

## *Perenniporiella chaquenia* sp. nov. and further notes on *Perenniporiella* and its relationships with *Perenniporia* (Poriales, Basidiomycota)

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**Abstract:** *Perenniporiella chaquenia* sp. nov. is described from Argentina. New records of *P. pendula* and *P. micropora* are discussed. A key to *Perenniporiella* species is presented. Preliminary phylogenetic relationships of *Perenniporiella* are inferred from parsimony and Bayesian analysis of a combined set of DNA sequence data (nuclear ribosomal partial LSU and ITS). It demonstrated that *Perenniporiella* forms a well resolved monophyletic clade distantly related to *Perenniporia* s.s. It also clearly showed that within *Perenniporia* as usually conceived other morphologically homogeneous group of taxa, such as the *P. ochroleuca* or *P. vicina* alliances, form well resolved clades, which could be recognized as distinct genera. The differentiation of the hyphal system and the basidiospores morphology are outlined as critical features for the definition of genera in the *Perenniporia* complex.

**Key words:** Neotropical polypores, phylogeny, taxonomy

### INTRODUCTION

In the frame of a revision of *Perenniporia*<sup>3</sup> Decock and Ryvardeen (2003) established *Perenniporiella* for a group

of three morphologically homogeneous species, namely *Perenniporiella neofulva* (syn.: *Perenniporia piperis* (Rick) Rajchenb., *Perenniporia albida* Wright & Rajchenb.), *Perenniporiella micropora*, and *Perenniporiella pendula*. However little is known about the last two species.

As a continuation of the studies of Neotropical *Perenniporia* s.l. (Decock and Herrera Figueroa 2000, Decock and Ryvardeen 1999, 2000, 2003) several field trips in Cuba and Argentina yielded new materials of the three known species of *Perenniporiella* and several collections of an additional taxon that could not be assigned to any of the *Perenniporiella* or *Perenniporia* s.l. species. Inferences of their phylogenetic relationships based on both partial nuclear ribosomal LSU and ITS DNA sequences data are discussed below. *Perenniporiella chaquenia* sp. nov. is described and a key to the species of *Perenniporiella* is provided.

### MATERIALS AND METHODS

**Morphology.**—Herbarium specimens are preserved at CORD and MUCL (herbarium acronyms are from Holmgren et al 1990). Strains in this study are preserved at BCCM/MUCL. Colors are described according to Kornerup and Wanscher (1981). Specimens were examined in Melzer's reagent, lactic acid cotton blue (Kirk et al 2001) and KOH 4%. All microscopic measurements were carried out in Melzer's reagent. In presenting the sizes of the microscopic elements 5% of measurements were excluded from each end and are given in parentheses, when relevant.  $\bar{x}$  = arithmetic mean,  $R$  = the ratio of length/width of basidiospores,  $\bar{x}_R$  = arithmetic mean of the ratio  $R$  and  $n$  = number of specimens examined. Thirty basidiospores were measured except when noted.

**Sequencing.**—The DNA was extracted from freshly collected mycelium from pure culture grown in liquid malt at 25 C in the dark. Extractions were carried out with the QIAGEN Dneasy plant Mini Kit (QIAGEN Inc.) and purified with GeneClean® III kit (Q-Biogene) following the manufacturer's recommendations. Primer pairs LROR-LR6 and NS7-ITS4 (White et al 1990) were used to amplify respectively the 5' end of the nr LSU DNA regions and ITS regions. Successful PCR reactions resulted in a single band observed on a 0.8% agarose gel, corresponding respectively to approximately 1200 and 900 bp. Polymerase chain reaction products were cleaned with the QIAquick® PCR purification kit (250) (QIAGEN Inc.) following the manufacturer's protocol. Sequencing reactions were performed with CEQ DTCS Quick Start Kit® (Beckman Coulter), according to the manufacturer's recommendations, with the primers LROR, LR3, LR3R, LR5 for the LSU and ITS1, ITS2, ITS3

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<sup>3</sup>Authorships of taxonomic names (TABLE I) are not repeated in the text.

TABLE I. Species/collections/sequences used in the phylogenetic studies and their GenBank accession numbers

Genus/species names Voucher specimens/cultures reference	Locality	GenBank accession numbers	
		28S	ITS
<b><i>Perenniporiella</i> Decock &amp; Ryvarden</b>			
<i>P. chaquenia</i> Robledo & Decock			
MUCL 47647 (PT)	Argentina	FJ393855	FJ411083
MUCL 47648 (PT)	Argentina	FJ393856	FJ411084
MUCL 49758 (T)	Argentina	FJ393857	FJ411085
<i>P. pendula</i> Decock & Ryvarden			
MUCL 46034	Cuba	FJ393853	FJ411081
MUCL 47129	Cuba	FJ393854	FJ411082
<i>P. micropora</i> (Ryvarden) Decock & Ryvarden			
MUCL 43581	Cuba	FJ393858	FJ411086
<i>P. neofulva</i> (Lloyd) Decock & Ryvarden			
MUCL 45091	Cuba	FJ393852	FJ411080
<b><i>Perenniporia</i> Murrill</b>			
<i>P. medulla-panis</i> (Jacq.:Fr.) Donk			
MUCL 43250 (T)	Norway	FJ393875	FJ411087
MUCL 49581	Poland	FJ393876	FJ411088
<i>P. cf. medulla-panis</i>			
MUCL 47876	China	FJ393879	FJ411089
<i>P. cf. medulla-panis</i>			
MUCL —	USA	FJ393878	FJ411090
MUCL 45934	Thailand	FJ393877	FJ411091
<i>P. martius</i> (Berk.) Ryvarden			
MUCL 41677	Argentina	FJ393859	FJ411092
MUCL 41678	Argentina	FJ393860	FJ411093
<i>P. fraxinea</i> (Bull.: fr.) Ryvarden			
MUCL 39326	France	FJ393861	FJ411094
<i>P. vicina</i> (Lloyd) Decock & Ryvarden			
MUCL 44779	Ethiopia	FJ393862	FJ411095
<i>P. subacida</i> (Petch) Donk			
MUCL 31402	Japan	FJ393880	FJ411103
<i>P. detrita</i> (Berk.) Ryvarden			
MUCL 42649	French Guyana	FJ393866	FJ411099
<i>P. ohiensis</i> (Berk.) Ryvarden			
MUCL 41036	USA	FJ393863	FJ411098
<i>P. ochroleuca</i> var. <i>brevispora</i> Corner			
MUCL 39726	Taiwan	FJ393865	FJ411098
<i>P. ochroleuca</i> (Berk.) Ryvarden			
MUCL 39563	Australia	FJ393864	FJ411097
<b><i>Abundisporus</i> Ryvarden</b>			
<i>A. violaceus</i> (Wakef.) Ryvarden			
MUCL 38617	Zimbabwe	FJ393867	FJ411100
<i>A. sclerosetosus</i> Decock & Laurence			
MUCL 41438 (T)	Singapore	FJ393868	FJ411101

TABLE I. Continued

Genus/species names Voucher specimens/cultures reference	Locality	GenBank accession numbers	
		28S	ITS
<i>A. cf. roseoalbus</i> (Jungh.) Ryvarden			
MUCL 49583	China	FJ393869	FJ411102
MUCL 49622	China	FJ393870	FJ411107
<i>Abundisporus sp.</i>			
MUCL 49566	China	FJ393871	FJ411108
<b><i>Donkioporia</i> Kotl. &amp; Pouz.</b>			
<i>D. expansa</i> (Desm.) Kotl. & Pouz.			
MUCL 35116	Belgium	FJ393872	FJ411104
<b><i>Pyrofomes</i> Kotl. &amp; Pouz.</b>			
<i>P. demidoffii</i> (Lev.) Kotl. & Pouz.			
MUCL 41034	Russia	FJ393873	FJ411105
<b><i>Microporellus</i> Murrill</b>			
<i>M. violaceo-cinerascens</i> (Petch) David & Rajchenb.			
MUCL 45229	Ethiopia	FJ393874	FJ411106

T, PT = Type, Paratype.

and ITS4 for the ITS regions (biology.duke.edu/fungi/mycology/primers). Nucleotide sequences were determined with a CEQ 2000 XL capillary automated sequencer (Beckman Coulter).

**Phylogenetic analysis.**—Nucleotide sequences initially were aligned automatically with Clustal X for Macintosh 1.5b, then manually adjusted as necessary with the editor in PAUP\* (4.0b10). The final LSU-ITS dataset comprised 29 sequences (23 taxa, TABLE I) and 1603 characters, including gaps. Ninety-five characters are excluded as ambiguously aligned. A total of 1108 characters are constant and 292 were parsimony informative.

