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Sarcodon in the Neotropics II: four new species from Colombia and a key to the regional species

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Abstract: This work reports on four species of the ectomycorrhizal (ECM) tooth fungus genus *Sarcodon* (Bankeraceae, Thelephorales, Basidiomycota) recently discovered in the Colombian Amazon. *Sarcodon colombiensis* sp. nov., *Sarcodon rufobrunneus* sp. nov., *Sarcodon pallidogriseus* sp. nov. and *Sarcodon bairdii* sp. nov. are described as new to science. These fungi occur in forests dominated by ECM trees in the genera *Pseudomonotes* (Dipterocarpaceae), *Dicymbe* (Fabaceae subfam. Caesalpinioideae) and *Aldina* (Fabaceae subfam. Papilionoideae). These records bring the number of *Sarcodon* species known from the Neotropics to 10. Each of the new species possesses the accepted diagnostic characters for the genus: pileate-stipitate stature, a dentate hymenophore, determinate basidiomata development, fleshy, non-zonate context, and brown, tuberculate basidiospores. Molecular phylogenetic analysis corroborated the generic placement of the species, and, in combination with morphological characters, confirmed that they are new to science. Macromorphological, micromorphological, habitat and DNA sequence data from the nuc rDNA internal transcribed spacer region (ITS) are provided for each of the new species. A key is provided that allows identification of all known Neotropical *Sarcodon* species and similar extralimital taxa.

Key words: Bankeraceae, Colombia, ectomycorrhizal fungi, Guiana Shield, Thelephorales, tooth fungi

Introduction

Grupe et al. (2015) summarized the current knowledge of the ectomycorrhizal (ECM) fungal genus *Sarcodon* Quél. ex P. Karst. (Bankeraceae, Thelephorales, Basidiomycota) in the Neotropics and described four new species from Belize, Guyana and Puerto Rico. These new *Sarcodon* species were associated with a diverse assemblage of putative ECM broadleaf host tree species in the genera *Dicymbe* (Fabaceae subfam. Caesalpinioideae), *Pakaraimaea* (Dipterocarpaceae) and *Quercus* (Fagaceae) and brought the number of species known from the Neotropics to six. Neotropical species diversity for this largely Nearctic, conifer-associated genus is still low, given that > 90 names have been proposed worldwide in *Sarcodon*.

Recent macrofungal collecting efforts in Amazonian Colombia have revealed a diverse assemblage of putatively ECM fungi (e.g. Vasco-Palacios et al. 2014). Here we describe *Sarcodon colombiensis* sp. nov. from forests dominated by the ECM trees *Pseudomonotes tropenbosii* A.C. Londoño, E. Alvarez & Forero (Dipterocarpaceae) and *Sarcodon rufobrunneus* sp. nov. from forests dominated by the ECM trees *Dicymbe uaiparuensis* R.S. Cowan (Fabaceae subfam. Caesalpinioideae) and *Aldina* sp. (Fabaceae subfam. Papilionoideae), from El Zafire, Amazonas. *Sarcodon pallidogriseus* sp. nov. and *Sarcodon bairdii* sp. nov. are described from a white sand forest dominated by *Dicymbe stipitata* R.S. Cowan in Monochoa, middle Caquetá region, Amazonas. In addition, these constitute the first records of *Sarcodon* for Colombia (Vasco-Palacios and Franco-Molano 2013).

Each of the four new species is morphologically similar to but distinguishable from a group of described *Sarcodon* species characterized by their overall somber colors and KOH-soluble bluish green pigments (Maas Geesteranus 1971). These include *Sarcodon atroviridis* (Morgan) Banker from temperate North America, Europe and eastern Asia, *Sarcodon thwaitesii* (Berk. & Br.) Maas G. from the Asian tropics and *Sarcodon bambusinus* (Baker & Dale) Maas G. from the Neotropics (Berkeley and Broome 1873; Morgan 1895; Baker and Dale 1951; Maas Geesteranus 1964, 1974a, 1975). Specimens putatively identified as *Sarcodon atroviridis*

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sensu lato were reported from Brazil but without any molecular data (Komura et al. 2015, Magnago et al. 2015).

The recently described Neotropical species *S. pakaraimensis* A. Grupe & T.W. Henkel, *S. portoricensis* A. Grupe & T.J. Baroni, *S. quercophilus* A. Grupe & D.J. Lodge and *S. umbilicatus* A. Grupe, T.J. Baroni & D.J. Lodge also fall into this narrow morphological group (Grupe et al. 2015). Nonetheless variation in key morphological characteristics corroborated by molecular phylogenetic analysis supports the recognition of the taxa treated here, *S. colombiensis*, *S. rufobrunneus*, *S. pallidogriseus* and *S. bairdii*, as unique species. Macromorphological, micromorphological, habitat and ITS rDNA sequence data are provided for each of the new *Sarcodon* species and contributed to the global molecular databases. A key is provided that allows identification of all known Neotropical *Sarcodon* species and similar extralimital taxa.

MATERIALS AND METHODS

Collections.—Collections of *Sarcodon colombiensis* and *S. rufobrunneus* were obtained in Jan 2012 from El Zafire in Amazonas, Colombia at 4°00′69″S, 69°53′97″W; ~180–220 m, along a trail in a mixed forest dominated by *Pseudomonotes tropenbosii* and white sand forests dominated by *Dicymbe uaiparuensis* and *Aldina* sp. Collections of *S. pallidogriseus* and *S. bairdii* were made in May 2005 from Resguardo de Monochoa, Comunidad de Chukiki, Puerto Santander, Amazonas, 0°40′S; 72′31″W; ~150 m, in forests where the putative ECM host is *Dicymbe stipitata*.

Macroscopic features of basidiomata were described fresh in the field. Colors were described subjectively and coded according to Kornerup and Wanscher (1978), with color plates noted in parentheses. Collections of fresh basidiomata were dried with silica gel desiccant beads. For *S. colombiensis* a minimal macromorphological description is provided, and a macroscopic image is lacking in that it was collected while travelling from the station to the city of Leticia. Micromorphological features of dried specimens were examined with an Olympus BX51 microscope with light and phase contrast optics and maximum magnification of 1000×. Separate mounts of fungal tissue were made in H_2O, 3% potassium hydroxide (KOH) and Melzer's solution. At least 20 individual basidiospores, basidia and other structures were measured per collection; for basidiospores dimensional measurements include ornamentation. Range and mean quotients of basidiospore length divided by width (Q) were calculated. Outlying measurements observed in less than 5% measured population are indicated in parentheses. Specimens were deposited in: HUA, University of Antioquia Herbarium; HSC, Humboldt State University (Index herbariorum: http://sweetgum.nybg.org/science/ih/).

DNA extraction, amplification, sequencing, and phylogenetic analyses.—DNA extraction, polymerase chain reactions (PCR), cloning and sequencing followed the standard protocols of Gardes and Bruns (1993) as modified by Grupe et al. (2015). Bidirectional sequencing was performed with ITS1F and ITS4 by the University of Florida ICBR sequencing center (www.biotech.ufl.edu). Sequences were edited with CodonCode aligner 3.5.7 (CodonCode Corp., Centerville, Massachusetts) and aligned with Mesquite 3.04 (Maddison and Maddison 2015). Accession numbers from GenBank (http://www.ncbi.nlm.nih.gov/) follow all species epithets for sequences of previously described taxa and those species described here as new (FIG. 1).

