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Sulzbacheromyces leucodontium (Basidiomycota, Lepidostromataceae), a new species of basidiolichen widely distributed in the Neotropics

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Abstract

As a result of botanical and lichenological expeditions in the Colombian Andean-Amazonian Piedmont, in the Brazilian Amazon, and in Veracruz, Mexico, a new species of *Sulzbacheromyces* was discovered and is here described based on morphological, anatomical, and molecular characters. *S. leucodontium* differs from other neotropical species in the genus by having white basidiomata and colonial algae in the thallus and represents the species with the widest distribution of the genus in the Americas, from Mexico to Brazil. In addition, the most complete phylogenetic reconstruction of the genus to date is presented as well as a key to the known species of *Sulzbacheromyces* in the Neotropics.

Key words: ITS barcoding, *Lepidostromatales*, maximum likelihood, phylogeny, soil inhabiting

Introduction

The Neotropics, due to historical, geographic, and climatic factors, is one of the most diverse regions of the world (Rull 2011, Hagen *et al.* 2021), with multiple ecosystems containing unique flora and fauna (Takhtajan 1989, Dick *et al.* 2019). Among the floristic regions proposed by Takhtajan (1989) is the Madrean Region (named after the Sierra Madre Occidental). Despite being within the geography of the Neotropics, Takhtajan (1989), included it within the Holarctic Kingdom in North America on account of its singularities and floristic affinities. This region occupies arid or semi-arid areas in the southern United States and northern Mexico and borders the Caribbean Region of the Neotropical Kingdom in the south. The point where these kingdoms, Holarctic and Neotropical, meet, and with them the Madrean and Caribbean regions, has an interesting connection with palynological and fossil records of both floras during the Oligocene-Miocene (Graham 1976, Rodríguez-Reyes *et al.* 2021).

In the Neotropics a region known as the Amazonian piedmont, which represents the transition between the Andean montane ecosystem and the Amazon basin, stands out. This region originated from the uplift of the Andes 10 My ago

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at the end of the Miocene. The Colombian Andean-Amazonian Piedmont has been strongly affected by anthropogenic pressures (Etter *et al.* 2006), experiencing great transformations in its natural ecosystems since the 1950s. These changes are mainly due to the colonization process, caused by the adaptation of the area for agricultural production (Avellaneda *et al.* 2016) and the exploitation of subsoil resources such as hydrocarbons, coal, gold, and other precious metal (Kairuz 2012, Ciontescu *et al.* 2019). Furthermore, the departments of Amazonas, Caquetá, and Putumayo have reported an alarming increase in deforestation rates (Hernández *et al.* 1992, Guio & Rojas 2019), generating the fragmentation of forests, a process that is known to lead to a reduction of ecosystem connectivity (Etter *et al.* 2006). The Andean-Amazonian Piedmont of Colombia is a biodiversity hotspot in southern Colombia (Kattan *et al.* 2004, Niño 2014, Avellaneda *et al.* 2016), representing approximately 37 % of the surface area of the Colombian Amazon (Guio & Rojas 2019), and a site of interest for biological conservation and research, due to the convergence of climatic and geomorphological factors from the Andes and the Amazon (Robertson & Castiblanco 2011).

The Indi-Wasi NNP has an area of 77,336 ha (Rojas *et al.* 2005) and is located on the eastern flank of the eastern mountain range of the Colombian Andes (Morales 2020), in the department of Caquetá in the municipalities of San José del Fragua and Belén de Los Andaquíes (Revelo 2019), on the basins of the Pescado and Fragua Grande rivers. This National Park is part of an important area for ecological connectivity as other protected sites in the national park system surround it. These sites include the Serranía de Los Churumbelos-Auka Wasi NNP, the Cueva de Los Guacharos NNP, Zona of the Amazon Forest Reserve, and the Andaki Regional Park (Delgado *et al.* 2021).

Despite being one of the most diverse places in the world, the lichenized fungi of the these ecosystems have been rarely studied. This is especially true for basidiolichens (Moncada *et al.* 2022), the different lineages of fungi within the Basidiomycota that have acquired the lichen lifestyle. Currently, there are eight genera of basidiolichens known in the Neotropics (ColFungi 2022), *viz*., *Acantholichen* Jørgensen (1998: 444), *Cora* Fries (1825: 300), *Corella* Vainio (1890: 242), *Cyphellostereum* Reid (1965: 336), and *Lichenomphalia* Redhead, Lutzoni, Moncalvo & Vilgalys (2002: 36) (family *Hygrophoraceae*, order *Agaricales*); *Multiclavula* Petersen (1967: 207) (family *Hydnaceae*, order *Cantharellales*); and *Lepidostroma* Mägdefrau & Winkler (1967: 15) and *Sulzbacheromyces* B.P. Hodk. & Lücking in Hodkinson *et al.* (2014: 176) (family *Lepidostromataceae*, order *Lepidostromatales*). Despite *Sulzbacheromyces* being one of the most recently described genera it has already been shown to be species rich (Sulzbacher *et al.* 2013, Coca *et al.* 2018).

Sulzbacheromyces is a pantropical genus of basidiolichens, that comprises eight species, *viz*., *S. bicolor* D.Liu, Li S.Wang & Goffinet in Liu *et al.* (2018: 735), *S. caatingae* (Sulzbacher & Lücking in Sulzbacher *et al.* 2013: 605) B.P. Hodk. & Lücking in Hodkinson *et al.* (2014: 176), *S. chocoensis* Coca, Lücking & Moncada (2018: 301), *S. fossicola* (Corner 1950: 691) D.Liu & Li S.Wang in Liu *et al.* (2018: 737), *S. miomboensis* De Kesel & Ertz. in Liu *et al.* (2018: 738), *S. sinensis* (R.H.Petersen & M.Zang 1986: 284) D. Liu & Li S. Wang in Liu *et al.* (2018: 740), *S. tutunendo* Coca, Lücking & Moncada (2018: 303), and *S. yunnanensis* D.Liu, Li S.Wang & Goffinet in Liu *et al.* (2018: 742), occurring in Africa, America, and Asia. The genus was proposed by Hodkinson *et al.* (2014), based on multi-gene phylogenetic analysis and thallus morphology. The taxon is characterized by a crustose to indistinct thallus, containing chlorococcoid algae of the genus *Bracteococcus* Tereg (1923: 191), and clavarioid to fusiform erect white to red fungal basidiomata. As a result of several recent expeditions to PNN Indi-Wasi in Colombia, to the Madrean-Caribbean Region in Veracruz, Mexico, and to Amazonian Rain Forests in western Brazil, we found a new species of *Sulzbacheromyces*, *S. leucodontium*, that we here describe based on integrated taxonomy from seven specimens collected in three different countries and by distinct research groups. This genus is reported for the first time from North America (in Mexico), and it presents a particular distribution of interesting transitional floristic regions of the Neotropics.

