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New record of *Schizophyllum* (Schizophyllaceae) from Mexico and the confirmation of its edibility in the humid tropics

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Abstract

The genus *Schizophyllum* is easily recognized within the order Agaricales. However, at the species level, taxonomic information for identification purposes is limited. The objective of the present study was to confirm the identity of the *Schizophyllum* species present in Tabasco, Mexico, by means of a detailed taxonomic revision of the macro- and micromorphological characters in more than 90 specimens, as well as phylogenetic analyses inferred from ITS sequence data. In total, three *Schizophyllum* species are described, of which one constitute a new record for Mexico. Finally, the edibility of *S. radiatum* is reported for the first time in the humid tropical region.

Keywords: Agaricales, split gills, microscopy, Internal Transcribed Spacer (ITS)

Introduction

The genus *Schizophyllum* E.M.Fr. in Observationes mycologicae (1815: 103) is taxonomically located in the family Schizophyllaceae, order Agaricales, and phylum Basidiomycota (Kirk *et al.* 2008). At the macroscopic level, this genus is characterized by the following features: basidiomes with pileus flabelliform, conchate, dimidiate or spatulate; margins lobed or dentate; surface villous and grayish white ($N_{30}M_{00}C_{00}$- Kueppers 1996); and a dry and leathery consistency (Figure 1A). The hymenium is located on split gills that are longitudinally divided into two parts (Figure 1B) (Linder 1933, Cooke 1961, Guzmán 2003) that can fold into the hymenophoral trama during long periods of drought to protect spores or that can open during periods of adequate moisture to liberate spores (Vellinga 2013, Piepenbring 2015).

At the microscopic level, the surfaces of the pileus have a villous layer, also called a "pellicle," composed of interwoven hyphae that vary with species in length and density. On the opposite side, a group of hyphae or "abhymenial hairs" is observed on the gills (Figure 1C). The spores are generally hyaline, elliptical, or cylindrical (Linder 1933).

Initially, Fries described the genus *Schizophyllum* in 1815 (Siqueira *et al.* 2016) and placed it within the family Agaricaceae (Cooke 1961). The name of this genus comes from the Latin words *schizo*, which means split, and *phyllum*, which means lamella. Therefore, its name appropriately describes its unique characteristics and distinctive morphology within the order Agaricales (Cooke 1961, Guzmán 2003).

For a long time, the taxonomy of the genus was uncertain and changed considerably because of the presence and observation of distinct morphological characters. These observations prompted researchers to place species of this genus within the order Polyporales or in the families Tricholomataceae and Thelephoraceae (Cooke 1961).

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Afterwards, Linder (1933) and Cooke (1961) significantly contributed to the taxonomy of *Schizophyllum* at the species level through a detailed revision of the distinctive macro- and micromorphological characters of numerous specimens from worldwide. These researchers formed the basis for identifying the different taxa and for establishing the affinities or frequencies of the species in temperate and tropical geographical regions. After these studies, taxonomic contributions on this genus have been scarce worldwide.

In Mexico, the *Schizophyllum* studies are attributed to Guzmán (1977) and Olivo-Aranda and Herrera (1994) who reported the species *Schizophyllum commune* E.M.Fr. in Observationes mycologicae (1815: 103), *Schizophyllum fasciatum* N.T.Pat. in Journal de Botanique (1887:169) and *Schizophyllum umbrinum* M.J.Berk. Journal of Botany (1851: 15) and generated the first taxonomic keys for the identification of the macromycetes in the country, in which they integrated to the genus, based mainly on the observation of macroscopic characters. After these contributions, there have been no taxonomic updates of this genus in Mexico and no molecular sequences have been generated from environmental samples (samples of wild origin) to verify their identity.

On the other hand, in the humid tropics of Mexico, numerous reports of the species *S. commune* and *S. umbrinum* can be highlighted (Cappello & Hernández-Trejo 1990, Cappello 2001, Cappello 2006, Cappello *et al.* 2013). However, the fungal diversity of the humid tropics has not been extensively explored (Guzmán 2008, Acosta-Aguirre *et al.* 2014), therefore an increase in the *Schizophyllum* records for this region is to be expected, as this region contains the highest biological richness within the country (Espinoza-Organista *et al.* 2008) and experiences annual rainfall levels that surpass 2 500 mm (Olvera-Salgado 2010). Furthermore, in the humid tropics and in other regions, at least 50% of *Schizophyllum* species are edible or have medicinal properties (Ying & Mao 1987, Chang & Miles 2004, Ruán-Soto *et al.* 2004, Boa 2005, Hobbs 2005, Ruán-Soto *et al.* 2006, Adejoye *et al.* 2007, Calonge 2011, Vázquez-Mendoza 2012, Moreno-Fuentes 2014). As a result, biotechnological interest has also been focused on species of this genus and their potential applications (Kumar *et al.* 2014, Turlo 2014, Horisawa *et al.* 2015, Siqueira *et al.* 2016).

Therefore, the generation of additional taxonomic information for *Schizophyllum* species is important for understanding, conserving, and using these species.

The objective of the present study was to confirm the identity of *Schizophyllum* species in Tabasco, Mexico by means of a detailed analysis of the macro- and micromorphological characteristics of wild specimens and from herbarium as well as the molecular analyses inferred from ITS sequence data.

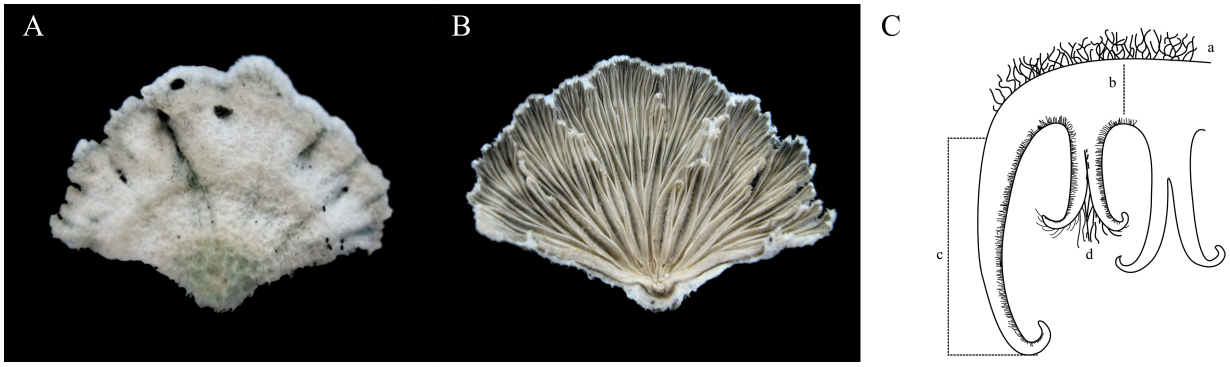

FIGURE 1. General appearance of A) the pileus and B) the hymenial gills of *Schizophyllum commune*. C) Illustration of the cross section of a basidiome (a = pellicle, b = context, c = gill length, d = abhymenial hairs). Photography by S. D. Carreño-Ruiz. Illustration taken and modified from Linder (1933).

