

# *Schizophyllum leprieurii* and the *Schizophyllum umbrinum* lineage (Agaricales, Basidiomycota) in Argentina

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► **Abstract** — Robledo, Gerardo L.; Orlando F. Popoff; Leonardo Amarilla; Jean-Marc Moncalvo; Carlos Urcelay. 2014. "*Schizophyllum leprieurii* and the *Schizophyllum umbrinum* lineage (Agaricales, Basidiomycota) in Argentina". *Lilloa* 51 (1). During the survey of wood decaying fungi in NW and Central Argentina, particular collections of *Schizophyllum* were found that macromorphologically (small brown basidiomata with orange-brown lamellae) resemble *Schizophyllum umbrinum*. On the basis of molecular evidence (ITS and LSU rDNA sequence analysis) and micromorphological examination it was found that they represent two species: *Schizophyllum leprieurii* Linder and *Schizophyllum cf. umbrinum*. *Schizophyllum leprieurii* Linder is a new record for Argentina and represents the southernmost and an extra tropical record of the species. Our results showed that *S. leprieurii* and *S. cf. umbrinum* are monophyletic within the *Schizophyllum umbrinum* lineage, a group in need of modern taxonomic revision.

**Keywords:** neotropical rare species, ITS, LSU, phylogeny, morphology, taxonomy.

► **Resumen** — Robledo, Gerardo L.; Orlando F. Popoff; Leonardo Amarilla; Jean-Marc Moncalvo; Carlos Urcelay. 2014. "*Schizophyllum leprieurii* y el linaje *Schizophyllum umbrinum* (Agaricales, Basidiomycota) en Argentina". *Lilloa* 51 (1). Durante el estudio de los hongos degradadores de la madera en el noroeste y el centro de Argentina se coleccionaron materiales particulares de *Schizophyllum*, que por su macromorfología (pequeños basidiomas marrones con laminillas marrón-anaranjadas) se parecían a *Schizophyllum umbrinum*. Sobre la base de evidencias moleculares (análisis filogenético de las secuencias de ADN ribosomal ITS y LSU) y análisis micromorfológicos, se encontró que representan dos especies: *Schizophyllum leprieurii* Linder y *Schizophyllum cf. umbrinum*. *Schizophyllum leprieurii* constituye un nuevo registro para Argentina y representa el registro más austral y extra tropical de la especie. Nuestros resultados muestran que *S. leprieurii* y *S. cf. umbrinum* son monofiléticos dentro del "linaje *Schizophyllum umbrinum*", un grupo que necesita una revisión taxonómica moderna.

**Palabras clave:** Especies neotropicales raras, ITS, LSU, filogenia, morfología, taxonomía.

## INTRODUCTION

*Schizophyllum* Fr. is a fungal genus easily recognizable by its macromorphology, mainly by the lamellar hymenophore with radial excentric lamellae that are longitudinally split at their edge. Due the particularity of its lamellar hymenophore, the genus has

been traditionally treated within the Agaricales (Singer, 1949) even though some authors suggested that it was related to cyphellaceous fungi in the Polyporales (Cooke, 1961). Based on morphological (*i.e.*, hyphal construction of the basidiome and basidiospores) and molecular evidence, Nakasone (1996) included *Schizophyllum amplum* (Lév.) Nakasone in the genus, a species with smooth hymenophore. Recent works dealing

with Agaricales in a phylogenetic framework have shown that *Schizophyllum* forms a monophyletic group, closely related to *Fistulina* Bull. and *Porodisculus* Murrill; these three genera were referred as the «schizophylloid clade» (Moncalvo *et al.*, 2002; Bodensteiner *et al.*, 2004; Matheny *et al.*, 2006). The only extensive taxonomic studies of the genus were by Cooke (1961) and Linder (1933). Despite the existence of several nomenclatural combinations and described species, most of them are generally considered synonyms of *Schizophyllum commune* Fr. Of the currently accepted species (Cooke, 1961) only one, *i.e.* *S. commune*, is regularly reported in surveys of fungal diversity around the world. *Schizophyllum commune* is the most widely known species of the genus, with a cosmopolitan distribution (James *et al.*, 2001), great morphological variability in shape and color, and of taxonomic/nomenclatural complexity (*cf.* synonymy, Cooke, 1961). Given its great morphological variability, little attention has been paid to species of this group during field works and, up to now, there are no modern taxonomic and systematic treatments of the genus.