Compatibility of datasets was tested with the partition homogeneity test (Farris et al 1995) as implemented in PAUP\* 4.0b10 (Swofford 2002).

Modeltest 3.06 (Posada and Crandall 1998) was used to evaluate the model of nucleotides substitution that best fit the provided dataset. The hierarchical likelihood ratio test was used to select the best-fit model.

Phylogenetic analysis of the aligned sequences was performed with the maximum parsimony method of PAUP\* 4.0b10 (Swofford 2002) and MrBayes 2.01 (Huelsenbeck and Ronquist 2001), both with gaps treated as missing.

The most parsimonious trees were identified with the best model of nucleotide as selected by Modeltest and a heuristic searches with random addition sequence (1000) and further evaluated by bootstrap analysis (bv), retaining clades compatible with the 50% majority rules in the bootstrap consensus tree. Analysis conditions were tree bisection addition branch swapping (TBR), starting tree obtained via stepwise addition, steepest descent not in effect, MULTREES effective.

The Bayesian phylogenetic tree was reconstructed with the

best model of nucleotide as selected by Modeltest. Two independent runs, each with four simultaneous Markov chains, were executed for  $1 \times 10^6$  generations, starting from random tree, keeping one tree every 100 generations. All topologies sampled before the average standard deviation reaching 5% were discarded as burn-in. The remaining trees were used to calculate a 50% majority rules consensus tree and to determine the posterior probabilities (bpp) for the individual branches. MAP tree with maximum posterior probability was determined with MESQUITE 2.01. (Madison and Madison 2004).

**Sequences.**—See TABLE I.

## RESULTS

**Compatibility of the LSU and ITS datasets.**—As a result of the partition homogeneity test, the two datasets were shown to be fully congruent ( $P > 0.05$ ), letting us combine them.

**Model of nucleotide substitution.**—The general time reversible model (GTR + I + G) was shown as the best fitting model. Variable sites were assumed to follow a gamma distribution (shape: 0.8207). Of the 10 000 trees obtained, the first 156 have been eliminated because they were obtained before the convergence.

Seven most parsimonious trees (MPT) resulted from the combined LSU-ITS based heuristic search (1460 steps in length, CI = 0.503, RI = 0.651, RC = 0.328). Two main topologies were recovered, being mostly concordant regarding the recovery of the different clades and their relative positions. (One tree is shown in

TABLE II. Pore size (pores/mm and pore diam in  $\mu\text{m}$ ) and basidiospore size ( $\mu\text{m}$ ) of *Perenniporiella* species

Species Status/herbarium	Pores		Basidiospores	
	Pores/mm	Range ( $\mu\text{m}$ )	$\bar{x}$ ( $\mu\text{m}$ )	Range ( $\mu\text{m}$ )
<b><i>P. neofutava</i></b>				
BRAZIL (Type)	6-7	(100)-100-157-(180)	126	(3.5)-3.5-4.5-(4.5) $\times$ (3.0)-3.0-4.0-(4.0)
ARGENTINA, Misiones ( <i>P. albida</i> Type)	7-8	no data		(3.5)-3.5-4.0-(4.5) $\times$ (3.0)-3.0-3.5-(3.5)
BRAZIL, Sao Leopoldo ( <i>P. piperis</i> Type)	7-8	(80)-89-150-(160)	125	(3.5)-3.5-4.5-(4.5) $\times$ (3.0)-3.0-4.0-(4.0)
BRAZIL, Cananea (SP 233707)	7-9	(72)-81-123-(124)	102	(3.5)-3.5-4.5-(5.0) $\times$ (3.0)-3.0-4.0-(4.0)
BRAZIL, Cananea (SP 233706)	5-6	(80)-88-120-(140)	104	(3.5)-3.5-4.5-(4.5) $\times$ (3.0)-3.0-3.5-(3.5)
BRAZIL, Sao Paulo (SP250939)	5-6(-7)	(80)-88-128-(128)	106	(3.5)-3.5-4.5-(4.5) $\times$ (3.0)-3.0-4.0-(4.0)
BRAZIL, Ubatuba (LR 24229, O, SP 213027)	7-8	(80)-80-104-(104)	91	(3.5)-3.5-4.5-(5.0) $\times$ (3.0)-3.0-4.0-(4.0)
BRAZIL, Cananea (LR 24801, O, SP 213599)	7-8(-9)	(76)-80-108-(120)	96	(3.5)-3.5-4.0-(4.0) $\times$ (3.0)-3.0-3.5-(3.5)
GUADALUPE, Petit Bourg (LY-AD)	7-8	(76)-76-112-(112)	91	(3.5)-3.5-4.5-(4.5) $\times$ (3.0)-3.0-4.0-(4.0)
<b><i>P. micropora</i></b>				
PERU, Huanoco, Tingo Maria (Type)	8-10	(56)-60-87-(100)	72	(4.5)-4.5-5.5-(5.5) $\times$ (4.0)-4.0-4.5-(4.5)
COSTA RICA (LR 29822)	10-12	(52)-60-84-(92)	70	(4.0)-4.0-5.0(-5.0) $\times$ (3.5)-3.5-4.0-(4.5)
CUBA, Sierra del Rosario (MUCL 43581)	8-9(-10)	75-87.5(-100)	82	(4.5)-4.5-5.0(-5.0) $\times$ (3.0)-3.5-4.0(-4.0)
<b><i>P. pendula</i></b>				
COLOMBIA, Nariño (Type)	7-(8)	(92)-92-131-(140)	112	(4.5)-5.0-6.0-(6.0) $\times$ (4.0)-4.5-5.0-(5.0)
CUBA, Topes de Collantes (MUCL 46034)	7-9	(75)-87.5-112.5(-125)	100	(5.0)-5.5-6.0(-6.0) $\times$ (4.0)-4.5-5.0(-5.0)
ARGENTINA, Jujuy (Robledo 393 CORD)	(6)-7-8(-9)	(66)-78-108(-120)	95	(4.5)-4.5-5(-5.5) $\times$ (3.5)-4.4-4.5(-5)
ARGENTINA, Salta (Robledo 1665 CORD)	(5)-6(-7)	(100)-110-150(-160)	129	(4.5)-5-5.5(-6) $\times$ (4-) 4-5(-5)
ARGENTINA, Salta (Robledo 1413 CORD)	(6)-7-8(-9)	(72)-78-96(-96)	86	(5-) 5-6(-6.5) $\times$ (4-) 4-5(-5.5)
<b><i>P. chaquenia</i></b>				
ARGENTINA, Córdoba (Type)	4-6	85-104(-110)	96	(5.5)-5.5-6.5(-7.5) $\times$ (4.5)-4.5-5.5(-5.5)
ARGENTINA, Córdoba (MUCL C47648)	4-6	(87.5)-100-113(-125)	106	(5.5)-5.5-6.0(-6.5) $\times$ (4.5)-4.5-5.0(-5.5)
ARGENTINA, Córdoba (MUCL C47647)	5-6(-7)	(75)-88-138(-162)	110	(5.5)-5.5-6.0(-6.5) $\times$ (4.0)-4.5-5.5(-5.5)
ARGENTINA, Córdoba (MUCL 49772)	4-6	(73)-80-104(-122)	90	(6.0)-6.0-6.5(-7.5) $\times$ (4.5)-4.5-5.5(-6.0)
ARGENTINA, Córdoba (MUCL 49773)	4-5(-7)	(73)-85-104(-110)	94	(6.0)-6.0-6.7(-7.2) $\times$ (4.8)-4.8-5.4(-6.0)
ARGENTINA, Córdoba (MUCL 49777)	4-6	(67)-73-104(-110)	87	(4.8)-5.4-6.0(-6.5) $\times$ (4.2)-4.8-5.4(-6.0)