New sequences were compiled and aligned with additional sequences from GenBank to generate a final alignment of 882 characters. The phylogenetic analyses included 21 sequences of *Sarcodon* species with one sequence from a *Hydnellum* sp. (AF351871) (Thelephorales) as outgroup. Maximum parsimony (MP) analysis was completed with default settings in PAUP* 4.0 (Swofford 2003). A maximum likelihood (ML) search was run in RAxML (Stamatakis 2014) with the GTR+G model on the CIPRES Science Gateway (Miller et al. 2010). Support for phylogenetic relationships was assessed based on 500 bootstrap replicates in PAUP (for MP) and RAxML (for ML). The alignment is available at: http://purl.org/phylo/treebase/phylows/study/TB2:S18131

RESULTS AND DISCUSSION

blastN queries and phylogenetic analyses.—blastN queries for ITS sequences of *S. colombiensis*, *S. rufobrunneus*, *S. pallidogriseus* and *S. bairdii* produced best matches to species of *Sarcodon* but none exceeded 95% similarity (SUPPLEMENTARY TABLE I). The best ML tree (FIG. 1, likelihood score = −ln 5816.46) differed slightly from the topology of the MP tree (1168 steps) in that the placement of some of the *Sarcodon* species outside the *S. atroviridis* clade had little to no bootstrap support in the MP tree (data not shown) but not the ML tree. The phylogenetic analyses demonstrated that *S. colombiensis*, *S. rufobrunneus*, *S. pallidogriseus* and *S. bairdii* are phylogenetically distinct from other recently described Neotropical *Sarcodon* species. Our analysis focused on the placement of *S. colombiensis*, *S. rufobrunneus*, *S. pallidogriseus* and *S. bairdii* and could not resolve other phylogenetic relationships within the genus or address the position of *Sarcodon* within the Bankeraceae or Thelephorales. *Sarcodon colombiensis* had the closest affinity with *S. pakaraimensis*, with the two species occurring in the well-supported clade A along with *S. rufobrunneus* and *S. umbilicatus* (FIG. 1). *Sarcodon bairdii* and *S. pallidogriseus* occurred in a basal position to clades A and B, with low confidence on the actual placement of these species (FIG. 1).

TAXONOMY

Sarcodon rufobrunneus A.M. Vasco-Pal. & A. Grupe, sp. nov. FIGS. 2, 3

MycoBank MB813077

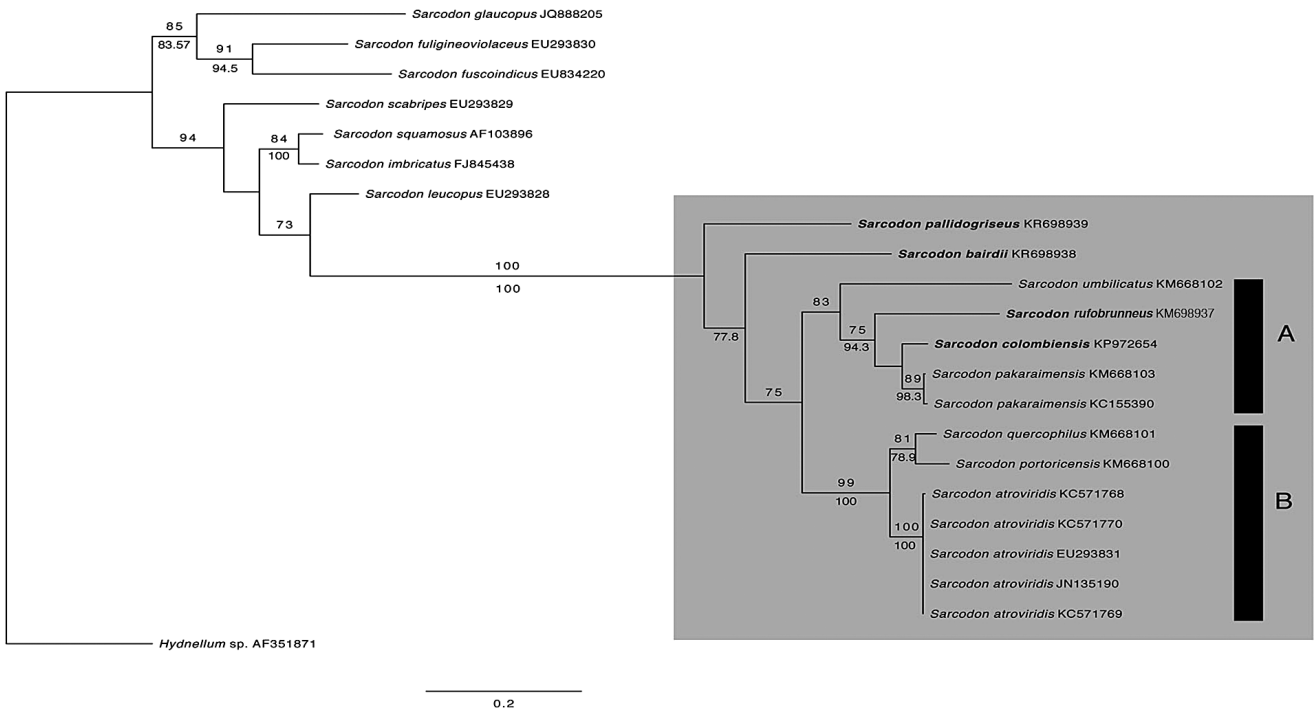

FIG. 1. Maximum likelihood phylogram based on internal transcribed spacer (ITS) ribosomal DNA sequences depicting phylogenetic relationships of *Sarcodon* species from Colombia. Support above the nodes are maximum likelihood bootstrap values. Support below the nodes are maximum parsimony bootstrap values. The gray box demarcates the *S. atroviridis* clade and the well-supported clade A and clade B illustrated with thick black boxes.

Diagnosis: Sarcodon rufobrunneus differs from other species of *Sarcodon* in its combination of dark reddish brown (7F8–8F8), umbonate pileus with a smooth to fibrillose pileus surface, unchanging pileus trama, grayish brown (7F3–7F4) stipe with initially reddish brown trama, and unique ITS sequence.

Typification: COLOMBIA: AMAZONAS; El Zafire at 4°00′69″S; 69°53′968″W; ~180–220 m; along trail in white sand forests dominated by *Dicymbe uaiparuensis*, 9 Jan 2012, *Vasco 1989* (holotype: HUA 186216; isotype: HSC G1164). GenBank accession: ITS KR698937.

Etymology: Rufus (Latin adj. A) = adjectival prefix indicating reddish, and -brunneus (Latin adj. A) = adjectival suffix indicating brown, referring to the reddish brown fresh pileus.

Pileus conical when young, parabolic to plane with age, 12–70 mm broad, 2–3 mm thick, dark reddish brown (7F8-8F8), hygrophanous; surface smooth to fibrillose, umbonate; margin eroded; trama not staining upon exposure. Hymenophore dentate; teeth 2–4 mm long, apices sharply conical, concolorous with pileus, delicate, easily removed. Stipe subequal, 30–50 × 3–6 mm, cylindrical to slightly clavate, grayish brown (7F3-7F4); surface glabrous; interior trama initially reddish brown, turning black with damage or age; basal mycelium a low grayish tomentum. Odor not distinguishable; flavor bitter. Macrochemical reactions: KOH black on all surfaces of the fresh basidioma. Basidiospores 5–7 × 7–9 µm including ornamentation (mean = 5.75 × 7.7 µm; n = 20), Q range = 0.62–0.857, Q mean = 0.75, suboblate, tuberculate, gray-tan in H_2O, tan in KOH, inamyloid; tubercles prominent in polar view, less so in side view, predominantly exsculpate; hilar appendage 1–2 µm. Basidia (25–) 30–38(–42) × (9–)11–13 µm wide apically, 5–9 µm wide centrally, 3–4 µm at basal septum, clavate, gray in H_2O and KOH; basal septum with clamp connection; sterigmata four, curved, 5–7 µm long. Hymenial cystidia absent. Hymenophoral trama parallel, predominantly gray in mass in H_2O, bright blue-green in KOH; individual hyphae gray in H_2O, light gray or light blue-green in KOH, 3–5 µm wide, with copious granular dark gray-blue pigment bodies, these soluble in KOH. Pileipellis a cutis of repent hyphae, gray-blue in mass in H_2O, light tan or blue-green in KOH, with copious granular dark gray-blue pigment bodies, these soluble in KOH; individual hyphae gray to light tan in H_2O, light gray in KOH, 4–6 µm wide, cylindrical; terminal cells undifferentiated. Pileus trama tan to brown-orange in mass in H_2O, tan to light tan or bright blue-green where pigment bodies have dissolved in KOH, with copious granular dark gray-blue pigment bodies, these soluble in KOH; individual hyphae light gray to light tan in H_2O, gray or light blue in KOH,

FIG. 2. Basidiomata of *Sarcodon rufobrunneus* (holotype; *Vasco 1989*). Bar = 10 mm.

frequently terminating in bifurcating tips of unequal lengths, others cylindrical and unbranched, (3–)6–10 µm wide. Stipitipellis a cutis of repent hyphae, in mass brown-orange or dark blue where pigment bodies are dense in H_2O, tan or bright blue-green in KOH, with copious granular dark gray-blue pigment bodies, these soluble in KOH; individual hyphae light tan or light gray in H_2O, light gray or light blue-green in KOH, cylindrical, 2–4 µm wide; terminal cells undifferentiated. Stipe trama brown-orange in mass in H_2O, tan or blue-green in KOH, copious granular dark gray-blue pigment bodies present, soluble in KOH; individual hyphae light tan in H_2O, light tan or light gray in KOH, frequently terminating in bifurcated tips of unequal lengths, others cylindrical and unbranched, 4–8(–10) µm wide. Clamp connections abundant on hyphae of all tissues.