*Schizophyllum umbrinum* Berk. has been often reported from South America. It is characterized by a particular combination of macroscopical features, *i.e.* basidiome with a brown pilear surface with a whitish brilliant mycelial disc in the attachment point, and notorious orange-brown to brownish lamellae. This species was originally described from Caripi, Pará State, N Brazil (Berkeley, 1851) and was reported from several regions from central and tropical America (Linder, 1933; Cooke, 1961), but it still lacks a modern description.

During our survey of wood decaying fungi in NW and Central Argentina, we found some collections of *Schizophyllum* that fit *S. umbrinum* in macromorphology. However, micromorphological and phylogenetic studies revealed that at least two different species are involved, *Schizophyllum leprieurii* Linder and *Schizophyllum cf. umbrinum*. The aim of this work is to report *Schizophyllum*

*leprieurii* in Argentina and to discuss its phylogenetic position within the genus.

## MATERIALS AND METHODS

**Microscopy.**— Microscopic examinations and measurements were done on freehand sections mounted in 3–5% KOH, phloxine 1% and Melzer's reagent as mounting media. Materials studied are kept at CORD and CTES herbaria. Herbarium acronyms are from Thiers (2014).

**DNA extraction, amplification, and sequencing.**— DNA was extracted from dry basidiomata tissue using the CTAB method described in Doyle and Doyle (1990). ITS and LSU rDNA amplifications used primer pairs were ITS8-F / ITS6-R (Dentinger *et al.*, 2010) and LROR / LR5 (White *et al.*, 1990), respectively. PCR reactions were performed in 25 mL reaction tubes with 1.13 Reddy Mix TM PCR Master Mix (2.5 mM MgCl<sub>2</sub>) (AB-geneH, Thermo Fisher Scientific Inc., UK) following the manufacturer's instructions. ITS and LSU PCR products were checked for positive amplification on 1% agarose gels, and were sent to Macrogen Inc. (Seoul, South Korea) for purification and sequencing with the BigDye™ terminator kit and run on ABI 3730XL. ITS and LSU sequences of the two specimens generated for this study have been deposited in GenBank and were combined into a dataset with additional GenBank sequences (Table 1). *Fistulina hepatica* (Schaeff.) With., *Fistulina pallida* Berk. & Ravenel and *F. antarctica* Speg. were used as outgroup taxa for the analyses.

**Phylogenetic analysis.**— The materials and sequences used in this study are listed in Table 1. DNA sequences were initially aligned with Muscle v.3.6 (Edgar, 2004 a, b), followed by manual alignment in the data editor of BioEdit V7.0.1 (Hall, 1999). Retention and consistence indexes were calculated in MEGA 5 (Tamura *et al.*, 2011). Bayesian analyses were conducted using MrBayes version 3.0b4 (Huelsenbeck and Ronquist, 2001). Models for the molecular data were

**Table 1.** List of species, collections, ecological data and sequences used in the phylogenetic analyses. Boldface Accession Numbers are new sequences obtained in this work.

Specie Voucher/Isolate - origin	Substrate Species / habitat	GenBank Accession #	
		ITS	LSU
<i>Fistulina hepatica</i> REG593-USA		AY571038	AY571004
<i>Fistulina antarctica</i> CBS701.85		DQ486702	AY293181
<i>Fistulina pallida</i> CBS 508.63		DQ486702	AY293181
<i>Schizophyllum amplum</i> A-FCUG 1803	n/d	AF141873	AF141873
B-Strain NH1803 - Spain	n/d	DQ097353	AY293169
<i>Schizophyllum commune</i> A-M162	<i>Abies beshanzuensis</i> , endophytic	HM595560	HM595606
B-BCC26414, Thailand	<i>Elaeis guineensis</i> , endophytic	FJ372690	FJ372712.
C-BCC22128, Thailand	<i>Elaeis guineensis</i> , endophytic	FJ372688	FJ372710
D-MA56	Mangrove, endophytic	GQ254677	GQ254661
E-Isolate 2IV_2_2, Thailand	<i>Elaeis guineensis</i> , endophytic	FJ372683	FJ372705
F-Isolate M34, China?	<i>Abies beshanzuensis</i> , endophytic	HM595559	HM595605
G-PDD 103380, New Zealand	n/d	KF727408	KF727350
<i>Schizophyllum fasciatum</i> CBS 267.60, Mexico	n/d	L43385	AF261589
<i>Schizophyllum radiatum</i> CBS 301.32 (AFTOL 516), Panama	n/d	AY571060	AY571023
<i>Schizophyllum umbrinum</i> A-FL02.1, Florida, USA	n/d	AF249391	AF261590
<i>Schizophyllum cf. umbrinum</i> B-Robledo 2478, Córdoba, Argentina	<i>Lithraea molleoides</i> , fallen branch	KM098067	KM098068
<i>Schizophyllum leprieurii</i> Robledo 1313, Salta, Argentina	Undetermined fallen branch	KM098065	KM098066