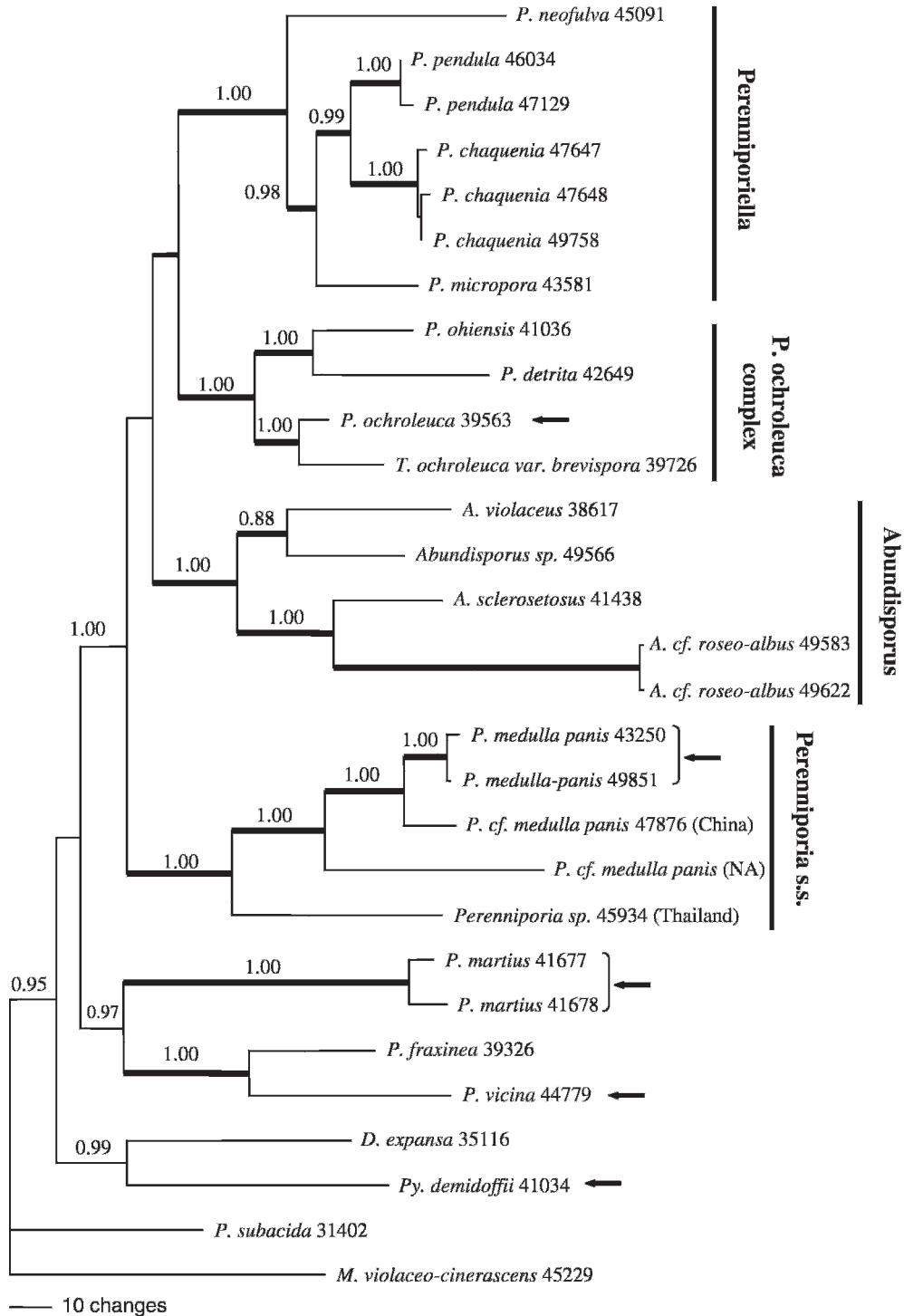


FIG. 1. One of the seven most parsimonious trees obtained from a heuristic search. *P* = *Perenniporia*; *Pa* = *Perenniporiella*; *T* = *Truncospora*; *A* = *Abundisporus*; *Py* = *Pyroformos*; *M* = *Microporellus*; *D* = *Donkioporia*; arrow indicates species for which a basidiospores germ pore has been evidenced by TEM studies. Numbers above branches = bvp; branches in bold = bp > 0.8.

FIG. 1.) Bayesian inference (MAP tree) yielded the same overall topology. Posterior probabilities of the MAP tree (205,100 generation; LnL: -8023.152) are added to the tree (FIG. 1).

*Perenniporiella* formed a strongly supported clade (bv 100%, bpb 1.00), distinct from the *Perenniporia* s.s. clade (bv 100%, bpb 1.00). All the morphologically based species of *Perenniporiella* are resolved as



terminal branches that are well supported for *P. pendula* and *P. chaquenien* revealing their status as individual species whereas *P. neofulva* and *P. micropora* are represented by a single sequence.

Members of *Perenniporia s.l.* (Ryvarden 1991, Ryvarden and Gilbertson 1994) included in our analysis, which represents a selection based on an analysis including a much larger number of species (Decock unpubl), are not all related to *P. medulla-panis s.s.* but dispersed into different, variably related clades, such as the *P. ochroleuca* complex (Decock and Ryvarden 1999a) or the *P. vicina* (Decock and Ryvarden 1999a) and *P. martius* alliances (Decock 2001). Other clades confidently confirmed correspond to morphologically homogenous alliances of species, such as the *Abundisporus* clade (bv 99%, bpp 1.00). However the relationships of these clades (or morphological alliances) are not resolved confidently in the current analysis, the basal branches being weakly supported or unsupported. In the Bayesian consensus tree the *Perenniporia s.s.*, *Abundisporus*, *P. ochroleuca* and *Perenniporiella* clades all collapse to form a large polytomous clade without internal hierarchy.

#### TAXONOMY

##### *Perenniporiella chaquenien* Robledo & Decock sp. nov.

FIGS. 2–12

Mycobank: MB 513051.

Basidiocarpo annuo ad biannuum, effusio ad effusum-reflexum, usque ad  $10 \times 5 \times 0.5$  cm. Superficie pilei crenea, alba in margine ad castaneam claram in basi; contexto cremeo claro, usque ad 2 mm crasso; poris circularibus, 4–6 per mm; systema hypharum dimitica, cum hyphis generativis hyalinis tenuitunicatis, 2–3.5  $\mu\text{m}$  et hyphis skeletis crassitunicatis, hyalinis et cyanophilis; contexto cum hyphis sceletis non ramosis ad pauce ramosas, pauce dextrinoidis 2.5–3.5  $\mu\text{m}$  ( $\bar{x} = 2.9 \mu\text{m}$ ) trama cum hyphis skeletis laxis arboriformibus, dextrinoidis, stipite 25–80(–93)  $\mu\text{m}$  longo ( $\bar{x} = 45 \mu\text{m}$ ), 2–3  $\mu\text{m}$  lato ( $\bar{x} = 2.5 \mu\text{m}$ ); ramulis 1–3, usque ad 245  $\mu\text{m}$  longis, 2–2.5  $\mu\text{m}$  latis; basidiis claviformibus, 14–23  $\times$  8–9  $\mu\text{m}$ ; basidiosporis ample ellipsoidis ad subgloboseas, hyalinis, crassitunicatis, cyanophilis et dextrinoidis, 5.5–6(–6.5)  $\times$  4.5–5(–5.5)  $\mu\text{m}$ ; chlamydosporis nullis.

HOLOTYPUS hic designatus: Argentina, Córdoba, Dpto Colón, Río Ceballos, Camino el Cuadrado (31°7'30S 64°19'44O) in ramulo mortuo *Celtis tala* vivens, 2 Sep 2004, Robledo 1720, in Herbario CORD conservatus est (ISOTYPUS in Herbario MUCL conservatus est, MUCL 49758; cultura vivens in collectium MUCL conservatus est, MUCL 49758).

*Basidiome* seasonal to reviscent, commonly resupinate, extending up to  $100 \times 50$  mm, 5 mm thick, occasionally effused reflex, the pilear portion up to  $25 \times 10 \times 6$  mm, dimidiate, solitary or made of several pilei laterally fused, applanate and convex, the *surface*

