted in MEGA version 6

(Tamura et al. 2013). The final ITS dataset comprised 32 sequences and 709 characters including gaps, the LSU dataset comprised 37 sequences and 876 characters including gaps, and the *tef1-α* comprised 19 sequences and 979 characters including gaps. The datasets were manually combined for concatenated analyses. The two concatenated data sets (ITS + 28S and ITS + 28S + *tef1-α*) were assessed for congruence using the Partition homogeneity test in PAUP* 4.0b10 (Swofford 2002). The substitution models that best fitted the sequence alignments were determined using the AIC criterion (Akaike 1974) implemented in jModelTest (Posada 2008; http://darwin.uvigo.es). The following models were used: (1) for ITS + 28S, TVM+I+G and TrN+I+G, respectively; (2) for ITS + 28S +*tef1-α*, the models selected were HKY+I, TIM2+I and TIM3ef+G, respectively. Phylogenetic analysis of the individual loci and combined data set were performed using maximum likelihood (ML) with RAxML 7.2.8 (Stamatakis et al. 2014) and Bayesian (BA) inferences of phylogenies in Mr Bayes v.3.0B4 (Ronquist & Huelsenbeck 2003). The number of included taxa for the concatenated ITS + 28S matrix was 35, the ITS and 28S partitions included 524 and 874 characters, respectively, for a combined data matrix of 1397 characters. While with the concatenated ITS + 28S + *tef1-α* matrix included 19 sequences with 866 ITS characters, 660 for 28S and 979 for ITS + 28S + *tef1-α*. Branch support was determined using nonparametric bootstrapping (1000 replicates) implemented in RAxML 7.2.8 (Stamatakis et al. 2014), using the default parameters, executed on the CIPRES (Cyber infrastructure for Phylogenetic Research) Science Gateway V. 3.1 (http://www.phylo.org/sub_sections/portal/, Miller et al. 2010). Bayesian phylogenetic analyses were performed using Mr Bayes v. 3.2.2 employing a Markov chain Monte Carlo (MCMC) algorithm (Ronquist and Huelsenbeck 2003). Four independent chains were run for 8 $\times 10^6$ generations, trees were sampled every 100 generations. Log files for each run were viewed in Tracer v1.6.0 (http://evolve.zoo.ox.ac.uk/software.html/tracer/) to determine convergence. Trees generated prior to stationarity were discarded and the reminder of the trees was summarized in a majority-rule consensus tree from the four independent runs. Branch support was assessed using posterior probabilities calculated from the posterior set of trees after stationarity was reached. Trees inferred from the ITS + 28S data set were rooted with *Nothophellinus andinopatagonicus* (J.E. Wright & J.R. Deschamps) Rajchenb. & M.B. Pildain (CIEFAPcc42) and *Fuscoporia gilva* (Schwein.) T. Wagner & M. Fisch. (ATCC26729). While the outgroups for the ITS+ 28S+ *tef1-α* were *Fomitiporia punctata* (P. Karst.) Murrill MUCL34101 and *Phellinus uncisetus* Robledo, Urcelay & Rajchenb. MUCL46231, as Rannala and Yang (2013) showed that including a closely related outgroup may

increase the statistical power of BA. Alignments and phylogenetic trees have been deposited at TreeBase: http://purl.org/phylo/treebase/phylows/study/20030.

## Results

### Phylogenetic analyses

Phylogenetic analyses based on the concatenated dataset ITS + 28S placed taxa in well resolved clades that included *Arambarria*, *Fomitiporella*, *Inocutis*, *Phellinotus* Drechsler-Santos & Robledo and the taxa *Fulvifomes inermis* (Ellis & Everh.) Y.C. Dai, *F. chinensis* (Pilát) Y.C. Dai and *Inonotus tenuissimus* H.Y. Yu, C.L. Zhao & Y.C. Dai (Zhao 2014, Rajchenberg et al. 2015)(BS=75%; PP=0.95). Combined and single loci phylogenetic analyses of ITS and 28S sequences (Fig. 1, Suppl. Fig. 1) confirm that *Arambarria* is a monophyletic genus and includes all specimens formerly identified as *Inocutis* spp. in southern South American countries (Argentina, Chile and Uruguay)(BS=90%; PP=1.0). We included sequences of *I. jamaicensis* from Arizona (USA, RLG15819) and of another species of *Inocutis* with available ITS and LSU sequences, *I. dryophila* (Berk.) Fiasson & Niemelä. A noteworthy discovery came from the inclusion of South African *Inocutis* Taxon 3 specimens (Cloete et al. 2015) that were placed as a basal group (BS=100%; PP=1.0) within *Arambarria*. Four major clades can be recognized within clade Arambarria based on the individual and concatenated dataset ITS + 28S (Fig. 1, Suppl. Fig. 1). The "destruens" (BS=60%; PP=0.99), "cognata" (BS=95%; PP=1.0) and "uruguay" (BS=85%; PP=0.98) clades, which are distributed across Argentina, Chile and Uruguay, and a basal one from South Africa (BS =100%; PP =1.0). Phylogenies of *Arambarria* based on individual loci and concatenated ITS + 28S + *tef1-α* reconstructed the same major clades (Fig. 2, Suppl. Fig.2) but only support the "destruens" clade (Fig. 2, Suppl. Fig.2). Combined ITS + 28S and individual analyses differentiate *Arambarria* from *Inocutis* s. str. The *I. jamaicensis* sequence from the North Hemisphere grouped basally within *Inocutis* but separated from the other species *I. dryophila*.