Materials and methods

Macro- and micromorphological study

The *Schizophyllum* specimens in the Fungal Collection of the Herbarium of the Biological Sciences Academic Division of the Juarez Autonomous University of Tabasco [Universidad Juárez Autónoma de Tabasco UJAT] were examined. Also, fresh basidiomes of the genus were examined; these specimens were obtained from 15 field trips to the municipalities of Centro, Tabasco, Macuspana, Tacotalpa, and Teapa and from one trip to the Diana Córdova de Balboa market in the municipal capital of Teapa, where the consumption and commercialization of *S. commune* had been previously reported (Ruán-Soto *et al.* 2006).

The macroscopic characteristics of the herbarium specimens were obtained from the labels of each reviewed specimen. The freshly collected basidiomes were macroscopically described and subsequently dried (Cifuentes *et al.* 1986, Cappello 2006). The color guide of Kueppers (1996) was used to determine the color of the fresh basidiomes. In addition, the microscopic structures of all fresh specimens were studied in preparations containing alcohol, 5% KOH, and Congo red dye under an Axiostar Plus Carl Zeiss microscope.

The taxa were identified by consulting several taxonomic keys proposed for the genus and the specialized literature (Linder 1933, Cooke 1961, Guzmán 1977, Olivo-Aranda & Herrera 1994, Robledo *et al.* 2014). The characteristics of the examined material were recorded in a database, and the examined materials were then incorporated into the Fungal Collection of the UJAT Herbarium.

Different strains of the specimens collected in the field and in the market were obtained and selected for their subsequent inclusion in the molecular study. These strains are deposited in the Cappello-García mushroom collection (CCG) UJAT.

Molecular study

DNA extraction, PCR and sequencing

DNA was extracted from isolated specimens, using CTAB + PVP (2%) methods described in Allen *et al.* (2006). The total extracted nucleic acids were visualized by electrophoresis in 1% agarose gel to verify the quality of the extracts. Subsequently, the ITS region of the 18S ribosomal gene was amplified by PCR, using the ITS4-ITS5 primers. The reaction mix contained 1X PCR buffer, 0.2 mM dNTPs, primers (0.2 pM), 1.5 mM $MgCL_2$, 1 U *Taq* polymerase, and 1 µl of a DNA dilution (1:20 or 1:50) prepared as a template using the primers ITS4 and ITS5 (White *et al.* 1990). The reaction was carried out under the following conditions: initial denaturation at 94 °C for 5 min, denaturation at 95 °C for 1 min, annealing at 55 °C for 1 min, extension at 72 °C for 1 min, and final extension at 72 °C for 5 min (40 cycles). The PCR product was purified using Quantum Prep PCR Klenn Spin Columns (Bio-Rad, no. cat 732┌6300). Each amplicon was sequenced in both directions according to the Sanger capillary method (Macrogen Inc., Korea).

Phylogenetic analysis

The dataset comprises nine sequences from specimens collected in the present study, in addition to 11 sequences derived from Genbank (Nakasone 1996, James *et al.* 2001, Siqueira *et al.* 2016). Sequences were aligned in MAFFT (Katoh & Standley 2013), then manually adjusted in BioEdit v. 7.0.4 (Hall 2007). The final alignment has been submitted to TreeBase (ID submission 242002) (obtained sequences in this study: MK585511, MF554594, MF554593, MK578042, MF554592, MF554591, MF554590.1, MK578041, MK578040. Sequences retrived from Genbank: LT217541, LT217537, LT217539, LT217531, LT217533, LT217535, LT217532, LT217560, AF249391, LT217559, L43382). The maximum likelihood (ML) analysis was performed in RAxMLHPC2 v. 8.2.4 (Stamatakis 2014) as implemented on the Cipres portal (Miller *et al.* 2010), under a GTRGAMMA model with one thousand rapid bootstrap (BS) replicates. Bayesian Inference (BI) analysis was performed with MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003). Six Markov chains were run for one million generations and sampled every 100th generation. Burn-in was determined by checking the likelihood trace plots in Tracer v. 1.6 (Rambaut *et al.* 2014) and subsequently discarded. The outputs were displayed in FigTree v1.4.0 (http://tree.bio.ed.ac.uk/software/figtree/).

Results

Morphological identifications

Ninety-three specimens of the genus *Schizophyllum* were examined, of which 61 were from the herbarium, 30 from the field, and 2 from the local market of Teapa, Tabasco. The following species were identified by their morphological characteristics: *S. commune*, *S. radiatum* E.M.Fr. Nova Acta Regiae Societatis Scientiarum Upsaliensis (1851: 41), and *S. umbrinum*.

Schizophyllum radiatum was the most abundant with 62 specimens, in contrast with *S. commune* and *S. umbrinum* with 28 and 3 specimens, respectively.

Schizophyllum radiatum constitute a new record for Tabasco and for Mexico. The specimens obtained from this species at the local market of Teapa, Tabasco, were further confirmed by molecular identification and thereby allowing the edibility of this species in the humid tropics to be inferred.