smooth to slightly concentrically sulcate, glabrous to faintly velutinous (under the lens), whitish when fresh and young, becoming cream to pale reddish brown and sometimes dark reddish to blackish toward the base, *margin* even or lobed, whitish to pale cream; *pore surface* whitish to cream when fresh and mature, unchanged on drying; *pores* even, round, 4–6/mm, ( $\bar{x} = 5$ ,  $n = 40$ ), (75–)88–137(–162)  $\mu\text{m}$  diam, ( $\bar{x} = 92 \mu\text{m}$ ,  $n = 30$ ); *dissepiments* smooth, entire, (42–)68–85(–105)  $\mu\text{m}$  thick ( $\bar{x} = 67 \mu\text{m}$ ,  $n = 120$ ); *context* homogeneous, up to 2 mm thick at the base in the reflexed portion, whitish to pale cream, with a fibrous consistency and texture; *tube layer* not stratified, concolorous with the context, with a corky consistency and a fibrous texture, up to 4 mm thick in the reflexed portion; *hyphal system* dimitic in the context and the trama of the tubes; *generative hyphae* difficult to observe, with clamps (clamps present at all septa on hyphae in culture), hyaline, thin-walled, 2–3.5  $\mu\text{m}$  thick; *vegetative hyphae* hyaline, cyanophilous, weakly dextrinoid in the context to strongly dextrinoid in the trama of the tubes; *context* mainly composed of nonbranched to sparingly branched vegetative hyphae, straight to sinuous, thick-walled, 2.5–3.5  $\mu\text{m}$  ( $\bar{x} = 2.9 \mu\text{m}$ ) in the main part; *trama* mainly composed of branched vegetative hyphae, with a loose arboriform branching pattern, with an unbranched, little differentiated, thick-walled basal stalk, 25–80(–93)  $\mu\text{m}$  long, ( $\bar{x} = 45 \mu\text{m}$ ), 2–3  $\mu\text{m}$  wide ( $\bar{x} = 2.5 \mu\text{m}$ ), straight to geniculated, then occasionally with lateral aborted processes and slightly widened at the apical branching point, branching of 1–3 levels, the branches long (< 245  $\mu\text{m}$ ,  $\bar{x} = 134 \mu\text{m}$ ), 2–2.5  $\mu\text{m}$  wide ( $\bar{x} = 2.1 \mu\text{m}$ ), thick-walled, straight to sinuous; *cystidia* absent; *basidia* clavate, with a basal clamp, hyaline, thin-walled, 14–23  $\times$  8–9  $\mu\text{m}$ , with four small sterigmata; basidioles clavate, clamped, hyaline, thin-walled, 14–22  $\times$  7–8  $\mu\text{m}$ ; *basidiospores* broadly ellipsoid to subglobose, thick-walled, with a small apiculus, hyaline, smooth, dextrinoid and cyanophilous, (4.8–)5.5–6.6(–7.5)  $\times$  (4.0–)4.5–5.8(–6.0)  $\mu\text{m}$  ( $\bar{x} = 6.1 \times 5.0 \mu\text{m}$ ),  $R = (1.0\text{--})1.1\text{--}1.4(1.7)$  ( $\bar{x}_R = 1.23$ ); *chlamydosporis* absent.

*Substratum*. dead branches attached to living *Celtis tala* (Ulmaceae).

*Type of rot*. white rot (laccase tested with syringaldazine [Harkin and Obst 1974]).

*Distribution*. known only from the Chaquean Mountain forests of central Argentina in Córdoba Province.

*Additional representative specimens examined*: ARGENTINA, PROVINCIA CÓRDOBA: Dpto Colón, Camino al Pan de Azúcar, 24°45'46.8"S, 64°42'58.1"W, 1950 m elevation, on dead stem of living *Celtis tala*, 4 Nov 2000, Robledo 23 (CORD); Río Ceballos, camino El Cuadrado, 31°7'30.8"S, 64°19'44.6"W,

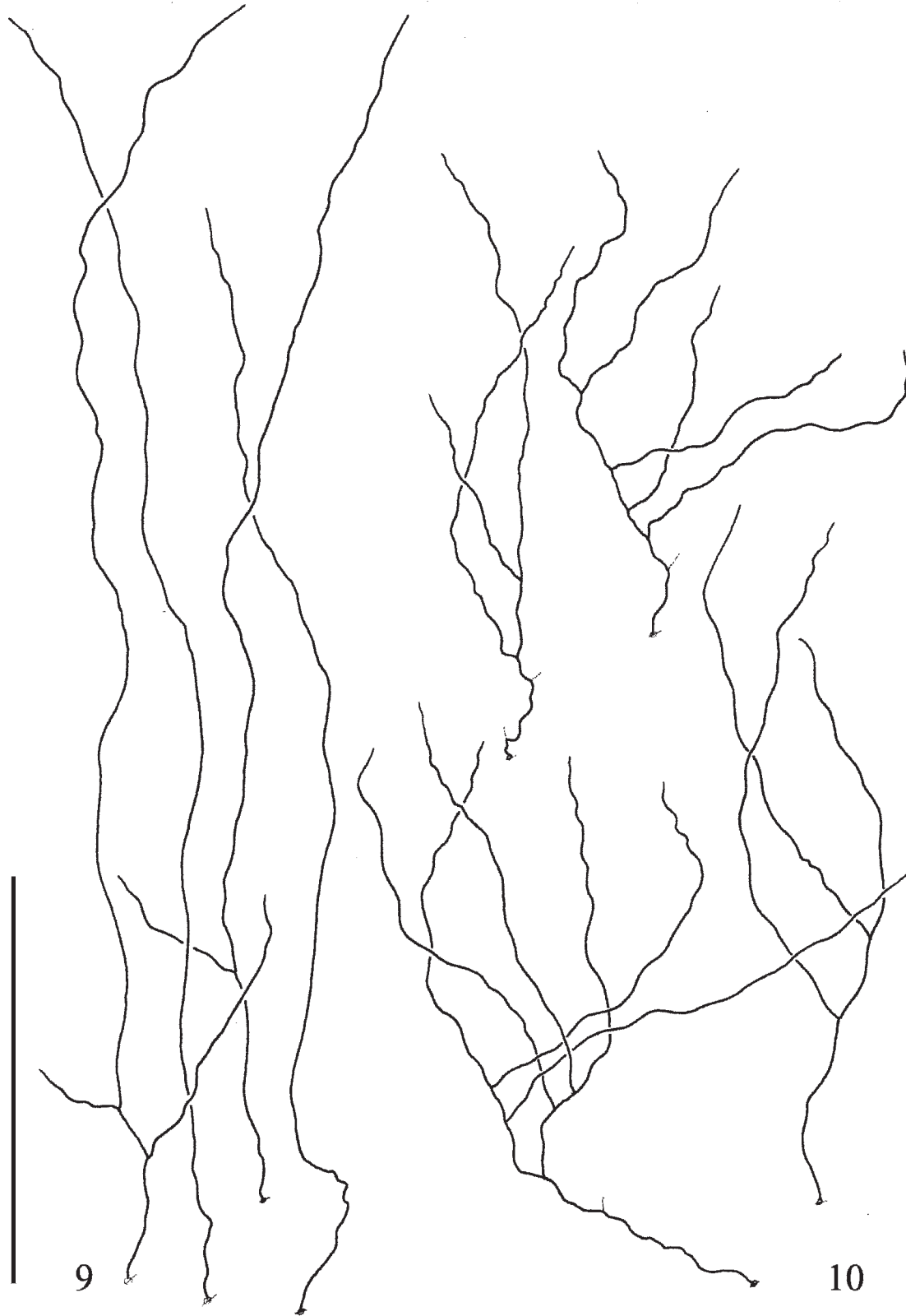




FIGS. 2–8. Macroscopic features of basidiomes of *Perenniporiella chaquenia* and *P. pendula*. 2–6. *P. chaquenia* (from Robledo 1720 HOLOTYPE CORD). 2. Basidiome, general view, bar = 1 cm. 3. pilear surface, bar = 0.5 cm. 4. Section trough basidiome showing context and tube layer, bar = 0.5 cm. 5–6. Details of the pore surface, bars = 0.5 cm. 7–8. *Perenniporiella pendula* (from Robledo 393 CORD, MUCL 49775) from NW Argentina. 7. Young pendant basidiome, bar = 0.5 cm. 8. Mature effused-reflexed basidiome, bar = 1 cm.