### Morphology &Taxonomy

*Arambarria cognata* (Bres.) Rajchenb. & Pildain comb. nov. Fig. 3

MycoBank MB820520

Bas.: *Polyporus rheades* Pers. var. *cognatus* Bres. Annls. Mycol. 18(1/3): 34, 1920.

Syn.: *Arambarria destruens* Rajchenb. & Pildain, Mycologia 107: 759, 2015 (Holotype BAFC!), MycoBank MB809350

For formal descriptions of this taxon see Gottlieb et al. (2002), Rajchenberg & Wright (1998), Martínez (2005, 2006), Rajchenberg (2006) and Rajchenberg et al. (2015) under *Inonotus* or *Inocutis jamaicensis*.

Specimens are variable macromorphologically, from resupinate, effused reflexed to strictly pileate. Pilei are triquetrous to ungulate, solitary or numerous imbricate, up to 3–7 × 2–4 × 0.5–1.5–3 cm; pilear surface is velutinous to slightly hispid but soon becomes glabrous and displays a smooth, sometimes radially wrinkled, hardened surface, chestnut, reddish brown to dark reddish brown; the margin is blunt, concolorous with pilear surface but cream coloured in large specimens. The context is homogeneous, presenting or not presenting a black line below the tomentum that runs partially or all along the pileus and is formed by the hardened pilear surface; a line may also be present in the base of tubes; context golden brown always lacking a granular core at the base. Pores are round to subgyrose, mostly 3-4-5/mm. The hyphal system is monomitic throughout, with simple-septate generative hyphae, with thin- to thick- hyaline to coloured walls. Setae are absent. Basidiospores are abundant, broadly ellipsoid, ellipsoid to ovoid, adaxially flattend, 5.7–6.8–7.1 × 3.8–5.0 µm,thick-walled, yellowish in water, chestnut in KOH 5%, IKI- and acyanophilous.

Some specimens from clade “uruguay” are prone to form large pileate basidiomata that lack resupinate portions (Fig. 3B; also cfr. Pérez et al. 2008 Fig. 1), but this was related to large and standing stems, as basidiomata similar to typical specimens from clades “destruens” and “cognata” (Fig. 3A, 3C) were also formed in thinner and inclined stems (cfr. Lupo et al. 2006, Fig. 1). Basidiospores showed a range of size variation that overlapped among specimens from the different clades (Tables 1 and 2). Nevertheless, Q values showed a progressive increase from “destruens” to “cognata” and “uruguay” specimens (Table 2).

A duplex context is the main morphological difference with *I. jamaicensis* s.str. and the lack of a distinct granular core being a general difference with species in *Inocutis*, though the granular core may be lacking in certain specimens of *I. jamaicensis* (Gilbertson and Ryvarden 1987, Valenzuela et al. 2013). Martínez (2006) described sclerified hyphae from rudimentary granular core in some Uruguayan specimens.

*Fomitiporella* is distinguished by perennial taxa with a dimitic hyphal system (Wagner and Fischer 2002). *Inocutis rheades* (Pers.) Fiasson & Niemelä is similar, but differs by the presence of a distinct granular core in the context, by somewhat larger pores 2-3-4/mm, and by mainly growing on *Populus*. Microscopically they are similar (Table 1) (Dai 2010; Ryvarden and Melo 2014).

Materials studied (specimens and/or strains):

Phylogenetic clade “cognata”

**ARGENTINA**, **CÓRDOBA**, leg. C. Spegazzini n°13, ad truncos (Holotype of *P. rheades* var. *cognatus*, S!). Ibid., leg. T. Stuckert 6847, 26 Apr 1899, det. C. Spegazzini (LPS 21857). Ibid, leg. ipse 6889 (LPS 21856).

**ARGENTINA, CÓRDOBA**, Punilla, Cuesta Blanca, on *Eupatorium buniifolium*, C. Urcelay 132, 136 and 137, 10 Jul 1999 (CORD). San Javier, La Ola, Pampa de Achala, on dead stem of standing *Polylepis australis*, Robledo 64, 18 Jun 2001. JUJUY, Santa Bárbara, El Fuerte, on stem of *Eupatorium* sp., 4623 Feb 2001. **MENDOZA**, Luján de Cuyo, *Vitis vinifera* L. var. C. Grande, isolated from wood-rot, leg. M. Gatica, 1999 (CIEFAPcc 198). **SAN JUAN**, Pocito, Carpintería, Finca Parralcha, *Vitis vinifera* var. Imperial Seedles, isolated from wood-rots, leg. D.B. Pappano, Oct-Nov 2014 (CIEFAPcc 16, 63, 72, 547, 550, 551, 552, 556 and 563, isolated from 8 different plants). **TUCUMÁN**, Trancas, 1229 asl, 26°17’21”LS 65°31’13.4” LW, on fallen branch, G.L. Robledo 940, 22 Mar 2007. Trancas, Dique El Cadillal, on living stem of *Cedrela*, 26°37’24.5” LS 65°11’55.6” LW, G.L. Robledo 788, 18 Feb 2007.