Habit, habitat and distribution: Gregarious on soil in forests with *Dicymbe uaiparuensis* and *Aldina* sp., known only from the type locality in El Zafire, Colombia.

Commentary: Sarcodon rufobrunneus is recognized in the field by its dark reddish brown, umbonate pileus with a smooth to fibrillose surface, unchanging pileus trama and grayish brown stipe with initially reddish brown trama. *Sarcodon rufobrunneus* can be differentiated from each of the other Neotropical species described in Grupe et al. (2015) and here based on pileus color and surface features, lack of a pileus staining reaction and the morphology of the pileus trama and stipe trama terminal cells (TABLE I).

Sarcodon rufobrunneus and the Neotropical *S. bambusinus* have a similar pileus shape, non-decurrent teeth, and similar tooth, stipe and basidium lengths, but *S. rufobrunneus* differs from *S. bambusinus* in its dark reddish brown pileus (vs. vinaceous drab, becoming fuscous or fuliginous with age), maximum pileus size (70 vs. 50 mm), smooth to fibrillose pileus (vs. villose to subfurfuraceous) and shorter basidiospores (5–7 vs. 6.5–9 µm) (Baker and Dale 1951, Maas Geesteranus 1974a).

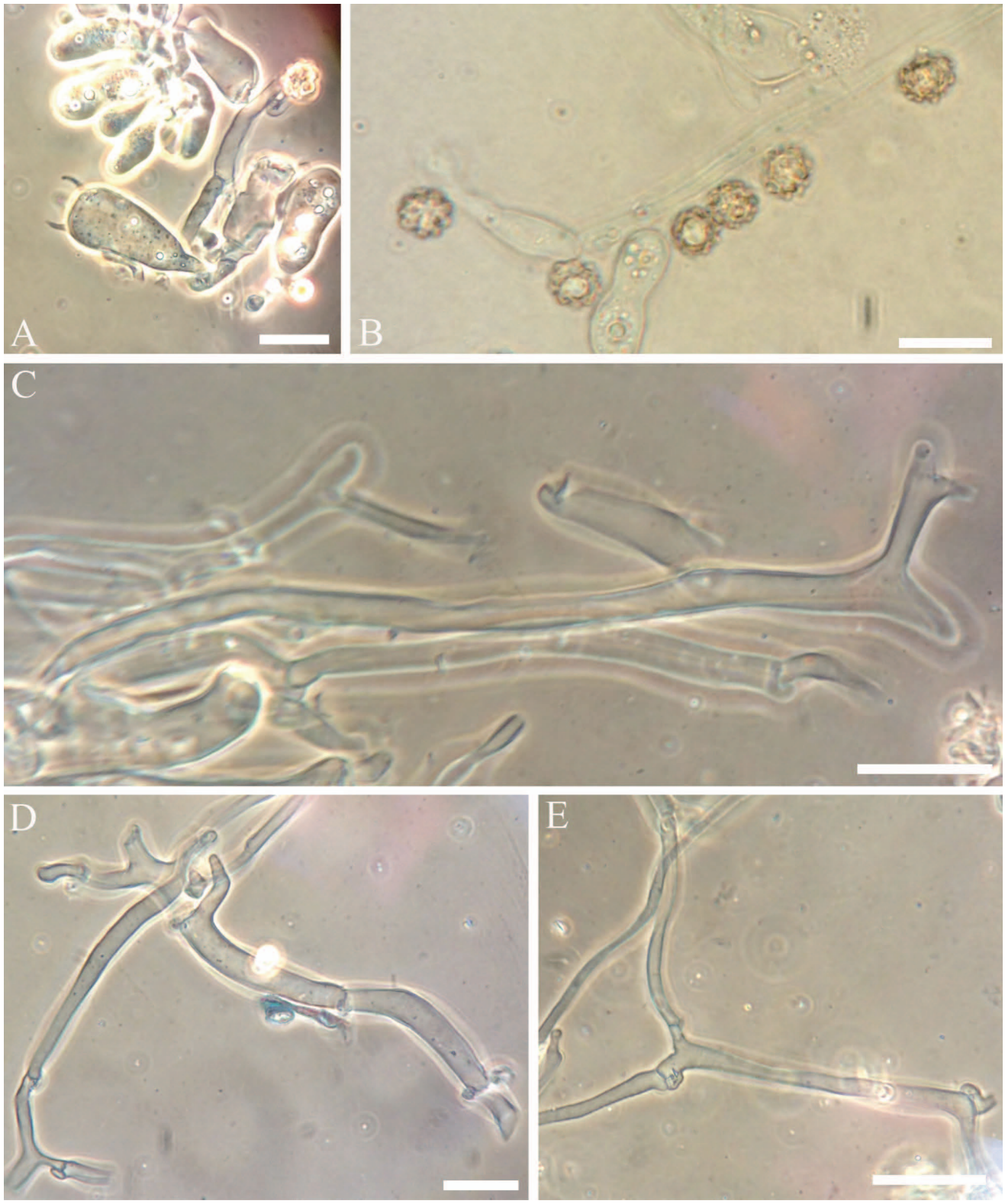

FIG. 3. Basidia (A), polar view of basidiospores (B) and terminal cells of the pileus (C, D) and stipe trama (E) of *Sarcodon rufobrunneus* (holotype; *Vasco 1989*). Bar = 10 µm.

TABLE I. Diagnostic morphological characters of Neotropical *Sarcodon* species

Species	Pileus surface	Pileus staining	Hymenophore attachment	Terminal cells of pileus and stipe trama	Tramal staining	Basidiospore ornamentation	Basidia	Stipitipellis terminal cells
S. colombiensis	Not recorded	Not recorded	Adnate	(Pileus) terminating in bifurcating tips of unequal lengths	Not recorded	Exsculpate; apices variable in height, blunt-rounded	Clavate 28–37 × 10–12 µm	Undifferentiated 3–4 µm wide
S. rufobrunneus	Smooth to fibrillose, umbonate	None	Adnate	(Pileus and stipe) terminating in bifurcating tips of unequal lengths	Absent	Prominent to low, predominately exsculpate	Clavate 30–38 × 11–13 µm	Undifferentiated, 3–4 µm wide
S. pallidogriseus	Slightly rugose, overall interwoven fibrillose, center with scales	None	Adnate	Undifferentiated	Absent	Apices rounded, frequently prominent and short, uncommonly exsculpate	Clavate 34–41 × 10–13 µm	Undifferentiated 3–4 µm wide
S. bairdii	Fibrillose, centrally squamulose	None	Adnate	Undifferentiated	Absent	Short, commonly rounded, infrequently flat topped, rarely exsculpate	Clavate 33–46 × 10–12 µm	Undifferentiated 4–7 µm wide
S. pakaraimensis	Glabrous, pitted	Black	Adnate	Undifferentiated	Pink	Rounded, rarely exsculpate	Clavate 27–47 × 5–7 µm	Undifferentiated, 3–9 µm wide
S. portoricensis	Fibrillose, areolate over disc	Black	Adnate	Undifferentiated	Black	Exsculpate, rounded corners	Clavate 33–44 × 7–12 µm	Subclavate to subcapitate, 2–3 µm wide
S. quercophilus	Appressed felted, substriate at margin	None	Adnate	Undifferentiated	Absent	Exsculpate, outward projecting corners	Short-clavate 22–30 × 5–10 µm	Serpentine, 2–4 µm wide
S. umbilicatus	Matted fibrillose, rugulose, umbilicate	Dark brown	Adnexed	Undifferentiated	Grayish brown	Rounded, rarely exsculpate	Clavate 32–38 × 5–7 µm	Undifferentiated, subcapitate, or subclavate, 2–5 µm wide