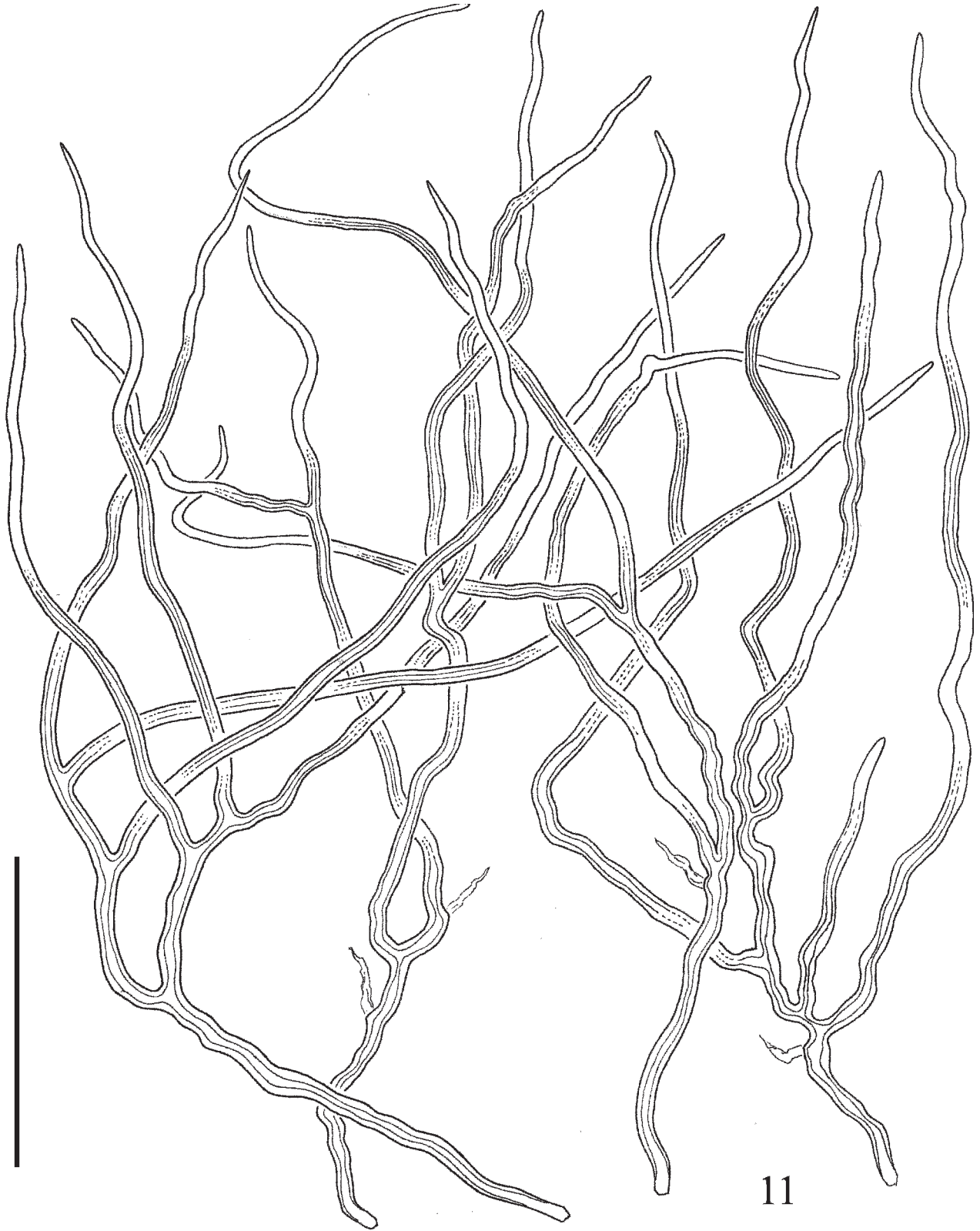
850 m elevation, on dead branch of living *Celtis tala*, 1 Apr 2001, Robledo 35 in CORD and MUCL (MUCL 49772); Reserva Hídrica La Quebrada, 31°8'5.6"S, 64°21'21.2"W, 950 m elevation, on dead branch of living *Celtis tala* in

Chaquena Mountains forests, 3 Apr 2006, Robledo 736 in CORD and MUCL (MUCL 47647, culture ex. MUCL 47647); Ibid Robledo 737 in CORD and MUCL (MUCL 47648, culture ex. MUCL 47648).

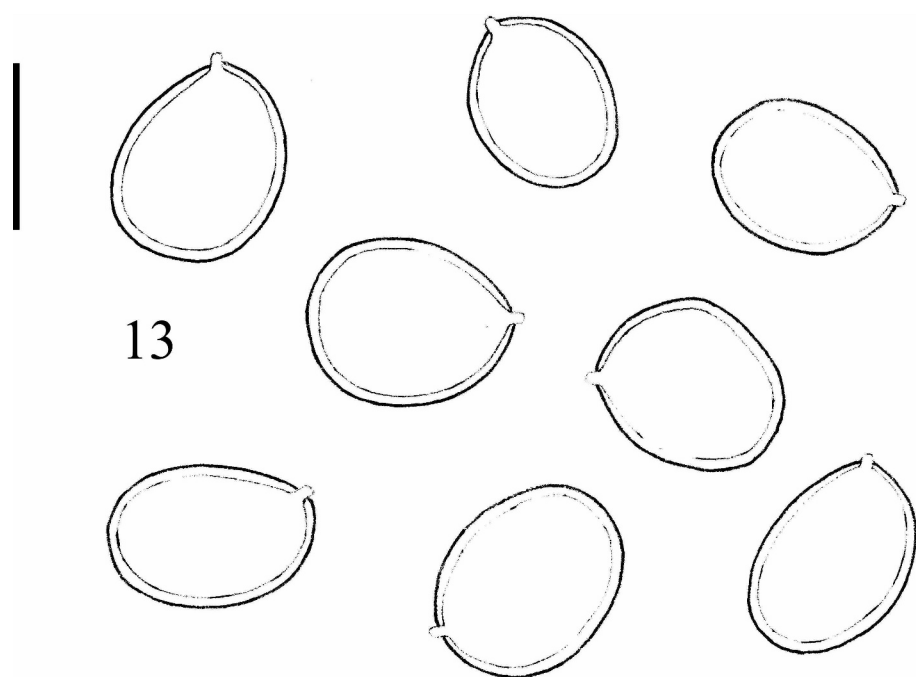
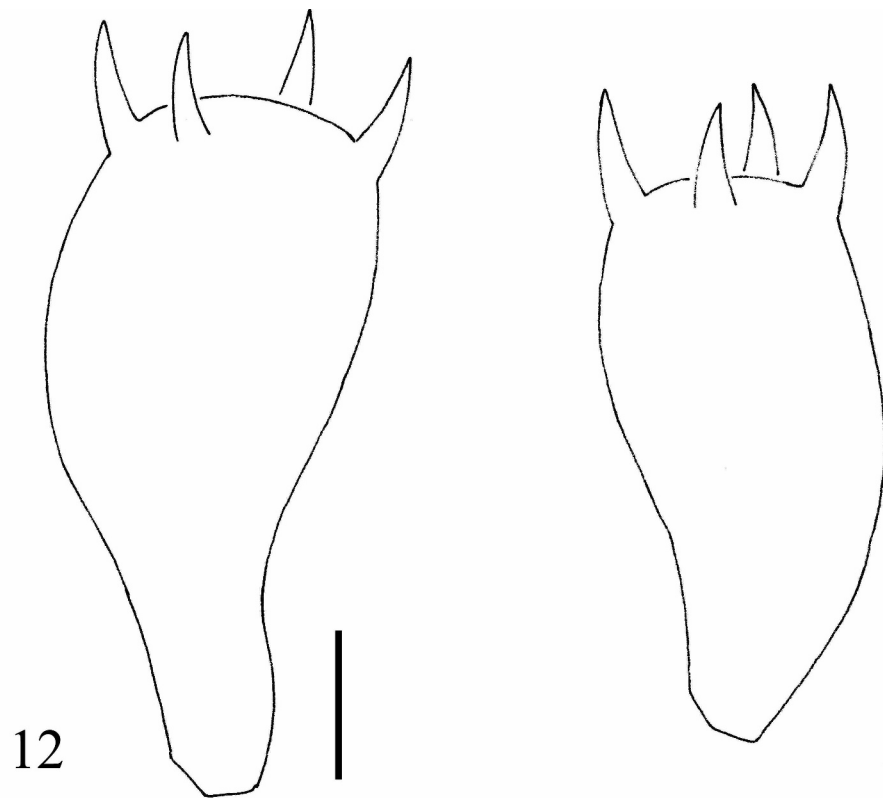


FIGS. 9–13. *Perenniporiella chaquenia*, microscopical features (from *Robledo 736* CORD, MUCL 47647). 9–10. Vegetative hyphae from the context (9) and the trama of the tubes (10), schematic. Bar = 100  $\mu$ m. 11. Vegetative hyphae from the trama. Bar = 40  $\mu$ m. 12. Basidia. Bar = 5  $\mu$ m. 13. Basidiospores. Bar = 5  $\mu$ m.





FIGS. 9-13. Continued.



FIGS. 9-13. Continued.

*Remarks.*—*Perenniporiella chaquenya* has all the typical features of *Perenniporiella*, including the hyphal system (FIGS. 2–4) and the basidiospores morphology (FIG. 6). The species is characterized macroscopically by a usually resupinate to occasionally effused reflexed basidiome and medium sized pores.