Material and Methods

Field and herbarium work

Fresh material was collected in the Indi Wasi National Natural Park on the Andean-Amazon Biogeographic Region (n=4). Additional samples were collected in Naranjal and Los Reyes in Veracruz, Mexico (n=2) and in the Reserva Extrativista do Cazumbá-Iracema in Acre, Brazil (n=1, Fig. 1). Specimens were gathered with remnants of the substrate (soil) in paper napkins and paper bags. Then the material was air-dried at room temperature. The specimens were examined under a NIKON SMZ800 dissecting microscope. Sections of the thallus and the basidiomata were studied under a NIKON E200 compound microscope. Microscope images were taken with a CANON Powershot G9X MarK

II camera. Measurements of all structures were done with the calibrated images using ImageJ 1.49 software (Schneider *et al.* 2012).

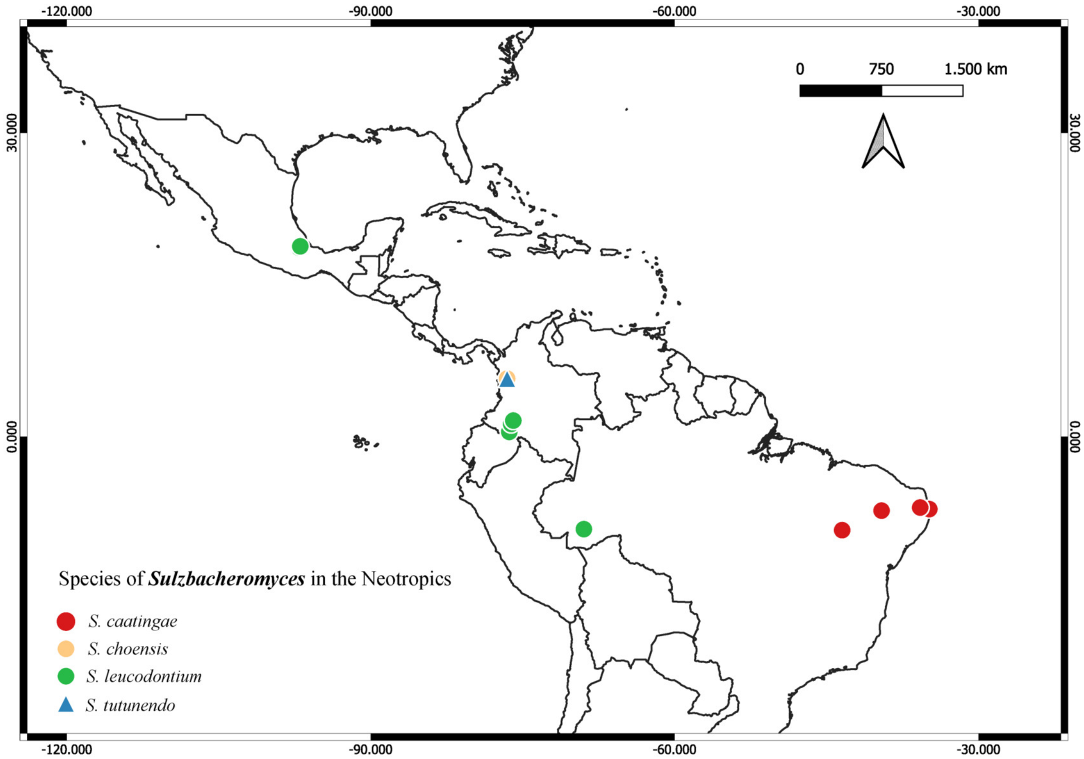

FIGURE 1. A. Distribution map of Neotropical *Sulzbacheromyces* species.

Molecular data

ITS sequences of *Sulzbacheromyces* samples (Table 1) were generated for this study in the Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution, using the ZR Fungal/Bacterial DNA MiniPrep™ (Zymo Research, Irvine, CA, USA) and Plant/Fungi DNA Isolation Kit (Norgen Biotek Corp., Canada) for DNA isolation following the manufacturer's instructions. Since our study focused on the mycobionts, only basidiomata were included in the DNA extraction tubes to avoid possible contaminants from the soil, The oldest basidiomata spent ten months as herbarium specimens between dehydration and sequencing at an average temperature of 19 °C. The primers used for amplification were ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990). PCR amplifications were carried out using 6 µL of MyTaq™ Red DNA Polymerase (Bioline, Taunton, MA, USA), 0.25 µL of each primer, 0.5 µL genomic DNA extract and 5 µL distilled water for a total of 12 µL. Thermal cycling parameters were: initial denaturation for 1 min at 95 °C, followed by 30 cycles of 15 s at 95 °C, 15 s at 53 °C, 10 s at 72 °C, and a final elongation for 10 s 72 °C. PCR samples were visualized on a 1 % ethidium bromide-stained agarose gel under UV light to check well bands. PCR products were cleaned with ExoSAP-IT (USB, Cleveland, OH, USA). The 10 µL cycle sequencing reactions consisted of 1–1.5 µL of BIG DYE Version 3.1 (Applied Biosystems, Foster City, California, U.S.A.), 2.5–3 µL of BIG DYE buffer,6 µM primer, 0.75–2 µL PCR product and water. Samples were sequenced with PCR primers in the Pritzker Laboratory (Chicago, USA) and Macrogen (Korea). The cycle sequencing conditions were as described in Coca *et al.* (2018) and sequences were assembled in GENEIOUS Pro 9.1.8 and submitted to GenBank (Table 1).

Phylogenetic analyses

ITS sequences of the new species were aligned with sequences of the same genus downloaded from GenBank. Five sequences of *Lepidostroma calocerum* (G.W.Martin 1940: 196) Oberwinkler (1984: 773) were used as outgroup (Table 1), following previous studies in the group (Sulzbacher *et al.* 2016, Coca *et al.* 2018). Sequences were aligned using GENEIOUS Pro 9.1.8 and with MAFFT using the auto option (Katoh & Toh 2005; Katoh *et al.* 2009). The final alignment was subjected to a maximum likelihood search with RAxML 8.2.0 (Stamatakis 2015) using the GTR-gamma model, and non-parametric bootstrapping using 1000 replicates. Likewise, a Bayesian analysis was carried out in MrBayes, using the same alignment, GTR as a substitution model with gamma rate variation, starting from a random tree, and four Markov chains were run in parallel to sample trees using the Markov Chain Monte Carlo (MCMC) method. After the burn-in phase every 100.000 samples out of 200 generations was considered to ensure convergence and stability of the phylogenetic tree reconstruction.

TABLE 1. GenBank accession numbers of data used in the phylogenetic analyses. The sequences generated by this study are in bold. Specimens with an 'en' dash were not sequenced.