Phylogenetic clade “destruens”

**ARGENTINA**, **CHUBUT**, Lago Puelo National Park, W arm of Lago Puelo, oriental slope of Valle de las Lágrimas, Los Tineos stream, on stem and branches of a dead *Diostea juncea* in *Austrocedrus chilensis* (D.Don) Pic. Ser. et Bizzarri forest, 10 May 1996, M. Rajchenberg 11172 (holotype, BAFC 34575) (Ex-type strains BAFCcc 1500, CIEFAPcc192. GenBank accessions: ITS AY072033, 28S KP347520). Ibid., 4 May 1998, A. Greslebin AG1591. CHUBUT, Los Alerces National Park, Lago Verde, track to Lago Menéndez, ca. 50 m from the bridge on Arrayanes river, on fallen trunk of *Lomatia hirsuta*, 9 May 1996, M. Rajchenberg 11116 (BAFC 34592, isolate BAFCcc 1508, CIEFAPcc 194). Ibid., Lago Futalaufquen, Cerro Dedal, beginning of the track towards the mountain’s top, on fallen branch of *Diostea juncea*, 9 May 1997, M. Rajchenberg 11230 (BAFC 34591). Ibid., Lago Futalaufquen, ‘head’ of the Lake, on dead branches of living *Diostea juncea* at the lake shore, 12 Dec 2012, M. Rajchenberg 12504 and 12505. Ibid., 25May 2011, M. Rajchenberg 12478 (isolate CIEFAPcc 347.**CHILE**, **SANTIAGO**, Región Metropolitana Quebrada de la Plata, on *Baccharis* Sch.Bip. ex Walp. sp., P. Sandoval, 2012 (SGO 160477).

Phylogenetic clade “uruguay”

**ARGENTINA**, **BUENOS AIRES**, Magdalena, Estancia El Destino, M. Rajchenberg & D. Job, 28 Aug 1984 (BAFC 30218). La Plata, Villa Elisa, leg. & det. C. Spegazzini, 26 May 1921, on *Eucalyptus* sp. (LPS 21859). Ibid., leg. & det. ipse, May 1921, on *Eucalyptus globulus* Labill. (LPS 21860). **URUGUAY**, Montevideo, leg. & det. C. Spegazzini, May 1914 (LPS 21858). **URUGUAY**, **DURAZNO**, Ruta 5 km 205, on *Acacia melanoxylon*, G. Pérez CGP465, Apr 2014. **CANELONES**, Atlántida, Ruta Interbalnearia km 41, on *Acacia longifolia*, G. Pérez CGP 466, 467 and 468, Apr 2014. Ibid., on *Dodonaea viscosa*, G. Pérez CGP 473 and 474, Apr 2014. Ibid., monosporic culture from CGP 468, as CGP 469.**TACUAREMBÓ**, Balneario Iporá, plantation behind De las Pintangueras street, on *Eucalyptus globulus*, G. Pérez CGP 470, 471 and 472, Jul 2014. **LAVALLEJA**, Route 14 between Battle and Zapicán, Uruguay Forestal, on *Eucalyptus globulus*, R. Linares, Aug 2002. Estancia Ruralco, on stump of *E. globulus*, S. Lupo, L. Bettucci & S. Martínez (MVHC 5001).

*Inocutis jamaicensis*s.s. (specimens and/or strains):

**JAMAICA**, Mabess River, at 3000 ft, Underwood 23, Apr 1903 (Holotype, NY!).**USA**, **NEW MEXICO**, Mescalero I.R., on *Quercus gambelii* Nutt., F.G. Hawksworth 98525, 3 Sep 1952 (det. R.L. Gilbertson) (ARIZ 017567). **ARIZONA**, Cochise Co., Coronado National Forest, Chiricahua Mts., Rucker Canyon, on *Quercus arizonica*, E.R. Canfield 71121, 22 Jul 1971 (det. R.L. Gilbertson) (ARIZ 017566). Ibid., South Fork of Cave Creek, on *Q. arizonica* Sarg., R.L. Gilbertson 15819, 1 Sep 1985 (ARIZ 011096 duplic at USDA Forest Service Herbarium); strain RLG-15819 = CIEFAPcc 420.

**Discussion**

*Inocutis jamaicensis* was recorded in Uruguay as the pathogen responsible of a serious stem and rot-canker in *E. globulus* and *E. viminalis* Labill. plantations, also associated with white-rots in the trunks and major branches of vineyards. Cholorotic leafroll in Chile and 'hoja de malvón' in Argentina are major diseases of grapevine production in southern South America, similar to Esca disease in many other productive areas around the world. A white-rot is associated with these diseases, which has been the subject of many studies in order to establish its etiology, due to the fact that the fungus is one of the main isolated taxa and also partially responsible of 'hoja de malvón' symptomatology (Gatica et al. 2000). Cloete et al. (2015) summarized the knowledge on Hymenochaetales fungi associated to grapevine diseases worldwide. In Argentina and Chile the species associated with the white rot have been known as *I. jamaicensis* and *Fomitiporella* sp., respectively, the

latter named as 'Fomitiporella vitis' (Auger et al. 2003 and 2005; Surico et al. 2008) but was never formally described (cfr. Indexfungorum and MycoBank).