Taxonomy

Schizophyllum commune Fr. in Observationes mycologicae (1815: 103)

Description:—Pileus 4–64 mm wide × 4–44 mm long, flabelliform, semicircular to spatulate, sessile or semistipitate; margin lobed, irregular, crenate, ragged, slightly rolled toward the hymenium. Villous surface soft to the touch; hairs frequently matted; pellicle 151–213 µm thickness; white ($N_{00}M_{00}C_{00}$), light gray ($N_{30}A_{00}M_{00}$), dark gray ($N_{80}A_{00}M_{00}$), light yellow ($N_{20}A_{50}M_{20}$), or light brown ($N_{20}A_{30}M_{20}$); zonate or azonate appearance that varies in color; context 359–447 µm thick (Figure 2A). Hymenium with split gills, 399–1256 µm in length; white ($N_{00}M_{00}C_{00}$), dark gray ($N_{80}A_{00}M_{00}$), light brown ($N_{30}A_{60}M_{30}$), light yellow ($N_{20}A_{50}M_{20}$), or beige ($N_{00}A_{10}M_{00}$); abhymenial hairs simple, hyaline, clinging to the surface opposite to the gills, 4.4–4.5 µm diam., with granules frequently incrusted along the outer third of their length near the apex (Figure 2B); basidia 18–22 × 3.2–3.3 µm, narrow claviform; spores 4.5–7.2 × 1.5–3 µm, hyaline, cylindrical, obliquely apiculate.

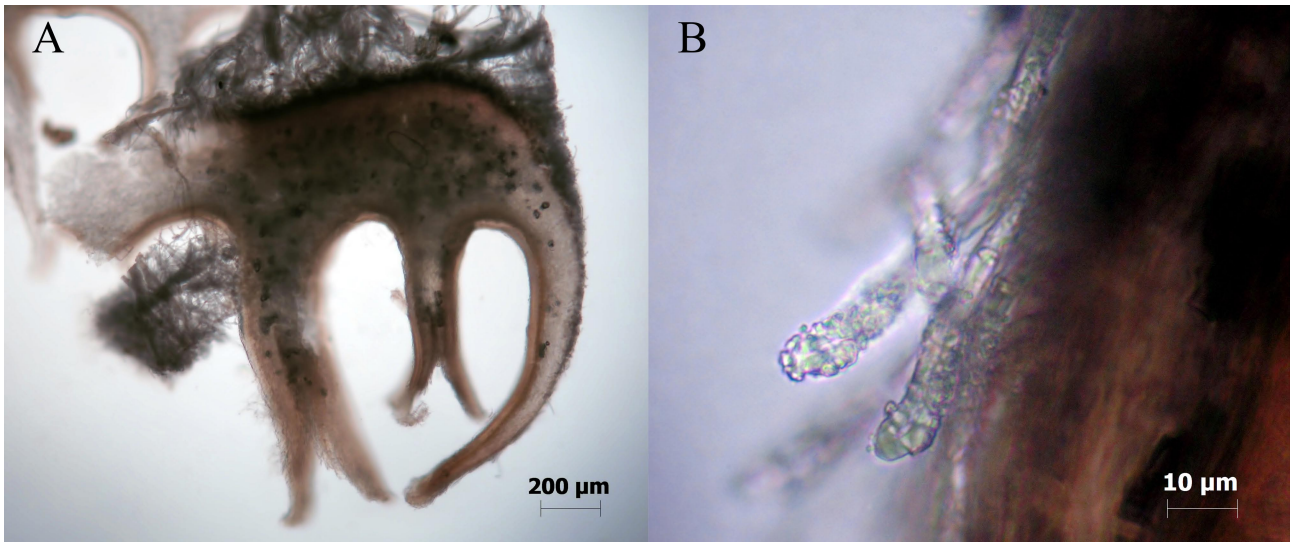

FIGURE 2. A) Cross section of the context and B) abhymenial hairs of *Schizophyllum commune*. Photography by A. A. Ávalos-Lázaro.

Habitat and Distribution:—Solitary or gregarious in large groups, saprotrophic or parasitic. This species has been reported on more than 500 hosts (Linder 1933, Cooke 1961, Olivo-Aranda & Herrera 1994, Vázquez-Mendoza 2013, Farr & Rossman 2017) and on fallen wood of *Ficus benjamina*. This species has a wide distribution and can be found throughout the year (Degreef *et al.* 1997). In Tabasco, it is distributed in the municipalities of Centro, Huimanguillo, Tacotalpa, Teapa, Tenosique, and Macuspana. In Mexico, it has been recorded in all states (Díaz-Moreno 2004, Olivo-Aranda & Herrera 1994). Worldwide, it is distributed on all continents except for Antarctica (Chang & Lui 1969, Adejoye *et al.* 2007, Ohm *et al.* 2010).

Examined material:—Mexico. Tabasco: Cárdenas, Poblado C29, elev. 10m, GPS 18º 03’ N, 96° 27’ W, 31 June 2009, Olmedo-López 1; Centro, Yumka´, elev. 10 m, GPS 18° 00’ W, 92º 50’ N, 06 September 2002, González 15; Villahermosa, elev. 15 m, GPS 18° 00’ N, 92º 50’ W, 04 September 2000, Sosa-Martínez 4; Jardín Botánico José Narciso Rovirosa, elev. 10 m, GPS 17° 59’ N, 92°58’ W, 04 December 2015, Carreño-Ruiz 800; 31 May 2016, Ovando 02; 25 November 2015, Carreño-Ruiz 711; Medellin y Pigua 3ª Sección, elev. 10 m, GPS 17° 74’ N, 93°18’ W, 14 February 2010, Pérez Hernández 02; 14 February 2010, Orduña-Rodas 1; Villa Las Fuentes Periférico, elev. 9 m, GPS 17° 58’ N, 92° 57’ W, 26 June 2001, Cappello 2142; Huimanguillo, Agua Selva, elev. 1000 m, GPS 17° 34’ N, 93° 59’ W, 18 November 2002, Domínguez 1; Estación Chontalpa, elev. 40 m GPS 17° 66´ N, 93° 48´ W, González 16, 16 October 2004; Tacotalpa, Sierra Tapijulapa, elev. 325 m, GPS 17°30 N, 92° 49’ W, 14 March 2003, Díaz-Contreras 57; Poblado Pomoquita, elev. 9 m, GPS 17°22´ N 92°43´ W, 22 October 2016, Carreño-Ruiz 658, 661; Parque Natural Villa Luz, elev. 120 m, 17° 26’ N, GPS 92° 45’ W, 23 November 2016, Carreño-Ruiz 710; Tapijulapa, elev. 900 m,