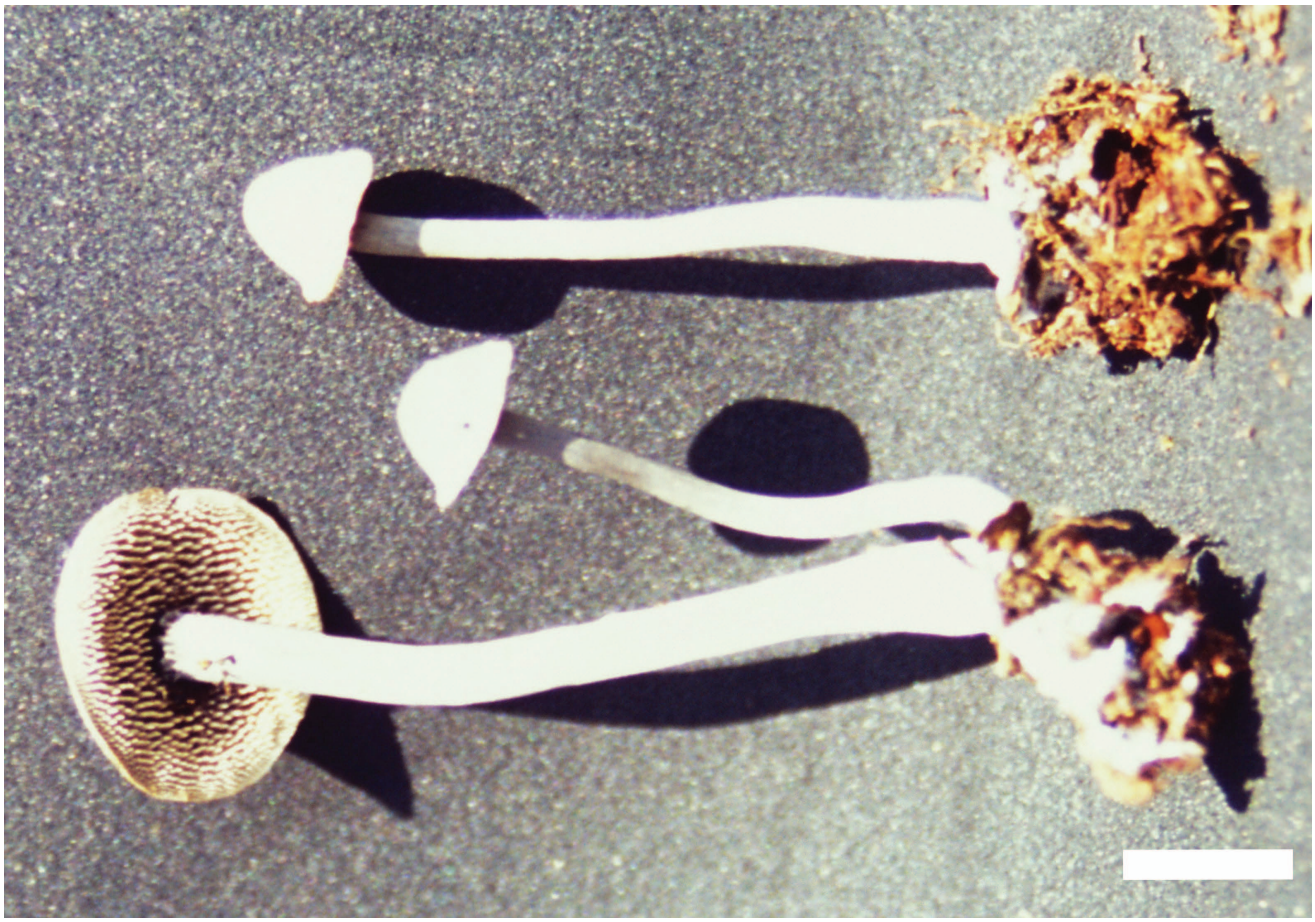

FIG. 4. Basidiomata of *Sarcodon pallidogriseus* (holotype; *Vasco 989*). Bar = 10 mm.

Sarcodon rufobrunneus resembles the Paleotropical *S. thwaitesii* in pileus shape, stipe length, surface texture of the stipe and basidium lengths. *Sarcodon thwaitesii* is distinguished by its grayish lilac to dark purple colors, tomentose pileus and taller basidiospores (7.6–9.4 vs. 5–7 µm) (Berkeley and Broome 1873; Maas Geesteranus 1964, 1971, 1974b).

Among extratropical species *Sarcodon rufobrunneus* is most similar to the north temperate *S. atroviridis* in that both have a similar range of pileus sizes and shapes, stipe surface texture and basidium sizes (Morgan 1895, Banker 1906, Coker and Beers 1951, Baird et al. 2013). *Sarcodon rufobrunneus* can be distinguished from *S. atroviridis* in its combination of a reddish brown pileus and grayish brown stipe (vs. brownish gray, grayish violet or black), unchanging pileus trama (vs. lilac, later bluish gray), shorter teeth (1–5 vs. 1–16 mm), shorter basidiospores (5–7 vs. 8–9 µm) and bifurcate pileus and stipe trama hyphae (vs. unbranching) (Morgan 1895, Banker 1906, Coker and Beers 1951, Baird et al. 2013). In addition, the ITS sequence of *S. rufobrunneus* is only ~82% similar to sequences of *S. atroviridis* from southeastern USA and these two species are distinct in the phylogenetic analysis (FIG. 1).

Sarcodon pallidogriseus A. Grupe & A.M. Vasco-Pal., sp. nov. FIGS. 4, 5
MycoBank MB813076

Diagnosis: Sarcodon pallidogriseus is distinct from all other described *Sarcodon* species in its combination of pale gray, campanulate, fibrillose, centrally scabrous pileus, unchanging pileus trama, velutinous stipe with unchanging trama and unique ITS sequence.

Typification: COLOMBIA: CAQUETA: Puerto Santander, Vereda Puerto Fresco, Chukiki, 0°40′S, 72°31′W, 150 m, in white sand forests with *Dicymbe stipitata*, 23 Sep 2005, *Vasco 989* (holotype: HUA 186217; isotype: HSC G1165). GenBank accession: ITS KR698939.

Etymology: Pallidus (Latin adj. A) = adjectival prefix indicating pale coloration, and -griseus (Latin adj. B) = adjectival suffix indicating gray, referring to the pale gray fresh basidiomata.

Pileus campanulate, 8–16 mm broad, 4 mm tall, gray (24D1, 24B1–24C1), drying to darker gray with orange