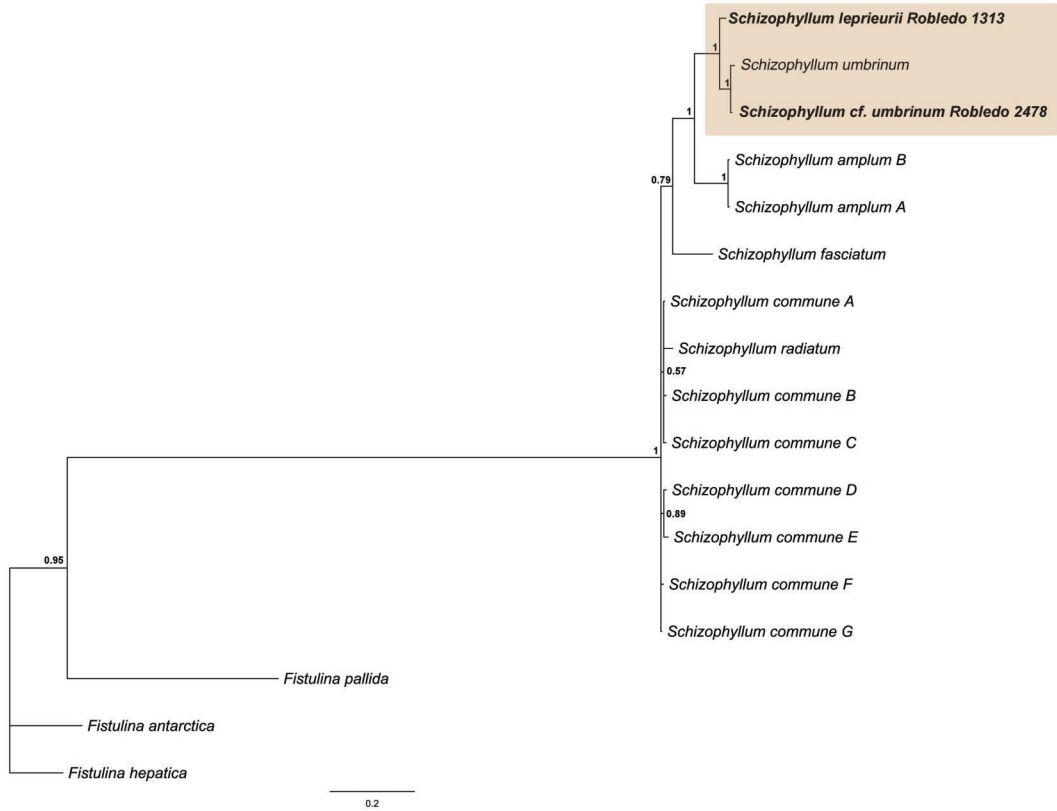
evaluated using the program jModelTest 2.1.3 (Darriba *et al.*, 2012) to find the best fit according to the Akaike information criterion (Akaike, 1974). The GTR+G + I model was found to be the most appropriate and Bayesian analyses were run with 20 million Metropolis-coupled Markov chain Monte Carlo (MCMCMC) generations with four chains, sampling trees every 100th generation. The log likelihood scores of sample points against generation time were plotted using TRACER version 1.3 (<http://evolve.zoo.ox.ac.uk/software.html>) to determine when the run reached stationarity. Nodes support was tested by posterior probabilities (PP), obtained from a 50% majority rule consensus tree after deleting 25% of the trees («burn-in»).