*Inocutis jamaicensis* was originally described from the Caribbean area (Murrill 1904), but its presence in several parts of the Americas has been reported continuously. It has been reported from Mexico (Chihuahua, Guanajato, Hidalgo, Oaxaca, Querétaro, Sonora and Veracruz States; Valenzuela et al. 2013), USA (New Mexico and SE Arizona States; Gilbertson and Ryvarden 1987), Brazil (Parana State; Baltazar et al. 2010), Argentina and Uruguay (cfr. Introduction). The species was originally described as a *Inonotus* species but two independent studies using molecular methods and published almost simultaneously showed that it belongs to *Inocutis* and not to *Inonotus* (Gottlieb et al. 2002, Wagner and Fischer 2002). Specimens of *I. jamaicensis* from the North Hemisphere (Arizona, USA; Wagner and Fischer 2002) grouped within *Inocutis* s.s., with the type species *I. rheades* (Pers.) Fiasson & Niemelä and *I. dryophilus* (Berk.) Fiasson & Niemelä, *I. ludovicianus* (Pat.) T. Wagner & M. Fisch. and *I. tamaricis* (Pat.) Fiasson & Niemelä, distant to South American specimens. They are herein considered to represent the 'true' *I. jamaicensis*. Specimens from Patagonia grouped within *Inocutis* (Gottlieb et al. 2002) but were later shown to represent a different genus (Rajchenberg et al. 2015). Based on preliminary studies that showed a relationship between the Patagonian strains and an isolate recovered from *Vitis vinifera* from Chile (Rajchenberg et al. 2015) we performed a wide sampling effort to compare strains from different parts. Our study showed that materials from Uruguay, Chile and Central and southern Argentina represent a different genus, *Arambarria*, with a wide distribution area and apparently restricted to the Southern Hemisphere. The results from the phylogenetic analyses shows that *I. jamaicensis* s.s. might probably have a more restricted distribution than previously recorded and assumed based on morphological studies. We did not include *I. jamaicensis* voucher specimen from Arizona, USA, viz. Gilb. 14740 (Genbank LSU sequence AY059048, Wagner and Fischer 2002) in this study because ITS sequence data were not available, but our results correlate well with those obtained in our previous work on the Hymenochaetaceae from Patagonia (Rajchenberg et al. 2015) where the specimen was used.

Whitin *Arambarria* the combined phylogenetic analysis showed the existence of 3, much related South American clades and a fourth, distinctly separated clade that corresponded to South African strains isolated from vineyards. The South American clades corresponded with several phytogeographic regions as follows: "destruens" in the Subantarctic Patagonian forest and Chilean Province, "cognata" in the Yungas forest, Monte and Chaco Serrano, and "uruguay" in the Pampas; in the three cases on native and cultivated trees. Within the

"destruens" clade, specimens from Patagonia (CIEFAPcc192 and CIEFAPcc194) isolated from basidiomata growing on the native trees *Diostea juncea* and *Lomatia hirsuta* grouped together with Chilean sequences (SGO160477, Fomitiporella sp. DQ459301) that belong to specimens collected from the native *Baccharis* sp. and the introduced *Vitis vinifera*, respectively. Clade "cognata" included strains CIEFAPcc 16, 550 and 563 isolated from *V. vinifera* wood-rots in San Juan province (Argentina) with specimen CORD132 from the native *Eupatorium buniifolium*. While clade "uruguay" includes collections from *Acacia* spp. and the native *Dodonaea viscosa*.

The possibility that 3 cryptic species might be involved was evaluated. Nevertheless, and despite of the phylogenetic groups that we could detect from our analyses, only one of them (clade "destruens") presented enough statistical support. Also, neither macro- nor micromorphological differences could be found. Only the spores' Q values showed a progressive increase from 1.36 to 1.63, a feature that might reflect an ongoing phylogenetic separation among these clades. Based on our data and given that only few materials comprised each clade, we could not find any supporting morphological feature to suggest recognizing these clades as different species at this time. Some specimens from clade "uruguay" form large, pileate basidiomata that lack resupinate portions, that were not found in specimens belonging to the other clades, but this was related to large and standing stems and, otherwise, basidiomata similar to typical specimens from clades "destruens" and "cognata" (Fig. 3A, 3C) were also formed in thinner and inclined stems. In this regard, it has been shown that logs with larger diameter might favor decay activity, fruitbody production and volume because they generally have more constant microclimatic conditions (Boddy 1983, 2001; Urcelay and Robledo 2009). Clade "destruens" was the only well-defined and supported phylogenetic group in all the analyses. Specimens from a wide geographic area along the Andes ranges and host diversity grouped together, from the Patagonian Andes forests in the south up to the Chile Province in the north. The record of the species is still scant in Chile, but found on *Baccharis*, which grows in areas where it has been replaced by vineyards. The concatenated ITS + 28S + *tef1-α* phylogeny did not support the clades "cognata" and "uruguay" as monophyletic, neither in BA nor in RAxML analyses (RAxML=60%; BA=0.9 for "cognata" and RAxML=< 60%; BA=0.9 for "uruguay"). In addition, mating experiments between monosporic cultures from *Eucalyptus* and *V. vinifera* from Uruguay and Argentina, respectively, demonstrated interfertility (Lupo et al. 2006). Therefore, while we were able to discriminate "destruens" among the South American clades, we cannot support the description of separate species due to the absence of morphological characteristics or other data that confirm the molecular analyses.