Taxon	Collection details	GenBank Accession Number (ITS)
Ertzia akagerae	Rwanda, Ertz *et al.* 7673 (BR)	KU999883
Lepidostroma calocerum	Colombia, Lücking 35836a, basidiome (F)	KT354923
Lepidostroma calocerum	Colombia, Lücking 35836b, basidiome (F)	KT354924
Lepidostroma calocerum	Colombia, Lücking 35836b, thallus (F)	KT354925
Lepidostroma calocerum	Colombia, Tisnes 1a, basidiome (F)	KT354926
Sulzbacheromyces bicolor	China, Wang & Wang 13-38188 (KUN-L)	KU999886
Sulzbacheromyces bicolor	China, Wang & Wang 13-38187 (KUN-L)	KU999887
Sulzbacheromyces caatingae	Brazil, Ovrebo 5034 (JPB51318, UFRN-Fungos 2502)	KT354928
Sulzbacheromyces caatingae	Brazil, Sulzbacher 237 (UFRN-Fungos 1479)	KC170320
Sulzbacheromyces caatingae	Brazil, Sulzbacher 235 (UFRN-Fungos 1478)	KC170321
Sulzbacheromyces caatingae	Brazil, Sulzbacher s. n. (UFRN-Fungos 2050)	KT354929
Sulzbacheromyces caatingae	Brazil, Sulzbacher s. n. (UFRN-Fungos 2049)	KT354930
Sulzbacheromyces caatingae	Brazil, Sousa 65 (UFRN-Fungos 2051)	KT354931
Sulzbacheromyces caatingae	Brazil, Wartchow 58-2013 (UFRN-Fungos 2105)	KT354932
Sulzbacheromyces caatingae	Brazil, Sulzbacher 235 (UFRN-Fungos 1478, isotype, basidiome)	KT354933
Sulzbacheromyces caatingae	Brazil, Sulzbacher 235 (UFRN-Fungos 1478, isotype, thallus)	KT354934
Sulzbacheromyces caatingae	Brazil, Sulzbacher 237 (UFRN-Fungos 1479, basidiome)	KT354935
Sulzbacheromyces caatingae	Brazil, Sulzbacher 237 (UFRN-Fungos 1479, thallus)	KT354936
Sulzbacheromyces caatingae	Brazil, Sulzbacher 235 (UFRN-Fungos 1478, type)	NR120240
Sulzbacheromyces chocoensis	Colombia, Coca 5821, LFC129 (FAUC, holotype)	MG434495
Sulzbacheromyces chocoensis	Colombia, Coca 5824, MON3373 (FAUC, paratype)	MG434496
Sulzbacheromyces chocoensis	Colombia, Coca 5821, MON3375 (B, isotype)	MG434497
Sulzbacheromyces fossicola	Thailand, Verbeken & R. Walleyn 2004-056 (GENT)	KX431120
Sulzbacheromyces fossicola	Thailand, Stubbe D. & Walleyn R. DS07-379 (GENT)	KX431121
Sulzbacheromyces fossicola	China, Wang *et al.* 14-44144 (KUN-L)	KU999888
Sulzbacheromyces leucodontium	**Brazil, ISE 50192 (ISE, ABL)**	**OQ650292**
Sulzbacheromyces leucodontium	**Colombia, Coca 9262 (FAUC, F)**	**OP890603**
Sulzbacheromyces leucodontium	Colombia, Coca 13505(JBB, FAUC)	–
Sulzbacheromyces leucodontium	Colombia, Coca 13248 (JBB, FAUC)	–
Sulzbacheromyces leucodontium	Colombia, Coca 13201(JBB, FAUC)	–
Sulzbacheromyces leucodontium	**Mexico, Torres-Cantú 3082 (XALU)**	**OP896860**
Sulzbacheromyces leucodontium	**Mexico, Guzmán-Guillermo 3008 (XALU)**	**OP896857**
Sulzbacheromyces miomboensis	Democratic Republic of Congo, De Kesel 5403	KX431122
Sulzbacheromyces miomboensis	Democratic Republic of Congo, De Kesel 6004	KX431123
Sulzbacheromyces sinensis	Japan, TUMH 50299	AB819619
Sulzbacheromyces sinensis	Japan, TUFC 100100	AB819620
Sulzbacheromyces sinensis	Japan, TUFC 14267	AB819622
Sulzbacheromyces sinensis	China, MCCNNU 140134	KR186216
Sulzbacheromyces sinensis	China, Wang & Liu 11-32786 (KUN-L)	KU999891
Sulzbacheromyces sinensis	China, Ma 12-4313 (KUN)	KU999892
Sulzbacheromyces sinensis	China, Jia FJ1034 (KUN)	KU999893
Sulzbacheromyces sinensis	China, Wang & Liu 11-32822 (KUN-L)	KU999894
Sulzbacheromyces sinensis	China, Wang *et al.* 12-38189 (KUN-L)	KU999895
Sulzbacheromyces sinensis	China, Wang *et al.* 14-44135 (KUN-L)	KU999896
Sulzbacheromyces sinensis	China, Wang *et al.*14-44136 (KUN-L)	KU999897
Sulzbacheromyces sinensis	China, Wang *et al.* 14-44138 (KUN-L)	KU999898
Sulzbacheromyces sinensis	China, Wang *et al.* 14-44146 (KUN-L)	KU999899
Sulzbacheromyces sp. (*fossicola*)	Thailand, NW1530	MW504984
Sulzbacheromyces sp. (*fossicola*)	Thailand, NW1531	MW504985
Sulzbacheromyces tutunendo	Colombia, Coca 5825, LFC126 (FAUC, paratype)	MG434489
Sulzbacheromyces tutunendo	Colombia, Coca 5823, LFC127 (FAUC, holotype)	MG434491
Sulzbacheromyces tutunendo	Colombia, Coca 5823, MON3372 (B, isotype)	MG434492

...continued on the next page

TABLE 1. (Continued)

Taxon	Collection details	GenBank Accession Number (ITS)
Sulzbacheromyces tutunendo	Colombia, Coca 5825, MON3385 (FAUC, paratype)	MG434493
Sulzbacheromyces tutunendo	Colombia, Coca 5822, MON3388 (FAUC, paratype)	MG434494
Sulzbacheromyces yunnanensis	China, Wang *et al.* 13-38191 (KUN-L)	KU999902
Sulzbacheromyces yunnanensis	China, Wang & Liu 11-32797 (KUN-L)	KU999903
Sulzbacheromyces yunnanensis	China, Wang & Liu 14-44141 (KUN-L)	KU999904
Sulzbacheromyces yunnanensis	China, Wang *et al.* 12-34448 (KUN-L)	KU999905
Sulzbacheromyces yunnanensis	China, Wang *et al.* 12-34445 (KUN-L)	KU999906
Sulzbacheromyces yunnanensis	China, Wang *et al.* 12-34614 (KUN-L)	KU999907
Sulzbacheromyces yunnanensis	China, Wang *et al.* 12-34446 (KUN-L)	KU999908
Sulzbacheromyces yunnanensis	China, Wang & Liu 14-44133 (KUN-L)	KU999909
Sulzbacheromyces yunnanensis	China, Wang *et al.* 14-44123 (KUN-L)	KU999910
Sulzbacheromyces yunnanensis	China, Wang *et al.* 12-34447 (KUN-L)	KU999911
Sulzbacheromyces yunnanensis	China, Wang *et al.* 12-34444 (KUN-L)	KU999912
Sulzbacheromyces yunnanensis	China, Wang *et al.* 13-38192 (KUN-L)	KU999913
Sulzbacheromyces yunnanensis	China, Wang *et al.* 13-38190 (KUN-L)	KU999914

Results and Discussion

Taxonomy

Sulzbacheromyces leucodontium Coca, Gómez-Gómez, Guzmán-Guillermo & Dal Forno *sp. nov*. (Figs. 2 and 3)

MycoBank No.: MB 000000

Type:—COLOMBIA. Caqueta: San José de Fragua, Parque Nacional Natural Alto Fragua Indi Wasi, terricolous in an open and humid area, 600 m elev., 1˚15'54.1" N, 76˚07'50.5" W, 27 October 2017, *Coca et al. 9262* (FAUC: holotype; JBB, F: isotypes).