*P. chaquenya* is comparable microscopically to *P. pendula*, with which it shares the basidiospores shape and size and the vegetative hyphae morphology. It differs in having larger and commonly widely effused basidiome and 4–6 pores/mm ( $\bar{x}$  = 5/mm) with thick dissepiments, compared to 7–9/mm ( $\bar{x}$  = 7.4/mm) in *P. pendula*. These species also have different ecological requirements as reflected in their habitat. *Perenniporiella chaquenya* so far has been found growing only on dead but still attached branches of living *Celtis tala*, in Chaquean Mountains forest of central Argentina (District “Chaqueño Occidental”, Cabrera 1976). These xerophilous forests are characterized by precipitation occurring mainly in summer and is 600–900 mm/y (average 480 mm/y), with dry and cold winters (Capitanelli 1979). *Perenniporiella pendula* (see below) originates from different, more humidity-buffered ecosystems (cloud/humid mountain forests) and occurs on decayed, fallen branches or twigs.

*Perenniporiella chaquenya* and *P. pendula* also are closely related phylogenetically (FIG. 1). They both form a well supported subclade together with *P. micropora*. *Perenniporiella neofulva* is more distant from the other three. This genetic divergence is also reflected in some morphological traits. *Perenniporiella neofulva* differs from all other *Perenniporiella* species in having larger and thicker, denser pilei and distinctly smaller basidiospores, on average ca. 4  $\mu$ m (TABLE II).

#### Notes on other species of *Perenniporiella*

*Perenniporiella pendula* Decock & Ryvar den, Mycol. Res. 107:99, 2003. FIGS. 13–14

*Perenniporiella pendula* was described on the basis of a single collection originating in Colombia (Decock and Ryvar den 2003). Since then the species has been collected in Cuba and Argentina, and the description is implemented below.

*Basidiome* seasonal, mainly pileate or with a slightly to broadly decurrent pore surface, solitary or 2–3 pilei laterally fused; *pileus* pendant and attached by a small discoid base to flabelliform, broadly attached, lobed, to 20 mm long, 25 mm wide, 4–5 mm thick, smooth to faintly concentrically sulcate, glabrous to faintly velutinous (under the lens), dull, white near the margin, progressively changing to cream, grayish orange (5B5), to light brown (6C[5–6], cinnamon) toward the base, with a few narrow light brown to brick red concentric zones; *margin* even or lobed,

thick, obtuse, white to pale cream; *pore surface* whitish to pale cream (probably white when fresh); *pores* even, round, 7–9/mm, (66–)75–121(–150) ( $\bar{x}$  = 100  $\mu$ m); *dissepiments* smooth, entire, (24–)30–60(–84)  $\mu$ m thick ( $\bar{x}$  = 40  $\mu$ m,  $n$  = 90); *context* homogeneous, 2–3 mm thick, pale cream to pale grayish orange, with a corky consistency, a fibrous texture, velvety to the touch; *tube layer* not stratified, concolorous with the context, with a corky consistency and a fibrous texture, up to 1.5 mm thick; *crust* absent; *hyphal system* dimitic in the context and the trama of the tubes; *generative hyphae* difficult to observe, with clamp, hyaline, thin-walled, 2–3  $\mu$ m wide; *vegetative hyphae* hyaline, slightly to distinctly cyanophilous, nondextrinoid in the context, weakly to strongly dextrinoid in the trama of the tubes, slightly swelling in KOH; *context* mainly composed of non-branched to sparingly branched vegetative hyphae, straight to sinuous, thick-walled but with a wide lumen, progressively widening from 2.5–3.5  $\mu$ m wide at the basal septum to 2.5–4.0  $\mu$ m wide ( $\bar{x}$  = 3.4  $\mu$ m) in the main part; *trama* mainly composed of branched vegetative hyphae, with a loose arboriform branching pattern, with an unbranched, barely differentiated, thick-walled basal stalk, 25–84(–90)  $\mu$ m long, ( $\bar{x}$  = 53  $\mu$ m), 2.0–3.5  $\mu$ m wide ( $\bar{x}$  = 2.7  $\mu$ m), with local (often apical) swelling to 6–9  $\mu$ m diam, straight to geniculated, then occasionally with lateral aborted processes, and 1–3 sparingly ramified, long (< 250  $\mu$ m long) apical branches, 1.5–2.0  $\mu$ m wide ( $\bar{x}$  = 1.7  $\mu$ m), thick-walled, straight to sinuous; few mature *basidia* observed, then clavate, clamped at the basal septum, hyaline, thin-walled, 14–16  $\times$  7–8  $\mu$ m, with four small sterigmata; *basidioles* clavate, hyaline 10–14  $\times$  5–7  $\mu$ m; *basidiospores* subglobose to globose, thick-walled, with a small apiculus, 0–1 guttulate, hyaline, weakly dextrinoid, which is more conspicuous when seen in mass, cyanophilous, (4.5–)4.5–6.0(–6.0)  $\times$  (3.5–)4.0–4.8(–5.0)  $\mu$ m,  $R$  = (1.0–)1.1–1.3(–1.5) ( $\bar{x}$  = 5.2  $\times$  4.4  $\mu$ m,  $\bar{x}_R$  = 1.2); *cystidia* and *chlamydospores* absent.

*Substratum.* dead, rotten branches of angiosperm (on *Dichrostachys cinerea* [Fabaceae] in Cuba).

*Type of rot.* white rot (laccase tested with syringaldazine) (Harkin and Obst 1974).

*Distribution.* known from Colombia (type locality), Cuba and NW Argentina.

*Type specimen:* COLOMBIA, PROVINCIA NARIÑO: Pasto Cicante, Reserva Planada, 30 Jul 1998, G. Müller (O, Holotype, MUCL 43375, Isotype).

*Additional specimens examined:* ARGENTINA, PROVINCIA JUJUY: Dpto Ledesma, Calilegua National Park, Mesada Las Colmenas, La Cascada path, 23°42'1.5"S, 64°51'56.8"W, 1170 m elevation, on dead branch of unidentified angiosperm, 6 Mar 2005, Robledo 393 in CORD and MUCL (MUCL 49775); Ibid, Abra de Cañas, 23°40'38.2"S, 64°53'46.3"W, 1730 m elevation, on dead

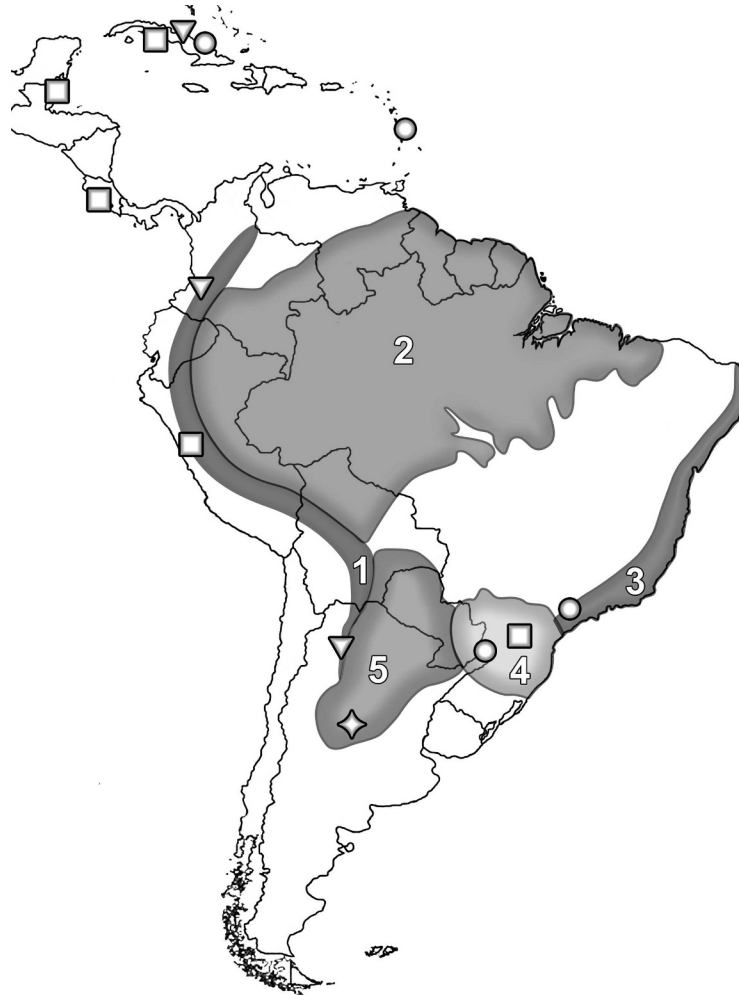


FIG. 14. Distribution of *Perenniporiella* species and the main forests types of the Amazonian domain in South America.  $\blacklozenge$  = *P. chaquenia*,  $\square$  = *P. micropora*,  $\circ$  = *P. neofulva*,  $\nabla$  = *P. pendula*, 1 = Yungas forests, 2 = Amazonian forests, 3 = Atlantic forests, 4 = Paranaense forests, 5 = Chaco forests. (Modified from Brown et al 2001).