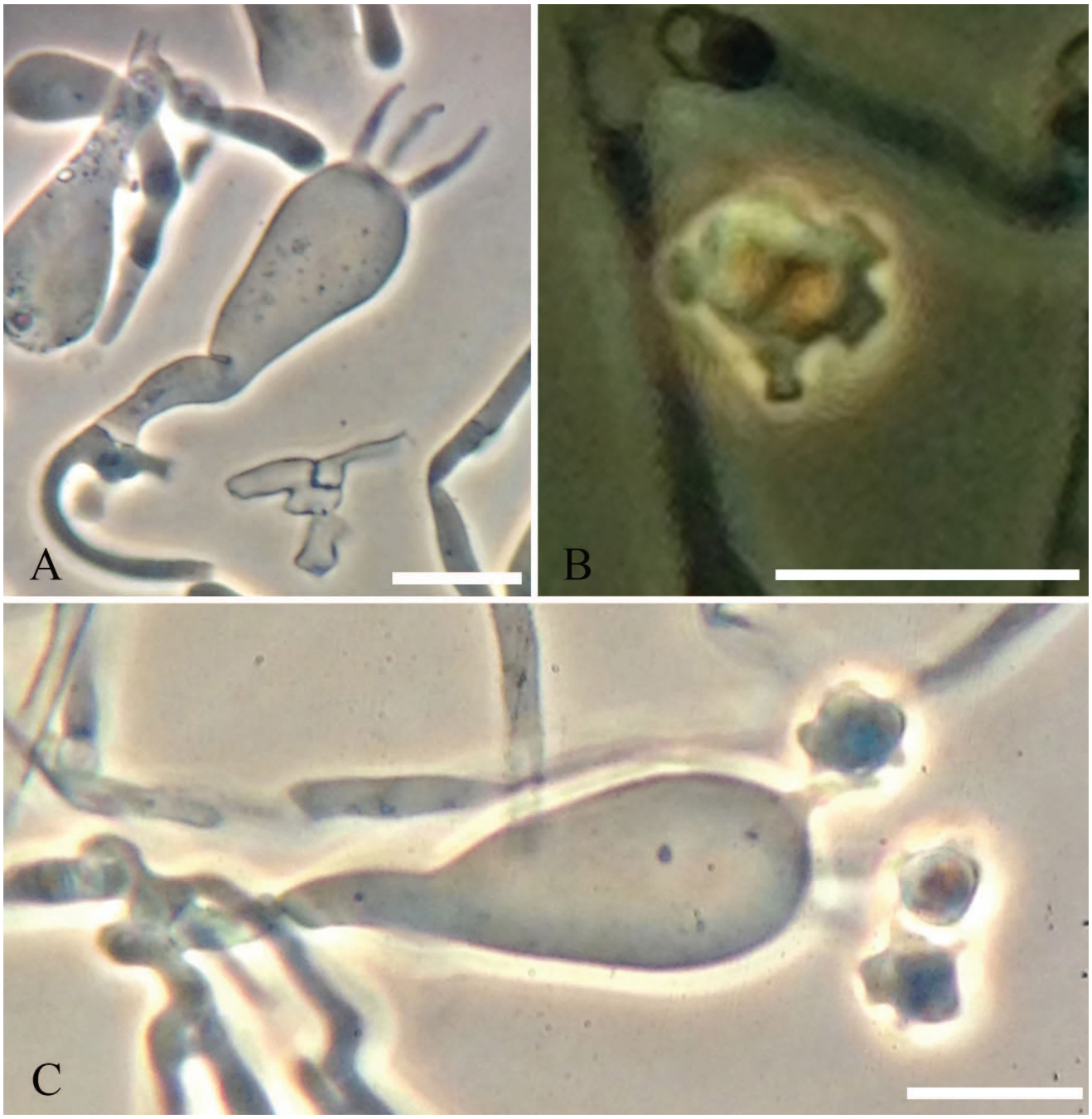

FIG. 5. Basidium (A), basidiospore (B), and basidium with basidiospores (C) of *Sarcodon pallidogriseus* (holotype; *Vasco 989*). Bar = 10 µm.

or green tones, hygrophanous; surface slightly rugose, overall interwoven fibrillose, center with scales; margin entire, gray with orange tones (5C4); trama gray (24D1), unchanging, soft. Hymenophore dentate, adnate; teeth 2 mm broad, smaller toward the margin, conical, acute apex, surface pale orange (6A3) to grayish orange when mature (5B2–5B3), drying to dark brown. Stipe subequal, 30–45 mm long, 2–5 mm broad, cylindrical, fragile, pale gray (24D1), bruising black; surface fibrillose; trama subsolid throughout development, cream (2A2), unchanging; basal mycelium white. Odor none; flavor bitter. Macrochemical reactions: KOH black on all surfaces of the fresh basidioma. Basidiospores 5–6(–7) × (6–)7–8 µm including ornamentation (mean = 5.65 × 7.15 µm; n = 20), Q range = 0.71–0.85(–1.0) µm, Q mean = 0.79 µm, suboblate, tuberculate, greenish brown in H_2O, pale golden brown in KOH, inamyloid; tubercles mostly

prominent and short; apices rounded, infrequently exsculpate, rarely pointed; hilar appendage 1–2 μm long. Basidia (30–)34–41(–44) × 10–13(–15) μm wide apically, (3–)5–8 μm wide centrally, 2–4 μm at basal septum, clavate, hyaline in H_2O and KOH; basal septum with clamp connection; sterigmata four, curved, 6–8 μm long. Hymenial cystidia absent. Hymenophoral trama interwoven, faint tan or light blue-green in mass in H_2O and KOH; individual hyphae light gray or pale blue-green in H_2O and KOH, 3–5 μm wide, with dense clusters of small, bluish green extracellular pigment bodies scattered throughout. Pileipellis a cutis of strongly repent hyphae, in mass light gray-green in H_2O, dark gray-blue in KOH, with dense clusters of small, bluish green extracellular pigment bodies scattered throughout, these dark blue-gray in H_2O, bright blue-green in KOH and eventually dissolving and leaching into solution; individual hyphae light gray-green in H_2O, faintly gray or gray-brown in KOH, 3–5 μm wide, cylindrical; terminal cells undifferentiated. Pileus trama in mass gray-brown to orange-brown in H_2O, light gray-tan in KOH, with highly scattered, extracellular, dark bluish green to nearly black granular pigment bodies in H_2O, these bluish green in KOH; individual hyphae light gray-brown in H_2O, light gray in KOH, cylindrical, (3–)4–7 μm wide. Stipitipellis a cutis of repent hyphae, in mass orange-brown to dark blue where pigment bodies are dense and copious in H_2O, in KOH light orange-brown or light blue-green; individual hyphae light gray in H_2O, faint gray to faint gray-blue in KOH, cylindrical, 3–4 μm wide; terminal cells undifferentiated. Stipe trama in mass orange-brown in H_2O, light brown-orange to light blue-green where pigment bodies have dissolved in KOH; individual hyphae faint gray to faint tan in H_2O, light gray in KOH, cylindrical, 5–8(–10) μm wide. Clamp connections abundant on hyphae of all tissues.

Habit, habitat and distribution: Gregarious on sandy soil under *Dicymbe stipitata*; known only from the type locality in the middle Caquetá region of Colombia.

Commentary: Sarcodon pallidogriseus is recognized in the field by its combination of pale gray colors, pileus that is campanulate, fibrillose, centrally scabrous, the unchanging pileus trama and velutinous stipe with unchanging trama. *Sarcodon pallidogriseus* can be differentiated from each of the other Neotropical species described in Grupe et al. (2015) and here based on its pale gray basidioma, shape and surface features of the pileus, lack of a tramal staining reaction, and surface features of the stipe (TABLE I).

Sarcodon pallidogriseus and the Neotropical *S. bambusinus* have a similar pileus shape, non-decurrent teeth of equal lengths, stipe lengths and basidium lengths, but *S. pallidogriseus* differs from *S. bambusinus* in its campanulate pileus (vs. orbicular, conical to planoconvex), pale gray basidioma (vs. vinaceous drab, becoming fuscous or fuliginous with age), rugulose, fibrillose, centrally scabrous pileus surface (vs. villose to subfurfuraceous), and shorter basidiospores (5–6 vs. 6.5–9 μm) (Baker and Dale 1951, Maas Geesteranus 1974a).

Sarcodon pallidogriseus resembles the Paleotropical *S. thwaitesii* in its black surface-staining reaction, lack of a tramal staining reaction, stipe length and basidium lengths. However, *S. thwaitesii* is distinguished by its grayish lilac to dark purple colors, tomentose pileus and longer basidiospores (7.6–9.4 vs. 5–6 μm) (Berkeley and Broome 1873; Maas Geesteranus 1964, 1971, 1974b).

Among extratropical species *S. pallidogriseus* is most similar to the north temperate *S. atroviridis* in that both have basidiomata that exhibit some shade of gray, stipe surface that stains black upon pressure, but lack a stipe-trama staining reaction and basidium sizes (Morgan 1895, Banker 1906, Coker and Beers 1951, Baird et al. 2013). *Sarcodon pallidogriseus* can be distinguished from *S. atroviridis* in its lack of a pileus trama staining reaction (vs. lilac, later bluish gray), orangish teeth (vs. white, yellowish, brown), rugulose, fibrillose, centrally scabrous pileus surface (vs. tomentose to felted or glabrous), fibrillose stipe surface (vs. felt-like but predominantly glabrous), cream stipe trama (vs. lilac to dark violet) and shorter basidiospores (5–6 vs. 8–9 μm) (Morgan 1895, Banker 1906, Coker and Beers 1951, Baird et al. 2013). In addition, the ITS sequence of *S. pallidogriseus* is only ~86% similar to sequences of *S. atroviridis* from southeastern USA and these two species are distinct in the phylogenetic analysis (FIG. 1).