GPS 17°27’ N, 92°41’ W, 23 August 2015, Carreño-Ruiz 646; Macuspana, Parque Estatal Agua Blanca, elev. 100 m, GPS 17°, 52’ N, 92° 29’ W, 06 July 2011, Mondragón-Sánchez 17; 05 April 2005, Díaz-Contreras 578; 11 July 2012, Carreño-Ruiz 118, Carreño-Ruiz 119, Carreño-Ruiz 707; Teapa, Ejido Vicente-Guerrero, elev. 100 m, GPS *17° 51’ N, 92° 92’ W,* 12 June 2005, Cappello 2206; Grutas del Coconá, elev. 150 m, 17° 34’ N, 93° 56’ W, 07 May 2015, Carreño-Ruiz 635; Sierra Madrigal, elev. 325 m, GPS 17° 30’ N, 92° 49’ W, 05 April 2003, Díaz-Contreras 55; 02 March 2016, Carreño-Ruiz 617; Mercado Diana Córdova de Balboa, elev. 100 m, GPS 17° 33’ N, 93° 57’ W, 08 May 2016, Carreño-Ruiz 634; Tenosique, Ranchería Santo Tomas, Vázquez 1, elev. 20 m, GPS 17° 17’ N, 91° 20’ W, 4 December 1987 (UJAT Herbarium).

Notes:—This species is distinguished by its very dense pellicle and by the slightly split radial lines that are occasionally observed on the surface of the pileus. Margins are rolled toward the hymenium. Spores are generally light yellow in color and basidiomes have a characteristic odor of dead wood. At the micromorphological level, the abhymenial hairs cling near the surface opposite to the gills and have crystalline granules along the outer third of their length.

Schizophyllum radiatum Fr. Nova Acta Regiae Societatis Scientiarum Upsaliensis (1851: 41)

Description:—Pileus 3–45 mm wide and 5–48 mm long, flabelliform, semicircular or spatulate, sessile or semistipitate; margin smooth, digitate or ragged, slightly rolled toward the hymenium (Figure 3A); pellicle 70 µm thickness; white ($N_{00}M_{00}C_{00}$), grayish white ($N_{20}A_{00}M_{00}$), or white with zones of light gray ($A_{20}M_{20}C_{30}$), dark gray ($N_{70}C_{00}A_{00}$), or brown ($N_{50}A_{80}M_{50}$); context of 113 to 384 µm thick (Figure 3B). Hymenium of split gills, 449 to 780 µm in length; yellow ($N_{10}A_{30}M_{30}$), light brown ($N_{50}A_{99}M_{50}$), grayish white ($A_{30}M_{10}C_{20}$), or golden brown ($N_{30}A_{50}M_{20}$); abhymenial hairs simple, 3.2–4 µm diam., either a) hyaline with crystalline granules at the apex (Figure 3C) or b) hyaline, smooth, and wavy near the apex (Figure 3D), separated from the surface opposite to the gills; basidia 19–20 × 3–3.6 µm, claviform or narrow claviform; spores 4.3–6 × 2–3 µm, hyaline, cylindrical, obliquely apiculate.