## RESULTS AND DISCUSSION

*Phylogenetic analyses.*— The combined ITS-LSU sequence dataset consisted of 17 taxa and 1464 characters, including gaps, of which 367 were variable and 264 were par-

simony-informative (CI = 0.86, RI = 0.90). The two Bayesian runs converged to stable likelihood values (-ln 2175.131, -ln 2230.688) after 10000000 generations. Results show that *Schizophyllum* forms a monophyletic clade (PP=1), including *S. amplum* with smooth hymenophore, being consistent with previous findings (Fig. 1) (Moncalvo *et al.*, 2002; Bodensteiner *et al.*, 2004; Matheny *et al.*, 2006). All collections preliminarily named as *S. umbrinum* group together in a well-supported clade (PP=1), hereafter named the «*S. umbrinum* lineage». Two putative species can be recognized within the *S. umbrinum* lineage; one clade consists of a single specimen from Yungas Forests of NW Argentina (PP=1); the second comprises one specimen from Chaco Serrano forests from Central Argentina and one from Florida, USA (sequence deposited as *S. umbrinum* in Genbank) (PP=1).

*Morphological analysis and taxonomic conclusions.*— *Schizophyllum leprieurii* is characterized macroscopically by the combina-



**Fig. 1.** 50% majority-rule consensus tree from Bayesian inference of the combined ITS-LSU dataset. Specimens from which new sequences were obtained in this work are in boldface. The *Schizophyllum umbrinum* lineage is indicated by a pale brown box.

tion of small brownish basidiomata with brownish lamellae and a small, whitish, brilliant mycelium disc at the attachment point to the substrate (Fig. 2A-E). Microscopically, three characters are diagnostic: yellowish-brown to brown basidiospores (Fig. 3C), a context dominated by simple septate generative hyphae with rather thick-walled gelatinized walls in KOH (Fig. 3D) and a particular hymenium with thick-walled basidia and basidioles, mainly at the apex (Fig. 3 A-C, E). Linder (1933) described *S. leprieurii* based on a single collection from French Guiana, pointing out that the species closely resembles *S. umbrinum* in color and size of basidiome, structure of context and basidia, but basidiospores were not observed. Later, Martin (1941) reported two specimens from the highlands areas in Colombia and described yellowish-brown to

brown basidiospores for this species. Based on this character, *i.e.* colored basidiospores, Cooke (1961) created *Phaeoschizophyllum* W.B. Cooke to accommodate *P. leprieurii* (Linder) W.B. Cooke. Cooke (1961) described clamp connections in the context and at the base of basidia of *S. leprieurii*, but referring to Martin’s (1941) drawings which in fact show simple septa as described by Martin himself, suggesting a mistake in Cooke’s description.

Both species, *S. umbrinum* and *S. leprieurii*, constitute the «*Schizophyllum umbrinum* stirpe» according to Singer (1959), which group species sharing basidiome color and morphology, presence of simple septa and the particular kind of hymenium composed by basidioles and basidia with thick and gelatinous walls. The two species differ in basidiospore morphology, being slightly

smaller and hyaline in *S. umbrinum* (Table 2), and in some characteristics of the abhymenial hairs, being thinner with some branched tips at the edge of lamellae in *S.*

*leprieurii* (Linder, 1933; Martin, 1941; Cooke, 1961).

All our newly collected specimens from Argentina shared the following macromor-



**Fig. 2.** Macroscopic features of Argentinian species of the *Schizophyllum umbrinum* lineage. A-E) *Schizophyllum leprieurii*. A) General view of the hymenophore. B) Detail view of the pilear surface and point of attachment. *Robledo 1313* (CORD). C) Detail view of the pilear surface and point of attachment. *Robledo 50* (CORD). D) General view of the hymenophore and the cyphelloid appearance of young basidiomata. *Robledo 408* (CORD). E) Detail view of the pilear surface and point of attachment. *Robledo 408* (CORD). F-H) *Schizophyllum* *cf.* *umbrinum*. F) General view in situ. G) Detail view of the pilear surface and point of attachment. H) Detail view of the hymenophore. *Robledo 2478* (CORD).

phological characters: relatively small brownish basidiomata, with brownish to orange-brown lamellae, with small disc of withish mycelium in the attachment point to the substrate (Figs. 2A-H). Micromorphological examinations showed that all specimens have simple septa throughout the basidiome (abhymenial hairs, contex hyphae, and at the base of basidia) (Figs. 3D-E, G), and all have yellowish-brown to brown basidiospores. At the same time they revealed a combination of morphological features, which define two morphological species that are consistent with the two clades/phylogenetic species within the *S. umbrinum* lineage recovered by the phylogenetic analysis (Fig. 1): basidia morphology and consequently, the hymenium morphology/configuration.