Diagnosis:—Thallus crustose forming a thin granulose film, terricolous in clay; basidiomata erect and unbranched, cylindrical to slightly fusiform, apically acute, and white. It differs from other species of *Sulzbacheromyces* with white basidiomata due to the absence of a prothallus, unbranched basidiomata, and the absence of clamp connections in the context hyphae.

Description:—*Thallus* crustose, terricolous in orange clay soil, forming a thin granulose film covering the substrate surface, presenting a moss green coloration, (25−)50−110 µm thick, homoiomerous, and compact. *Photobiont* trebouxioid, frequently grouped occasionally in a continuous layer, with spherical to ellipsoid cells 24–38 µm, with 6 to 26 chloroplast 5–8 µm, surrounded by hyphae. *Basidiomata* dispersed, fusiform to clavarioid, frequently with an inflated base, white to ivory white, (6)10–20 (25) mm high, 0.6–0.9 mm diam. at the base and 0.4–0.8 mm diam., unbranched at the apex, with solid context.

Context hyphae septate, 2–4 µm wide, thin-walled, without ornamentations, irregular, thickened towards the septum, and sparsely branched. *Subhymenial hyphae* septate, tightly arranged, irregular, and thin walled. *Hymenial hyphae* developed along the basidiomata. *Basidia* clavate, thin-walled, hyaline, 12 × 5 µm, bearing two small sterigmata, 4–5 µm. *Basidioles* 25–33 µm high, smooth-walled, and bearing oil droplets. *Basidiospores* ellipsoid and hyaline, thin-walled, 3 × 6 µm. *Clamp connections* not observed in any part.

Etymology:—The epithet refers to the unique white basidiomata within *Sulzbacheromyces* and its shape that is reminiscent of the elongated ivory tusks of elephants.

Distribution and ecology:—*Sulzbacheromyces leucodontium* is a terricolous species found on orange clay soil. It has been found in Colombia in the departments of Caquetá and Putumayo, in a tropical rainforest from the Andean-Amazon Piedmont. In Brazil, it has been reported a single time on soil from the Amazonian Rainforest from an extractive reserve and conservation area, where locals use the forest resources, such as rubber, sustainably. It has also been found in Mexico in the municipalities of Naranjal and Los Reyes near Pico de Orizaba.

Ranging from Mexico to western Brazil, this species has the broadest geographical distribution of the genus in the Americas observed to date. The two other Colombian species, *S. chocoensis* and *S. tutunendo*, are so far restricted to their type localities, while the Brazilian species, *S. caatingae*, has so far only been found in Northeastern Brazil, although in three different biomes (Sulzbacher *et al.* 2016). This pattern of one species from the genus with a broad

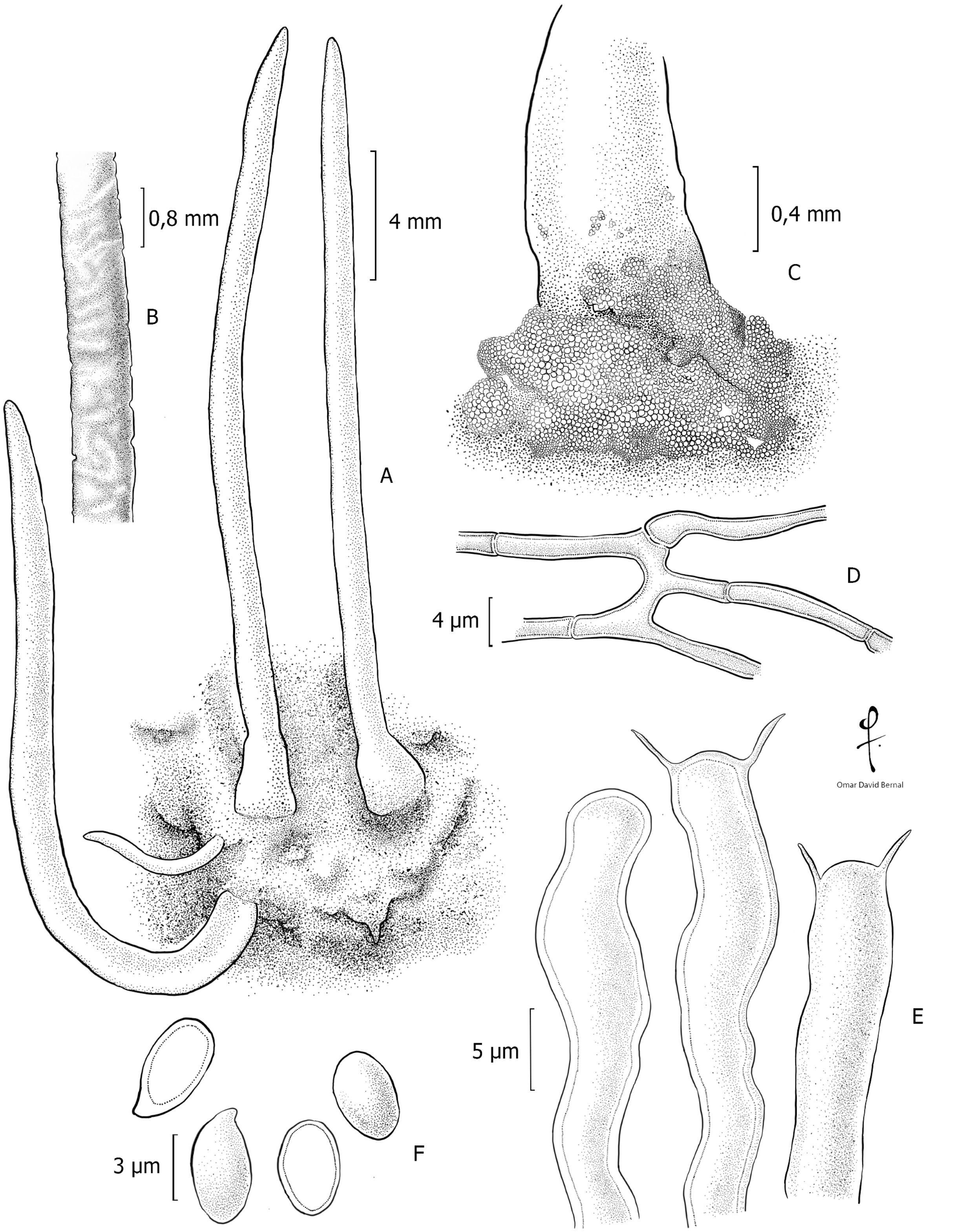

FIGURE 2. *Sulzbacheromyces leucodontium*. **A.** Thallus and basidiomata. **B.** Detail of the cracked basidiomata. **C.** Insertion of basidiomata and thallus, note the clustering of the photobiont in small spheres in the thallus. **D.** Hyphae of the context. **E.** Basidia and basidioles **F.** Basidiospores (Coca 13248 JBB). Drawings by: Omar Bernal