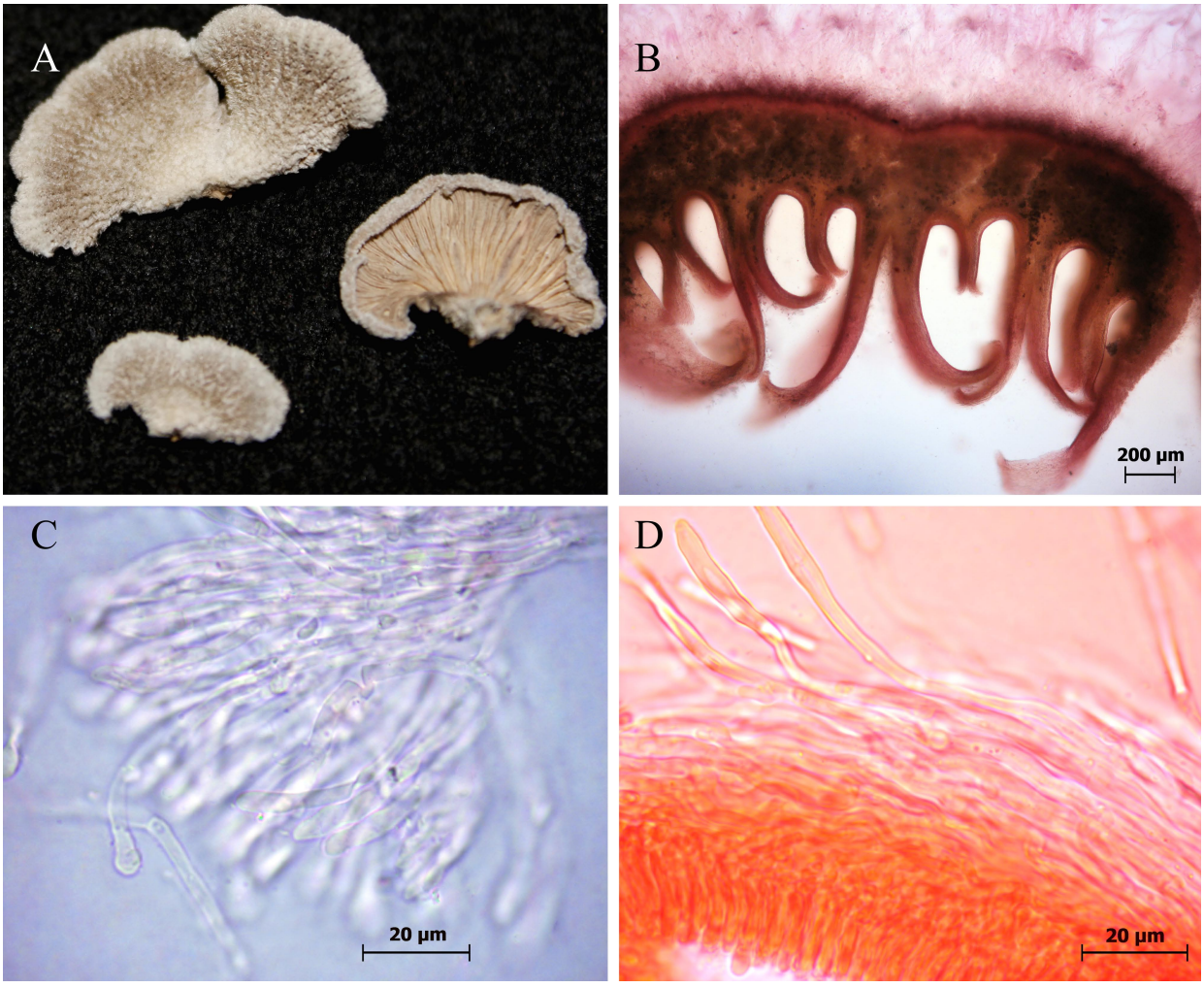

FIGURE 3. A) Pileus with a zonate appearance, B) context, C) abhymenial hairs with crystalline granules at the apex, and D) smooth abhymenial hairs of *Schizophyllum radiatum*. Photography by A. A. Ávalos-Lázaro.

Habitat and distribution:—Solitary or gregarious in large groups, saprotrophic. This species has been reported on wood of *Magnolia mexicana*, *Persea americana* (Linder 1933), and *Gossypium arboreum* (Farr & Rossman 2017). In the present study, it was also found on fallen wood of *Ficus benjamina, Ormosia macrocalix*, and *Gliricidia sepium*. In Tabasco, it is distributed in the municipalities of Centro, Cárdenas, Huimanguillo, Jalpa, Macuspana, Paraíso, Tacotalpa, and Tenosique. In Mexico, it is a new record. Worldwide, it has been reported in the United States (Farr & Rossman 2017) and in tropical regions of the American continent, including Bolivia, Cuba, Ecuador, Guatemala, French Guiana, Honduras, Jamaica, Panama, Puerto Rico, Venezuela, and Suriname (Linder 1933).

Examined material:—Mexico. Tabasco: Cárdenas, Heroica Cárdenas, elev. 15 m, GPS 17° 59' N 93° 20' W, 09 September 2008, Mondragón-Sánchez 1; Centro, Jardín Botánico José Narciso Rovirosa, elev. 10 m, GPS 17° 59' N, 92°58' W, 27 October 2000, García-Arellano 1; 20 May 2004, Cappello-García 3127; 30 September 2005, Juárez 1; 21 October 2015, Carreño-Ruiz 501; 29 September 2016, Carreño-Ruiz 643; 01 July 2016, Carreño-Ruiz 635, 637; 22 September 2016, García 3; 03 September 2016, Carreño-Ruiz 639; 17 November 2016, Carreño-Ruiz 663, 664; Paseo Tabasco Villahermosa, elev. 10 m, GPS 18° 00' N, 92° 50' W, 13 September 2016, Carreño-Ruiz 638; Villa Luis Gil Pérez, elev. 10 m, GPS 17° 52' N, 93° 04' W, 29 September 2010, Montecinos 2; Ranchería Medellín y Madero 1a Secc., elev. 10 m, GPS 18.1176 N, 92.8347 W, 08 February 2005, Contreras-Godoy 1; Tamulte de las sabanas, elev. 10 m, GPS 18° 16' N, 92° 78' W, 21 September 2009, Gerónimo-Valencia 4; Parque Museo La venta, elev. 15 m, GPS 18° 00' N, 92° 50', 11 November 1997, López-Bonilla 32; 07 October 2018, Carreño-Ruiz 709; Comalcalco, Rancheria Centro Tular 2a secc., elev. 10 m, GPS 18° 19' N, 93° 23, 07 March 1999, Izquierdo-Pérez 1; Huimanguillo, Agua Selva, elev. 1000 m, GPS 17° 34' N, 93° 59' W, 5 September 1999, Cappello 915; Malpasito, elev. 411 m, GPS 17.345833 N, 93.591389 W, 23 September 2005, López-González 01; Jalapa, Ranchería Víctor Fernández Manero 1 secc, elev. 10 m, GPS 17° 85' N, 92° 81' W, 17 September 2005, Lucio 3; 19 May 2004, Camacho 19; Macuspana, Parque Estatal Agua Blanca, elev. 100 m, GPS 17°, 52' N, 92° 29' W, 28 October 2011, Gómez-García 82; 28 February 2012; Morales-López 173; 27 September 2016, Carreño-Ruiz 644; 09 August 2006, Bautista-Lorenzo 3; 28 February 2012, Mondragón-Sánchez 49; 11 July 2016, Carreño-Ruiz 117, 120; 11 March 2011, Fajardo 75; 28 February 2012, Mondragón 99; 23 March 2007, Bolivar 3; 14 March 2005, Díaz-Contreras 556; Carretera Apasco-Chivalito, elev. 100 m, GPS 17° 37' N, 92° 26' W, 04 July 2011, Ruiz-Villareal 16; Paraíso, Puerto Ceiba, elev. 10 m, GPS 18° 41' N, 93° 18' W, 04 November 2004, López-Pérez 1; Tacotalpa, Poblado Pomoquita, elev. 9 m, GPS 17°22´ N 92°43´ 44 W, 22 October 2016, Carreño-Ruiz 557, 660, 659, 665, 656, 653, 654; Ejido Agua Blanca Sierra Tapijulapa, elev. 20 m, GPS 17° 48' N, 92° 62' W, 29 March 2003, Díaz-Contreras 280; 15 March 2003, Díaz-Contreras 283; 30 August 2003, Díaz-Contreras 186; 14 March 2003, Díaz-Contreras 57; Ejido Yajaloh Rio Seco Sierra Tapijulapa, elev. 50 m, GPS 17° 27' N, 92°43' W, 28 July 2003, Díaz-Contreras 130; 31 August 2003, Díaz-Contreras 180; Lomas Alegres Sierra Poana, elev. 54 m, GPS 17° 35' N, 92° 47' W, 31 August 2003, Díaz-Contreras 197; Villa Luz, elev. 120 m, GPS 17° 26' N, 92° 45' W, 23 August 2015, Carreño-Ruiz 507, 508, 509; Teapa, Mercado Diana Córdova de Balboa, elev. 100 m, GPS 17° 33' N, 93° 57' W, 02 March 2016, Carreño-Ruiz 619; Sierra Madrigal, elev. 325 m, GPS 17° 30' N, 92° 49' W, 24 August 2003, Díaz-Contreras 60; 7 June 2003, Díaz-Contreras 268; Puyacatengo Cruce Chapingo, elev. 800 m, GPS 17º 37' N, 92º 52' W, 04 March 2015, Díaz-Contreras 532; 02 March 2016, Carreño-Ruiz 618; Tenosique, Rancho Tigre, elev. 50 m, GPS 17º 26' N, 91º 08 W, 27 May 1988, Hernández-Trejo 30; Estapilla, elev. 20 m, GPS 17° 54' N, 91° 40' W, 29 June 2006, Hernández-Sánchez 1; 21 June 2006, Hernández-Sánchez 5; Ranchería Santo Tomas Arroyo, elev. 20 m, GPS 17° 17' N, 91° 20' W, 04 December 1987, Aguilar-Cruz 1 (UJAT Herbarium).