Sarcodon bairdii A. Grupe & A.M. Vasco-Pal., sp. nov. FIGS. 6, 7

MycoBank MB812925

Diagnosis: Sarcodon bairdii differs from all other described species of *Sarcodon* in its combination of yellow-gray, convex to plane, subumbilicate pileus that has a fibrillose and centrally squamulose surface, yellow-gray, unchanging pileus trama, brownish gray, fibrillose stipe and unique ITS sequence.

Typification: COLOMBIA: CAQUETA: Puerto Santander, Vereda Puerto Fresco, Chukiki, white sand soil forests with *Dicymbe stipitata*, 0°40′S, 72°31′W, 150 m, 23 Sep 2005, *Vasco 990* (holotype: HUA 186218; isotype: HSC G1166). GenBank accession: ITS KR698938.

Etymology: The species is named after Dr Richard E. Baird, an authority on hydnoid fungi of the Thelephorales.

Pileus broadly convex to plane, subumbilicate, 26–45 mm broad, yellowish gray (4B4–4B5), slightly hygrophanous; fibrillose, centrally squamulose; margin

FIG. 6. Basidiomata of *Sarcodon bairdii* from Colombia (holotype; *Vasco 990*). Bar = 10 mm.

eroded, rimose, with olive tones (4E4–4E3); trama 2 mm wide, spongy, yellow-gray (4B2), unchanging. Hymenophore dentate, adnate, teeth 1–3 mm long, tapered, with acute apices, grayish brown (5F2), teeth shorter at margin. Stipe equal, 30–50 mm long, 3–11 mm wide, cylindrical, tapering gradually toward the base, brittle, brownish gray (5D2) toward apex, darker toward the base (5E3–5D3); surface fibrillose, bruising black; trama solid to substuffed, spongy, yellow-gray (4B2), bruising dark blue. Odor non-distinguishable;

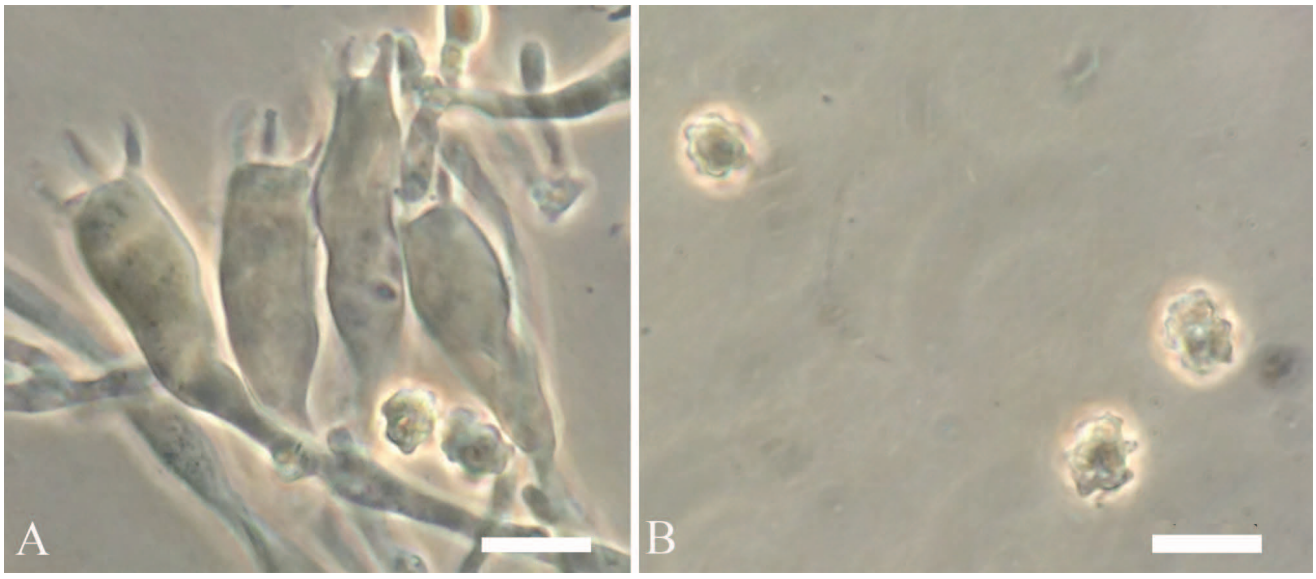

FIG. 7. Basidia and basidiospores of *Sarcodon bairdii* (holotype; *Vasco 990*). Bar = 10 µm.

flavor bitter. Macrochemical reactions: KOH black on all surfaces of the fresh basidioma. Basidiospores (5–) 6–7 × 7–8(–9) μm including ornamentation (mean = 6.2 × 7.8 μm; n = 20), Q range = 0.66–0.88, Q mean = 0.79, oblate, tuberculate, dark gray to light tan in H_2O, light tan in KOH, inamyloid; tubercles short, commonly rounded, infrequently flat topped, rarely exsculpate; hilar appendage 1–2 μm. Basidia (28-)33–46 × 10–12(–14) μm wide apically, (2–)4–9 (–11) μm wide centrally, 2–3 μm at basal septum, clavate, light gray in H_2O, light gray to light tan in KOH; basal septum with clamp connection; sterigmata four, curved, 5–7 μm long. Hymenial cystidia absent. Hymenophoral trama parallel, in mass greenish brown in H_2O, orange-brown to dark gray-blue in KOH; individual hyphae light gray in H_2O, light tan or light gray in KOH, 5–7(–10) μm wide, with copious granular dark grayish blue pigment bodies, these soluble in KOH. Pileipellis a cutis of repent hyphae, dark grayish green to brown-green in mass in H_2O, orange-brown or dark grayish blue in KOH, with copious granular dark gray-blue pigment bodies, these soluble in KOH; individual hyphae light gray in H_2O, light gray to light tan in KOH, 6–9 μm wide, cylindrical; terminal cells undifferentiated. Pileus trama dark grayish green to brown-green in mass in H_2O, orange-brown or dark grayish blue in KOH, with copious granular dark gray-blue pigment bodies, these soluble in KOH; individual hyphae light gray in H_2O, light gray to light tan in KOH, cylindrical, 7–10(–12) μm wide. Stipitipellis a cutis of repent hyphae, in mass dark orange in H_2O, dark orange to darkest blue in KOH, with copious granular dark grayish blue pigment bodies, these soluble in KOH; individual hyphae light gray in H_2O, light gray to light tan in KOH, more or less cylindrical, with irregular bulges and constrictions, 4–7 μm wide; terminal cells undifferentiated. Stipe trama brownish green in mass in H_2O, light tan or dull blue-green in KOH, with copious granular dark grayish blue pigment bodies, these soluble in KOH; individual hyphae light brown-green in H_2O, light gray to light tan in KOH, 10–16 μm wide. Clamp connections abundant on hyphae of all tissues.

Habit, habitat and distribution: Gregarious on white sand soil in forest with *Dicymbe stipitata*, known only from the type locality in the middle Caqueta region of Colombia.

Commentary: Sarcodon bairdii is recognized in the field by its yellow-gray pileus that is convex to plane, subumbilicate, fibrillose and centrally squamulose, yellow-gray, unchanging pileus trama, brownish gray, fibrillose stipe, and stipe trama that bruises blue. *Sarcodon bairdii* can be differentiated from each of the other Neotropical species described in Grupe et al. (2015) and here based on overall basidioma color, shape and surface features of the pileus, lack of a pileus trama staining reaction and surface features of the stipe (TABLE I).