One species has a particular hymenium with highly thick-walled elements (basidia and basidioles) with sinuous capillary lumen (Fig. 3A-C, E), a feature that was described and illustrated for *S. leprieurii*; see for instance Plate 36-Fig. 12 by Linder (1933) and Fig. 24 by Martin (1941). At first impression it suggests an immature, sterile hymenium; however basidia in several stages of development were observed (Fig. 4). The thin capillary lumen grows up and widens towards the apex, then it emerges as a resinous drop of brown color and develops sterigmata and basidiospores and, finally, it collapses after maturation and liberation of basidiospores. Based on these features, the collection *Robledo*

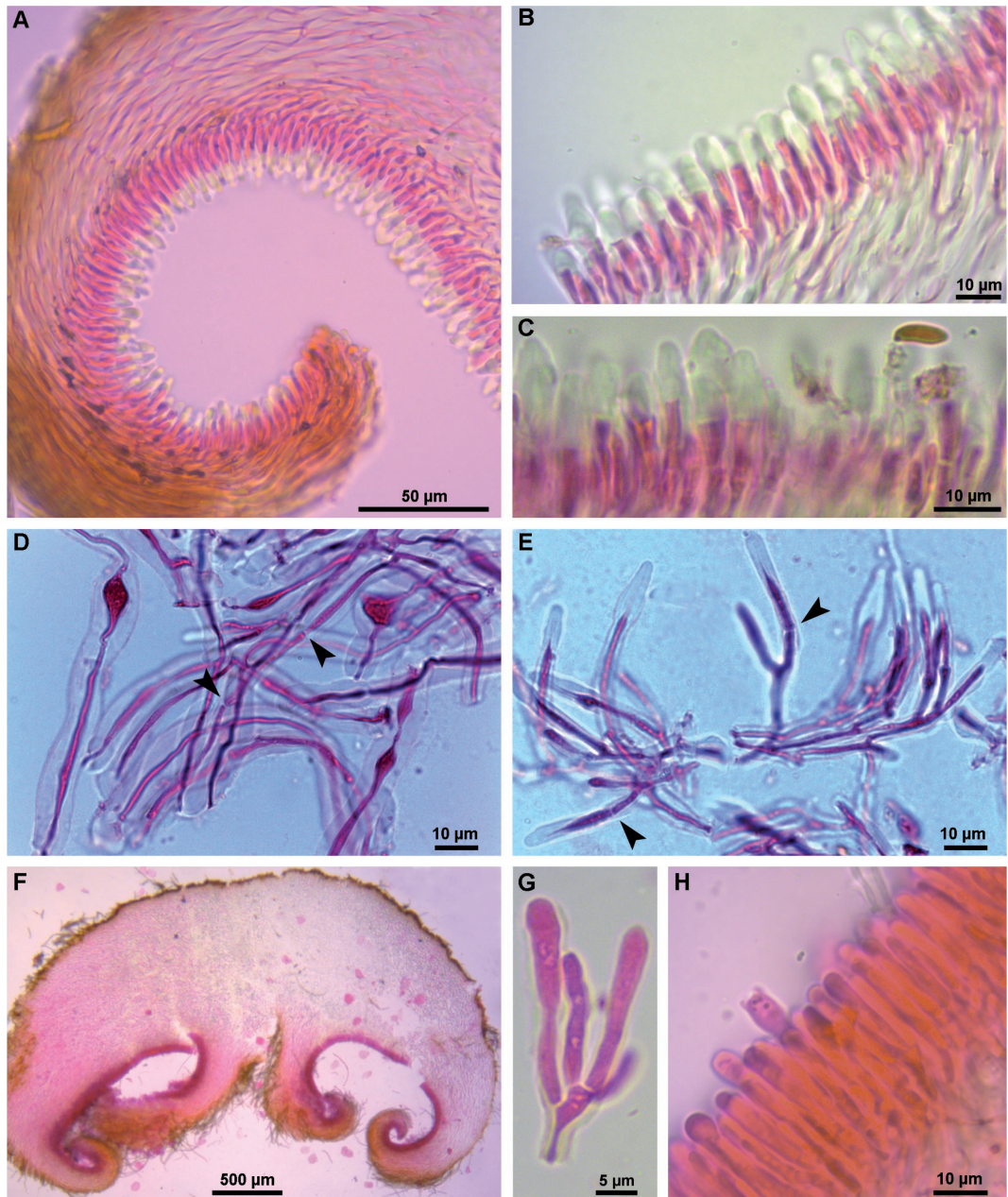
*do 1313*, which is also distinguished phylogenetically (Fig. 1), is considered to be *Schizophyllum leprieurii*.