Notes:—At the macroscopic level, this species can be distinguished by the surface of the pileus, which has concentric color patterns of white to dark gray and mainly white spores. In addition, it has a typical fruity aroma that contrasts with the aroma of other species in this genus. It can be confused with *S. commune*. However, *S. radiatum* has two types of abhymenial hairs: The first, which are very similar to *S. commune*, are incrusted with crystalline granules yet are located at the apex. The second are simple and wavy or wavy at the apex. Both types separated from the surface opposite to the gills.

Schizophyllum umbrinum Berk. Journal of Botany (1851: 15)

Description:—Pileus 6–11 mm wide × 4–7 mm long, conchate, digitate; sessile or laterally stipitate (Figure 4A); when stipe is present, a strigose zone is observed near the basal area; rigid consistency; pellicle 170 to 174 µm thickness; grayish white ($A_{30}M_{10}C_{20}$) to light brown ($N_{30}A_{20}M_{00}$); context 315 to 320 µm thick (Figure 4B). Hymenium with gills 231 to 299 µm in length, tightly rolled; abhymenial hairs 4 µm diam., hyaline and smooth, apexes slightly wavy or spiraled (Figure 4C, D); spores 4.7–5.4 × 2–2.6 µm, hyaline, ellipticals (Figure 4E).

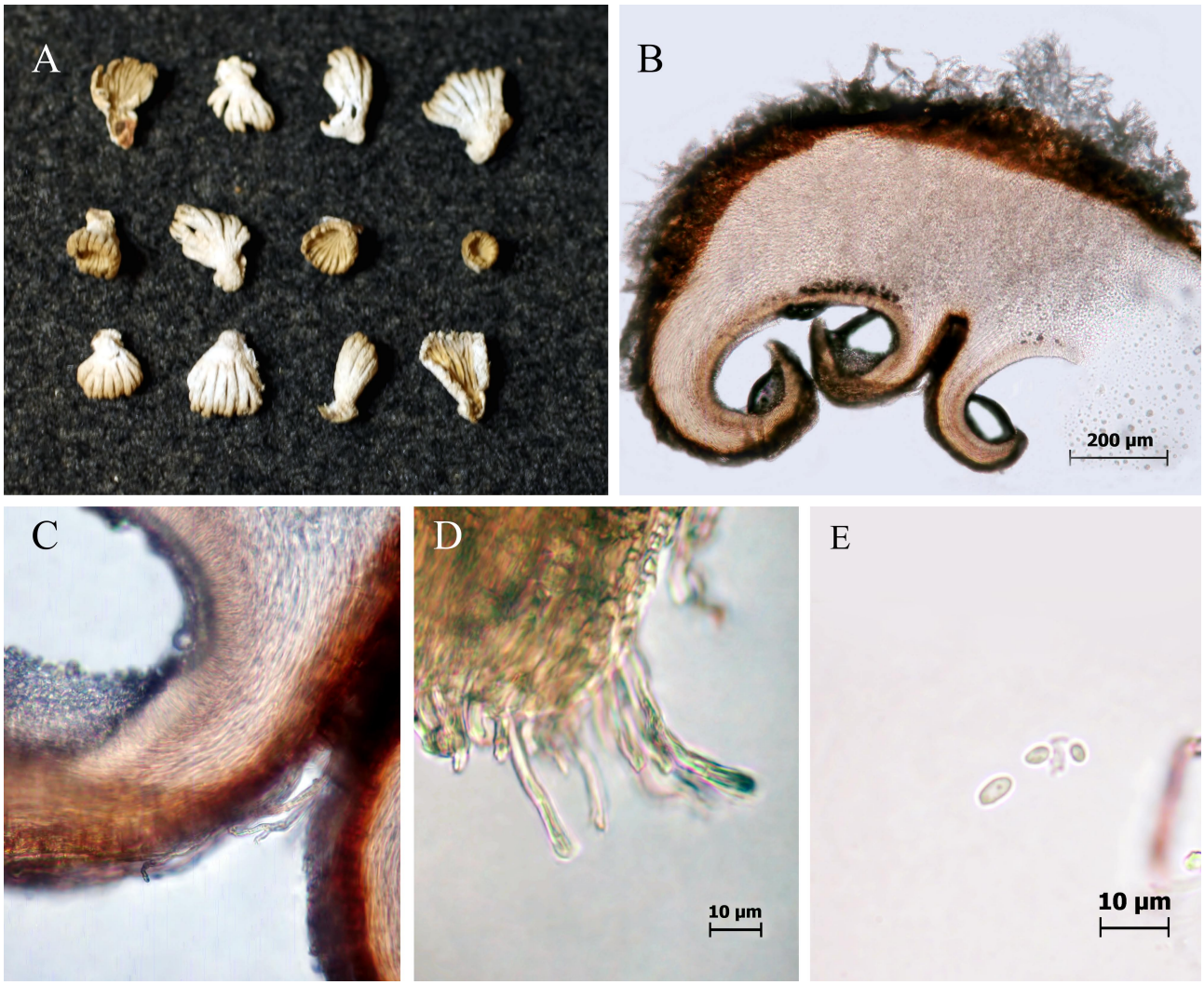

FIGURE 4. A) Digitate pileus, B) cross section of the context, C) general view of the location of the abhymenial hairs, D) abhymenial hairs with smooth apices and E) hyaline spores of *Schizophyllum umbrinum*. Photography by A. A. Ávalos-Lázaro.