distribution and several more species of the genus having narrower distributions has also been observed in Asia, where *Sulzbacheromyces sinensis* is found in several countries (Japan, China, South Korea, Taiwan, Philippines) and *S. bicolor*, *S. yunnanensis* and *S. fossicola* are more restricted. Unfortunately, we are yet to see what the evolutionary and distributional patterns are in Africa, since so far, only one species in the genus has been reported for the Democratic Republic of Congo, namely *S. miomboensis*. The monotypic *Ertzia akagerae* (Eb. Fischer, Ertz, Killmann & Sérusiaux) Hodkinson & Lücking in Hodkinson *et al.* (2014:175) is the only other species reported from the order *Lepidotromatales* in the African Continent, more specifically, in Rwanda. This emphasizes a lot more studies are needed in this part of the world, not only in basidiolichens, but in lichenology overall, since large parts of this continent remain underexplored (Fryday *et al.* 2022).

Remarks:—*Sulzbacheromyces leucodontium* is the only Neotropical *Sulzbacheromyces* species with persistently large white basidiomata. *S. chocoensis* may have white basidiomata at the base, but from the third middle upwards, they are usually reddish orange. In the Paleotropics, two species with pale basidiomata are recognized, *S. bicolor* and *S. fossicola.* However, *S. bicolor* is distinguished by having basidiomata with yellow apices, a thallus with a white prothallus, and hyphae with clamp connections. *S. fossicola* differs by having a chlorococcoid photobiont and white basidiomata that branch at the base of the sporome. In addition, the two species are only distantly related to our new species and have not been reported from the Neotropics.

Despite belonging to a distinct order, *Multiclavula mucida* (Pers.) R.H. Petersen (1967:212), (Cantharellales), is the most phenotypically similar species that occurs in the Neotropics to *Sulzbacheromyces leucodontium*. Nonetheless, the ecology of these species is different, with *M. mucida* growing primarily in rotten logs versus the terricolous habit of *S. leucodontium*. Additionally, *Multiclavula* occurs more frequently in mountain ecosystems, whereas *Sulzbacheromyces* is restricted to lowland and sub lowland forests.

Specimens examined (Paratypes):—COLOMBIA. Caquetá: Belén de los Andaquíes, Parque Municipal Natural Andakí, 1100 m elev., 1˚36' N 75˚58' W, 5 October 2021, *Coca et al. 13505* (JBB). Belén de los Andaquíes, Entre la vereda Las Verdes y vereda Quisayá, 575 m elev., 1˚36' N 75˚55' W, 4 October 2021, *Coca et al. 13248* (JBB). Putumayo: Puerto Asís, Vereda Las Acacias, 260 m elev., 0˚29' N 76˚19' W, 19 August 2021, *Coca 13201* (FAUC, JBB). MEXICO. Veracruz: Naranjal, UMA environmental station Tequecholapa, ca. 700 m elev. 18°48' N 96°57' W, 7 October 2022, *Torres-Cantú 3082* (XALU). Los Reyes, Zoquiapan, 700 m elev., 18°39'N 97°03'W, ca. 7 October 2022 *Guzmán-Guillermo 3008* (XALU). BRAZIL. Acre: Sena Madureira, Reserva extrativista Cazumbá-Iracema, Núcleo Cazumbá, disturbed tropical rain forest 150 m elev., 09˚07' S 68˚57' W, 10 April 2019, *M. Cáceres, A. Aptroot & J.G. Cavalcante ISE 50192* (ISE, ABL).

Phylogeny

The alignment used was 615 bp in length, with an estimate of 40 % invariable sites. *Sulzbacheromyces* is presented as a monophyletic taxon that supports previously proposed phylogenies (Hodkinson *et al.*, 2014; Coca *et al.*, 2018 Liu *et al.*, 2018, 2019). The inferred genus phylogenetic tree showed two main lineages (Fig. 4), one with Asian species and another with American and African species, however, lacking strong support. This result is not consistent with previous studies (Coca *et al.*, 2018; Liu *et al.*, 2018). However, the relationships did not receive strong support either in our studies or previous studies.

The Neotropical species remain monophyletic (66ML/0.99PP) consistent with our previous study (Coca *et al.* 2018); however, the relationships between the species are poorly supported. *Sulzbacheromyces leucodontium* collected in Brazil, Colombia and Mexico grouped with other Colombian species but the sister group relationships lack support. We hypothesize this may be due to the lack of undiscovered taxa and the phylogeny being inferred from a single locus (ITS only). Nonetheless, ITS seems to be of extreme importance in helping establish species boundaries in this group, especially because so few morphological characters are present and of taxonomic importance. We further anticipate more species in this genus to be discovered and promote the use of integrative taxonomy to test how much phenotypic plasticity these species present, which will help us better understand patterns of diversity and speciation in the genus. The relatively simple thallus and basidiomata of *Sulzbacheromyces* give limited morphological information and make species delimitation challenging. Although the Neotropical species *S. caatingae, S. chocoensis*, *S. tutunendo* and the new species *S. leucodontium* show a rather similar overall morphology, they present distinct ecological and geographical distribution patterns. *S. caatingae* is found in the altitudinal range between 0 and 500 m and is almost restricted to the Caatinga ecosystem, extending to the adjacent Atlantic Rainforest (Sulzbacher *et al.* 2016). *S. chocoensis* and *S. tutunendo* are sympatric occurring in the tropical rainforest of the Colombian Chocó region. Coca *et al.* (2018) considered these two species semi-cryptic, as defined by Vondrák *et al.* (2009).

The new species, *S. leucodontium*, occurs in the Colombian Andean-Amazonian Piedmont, the Brazilian Amazon and the Madrean-Caribbean transition in Mexico. It is readily distinguished from other neotropical *Sulzbacheromyces* species by having white basidiomata, and the presence of colonial, trebouxioid algae in the thallus.