Sarcodon bairdii and the Neotropical *S. bambusinus* have a similar pileus shape, non-decurrent teeth of equal lengths, stipe lengths, and basidium lengths, but *S. bairdii* differs from *S. bambusinus* in its pileus being convex to plane, subumbilicate in the center (vs. orbicular, conical to plano-convex), basidioma yellowish gray (vs. vinaceous drab, becoming fuscous or fuliginous with age), pileus surface that is fibrillose with interspersed fibers and centrally squamulose (vs. villose to subfurfuraceous) and basidiospores that are both shorter and wider (6–7 × 7–8 vs. 6.5–9 × 5–7 μm) (Baker and Dale 1951, Maas Geesteranus 1974a).

Sarcodon bairdii resembles the Paleotropical *S. thwaitesii* in its non-staining pileus trama, stipe and basidium lengths. *Sarcodon thwaitesii* is distinguished by its grayish lilac to dark purple colors, tomentose pileus and basidiospore dimensions (7.6–9.4 × 5.4–7.2 vs. 6–7 × 7–8 μm) (Berkeley and Broome 1873; Maas Geesteranus 1964, 1971, 1974b).

Among extratropical species, *Sarcodon bairdii* is most similar to the north temperate *S. atroviridis* in that both have basidiomata that exhibit some shade of gray, stipes that bruise black, comparable basidiospore widths and basidium sizes (Morgan 1895, Banker 1906, Coker and Beers 1951, Baird et al. 2013). *Sarcodon bairdii* can be distinguished from *S. atroviridis* in its pileus surface being fibrillose and centrally squamulose (vs. tomentose to felted or glabrous), unchanging pileus trama (vs. lilac, later bluish gray), fibrillose stipe surface (vs. felt-like to pubescent or glabrous), stipe trama that is yellow-gray before bruising dark blue (vs. lilac to dark violet) and shorter basidiospores (6–7 vs. 7–9 μm) (Morgan 1895, Banker 1906, Coker and Beers 1951, Baird et al. 2013). In addition, the ITS sequence of *S. bairdii* is only ~86% similar to sequences of *S. atroviridis* from southeastern USA and these two species are distinct in the phylogenetic analysis (FIG. 1).

Sarcodon colombiensis A.M. Vasco-Pal. & A. Grupe, sp. nov. FIG. 8

MycoBank MB811919

Diagnosis: Sarcodon colombiensis differs from other species of *Sarcodon* in its dark gray to black basidioma, umbonate pileus and unique ITS sequence.

Typification: COLOMBIA: AMAZONAS: El Zafire, 4°00′69″S; 69°53′968″W, ~180–220 m; along trail in forest under *Pseudomonotes tropenbosii*, 9 Jan 2012, *Vasco 2084* (holotype: HUA 186215; isotype: HSC G1167). GenBank accession: ITS KP972654.

Etymology: Colombiensis (-ensis Latin adj. B) = adjectival suffix indicating origin or place, referring to the type locality of the country of origin, Colombia.

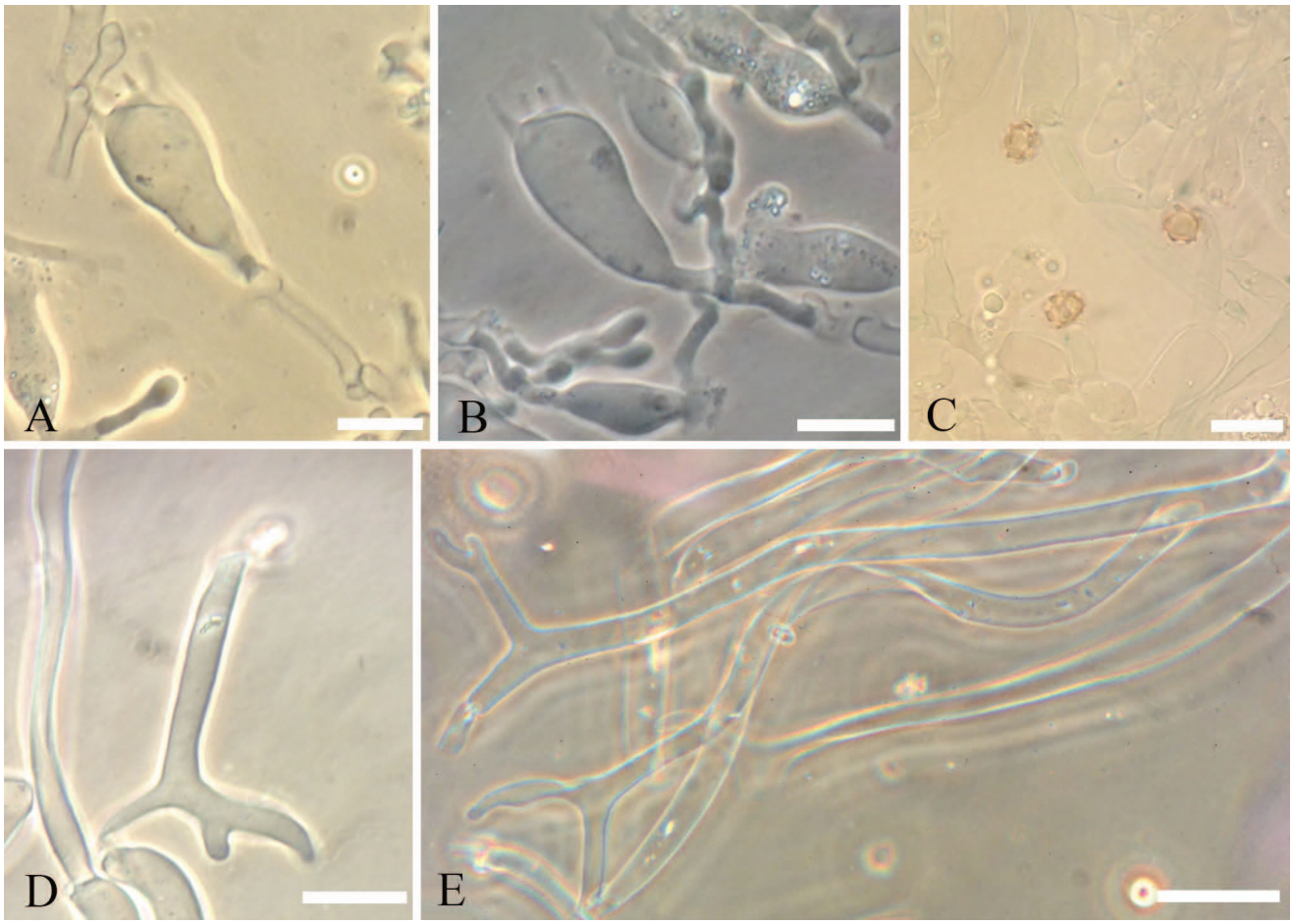

FIG. 8. Basidia (A, B), basidiospores (C) and terminal cells of the pileus trama (D, E) of *Sarcodon colombiensis* (holotype; *Vasco 2084*). Bar = 10 µm.

Pileus umbonate, up to 30 mm broad, hygrophanous, dark gray to nearly black; pileus staining reactions, surface features and trama characteristics not recorded. Hymenophore dentate, adnate, teeth up to 3 mm long, sharp, yellowish. Stipe equal, up to 50 mm long, 3–4 mm wide, smooth surface, concolorous with the pileus, hygrophanous. Odor and flavor not recorded. Macrochemical reactions: KOH dark blue to black on all tissues of the dried basidioma. Basidiospores 5–6(–7) × (6–)7–8 µm including ornamentation (mean = 5.95 × 7.45 µm; n = 20), Q range = 0.75–0.86, mean Q = 0.80, oblate, tuberculate, light brown in H_2O, light tan in KOH, inamyloid; tubercle apices variable in height, blunt-rounded, exsculpate; hilar appendage 1 µm long. Basidia (25-)28–37(–41) × 10–12 µm apically, 6–8(–10) µm centrally, 2–4 µm at basal septum, clavate, occasionally with a central constriction, light tan to light gray in H_2O, faint gray in KOH; basal septum with clamp connection; sterigmata four, curved, 4–5(–7) µm long. Hymenial cystidia absent. Hymenophoral trama subparallel to slightly divergent, in mass light reddish brown to light gray in H_2O, bright green-blue in KOH; individual hyphae light tan to light gray in H_2O, faint gray to faint green-blue in KOH, (3–) 5(–10) µm wide, with copious dark blue, nearly black pigmented bodies. Pileipellis a cutis of repent hyphae, in mass light tan to light gray in H_2O, light tan to light blue-green in KOH, with dark blue, nearly black pigment bodies scarce compared to other tissues, these eventually dissolving and leaching into solution; individual hyphae light tan to faint gray in H_2O, light gray in KOH, 4–6(–10) µm wide, infrequently branching near the basal clamp connection; terminal cells undifferentiated. Pileus trama in mass brown-orange in H_2O, green-blue or light tan in KOH, pigment bodies present, of two types, some small, clustered, dark blue, nearly black, dissolving to bluish green and leaching into solution in KOH, others relatively large and copious, dark yellow-orange in H_2O, more or less soluble in KOH; individual hyphae frequently terminating in bifurcating tips of unequal lengths, others cylindrical and unbranched,