Habitat and distribution:—Gregarious in small groups, saprotrophic. This species has been reported on wood of *Acacia sp.*, *Persea americana*, *Eucalyptus sp*. (Olivo-Aranda & Herrera 1994), *Hevea brasiliensis*, and *Mangifera indica* (Farr & Rossman 2017). In the present study, it was mainly found in medium-height rainforest in Macuspana, Tabasco. In Mexico, it has been reported in the northern and central regions of the country in the states of Colima, Durango, Michoacán, Jalisco, Nuevo León, Nayarit, Morelos, and the State of Mexico and in the southeastern states of Veracruz, Guerrero, Chiapas, Yucatán, and Quintana Roo (Olivo-Aranda & Herrera 1994). Worldwide, it is distributed throughout the northern United States, Nicaragua, Cuba, Paris (Linder 1933), and Argentina (Robledo *et al.* 2014).

Examined material:—Mexico. Tabasco: Macuspana, Parque Estatal Agua Blanca, elev. 100 m, GPS 17°, 52' N, 92° 29' W, 25 March 2012, Gómez-García 250; 26 March 2012, Mondragón-Sánchez 106; 05 November 2018, Carreño-Ruiz 708 (UJAT Herbarium).

Notes:—This species can be confused with *S. leprieurii* D.H.L. *American Journal of Botany* (1933: 561). However, at the macroscopic level, *S. umbrinum* has a pileus of light brown to light gray color. At the micromorphological level, it has elliptical hyaline spores and smooth abhymenial hairs with wavy endings. In contrast, *S. leprieurii* has a pileus of dark brown to bright golden brown color, cylindrical yellowish brown or light brown spores and abhymenial hairs light brown with granules or crystals along the apical portion (Linder 1933, Robledo *et al.* 2014).

Dichotomous key for *Schizophyllum* species in the Mexican humid tropics

1a. Basidiome spatulate, semicircular, flabelliform, gills longer than the width of the context 2
1b. Basidiome conchate, gills smaller of length than the width of the context; smooth abhymenial hairs, wavy to spiraled or with wavy ends ..... ***S. umbrinum***.

2a. Abhymenial hairs matted to gills, thick, hyaline, simple, slight granulation present at the apexes, smooth with swollen or slightly bifurcate ends..... ***S. radiatum***.

2b. Abhymenial hairs separated from gills, thick walls, hyaline, simple with abundant granulation along approximately one-third of their outer length near the apex ..... ***S. commune***.

Phylogenetic analyses

The final ITS alignment contains 569 characters including gaps. *Schizophyllum amplum* K.K.N. Mycologia (1996: 771) was used as outgroup. The resulting ML and Bayesian trees had highly similar topologies. The ML tree is shown in the Figure 5 and branches with Bayesian posterior probabilities higher than 80% are thicker. Samples from Mexico were placed in two clades: one clade included strains of *S. commune* and *S. radiatum* (CBS301.32 is the epitype), which were not well separated, and another clade included only strains of *S. umbrinum* with full support.

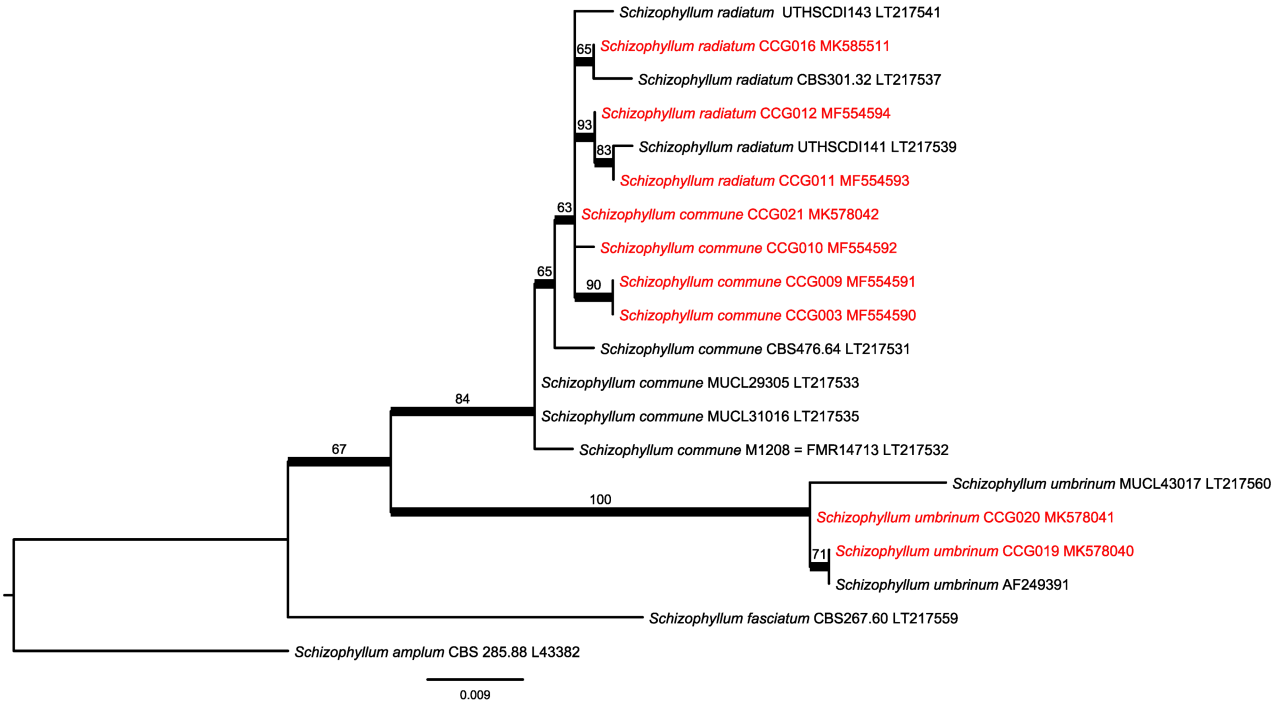

FIGURE 5. Maximum likelihood phylogram of *Schizophyllum* resulting from analysis of ITS sequence data. The bootstrap support values greater than 50% are indicated, and branches with Bayesian posterior probabilities greater than 0.8 are in bold. Species sampled from Mexico are in red. Codes of the herbarium records corresponding to the strains: Carreño-Ruiz 709 (CCG016), 619 (CCG012), 618 (CCG011), 707 (CCG021), 617 (CCG010), 119 (CCG009), 118 (CCG003), 708 (CCG020) & Mondragón-Sánchez 106 (CCG019) (The origin of the herbarium records are within the section of material examined by each species).