The second species differs in the morphology of basidia and hymenium. Basidia are thick-walled at the base only (Fig. 3G) and develop in a typical palisade (Fig. 3H). This species is represented by a specimen found in subxerophytic Chaco Serrano forests in Central Argentina. In our phylogenetic analysis, it clusters with a sequence deposited in Genbank labeled *S. umbrinum* from Florida, USA. *Schizophyllum umbrinum* was described with hyaline basidiospores (Linder, 1933; Cooke, 1941), but our specimen presents yellowish-brown to brown colored basidiospores. Linder (1933) stated that basidia of *S. umbrinum* frequently present a brown secretion on the apex, suggesting that basidia and hence probably basidiospores, should present this yellowish-brown color. Unfortunately, to the best of our knowledge, no modern descriptions of *S. umbrinum* are available. In our material (*Robledo 2478* CORD) basidiospores darken as they mature since those still attached to basidia are pale yellowish while those free and/or deposited on the abhymenial hairs are yellowish-brown to brown. A revision of original and type materials should be done to clear up the situation; meanwhile we name our specimen as *Schizophyllum cf. umbrinum*.

Regarding the taxonomic position of the *Schizophyllum umbrinum* lineage, Martin

**Table 2.** Micromorphological characters of species within the *Schizophyllum umbrinum* lineage.

Species Voucher/reference	Basidiospores		
	Size ( $\mu\text{m}$ )	color	Septa
<b><i>Schizophyllum umbrinum</i></b>			
Linder (1933)	4.5-6 x 2-2.5	hyaline	simple
Cooke (1961)	4.5-6 x 2-2.5	hyaline	simple
<b><i>Schizophyllum cf. umbrinum</i></b>			
Robledo 2478 (CORD), Arg.	7-8 x 3	brown	simple
<b><i>Schizophyllum leprieurii</i></b>			
Robledo 50 (CORD), Arg.	7-8 (9) x 3-3.5	brown	simple
Robledo 1313 (CORD), Arg.	(6.5)7-8.5(10) x 2.5-3	brown	simple
Robledo 408 (CORD), Arg.	6-8 x 2.5-3	brown	simple
Linder (1933)	Not observed		n/d
Martin (1941)	6-8 x 2-2.5	brown	simple
Cooke (1961)	5.6-7.5 x 2.5-4	brown	clamped



**Fig. 3.** Microscopic features of Argentinian species of the *Schizophyllum umbrinum* lineage. A-E) *Schizophyllum leprieurii*. A) Section throughout lamellae. B) Hymenium with highly thick-walled elements with capillar sinuous lumen. C) Detail view of the hymenium with brown basidiospores. *Robledo 1313* (CORD). D) Gelatinized hyphae of the context, simple septa are indicated with black arrowheads. *Popoff 4867* (CTES). E) Thick-walled hymenial elements, simple septa are indicated with black arrowheads. *Robledo 2478* (CORD). F-H) *Schizophyllum cfr. umbrinum*. F) Section through basidiome. G) Thick-walled hymenial elements. H) Detail view of the hymenium. *Robledo 2478* (CORD).

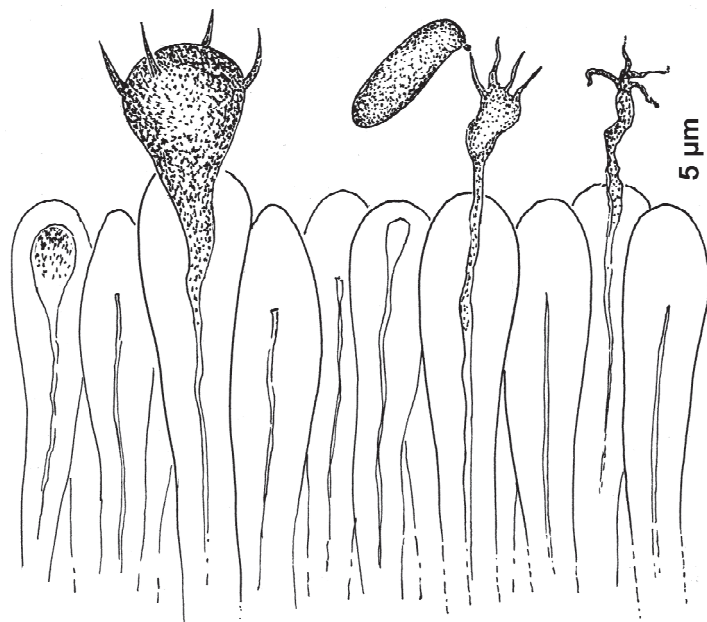


Fig. 4. Sequence of basidium formation observed in *Schizophyllum leprieurii*, from left to right lumen grows up to the basidiolium apex, then the basidium emerges and develops basidiospores, finally it collapses. Robledo 1313 (CORD).