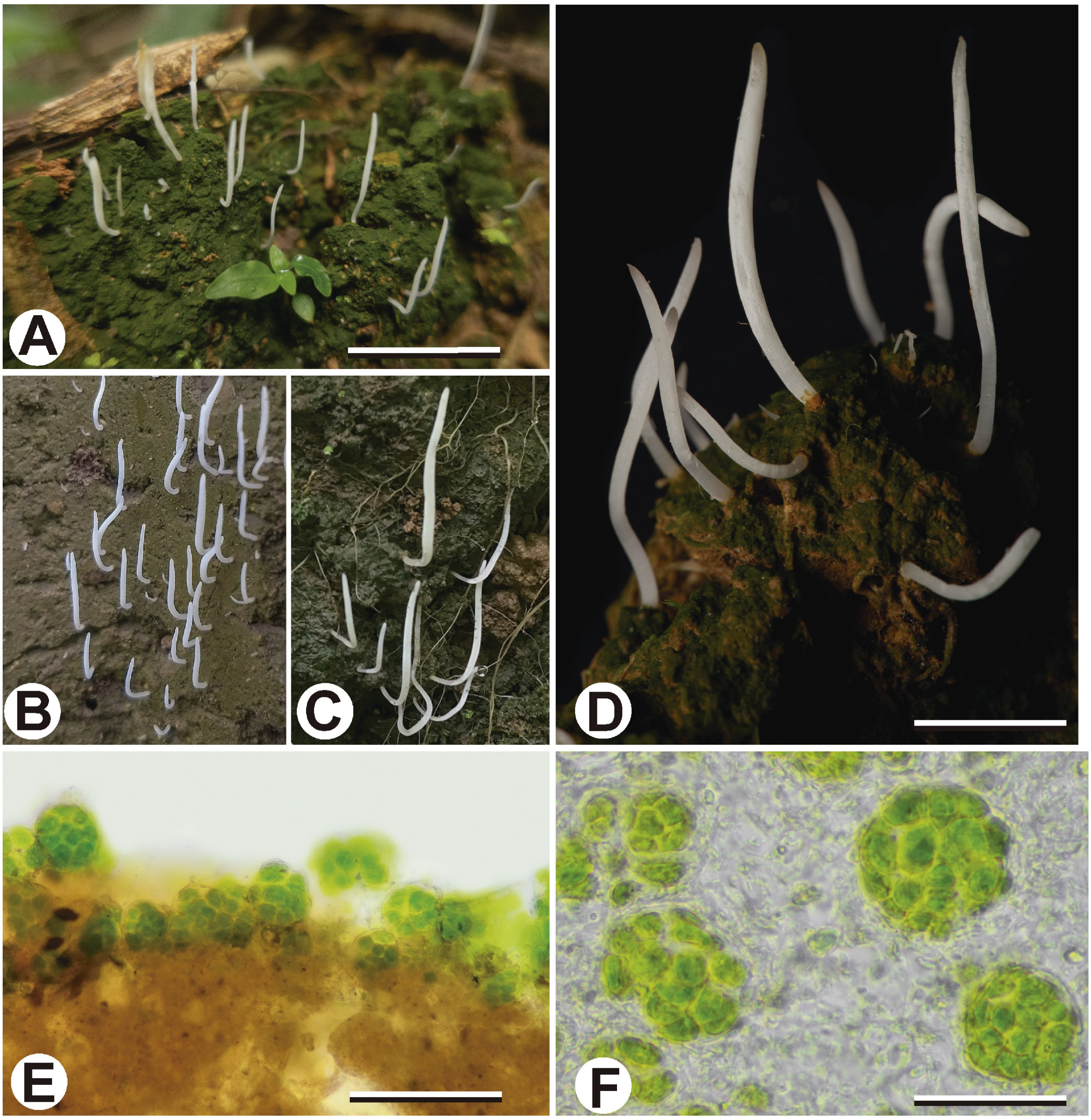

FIGURE 3. Field and lab pictures of *Sulzbacheromyces leucodontium*. **A.** Specimen in field with thallus and basidiomata (Putumayo, Coca 13201, scale 27 mm). **B.** Type specimen in field (Caquetá, Coca 9262)**. C.** Specimen in field with thallus and basidiomata (Mexico, Veracruz, Guzmán-Guillermo 3008) **D.** Detail of the thallus and basidiomata (Putumayo, Coca 13201, scale 9 mm). **E.** Cross section of the thallus of *S. leucodontium* on soil **(**Caquetá, Coca 13248, Scale 52 µm.). **F.** trebouxioid photobiont **(**Caquetá, Coca 13248, Scale 25 µm). Photos by: L.F.Coca (A-B, D-F); J.Guzmán Guillermo (C)