Also, the moderate support of "cognata" and "uruguay" clades suggest an unresolved structure within the South American specimens even with multilocus analyses. It would be necessary to include more specimens from the wide distributional range of this genus in order to confirm or reject the hypothesis of new species within *Arambarria*. For example, it was demonstrated for the phytopathogenic fungus *Colletotrichum* Corda that the addition of new strains into a group containing two originally well supported sister clades the distinctiveness of the two clades collapsed (Liu et al. 2016). Therefore, obtaining a sufficient number of strains from diverse origins is crucial for delimiting species or introducing a novel one. Another scenario to consider is the case of sympatric speciation, where mechanisms of reproductive isolation may evolve much later than DNA divergence. In this case, phylogenetic studies discriminate the speciation process more accurately than the Biological Species criterion, and closely related species may remain interfertile in *in vitro* crosses for some time (Cai et al. 2011).

After considering the distinctiveness and the wide geographical range of *Arambarria* specimens from southern South America we proceeded to review former names and available materials. It came to our attention the name *Polyporus rheades* (Pers.) Bondartsev & Singer var. *cognatus* Bres., which was used for a specimen collected by Spegazzini from Córdoba Province, Argentina (Bresadola 1920). It was considered an accepted variety of *P. rheades* by Pegler (1964), but a synonym of *I. jamaicensis* by Gottlieb et al. (2002). The morphological study of several of Spegazzini's specimens of var. *cognatus* (also registered by him from elsewhere in Argentina, as stated in the Introduction) and the inclusion of molecular data from a specimen from Córdoba proved to be the previous available species name and the new combination *A. cognata* has been proposed. As a conclusion, with the available data at this time we support the existence of a single species *A. cognata* in Argentina, Chile and Uruguay.

*Arambarria* in southern South America represents a wood-rotting pathogen that has a wide geographical distribution, grows on numerous native hosts and that has jumped from indigenous to introduced exotic hosts. Host jumps are common for fungal pathogens (Wingfield 2003). This has been the case for other Hymenochaetales described from vineyards worldwide such as *Fomitiporia mediterranea* M. Fisch., *F. australiensis* M. Fisch., J. Edwards, Cunningt. & Pascoe and *F. capensis* M. Fisch., M. Cloete, L. Mostert & F. Halleen that are responsible of the white-rot decays in vineyards in the Mediterranean, Australian and South African areas, respectively (Cloete et al. 2014, Fischer 2002, Fischer et al. 2005). *Inonotus rickii* (Pat.) D.A. Reid

(a Neotropical species) is a pathogen of *Platanus acerifolia* Mill. ex Münchh. and *Acer negundo* L. in planted tree areas/streets of Buenos Aires city (Rajchenberg and Robledo 2013). In South Africa, several *Ganoderma* species have been described attacking introduced *Jacaranda mimosifolia* D. Don. trees in Pretoria (Coetzee et al. 2015). In Sumatra, *G. philippii* (Bres. & Henn. ex Sacc.) Bres. is responsible for root rot of exotic *Acacia mangium* Willd. and *Eucalyptus* trees (Coetzee et al. 2011). Fungal host jump events are connected with anthropogenic introduction (Slippers et al. 2005). In this context it is also worthy to note that an intensive trade of vine cuttings from Chile to Argentina either formal or informally occurred in the 1990s due to laws that aimed to stimulate agricultural development, securing interchange of biological materials in the two neighboring wine growing areas of Chile and Argentina. Present knowledge regarding pathogen-host interaction shows that some plant pathogens have a broad host range and are capable of parasitizing host plants of different families, being host jump and host expansion the common evolutionary mechanisms that enables host specific pathogens to shift from one host to another or to acquire new host and, in most cases, host shift consequently produces the most devastating disease outbreaks (Woolhouse et al. 2005).

Our study recovered *Inocutis* Taxon 3 of the Hymenocohaetales isolated from South African vineyards (Cloete et al. 2015) within the clade "Arambarria". However, it might represent a species different from the South American *A. cognata*. The record of *I. jamaicensis* on *Phylica* L. sp. (Rhamnaceae) from Tristan da Cunha island (Reid 1955) may be a clue of the existence of a species morphologically similar to the North Hemisphere *I. jamaicensis* and to the South American *A. cognata.* The island is very isolated but is phytogeographically related to the South African Cape Floral Kingdom, where fynbos formation presents most of the species diversity in *Phylica* (Richardson et al. 2001). Based on the morphological similarity between *I. jamaicensis* and *A. cognata*, the possibility exists that Reid's record found in that island is a specimen of the South African *Inocutis* Taxon 3 of the Hymenochaetales, and an indication that it might be found on *Phylica* in the continent. According to the above facts, we expect to find a taxon that might be morphologically very similar to the southern South American taxon, but phylogenetically distinct.