branch, 21 May 2007, *Robledo 1513* in CORD; Dpto San Antonio, Dique Los Alisos,  $24^{\circ}15'33.3''S$ ,  $65^{\circ}19'55.4''W$ , 1392 m elevation, on dead branch, 21 Feb 2007, *Robledo 887* in CORD; PROVINCIA SALTA: Dpto Anta, El Rey National Park, Pozo Verde,  $23^{\circ}42'1.5''S$ ,  $64^{\circ}51'56.8''W$ , 1303 m elevation, on dead branch of unidentified angiosperm, 26 May 2007, *Robledo 1665* in CORD and MUCL (MUCL 49771); Ibid, "Las Chuñas" path,  $24^{\circ}43'1.5''S$ ,  $64^{\circ}38'51.5''W$ , 886 m elevation, on dead branch, 24 Mar 2007, *Robledo 1005* in CORD; Ibid, "El Chañar" hill,  $24^{\circ}45'46.8''S$ ,  $64^{\circ}42'58.1''W$ , 1950 m elevation, on dead branch, 28 May 2007, *Robledo 1683* in CORD; Dpto La Caldera, Abra de la Sierra, National road n° 9,  $24^{\circ}31'12''S$ ,  $65^{\circ}20'56.8''W$ , 1531 m elevation, on dead branch, 19 Feb 2007, *Robledo 847* in CORD; Dpto Santa Victoria Oeste, Baritu National Park, path to "Campo Grande",  $22^{\circ}26'10''S$ ,  $64^{\circ}43'40''W$ , 1190 m elevation, on dead branch of unidentified angiosperm, 09 May 2007, *Robledo 1413* in CORD and MUCL (MUCL 49776); Ibid, *Cedrella lilloi* forests in the path between Lipeo and Baritu,  $22^{\circ}27'20.8''S$ ,  $64^{\circ}44'34.5''W$ ,

1653 m elevation, on dead branch, 8 May 2007, *Robledo 1351* in CORD; CUBA, PROVINCIA SANCTI SPIRITUS: Topes de Collantes, on dead fallen branches of *Dichrostachys cinerea*, in secondary forest, 15 Sep 2004, *Cony Decock CU/04-161*, MUCL 46034 (culture ex. MUCL 47129 = CRGF 349); on dead fallen branches of *Dichrostachys cinerea*, in secondary forest, 20 Sep 2005, *Cony Decock & Sara Herrera Figueroa CU/05-182*, MUCL 47129 (culture ex. MUCL 47129 = CRGF 763).

*Remarks.*—*Perenniporiella pendula* is characterized by a pendant to broadly attached basidiomes, occasionally with a decurrent part, easily detachable when mature, a dimitic hyphal system with unbranched to sparingly branched vegetative hyphae in the context, then with a wide lumen, branched vegetative hyphae in the trama, then with a loose arboriform branching pattern, and subglobose to globose, dextrinoid basidiospores. The vegetative hyphae are nondextri-



noid in the context but are dextrinoid in the trama of the tubes.

The species currently is known from northwestern (NW) Argentina, Colombia and Cuba (FIG. 14). In Argentina the species so far has been collected only in the NW subtropical mountains forests, known as the Andean Yungas Forest (Brown 2005), which is a cloud mountainous ecosystem. These forests constitute the southernmost extremity of the Neotropical mountain forests (FIG. 14), with precipitation of 1000–2000 mm/y, depending on altitude (Brown et al 2001). In Cuba the species also was collected in wet, tropical forest above 700 m (“bosque pluvial de montaña”, Capote 1984).

*Perenniporiella micropora* (Ryvarden) Decock & Ryvarden, Mycol. Res. 107:99, 2003.

≡ *Perenniporia micropora* Ryvarden, Mycotaxon 28:533, 1987.

A description of this species can be found in Decock and Ryvarden (2003).

*Type specimen:* PERU: Dpto Huanoco: Parque National Tingo Maria, ca. 5 km from Tingo Maria, on the Tingo Maria-Monzon Road, 2600 ft. elevation., on undetermined log, 6 Jul 1976, *K.P. Dumont PE-1039* (O, Isotype).

*Additional specimens examined:* COSTA RICA: PROVINCIA PUNTARENAS: Carara Biological Reserva, 50 m. elevation, 14 Jun. 1991, *L. Ryvarden 29822* (O, MUCL, USJ55794); CUBA, PROVINCIA PINAR DEL RÍO: Reserva de la Biosfera “Sierra del Rosario”, Soroa, on dead fallen branch of unidentified angiosperm, 11 Sep. 2001, *C. Decock and S. Herrera Figueroa CU-184*, in MUCL as MUCL 43581 (culture ex. MUCL 43581 = CRGF 509).

*Remarks.*—The species so far has been known from two collections originating in Peru (type locality) and Costa Rica. It since has been reported from Belize (Ryvarden 2007), Brazil (Ryvarden and de Meijer 2002) and here is reported from western Cuba. The duplex context, with an upper soft and loose layer and a lower more compact layer and the small pores (8–10[12]/mm) are characteristics that distinguish the species in the genus.

#### DISCUSSION

Traditionally, and since Corner’s (1932, 1953) precursor works, the differentiation of the generative hyphae into various forms of so-called vegetative hyphae to form the hyphal systems (mono-, di- or trimitic) have played a pivotal role in the taxonomy of polypores. Basidiospores features including wall thickness and chemical composition (shown by various reactions in staining reagent—mainly iodine and cotton blue—(Gilbertson and Ryvarden 1986, Ryvarden 1991) and

the type of rot (Nobles 1965, 1971, Gilbertson and Ryvarden 1986) also are critical features.

However in most treatments of *Perenniporia* (e.g. Dai et al 2002, Gilbertson and Ryvarden 1987, Lehmkuhl Gerber et al 1999, Niemelä et al 1992, Núñez and Ryvarden 2001, Ryvarden and Johansen 1980, Ryvarden and Gilbertson 1994), although with the remarkable exception of Corner (1987, 1989), the diversity of hyphal systems and vegetative hyphae have been rarely emphasized or critically analyzed (however see e.g. Decock 2001, 2007, Decock and Ryvarden 1999a, b, Decock and Stalpers 2006b, Decock et al 2007). The genus was (and still is) variously described as di- or trimitic without much further qualification of the vegetative hyphae morphology with, as a consequence, the merging of different hyphal constructions (Corner 1993, Decock 2001, 2007). Moreover the basidiospores ultrastructure and especially the presence, ontogenesis and resulting morphology of a germ pore (Capellano 1973, Keller 1974, 1986) were poorly considered, if at all (Decock 2007).

This situation, combined with a historically unclear generic concept based on an uncertain type species (Decock and Stalpers 2006a, b), has resulted in fine in a large but morphologically heterogeneous assemblage of taxa of presumably distant (see Corner 1993, Decock et al 2000, Decock 2001, 2007) or uncertain affinities (see Decock and Ryvarden 1999a, Decock et al 2001). Smaller, morphologically based entities obviously could be recognized within *Perenniporia s.l.* based on such characters as differentiation of the vegetative hyphae and/or basidiospores morphology (Corner 1993, Decock 2007, Decock and Ryvarden 1999, 2003, Decock et al 2001).

However from a cladistic standpoint the pertinence of these characters and the entities they potentially delimit were barely evaluated with other nonmorphological data such as DNA sequences data.

*Perenniporiella* illustrates the case to some extent. The genus was established on the basis of such morphological features as the basidiospores morphology and vegetative hyphae differentiation, both considered as critical and deviating from *Perenniporia s.s.* (Decock and Ryvarden 2003). The hyphal system thus was characterized as dimitic with variably branched vegetative hyphae in the context, non- to sparingly, loosely arboriform and skeletobinding hyphae with a poorly differentiated arboriform pattern in the hymenophoral trama. Intermediates exist between the unbranched vegetative hyphae of the context and the arboriform skeletobinding hyphae on the hymenophoral trama, forming in fine a continuum from one extreme to the other (see also e.g. Decock and Laurence 2001). Basidiospores are

subglobose to globose (FIG. 6) and without germ pore (at least under optical microscopy).

*Perenniporiella chaquenia* share these main morphological characteristics with *P. neofulva* (type species), *P. pendula* and *P. micropora*, justifying the generic placement. These species also are more closely related to each other phylogenetically than to *P. medulla-panis* s.s. (FIG. 1), supporting their segregation into a different generic entity.