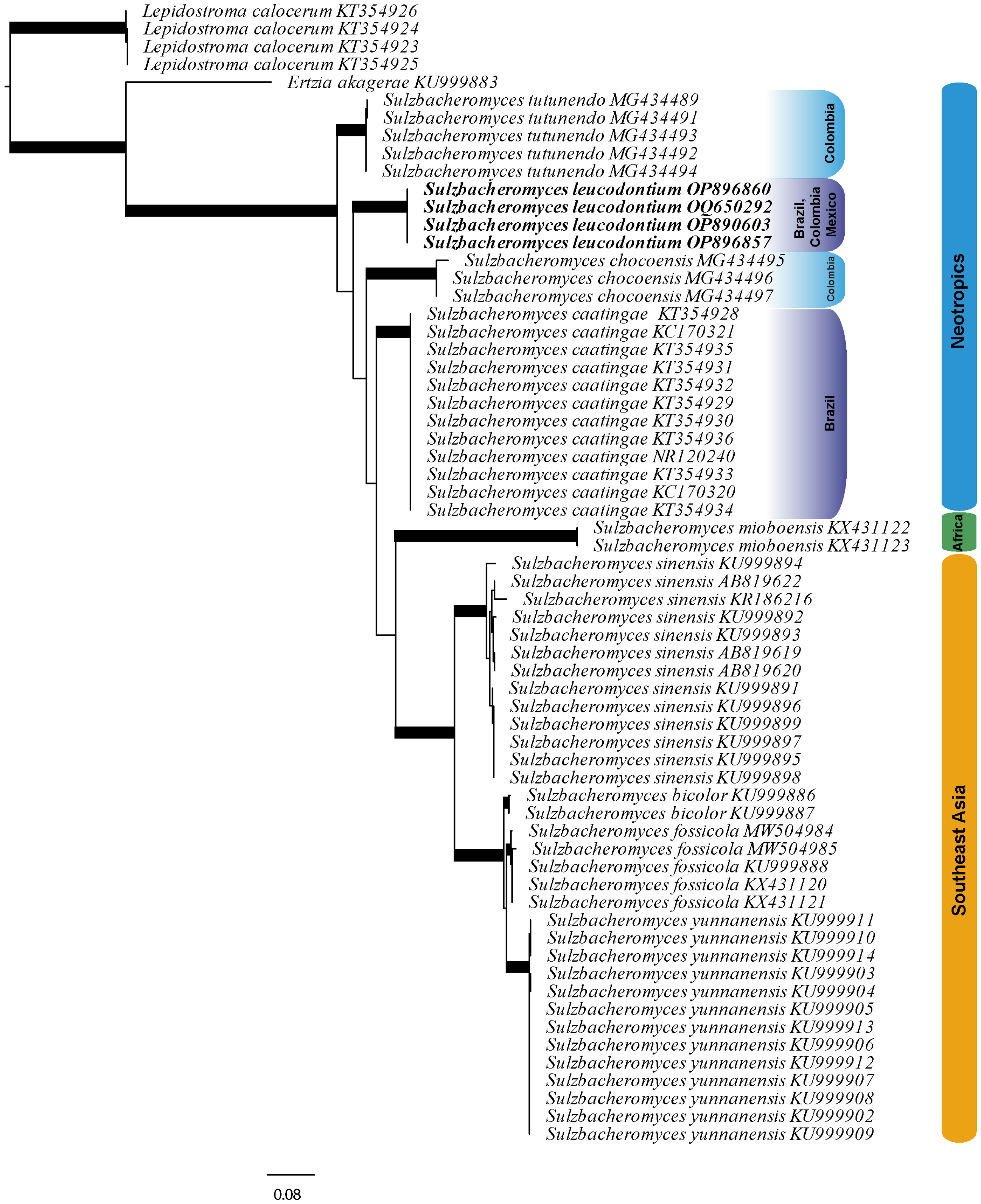

FIGURE 4. Best-scoring Maximum Likelihood tree using the ITS barcoding marker for the known *Sulzbacheromyces* species. Supported branches (bootstrap values ≥70 and posterior probability >0,95) are thickened and bootstrap support values are indicated below branches, Asian species are present in warm color, Neotropical species are present in cool color and African species in green.

Key to the species of *Sulzbacheromyces* in the Neotropics

1a Thallus microsquamulose, with clearly distinguishable green squamules .... *Lepidostroma*
1b Thallus crustose, formed by clustered algal populations at the base [*Sulzbacheromyces*] 2

2a Basidiomata consistently white .... *S. leucodontium*
2b Basidiomata flesh color, orange, yellow or reddish 3

3a Basidiomata usually branched and frequently curly at the tip, orange or flesh color, found in tropical rain forests in Northwestern South America .... *S. tutunendo*
3b Basidiomata unbranched 4

4a Basidiomata short (mostly up to 1 cm), reddish to yellowish, often with a white stipe or lighter at the base, found in tropical rain forests in Northwestern South America .... *S. chocoensis*
4b Basidiomata tall (up to 3.6 cm), yellow to orangish, sometimes widened at the tip, found in Northeastern Brazil .... *S. caatingae*

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References

Avellaneda, A., Monroy, K.F. & Cardona-Guzmán, D.P. (2016) Análisis socio ecológico de los sistemas agropecuarios en la Amazonia Colombiana, estudio de caso La Macarena-Meta, Colombia. *Revista Iberoamericana de Economía Ecológica* 26: 141–154.

Ciontescu, N., Ortega, D., Guerrero, J. & Zambrano, H. (2019) Análisis de conectividad ecológica en el Piedemonte Andino Amazónico, Departamento del Caquetá. USAID, Patrimonio Natural y Conservación y Gobernanza. Bogotá. Available from: https://pdf.usaid.gov/pdf_docs/PA00X3PF.pdf (Accessed 25 January 2021)

Coca, L.F., Lücking, R. & Moncada, B. (2018) Two new, sympatric and semi-cryptic species of *Sulzbacheromyces* (Lichenized Basidiomycota, Lepidostromatales) from the Chocó Biogeographic Region in Colombia. *Bryologist* 121: 297–305. https://doi.org/10.1639/0007-2745-121.3.297

ColFungi. (2022) Useful Fungi of Colombia. Facilitated by the Royal Botanic Gardens, Kew. Available from: https://colfungi.org/ (Accessed: 18 October 2022).

Corner, E.J.H. (1950) A monograph of *Clavaria* and allied genera. *Annals of Botany Memoirs* 1: 1–740.

Delgado-Forero, D.A., Sandoval-Jurado, J-F., Vives, A.L. & Gómez, M. (2021) La siembra de cultivos de coca y la deforestación como hecho regional en los parques nacionales naturales: Caso Parque Nacional Natural Alto Fragua Indi Wasi. Available from: https://cider.uniandes.edu.co/sites/default/files/noticias/2021/noviembre/COCA-PARQUES-NACIONALES-NATURALES-2.pdf (accessed 25 January 2023)

Dick, W.C. & Pennington, R.T. (2019) History and Geography of Neotropical Tree Diversity. *Annual Review of Ecology, Evolution, and Systematics* 50: 279–301. https://doi.org/10.1146/annurev-ecolsys-110617-062314

Etter, A., McAlpine, C., Phinn, S., Pullar, D. & Possingham, H. (2006) Characterizing a tropical deforestation wave: a dynamic spatial analysis of a deforestation hotspot in the Colombian Amazon. *Global Change Biology* 12: 1409–1420. https://doi.org/10.1111/j.1365-2486.2006.01168.x

Fries, E.M. (1825) *Systema Orbis Vegetabilis I*. Typographia Academica, Lund, 369 pp.

Fryday, A.M., Beckett, R.P. & Kirika, P.M. (2022) Lichenology in Africa. *Lichenologist* 54: 227–230. https://doi.org/10.1017/S0024282922000329

Gardes, M. & Bruns, T.D. (1993) ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae

and rusts. *Molecular Ecology* 2: 113–118.
https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Graham, A. (1976) Studies in Neotropical Paleobotany. II. The Miocene Communities of Veracruz, Mexico. *Annals of the Missouri Botanical Garden* 63: 787–842.
https://doi.org/10.2307/2395250

Guio, C.A. & Rojas, A. (2019) Amazonia colombiana: dinámicas territoriales. *Ideas Verdes, análisis político* 22: 1–52.

Hagen, O., Skeels, A., Onstein, R.E. & Pellissier, L. (2021) Earth history events shaped the evolution of uneven biodiversity across tropical moist forests. *Proceedings of the National Academy of Sciences* 118: e2026347118.
https://doi.org/10.1073/pnas.2026347118

Hernandez, J., Ortiz, R., Walschburger, T. & Hurtado, A. (1992) Estado de la biodiversidad en Colombia. *In*: Halffter, G. (ed.) *La diversidad biologica de Iberomaerica I*. Instituto de Ecología, Veracruz, pp. 123–124.

