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Sarcodon in the Neotropics I: new species from Guyana, Puerto Rico and Belize

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Abstract: Four species of the ectomycorrhizal (ECM) genus *Sarcodon* (Bankeraceae, Thelephorales, Basidiomycota) are described as new to science. *Sarcodon pakaraimensis* sp. nov. is described from forests dominated by the ECM trees *Pakaraimaea dipterocarpacea* (Dipterocarpaceae) and *Dicymbe jenmanii* (Fabaceae subfam. Caesalpinioideae) in the Pakaraima Mountains of Guyana. *Sarcodon portoricensis* sp. nov. is described from lower montane wet forest within the El Yunque National Forest of Puerto Rico. *Sarcodon quercophilus* sp. nov. and *Sarcodon umbilicatus* sp. nov. are described from *Quercus* (Fagaceae) cloud forests within the Maya Mountains of Belize. The discovery of these species is significant given that the majority of the approximately 87 described *Sarcodon* species are north temperate or boreal in distribution and frequently associate with coniferous host plants; these constitute the most recent records for *Sarcodon* from the greater Neotropics. Each of the new species is morphologically consistent with accepted diagnostic characters for *Sarcodon*: pileate-stipitate stature, a dentate hymenophore, determinate basidiomatal development, fleshy, non-zonate context and brown, tuberculate basidiospores. DNA (ITS) sequence analysis corroborated the generic placement of *S. pakaraimensis*, *S. portoricensis, S. quercophilus* and *S. umbilicatus* and, along with morphological differences, supported their recognition as distinct species. 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 to Neotropical *Sarcodon* species and similar extralimital taxa is provided.

Key words: Bankeraceae, Caribbean, Central America, ectomycorrhizal fungi, Guiana Shield, Thelephorales, tooth fungi

Introduction

Sarcodon Quél. ex P. Karst. (Bankeraceae, Thelephorales) is an ectomycorrhizal (ECM) basidiomycete genus characterized by stipitate, pileate basidiomata with determinate development, fleshy, non-zonate context, dentate hymenophore, variably tuberculate, brown basidiospores, and the presence or absence of clamp connections (Banker 1906, Maas Geesteranus 1971). Approximately 87 species of *Sarcodon* have been described worldwide, mostly from high latitude forest environments (Coker and Beers 1951, Maas Geesteranus 1971, McNabb 1971, Harrison 1973, Baird 1986, Baird and Khan 1986, Harrison and Grund 1987, Agerer 1991, Stalpers 1993, Visser 1995, Shiryaev 2008, Mleczko et al. 2011, Baird et al. 2013, Vizzini et al. 2013). All known species of *Sarcodon* fruit on the soil in spatial association with ECM plants and available evidence suggests that Thelephorales species, including those of *Sarcodon*, are ECM (Stalpers 1993, Tedersoo and Smith 2013). The ECM status of *Sarcodon* has been confirmed for *Sarcodon imbricatus* (L.) P. Karst. on *Picea abies* (L.) H. Karst. in Germany (Agerer 1991), *Sarcodon scabrosus* (Fr.) P. Karst. on *Pinus banksiana* Lamb. (Visser 1995) in Canada, *Sarcodon leucopus* (Pers.) Maas Geest. & Nannf. with other Pinaceae hosts in Poland (Mleczko et al. 2011), and *Sarcodon atroviridis* (Morgan) Banker on *Abies pindrow* (Royle ex D. Don) Royle in Pakistan (Niazi 2008). While largely Holarctic in distribution, some *Sarcodon* species are known from the Paleotropics (Maas Geesteranus 1964, 1967, 1971, 1974a, Watling and Lee 1995), but records from the Neotropics are scarce (Baker and Dale 1951, Snell and Dick 1958, Maas Geesteranus 1974b, Singer et al. 1983). Here we provide new reports for the genus in the Neotropics from the Guiana Shield, northern Caribbean, and Central America. *Sarcodon pakaraimensis* sp. nov. is described from Guyana, in forests dominated by the

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endemic ECM trees *Pakaraimaea dipterocarpaceae* Maguire & P.S. Ashton (Dipterocarpaceae) and *Dicymbe jenmanii* Sandw. (Fabaceae subfam. Caesalpinioideae). *Sarcodon portoricensis* sp. nov. is described from a lower montane wet forest of the El Yunque National Forest of Puerto Rico. *Sarcodon quercophilus* sp. nov. and *Sarcodon umbilicatus* sp. nov. are described from ECM *Quercus*-dominated (Fagaceae) cloud forests of the Maya Mountains of Belize.