In conclusion, this study confirms the distinctiveness of *Arambarria* as a pathogen within the Hymenochaetaceae especially so *vis à vis Inocutis*. It also shows the existence of two distinct species, *A. cognata* present in Argentina, Chile and Uruguay, and an unnamed species in South Africa. Both species are associated to native and introduced forest and agriculturally important trees. From a pathological perspective, it seems likely that these taxa jumped from native hosts to introduced ones given their geographic distribution

and hosts diversity. Future work will be needed to determine if the present phylogenies reflect population structure or species delimitation in southern South America and the proper taxonomic delimitation of the South African taxon.

**Acknowledgments**

This study was funded by PIP-CONICET 11220110100388 (to MR), SECITI - 1400-0114-2012 (to DBP), and MinCyT PICT-1676 to Carlos Urcelay (IMBIV-CONICET, Argentina). Pablo Sandoval Leiva (Museo de Ciencias Naturales, Santiago, Chile) is acknowledged for allowing us to record his specimen of *A. cognata* collected in Chile. Drs. A.E. Arnold (Herbarium ARIZ, USA), A. Romero (Herbarium BAFC, Argentina) and M. Cabello (LPS, Argentina) are deeply acknowledged for lending specimens and/or cultures at their keeping. Three anonymous reviewers are acknowledged for their critical comments and text improvement.

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**Captions of Tables and Figures**

*Table 1.* Basidiospore measurements of *Arambarria cognata* and related taxa.

*Table 2*. Concise basidiospores size variation in specimens from different clades.

*Fig. 1.* Phylogenetic relationships of *Arambarria* inferred from ITS and LSU sequences via maximum likelihood (ML) and Bayesian (BA). Thick vertical black bars show the root branch for the specific lineage indicated by the adjacent label. Thick horizontal branches are supported by bootstrap value greater than 60% (ML) and 0.9 (BPP). PAT, Patagonia; SJ, San Juan; ARG, Argentina; CH, Chile; SA, South Africa; UR, Uruguay; USA United States of America; TAC, Tacuarembó; CAN, Canelones; STE, Stellenbosch. Sequences in bold were generated in this study. T, sequences obtained from the genus type species.

*Fig. 2*. Phylogram generated from ITS+28S+ *tef1-α* combined sequence data with maximum likelihood and Bayesian analysis. Thick vertical black bars show the root branch for the specific lineage indicated by the adjacent label. Thick horizontal branches are supported by bootstrap value greater than 60% (ML) and 0.9 (BPP). PAT, Patagonia; SJ, San Juan; ARG, Argentina; CH, Chile; UR, Uruguay. T, sequences obtained from the genus type species.

*Fig. 3*. A-C, Basidiomata of *Arambarria cognata*. A. on *Diostea* (Patagonia, Argentina). B. on *Eucalyptus* (Uruguay). C. on *Eupatorium buniifolium* (Córdoba Prov., Argentina). D. Wood rot in *V. vinifera* from where isolate CIEFAPcc72 was obtained.

Suppl. Fig. 1. Phylograms generated from 28S and ITS sequence data with maximum likelihood and Bayesian analysis. Thick vertical black bars show the root branch for the specific lineage indicated by the adjacent label. Thick horizontal branches are supported by bootstrap value greater than 60% (ML) and 0.9 (BPP). PAT, Patagonia; SJ, San Juan; ARG, Argentina; CH, Chile; UR, Uruguay. T, sequences obtained from the genus type species.

Suppl. Fig. 2. Phylograms generated from 28S, ITS and *tef-α* sequence data sets with maximum likelihood and Bayesian analysis. Thick vertical black bars show the root branch for the specific lineage indicated by the adjacent label. Thick horizontal branches are supported by bootstrap value greater than 60% (ML) and 0.9 (BPP). PAT, Patagonia; SJ, San Juan; ARG, Argentina; CH, Chile; UR, Uruguay. T, sequences obtained from the genus type species.