Hodkinson, B.P., Moncada, B. & Lücking, R. (2014) Lepidostromatales, a new order of lichenized fungi (Basidiomycota, Agaricomycetes), with two new genera, *Ertzia* and *Sulzbacheromyces*, and one new species, *Lepidostroma winklerianum*. *Fungal Diversity* 64: 165–179.
https://doi.org/10.1007/s13225-013-0267-0

Jørgensen, P.M. (1998) *Acantholichen pannarioides*, a new basidiolichen from South America. *Bryologist* 101: 444–447.
https://doi.org/10.2307/3244185

Kattan, G., Franco, P., Rojas, V. & Morales, G. (2004) Biological diversification in a complex region: a spatial analysis of faunistic diversity and biogeography of the Andes of Colombia. *Journal of Biogeography* 31: 1829–1839.
https://doi.org/10.1111/j.1365-2699.2004.01109.x

Katoh, K. & Toh, M. (2005) MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* 33: 511–518.
https://doi.org/10.1093/nar/gki198

Katoh, K., Asimenos, G. & Toh, H. (2009) Multiple alignment of DNA sequences with MAFFT. *Methods in Molecular Biology* 537: 39–64.
https://doi.org/10.1007/978-1-59745-251-9_3

Liu, D., Goffinet, B., Ertz, D., Kesel, A., Wang, X., Hur, J., Shi, H., Zhang, Y., Yang, M. & Wang, L. (2018) Circumscription and phylogeny of the Lepidostromatales (lichenized Basidiomycota) following discovery of new species from China and Africa. *Mycologia* 109: 730–748.
https://doi.org/10.1080/00275514.2017.1406767

Liu, D., Wang, X.Y, Wang, L.S., Maekawa, N. & Hur, J.S. (2019) *Sulzbacheromyces sinensis*, an Unexpected Basidiolichen, was Newly Discovered from Korean Peninsula and Philippines, with a Phylogenetic Reconstruction of Genus *Sulzbacheromyces*. *Mycobiology* 47 (2): 191–199.
https://doi.org/10.1080/12298093.2019.1617825

Mägdefrau, K. & Winkler, S. (1967) *Lepidostroma terricolens* n. g. n. sp., eine Basidiolichene der Sierra Nevada de Santa Marta (Kolumbien). Mitteilungen des Institute Colombo-Alemán. *Investigaciones Científicas* 1: 11–17.
https://doi.org/10.25268/bimc.invemar.1967.1.0.600

Martin, G.W. (1940) Some tropical American "Clavarias". *Lilloa* 5: 191–196.

Moncada, B., Coca, L.F., Díaz-Escandón, D., Jaramillo-Ciro, M. Simijaca-Salcedo, D., Soto Medina, E & Lücking, R. (2022) Diversity, Ecogeography, and Importance of Lichens of Colombia. *In:* de Almeida, R.F., Lücking, R., Vasco-Palacios, A.M., Gaya, E. & Diazgranados, M. (eds.) *Catalogue of Fungi of Colombia*. Kew Publishing, Royal Botanic Gardens, Kew, London, pp. 77–90.

Morales, M.A. (2020) Lista de especies cinegéticas en tres sectores del parque Nacional Natural Alto Fragua Indi Wasi, Caquetá, Colombia. *Rev Colombiana Cienc Anim. RECIA* 12: e764.
https://doi.org/10.24188/recia.v12.n2.2020.764

Niño, I. (2014) *WWF en el Piedemonte Andino-Amazónico de Colombia.* Piedemonte. pp. 1–14.

Oberwinkler, F. (1984) Fungus-alga interactions in basidiolichens. *Beihefte zur Nova Hedwigia* 79: 739–774.

Petersen, R.H. (1967) Notes on clavarioid fungi. VII. Redefinition of the *Clavaria vernalis C. mucida* complex. *The American Midland Naturalist* 77: 205–221.
https://doi.org/10.2307/2423440

Petersen, R.H. & Zang, M. (1986) New or interesting clavarioid fungi from Yunnan, China. *Acta Botanica Yunnanica* 8: 2815–294.

Redhead, S.A., Lutzoni, F., Moncalvo, J.M. & Vilgalys, R. (2002) Phylogeny of agarics: partial systematics solutions for core omphalinoid genera in the Agaricales (Euagarics). *Mycotaxon* 83: 19–57.

Reid, D.A. (1965) A monograph of the stipitate stereoid fungi. *Beihefte zur Nova Hedwigia* 18: 1–382.

Revelo, J. (2019) ¿Para qué sirven los parques naturales? Legibilidad estatal en el Parque Alto Fragua Indi Wasi, Colombia. *Colombia*

Internacional 100: 121–145.
https://doi.org/10.7440/colombiaint100.2019.06

Robertson, K. & Castiblanco, M. (2011) Amenazas fluviales en el piedemonte amazónico Colombiano. *Revista Colombiana de Geografia* 20: 125–137.
https://doi.org/10.15446/rcdg.v20n2.27185

Rodriguez-Reyes, O., Estrada-Ruiz, E., Monje Dussan, C., Andrade Brito, L. & Terrazas, T. (2021) A new Oligocene-Miocene tree from Panama and historical Anacardium migration patterns. *PLoS ONE* 16: e0250721.
https://doi.org/10.1371/journal.pone.0250721

Rojas, M., Solano, A., Chitiva, L.Y., Jacanamejoy, C.J., Cuellar, M.P., Garcia, R., Sarmiento, I. & Suarez, J.C. (2005) Linea base para la planeación del manejo del Parque Nacional Natural (Nukanchipa Alpa) Alto Fragua Indi Wasi. Parques Nacionales Naturales de Colombia, direccción territorial Amazonia. Available from: https://www.parquesnacionales.gov.co/portal/wp-content/uploads/2020/10/pm-altofragua_2007.pdf (accessed: 25 January 2023).

Rull, V. (2011) Neotropical biodiversity: timing and potential drivers. *Trends in Ecology & Evolution* 26: 508–513.
https://doi.org/10.1016/j.tree.2011.05.011

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671–675.
https://doi.org/10.1038/nmeth.2089

Stamatakis, A. (2015) Using RAxML to Infer Phylogenies. *Current Protocols in Bioinformatics* 51: 6.14.1–6.14.14.
https://doi.org/10.1002/0471250953.bi0614s51

Sulzbacher, M., Baseia, I., Lücking, R., Parnmen, S. & Moncada, B. (2013) Unexpected discovery of a novel basidiolichen in the threatened Caatinga biome of northeastern Brazil. *The Bryologist* 115: 601–609.
https://doi.org/10.1639/0007-2745-115.4.601

Sulzbacher, M.A., Wartchow, F., Ovrebo, C.L., Sousa, J.O., Baseia, I.G., Moncada, B. & Lücking, R. (2016) *Sulzbacheromyces caatingae*: notes on its systematics, morphology and distribution based on ITS barcoding sequences. *Lichenologist* 48: 61–70.
https://doi.org/10.1017/S0024282915000420

Takhtajan, A. (1986) *Floristic regions of the world.* University of California Press, California, 247 pp.
https://doi.org/10.5962/bhl.title.2741

Tereg, E. (1923) Einige neue Grünalgen. *Beihefte zum Botanischen Centralblatt* 39: 179–195.

Vainio, E.A. (1890) Étude sur la classification naturelle et la morphologie des Lichens du Brésil. Pars prima. *Acta Societatis pro Fauna et Flora Fennica* 7: 1–247.

Vondrák, J., Říha, P., Arup, U. & Søchting, U. (2009) The taxonomy of the *Caloplaca citrina* group (Teloschistaceae) in the Black Sea region; with contributions to the cryptic species concept in lichenology. *Lichenologist* 41: 571–604.
https://doi.org/10.1017/S0024282909008317

White, T.J., Bruns, T., Lee, S.B. & Taylor, J.W. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In:* Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (eds.) *PCR Protocols*. Academic Press, San Diego, pp. 315–322.
https://doi.org/10.1016/B978-0-12-372180-8.50042-1