(1941) considered that difference in spore color is not a sufficient character to warrant generic segregation. However, the combination of macromorphological (*i.e.* brownish basidiomata), micromorphological (*i.e.* colored basidiospores and simple septa) and molecular (*i.e.* their grouping in a monophyletic clade) evidences might support the recognition of *Phaeoschizophyllum* to best accommodate the members of this unique lineage. More in depth studies involving additional collections and DNA markers are needed to clarify the validity of *Phaeoschizophyllum*.

There is little information available at the moment to comprehensively infer the ecology and distribution of the two species examined here, but some patterns seem to arise. The *Schizophyllum umbrinum* lineage (*i.e.* *S. umbrinum*, *S. cf. umbrinum* and *S. leprieurii*) is so far endemic to tropical and subtropical America. *Schizophyllum leprieurii* has several records at high altitudes along the Andes within the tropics and specimens of NW Argentina were recorded along the subtropical mountain rain forest (Yun-

gas) at 1500 m. Similarly, Martin (1941) reported this species at 1300 and 2300 m. in the Andean region of Colombia. *Schizophyllum umbrinum* was originally described from lowland tropical rain forests in N Brazil and, based on the original works of Linder (1933) and Cooke (1941), its distribution was concentrated in Central America and the Caribbean. Recent records of this species were also made from Florida (James *et al.*, 2001), Brazil (Cortellini Abrahão *et al.*, 2012) and Colombia (López-Quintero *et al.*, 2011). Finally, in the light of our results and the discussion presented above, some past record of *S. umbrinum* may be inaccurate since this name encompasses two or more cryptic species; see for instance the report of *Schizophyllum sp.* from Ecuador tropical rain forests by Læssøe and Petersen (2008).

*Studied material.*— *Schizophyllum leprieurii*: ARGENTINA. Prov. Jujuy, Dpto. Le-desma, Parque Nacional Calilegua, Abra de Cañas, Monolito, on dead fallen twig of *Alnus acuminata*, 23°40'54.8"S, 64°54'2.4"W,



Alt. 1702 m, 22-II-2001, *Robledo 50* (CORD); *ibid.*, Sendero Momota, on dead fallen branch, 23°48'48"S, 64°51'1.5"W, Alt. 600 m, 28-III-2007, *Robledo 1515* (CORD); *ibid.*, Sendero Tataupá, on dead fallen branch, 23°44'12"S, 64°50'60"W, Alt. 800 m, 28-III-2007, *Gallo 172* (CORD); *ibid.*, Sendero La Lagunita, on dead fallen branch, 23°45'18"S, 64°51'13"W, Alt. 717 m, 6-III-2005, *Gallo 408* (CORD); Prov. Salta, Dpto. Santa Victoria Oeste, Parque Nacional Baritu, Abra de minas, on dead fallen branch, 22°28'15"S, 64°44'47"W, Alt. 1760 m, 7-V-2007, *Robledo 1313* (CORD); *ibid.*, Reserva Nacional El Nogalar, 22°16'46.6"S, 64°42'35"W, 1677 m, *Popoff et al. 4867* (CTES); *ibid.*, Dpto. Anta, Parque Nacional El Rey, Cerro El Chañar, Bosque de Aliso, Pino y Queñoa, on dead fallen branch of *Alnus acuminata*, 24°45'46.8"S, 64°42'58.1"W, 1950 m, 28-V-2007, *Gallo 778* (CORD). *Schizophyllum cf. umbrinum*: ARGENTINA. Prov. Córdoba, Dpto. San Javier, Los Hornillos, on fallen log of *Lithraea molleoides* (Anacardiaceae), 31°54'24.1"S, 64°55'59.9"W, 1280 m, 27-IV-2012, *Robledo 2478* (CORD).

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