*Table 1*. Basidiospore measurements of *Arambarria cognata* and related taxa

| Species/ Lineage | Specimen* | Mean Spore Length ± SD (L) | Mean Spore Width ± SD (W) | Spore Length | Spore Width | Q= L / W |
|---|---|---|---|---|---|---|
| *A. cognata* "destruens clade" | *destruens* type BAFC 34575 Chubut, ARG | 6.00 ± 0.31 | 4.43 ± 0.36 | 5.69-6.31 | 4.07-4.79 | 1.35 |
| | BAFC 34592 Chubut, ARG | 5.96 ± 0.22 | 4.23 ± 0.31 | 5.74-6.18 | 3.92-4.54 | 1.41 |
| | MR 12504 Chubut, ARG | 6.24 ± 0.35 | 4.60± 0.36 | 5.89-6.59 | 4.24-4.96 | 1.36 |
| | SGO160477 CHILE | 6,30 ±0,41 | 4,5 ±0,39 | 5.89-6.71 | 4.11-4.89 | 1.40 |
| *A. cognata* "cognata clade" | *cognatus* type Córdoba, ARG | 6.38 ± 0.36 | 4.55 ± 0.35 | 6.02–6.74 | 4.20-4.90 | 1.40 |
| | Urcelay 132 Córdoba, ARG | 6.10 ± 0.25 | 4.18 ± 0.35 | 5.85-6.35 | 3.83-4.53 | 1.46 |
| | Robledo 64 Córdoba, ARG | 6.09 ± 0.32 | 4.29 ± 0.30 | 5.77-6.41 | 3.99-4.59 | 1.42 |
| | Robledo 46 Jujuy, ARG | 5.97 ± 0.22 | 4.08 ± 0.25 | 5.75-6.19 | 3.83-4.33 | 1.46 |
| | Robledo 788 Jujuy, ARG | 5.94 ± 0.19 | 4.04 ± 0.12 | 5.75-6.13 | 3.92-4.16 | 1.47 |
| *A. cognata* "uruguay clade" | Linares URU | 6.85 ± 0.27 | 4.21 ± 0.21 | 6.58-7.12 | 4.0-4.42 | 1.63 |
| | MVHC 5001 URU | 6.37 ± 0.49 | 4.14 ± 0.18 | 5.88-6,86 | 3,96-4.32 | 1.54 |
| | CGP 557 URU | 6.39 ± 0.35 | 4.21 ± 0.27 | 6.04-6.74 | 3.94-4,48 | 1.52 |
| *Inocutis jamaicensis* | *jamaicensis* RLG15819, USA | 6.38 ± 0.45 | 4.51 ± 0.37 | 5.93-6,83 | 4.14-4,88 | 1.41 |
| | *jamaicensis* Hawks98525, USA | 6.63 ± 0.41 | 4.72 ± 0.34 | 6.22-7.04 | 4.38-5,06 | 1.40 |
| | *jamaicensis* Canf71121, USA | 6.86 ± 0.28 | 4.89 ± 0.34 | 6.58-7.14 | 4.55-5.19 | 1.40 |
| *Inocutis rheades* | *rheades* type FRANCE | 6.98 ± 0.20 | 5.01 ±0,47 | 6.78-7.18 | 4.54-5.48 | 1.39 |

*number of spores measured per specimen = 30. For specimen's data see text
ARG: Argentina, URU: Uruguay