*Perenniporia* s.s. based on its type species *P. medulla-panis* (Decock and Stalpers 2006a) presents a morphologically related hyphal system, dimitic with arboriformly branched skeletobinding (Decock and Stalpers 2006b). It differs from *Perenniporiella* in its basidiospores characterized by a large apical germ pore whose development finally causes the apex to collapse, producing the typical truncate aspect (Decock 2007, Decock and Stalpers 2006b). *Perenniporia medulla-panis* s.s. and related species (the *P. medulla-panis* complex) also form a monophyletic clade distinct from the *Perenniporiella* clade.

The affinities of *Perenniporiella* and of *Perenniporia* s.s. are not clearly resolved in the current analysis and in all probability would require a more extended taxon sampling and possibly other molecular markers. However they both belong to the polyporoid clade and in all probability to the core polyporoid clade as defined by Binder et al (2005).

Members of *Perenniporia* as commonly accepted (*Perenniporia* s.l.) are not all closely related to *P. medulla-panis*, as shown in the present analysis, but instead are scattered into distinct clades. Each of these clades also represents a singular combination

of morphological traits (synapomorphies) that support recognition at genus level, despite the fact that their relationships with *Perenniporia* s.s. and within the polyporoid clade are not yet fully resolved.

Consequently other taxonomic entities will doubtless emerge from *Perenniporia* s.l., for example the *P. vicina* complex (Lloyd) Decock & Ryvardeen, which corresponds partly to *Vanderbylia* Reid (Reid 1973, Decock and Ryvardeen 1999a), the *P. martius* (Berk.) Ryvardeen complex, which also partly corresponds to *Vanderbylia* Reid (Reid 1973, Decock 2001), the *P. ochroleuca* (Berk) Ryvardeen complex, corresponding to *Truncospora* Pilát ex Pilát, (Decock and Ryvardeen 1999a), along with the *P. contraria*/*P. subannosa* group (Decock et al 2001) or the *P. subacida* complex. These complexes are internally homogeneous as regards their hyphal system, vegetative hyphae differentiation and basidiospores morphology including ultrastructure (synapomorphies). They also are resolved as monophyletic clades in DNA based phylogenetic analysis (Decock pers obs). They will be treated separately.

*Perenniporiella* is known so far only from South and Central America, Cuba, possibly constituting its northernmost limit of distribution, and down to central Argentina (FIG. 14). It might represent an endemic New World genus. Analysis of a set of about 200 DNA sequences data (both partial LSU and ITS) of *Perenniporia* s.l. species originating from both tropical and temperate areas has failed to reveal for the time being any related species outside the Neotropics.

PRELIMINARY ANNOTATED KEY TO THE SPECIES OR SPECIES COMPLEX WITHIN NEOTROPICAL *PERENNIPORIA* S.L.  
HAVING A PILEATE BASIDIOM

- 1 Basidiospores apically sub- to distinctly truncate, with an apical germ pore . . . . . 2
- 1' Basidiospores not apically truncate but might appear angular on drying, germ pore absent . . . . . 7
- 2 Basidiome stipitate; seasonal . . . . . *Perenniporia stipitata* Ryvardeen  
For a description, see Ryvardeen (1987) and Decock and Ryvardeen (1998).
- 2' Basidiome sessile, seasonal to perennial . . . . . 3
- 3 Vegetative hyphae unbranched and strongly dextrinoid, both in the context and the trama of the tubes; basidiospores ovoid-elongated (pip-shaped), apically narrowed and subtruncate, dextrinoid; basidiome usually large, with a thick dark crust . . . . . *Hormodermoporus* Teix.  
= *P. martius* (Berk.) Ryvardeen 1972;  
For a description, see Decock and Herrera Figueroa (2000) and Ryvardeen and Johansen (1980).
- 3' Some vegetative hyphae branched, at least in the trama of the tubes, variably dextrinoid; basidiospores ellipsoid to subglobose, distinctly apically truncate, variably dextrinoid . . . . . 4
- 4 Basidiospores ellipsoid, apically largely truncate, equal or longer than 10 µm; vegetative hyphae in the context mostly unbranched, skeletal-like, to sparingly branched in the hymenophoral trama . . . . .  
. . . . . *Truncospora* Pilát ex Pilát complex  
= *Perenniporia detrita* (Berk.) Ryvardeen, *P. ohioensis* (Berk.) Ryvardeen, and *P. ochroleuca* (Berk.) Ryvardeen; these species have been reported from the Neotropics, however careful examinations of the collections are necessary to ascertain the identity of the taxa present in the area. For a description see Decock and Ryvardeen (1999a).
- 4' Basidiospores on average shorter than 10 µm; vegetative hyphae in the trama always branched, usually with an arboriform branching pattern . . . . . 5

- 5 Basidiome strongly concentrically sulcate, brown to dark brown; context and trama pale brown to brown; vegetative hyphae faintly yellowish to yellow brownish; basidiospores on average shorter than 6  $\mu\text{m}$  long . . . . . 6
- 5' Basidiome not concentrically sulcate, whitish, cream (to brown); context whitish to pale grayish orange, tubes darker, cream-colored to grayish orange; vegetative hyphae hyaline not to faintly dextrinoid; basidiospores 7–9  $\times$  4–5  $\mu\text{m}$  . . . . . *Perenniporia sprucei* Decock & Ryvar den  
For a description see Decock and Ryvar den (1999a).
- 6 Pore surface grayish; tube layers and context brown, grayish brown; pores 8–10/mm; basidiospores ellipsoid to subglobose, 5.0–6.5  $\times$  4–4.5  $\mu\text{m}$  . . . . . *Perenniporia inflexibilis* (Berk.) Ryvar den  
*Perenniporia inflexibilis* is usually found with completely resupinate basidioma but occasionally can develop pilei when growing on vertical substrate. For a description see Ryvar den and Johansen (1980).
- 6' Pore surface white; tube layer and trama wood- to pinkish brown; pores (5)–6–7/mm; basidiospores ellipsoid 3.5–4.0  $\times$  2.5–3  $\mu\text{m}$  . . . . . *Perenniporia* cf. *decurrata* Corner  
*Perenniporia decurrata* originally was described from southeastern Asian tropical forest (Corner 1989). It has been collected recently in tropical South America (Venezuela and French Guyana, unpubl). For a description see Corner (1989).
- 7 Vegetative hyphae unbranched and strongly dextrinoid, both in the context and trama of the tubes; basidiospores ellipsoid to broadly ellipsoid, thick-walled, not dextrinoid; pileus (creamy) but mainly brown to dark brown; context and tube layer whitish to creamy . . . . . 8
- 7' Vegetative hyphae always branched in the trama of the tubes, unbranched to branched in the context, dextrinoid or not; basidiospores subglobose, weakly dextrinoid; pileus white, whitish creamy to grayish orange, more rarely light brown from the base; context and tube layer creamy to grayish orange . . . . . *Perenniporiella* Decock & Ryvar den
- 8 Margin of the pileus progressively sharpened; pores (5)–6–8 /mm, 70–104  $\mu\text{m}$  diam; skeletal hyphae in the context 2.5–4.0  $\mu\text{m}$  diam . . . . . *Perenniporia contraria* (Berk. & Curtis) Ryvar den  
For a description see Decock et al (2001).
- 8' Margin of the pileus abrupt, rounded; pores 3–4(–5)/mm, 100–220  $\mu\text{m}$  diam; skeletal hyphae in the context 3.5–6.7  $\mu\text{m}$  diam . . . . . *Perenniporia subannosa* (Bres.) Decock et al  
For a description see Decock et al (2001).

KEY TO SPECIES OF *PERENNIPORIELLA*

- 1 Context heterogeneous (duplex), with a loose upper layer and a denser lower layer; pores 8–10(–12)/mm . . . . . *Perenniporiella micropora*
- 1' Context homogeneous. . . . . 2
- 2 Basidiospores on average less than 5  $\mu\text{m}$  long, 3.5–4.5  $\times$  3–4  $\mu\text{m}$  . . . . . *Perenniporiella neofulva*
- 2' Basidiospores on average longer than 5  $\mu\text{m}$  . . . . . 3
- 3 Pores 8–9/mm; basidiospores subglobose to globose, 4.5–6.0  $\times$  4.0–4.8  $\mu\text{m}$ , on average 5.2  $\times$  4.5  $\mu\text{m}$  . . . . . *Perenniporiella pendula*
- 3' Pores 5–7/mm; basidiospores broadly ellipsoid to subglobose, 5.5–6.6(–6.5)  $\times$  4.5–5.8  $\mu\text{m}$ , on average 6.1  $\times$  5.0  $\mu\text{m}$  . . . . . *Perenniporiella chaquenia*

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