(4–)8–11(–12) μm wide. Stipitipellis a cutis of repent hyphae, in mass gray or tan in H_2O, light tan in KOH, with scattered clusters of irregularly shaped, extracellular, granular pigment bodies, these dark blue, nearly black in H_2O, bluish green in KOH and eventually dissolving and leaching into solution; individual hyphae light gray to faint tan in H_2O, gray in KOH, cylindrical, (2–)3–4(–5) μm wide; terminal cells undifferentiated. Stipe trama in mass brown-orange or faint tan in H_2O, light tan to light green-blue in KOH, with scattered extracellular granular pigment bodies, these darkest blue to nearly black in H_2O, dark bluish green in KOH; individual hyphae light gray to faint tan in H_2O, light gray to light green-blue in KOH, more or less cylindrical, (5–)8–11(–15) μm wide. Clamp connections abundant on hyphae of all tissues.

Habit, habitat and distribution: Solitary, on soil in forest with *Pseudomonotes tropenbosii*; known only from the type locality in El Zafire, Colombia.

Commentary: Sarcodon colombiensis is recognized in the field by its dark gray to black basidioma and umbonate pileus. *Sarcodon colombiensis* can be differentiated from each of the four Neotropical species described in Grupe et al. (2015) and here based on key features of basidioma color and terminal cells of the pileus trama hyphae (TABLE I).

Sarcodon colombiensis and the Neotropical *S. bambusinus* have a similar pileus shape, non-decurrent teeth, similar tooth lengths, stipe lengths and basidium lengths, but *S. colombiensis* differs from *S. bambusinus* in its dark gray to black (vs. vinaceous drab, becoming fuscous or fuliginous with age) basidioma colors, yellowish teeth (vs. pallid fuliginous to ochraceous) and shorter basidiospores (5–6 vs. 6.5–9 μm) (Baker and Dale 1951, Maas Geesteranus 1974a).

Sarcodon colombiensis resembles the Paleotropical *S. thwaitesii* in pileus shape, stipe length, surface texture of the stipe and basidium lengths. *Sarcodon thwaitesii* is distinguished from *S. colombiensis* by its grayish lilac to dark purple colors, white, grayish, or brown teeth (vs. yellowish), and shorter basidiospores (5–6 vs. 7.6–9.4 μm) (Berkeley and Broome 1873; Maas Geesteranus 1964, 1971, 1974b).

Among extratropical species *S. colombiensis* is most similar to the north temperate *S. atroviridis* in that both have a similar stipe surface texture and basidium sizes (Morgan 1895, Banker 1906, Coker and Beers 1951, Baird et al. 2013). *Sarcodon colombiensis* can be distinguished from *S. atroviridis* by its umbonate pileus (vs. convex to planar), shorter teeth (≤ 3 vs. 1–16 mm), shorter basidiospores (5–6 vs. 8–9 μm), and bifurcate pileus trama hyphae (vs. unbranching) (Morgan 1895, Banker 1906, Coker and Beers 1951, Baird et al. 2013). In addition, the ITS sequence of *S. colombiensis* is only ~85% similar to sequences of *S. atroviridis* from southeastern USA and these two species are distinct in the phylogenetic analysis (FIG. 1).

KEY TO NEOTROPICAL *SARCODON* SPECIES WITH SELECTED EXTRALIMITAL TAXA

1. Pileus pinkish gray (7B2–7C2 KW), with irregular darker purplish spots, with age developing irregular black auto-oxidative patches, or grayish lilac or dark purple when young 2
1. Pileus not as above; some shade of grayish, orangish, yellowish brown or with reddish tones . . . 4
2(1). Pileus surface irregularly pitted; a densely interwoven mat under hand lens; trama slowly staining pink (11A2–11B2) upon exposure; Guyana, in *Pakaraimaea* forests. . . . . *Sarcodon pakaraimensis*
2. Pileus surface not as above; trama unchanging or not staining as above. 3
3(2). Pileus surface appressed, felt-like; substriate at extreme margin, basidia predominately 22–30(–36) × 10–16 μm; stipitipellis hyphae terminal cells with 2–8 serpentine undulations; Belize, in montane *Quercus* forests . . . . . *Sarcodon quercophilus*
3. Pileus surface a fine erect tomentum or velutinous; eventually areolate before collapsing to glabrous; stipitipellis terminal cells undifferentiated; Malaysian Archipelago and New Guinea, in Dipterocarpaceae and Fagaceae forests, New Zealand in *Nothofagus* forests . . . . . *Sarcodon thwaitesii*
4(1). Pileus surface tomentose, felt-like or pubescent, eventually glabrous; basidioma some shade of orange white (5A2), orange gray (5B2), pale orange (5B3), reddish blond (5C3), teeth up to 16 mm long; whole basidioma drying olivaceous; eastern North America, Europe, eastern Asia . . . . . *Sarcodon atroviridis*
4. Pileus surface not as above or not with those combinations; basidioma some shade of gray, grayish brown, yellowish gray (4B2), dark reddish brown (7F8–8F8) or fuscous; teeth not exceeding 6 mm, basidioma not drying olivaceous 5
5(4). Pileus regularly with a deep, prominent umbilicus; Belize, in montane *Quercus* forests . . . . . *Sarcodon umbilicatus*
5. Pileus without an umbilicus or not deep and prominent 6
6(5). Pileus surface matted fibrillose throughout, with age finely areolate over disk; all tissues staining black under pressure or exposure; Puerto Rico, in lower montane wet forests . . . . . *Sarcodon portoricensis*

6. Pileus surface not as above or not becoming areolate, not all tissues staining black under pressure or exposure 7

7(6). Pileus with an umbo; hyphae of the pileus commonly branching dichotomously at septa 8

7. Pileus without an umbo; hyphae of the pileus trama not as above 9

8(7). Pileus dark reddish brown (7F8–8F8); surface smooth to fibrillose, stipe grayish brown, trama reddish brown before turning black; hyphae of both the pileus and stipe commonly branching dichotomously at septa; Colombia, in *Pseudomonotes* forests . . . . . *Sarcodon rufobrunneus*

8. Pileus dark gray to nearly black, without reddish tones; surface as above or not; stipe trama not initially reddish brown; hyphae of the stipe not as above; Colombia, in *Pseudomonotes* forests . . . . . *Sarcodon colombiensis*

9(7). Pileus surface smooth, villose or subfurfuraceous, more repent fibrillose near margin; stipe staining slowly fuliginous or fuscous with contact or age; Trinidad, Brazil, in lowland tropical rain forests . . . . . *Sarcodon bambusinus*

9. Pileus surface smooth to fibrillose, or slightly rugose, overall interwoven fibrillose with scales centrally, or centrally squamulose, and lacking a fuliginous or fuscous staining reaction. 10

10(9). Pileus broadly convex to plane, yellowish gray, centrally squamulose; stipe bruising black; trama yellow-gray, bruising dark blue; Colombia, in *Dicymbe* forests . . . . . *Sarcodon bairdii*

10. Pileus campanulate, gray, drying to darker gray with orange or green tones, surface with scales centrally; stipe bruising black; trama cream, not bruising; Colombia, in *Dicymbe* forests . . . . . *Sarcodon pallidogriseus*

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