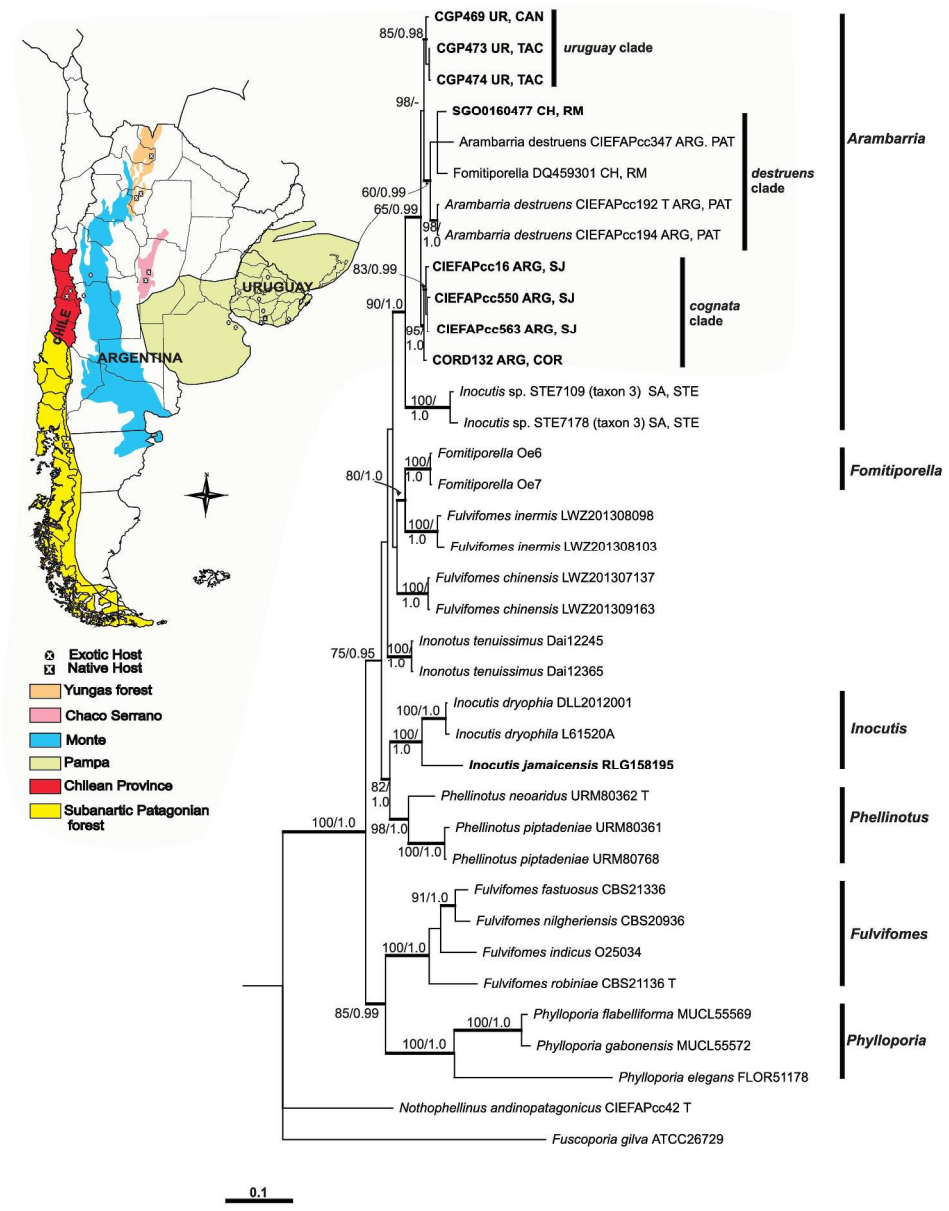


Fig. 1. Phylogenetic relationships of Arambarria inferred from ITS and LSU sequences via maximum likelihood (ML) and Bayesian (BA). Thick vertical black bars shows the root branch for the specific lineage indicated by the adjacent label. Thick branches in bold are supported by bootstrap value greater than 60% (ML) and 0.9 (BPP). PAT, Patagonia; SJ, San Juan; ARG, Argentina; CH, Chile; SA, South Africa; UR, Uruguay; USA United States of America; TAC, Tacuarembó; CAN, Canelones; STE, Stellenbosch. Sequences in bold were generated in this study. T, sequences obtained from the genus type species.

266x339mm (300 x 300 DPI)

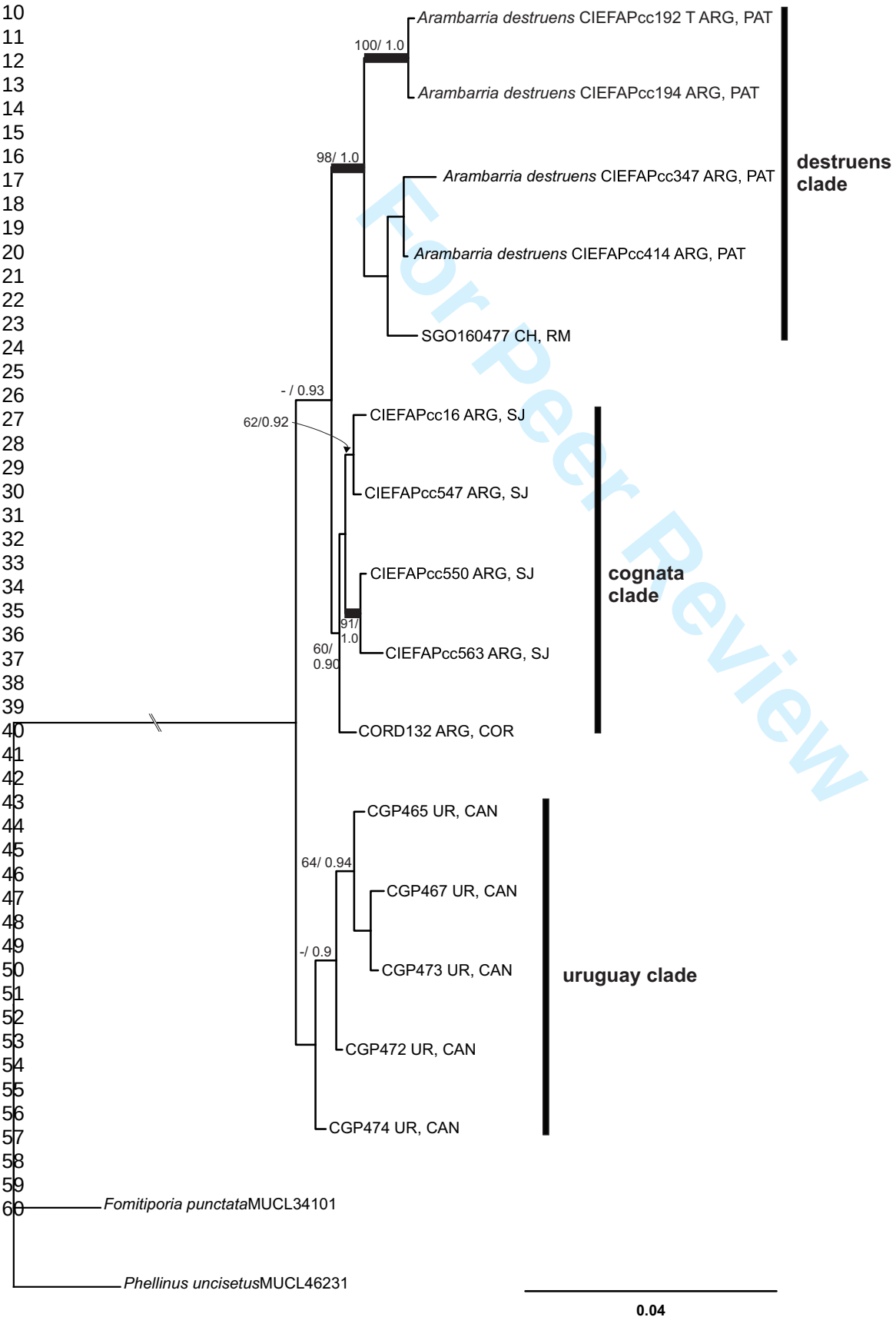

Table 2. Concise basidiospores size variation in specimens from different clades.

| *Arambarria cognata* clades | Spore size range (µm) | Q variation |
|---|---|---|
| destruens | 5.69-6.71 × 3.92–4.96 | 1.36–1.40 |
| cognata | 5.75–6.74 × 3.83–4.90 | 1.40–1.47 |
| uruguay | 5.88–7.12 × 3.94–4.48 | 1.52–1.63 |