Discussion

In the present study three of the six validated species of *Schizophyllum* are reported from the Mexican humid tropics, according to the taxonomic studies of Linder (1933), Cooke (1961) and Robledo *et al.* (2014).

In the context of traditional taxonomy, the identification of species should mainly be based on the observation of microscopic characters, such as the size of the context as well as the morphology, size, and color of the abhymenial hairs and spores, according to the criteria proposed by Linder (1933) and Cooke (1961). Meanwhile, the macromorphological characters presented by different species of *Schizophyllum* are highly variable yet, in some cases, also very similar; so, these taxa cannot be delimited based on macromorphological characters alone. For some time, the size of the basidiomes was considered to be one important reference for separating species (Linder 1933, Cooke 1961, Guzmán 1977, Olivo-Aranda & Herrera 1994). For example, *S. commune* and *S. radiatum* were previously associated with pileus larger than 15 mm in diameter. However, in the present study, these fungi were found as small as 5 mm in size in the form of flabelliform basidiomes; therefore, at first sight, these could be confused with species like *S. umbrinum* or *S. leprieurii*. These latter two fungi have been categorized as part of the lineage of small basidiomes within the genus *Schizophyllum* with pileus less than 15 mm in diameter (Linder 1933, Cooke 1961, Robledo *et al.* 2014).

In the present study, 64% of identified specimens were *S. radiatum*. In addition, this study is the first report for this species in the humid tropics of Mexico and coincides with the study of Linder (1933), who confirmed the high frequency of this species within tropical regions of the American continent, including Bolivia, Cuba, Ecuador, Guatemala, French Guiana, Honduras, Jamaica, Panamá, Puerto Rico, Venezuela, and Suriname, among others. The findings of the present study therefore contrast with recent studies about fungi diversity of Tabasco, Mexico that highlight *S. commune* as the more frequent species (Ruán-Soto *et al.* 2004, Ruán-Soto *et al.* 2006, Sánchez-Hernández *et al.* 2010, Moreno-Fuentes 2014).

Additionally, the confusion surrounding the differentiation of *S. commune* and *S. radiatum* and the quantity of records attributed to the first species, especially in tropical areas, may be due to the high degree of morphological similarity of these species. For this reason, we recommend in particular for these species, that the taxonomist should make at least 10 cuts of the cross section of the basidiome for observe the abhymenial hairs in the lamellas until verify that in the specimen exist only one type of abhimenial hair, or by the otherwise, check if two types are found, which is very useful to determine if the specimen that is reviewed corresponds to *S. commune* or *S. radiatum*.

In this sense, in the present study it was considered important to generate a phylogenetic tree based on the analysis of the molecular sequences obtained for the species, with the universal DNA barcode marker ITS. However, the result showed that with ITS alone, it is not sufficient for species differentiation. Additional markers such as the translation elongation factor-1α (TEF-1α) and the second largest subunit of RNA polymerase II (Rpb2) with higher resolution power are necessary for better differentiation.

The results obtained in our tree, on the one hand, complement the data generated by the traditional taxonomy, with respect to the identity of the species, observing that, in the analysis of the macro and micromorphological characters as in the molecular level, these species show a high similarity. Even these results coincide with the results of the phylogenetic studies previously conducted by Moncalvo *et al.* (2002) and Siqueira *et al.* (2016), who have considered these species as sisters, with a very close relationship.

Furthermore, the results of phylogenetic tree also suggest new questions regarding the molecular separation of the strains tested in this study, not being entirely conclusive, which could be attributed to the situation of the species in terms of availability of the molecular sequences that exist in the actuality. Although the GenBank database contain a large amount of molecular sequences for *S. commune* and *S. radiatum*, there is not sufficient generated molecular sequences from environmental samples of strains from basidiomes of wild origin and moreover, in a careful selection of such sequences, those showing a strong molecular support come from clinical specimens and simultaneously, part of these sequences do not reveal the corresponding taxonomic support, because no feature analysis macro- and micromorphological characters that support them, which has caused that many researchers do not have the certainty that they are the species they have named as *S. commune* or *S. radiatum*.

In this sense, the results generated, in addition to knowledge of the molecular and phylogenetic situation presented by these species based on the molecular sequences available up to now, indicate that it is important to continue with the development of these studies, in which it is necessary the use of more than one molecular marker to have greater certainty when elucidating the phylogenetic differences of these species, as they suggest (Sharma *et al.* 2015, Vellinga *et al.* 2015, Jeewon & Hyde 2016) together with the taxonomic evidence that helps to avoid ambiguities. For this reason, it is expected that the taxonomic descriptions presented here, contribute to the adequate identification of the species of *Schizophyllum*, by offering new knowledge for the field of human and animal health, mainly due to some existing controversies regarding the detected pathogenicity in species such as *S. commune* and *S. radiatum* (Chan *et al.* 2014), likewise for the pharmaceutical and biotechnological industries, which have focused their interest on the adequate identification of *S. commune*, due to its medicinal properties and its genetic qualities, among other aspects in the that it is necessary to guarantee that it is the appropriate organism.

Finally, the edibility of *S. radiatum* was confirmed for the first time in the Mexican humid tropics. Therefore, *S. radiatum* can be added to the list of edible fungal species in Mexico. Currently, this species, as well as *S. commune*, is locally commercialized in the market of Teapa, Tabasco. The potential economic value of *S. radiatum* for the communities where it is collected or located can be estimated based of the findings of the present study.

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