All of the new species are morphologically similar but distinguishable from each other, and similar to a group of previously described species defined by their non-scaly pilei, overall somber basidioma colors, and KOH-soluble bluish green pigments (Maas Geesteranus 1971), in particular *Sarcodon atroviridis* (Morgan) Banker from temperate North America, Europe, and East 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, 1974b, 1975). Variation in key morphological characteristics corroborated by molecular phylogenetic analysis warrant the erection of the four new species, and indicate their close relationship within the genus. 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 to Neotropical *Sarcodon* species and similar extralimital taxa is provided.

MATERIALS AND METHODS

Collections.—Guyana collections were made during the Dec–Jan rainy season of 2010–2011 from the Upper Mazaruni River Basin in the Pakaraima Mountains, in the vicinity of a base camp at 5°26′21.3″N, 60°04′43.1″W; ~ 800 m. This area is ~ 15 km west of Mount Ayanganna (2200 m) and characterized by a mixture of open savannas and closed canopy forests on white sand soils (Smith et al. 2013). Collections were made in forests co-dominated by the ECM trees *P. dipterocarpacea* and *D. jenmanii*. Puerto Rico collections were made Jun–Jul 1998 in a lower montane wet forest along the Pico El Toro Trail in the El Yunque National Forest (previously known as the Caribbean National Forest) in the general locality of 18°17′N 65°51′W; 650–710 m. Belize collections were made in Aug 2004 and Aug 2007 from Doyle's Delight Mountain within the Maya Mountains near 16°29′N, 89°2′W; ~ 1000 m, from cloud forests dominated by species of *Quercus*.

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 or as capitalized Ridgway colors as reproduced by Smithe (1975). Collections of fresh basidiomata were dried in the field with silica desiccant beads or were warm air-dried with food dehydrators or a forced-air drying oven. Micromorphological features of dried specimens were examined with an Olympus BX51 microscope with light and phase contrast optics. Fungal tissue was mounted in H_2O, 3% potassium hydroxide (KOH), or Melzer's solution. At least 20 individual basidiospores, basidia and other structures were measured per collection; for basidiospores measurements were taken from spore deposits when possible, with dimensional measurements including ornamentation. Range and mean quotients of basidiospore length divided by width (Q) were calculated. Outlying measurements observed in less than 5% of the measured population are indicated in parentheses. Line drawings were made with tracing paper and modified with Photoshop CS5 (Adobe, San Jose, California). Specimens were deposited in these herbaria (Holmgren et al. 1990): BRG, University of Guyana; HSU, Humboldt State University; CORT, State University of New York at Cortland; NY, New York Botanical Garden; BRH, Forest Department Herbarium, Ministry of Natural Resources, Local Government and the Environment of Belize; UPRRP, University of Puerto Rico at Rio Piedras.

DNA extraction, amplification, sequencing and phylogenetic analyses.—DNA extraction, polymerase chain reactions (PCR), cloning and sequencing protocols followed Gardes and Bruns (1993), with the following modifications. DNA was extracted from dried basidiomata by placing tissue samples into 1.5 mL tubes with 0.1 mm glass beads and 400 μL CTAB heated to 60 C. Tissues were ground with a plastic micropestle, incubated overnight at 57 C with 700 rpm shaking on an Eppendorf Thermomixer R (Eppendorf International, http://www.eppendorf.com). This resulted in dark samples, presumably from the copious pigments present in the basidiomata. The tubes were centrifuged at 8 000 rpm to pelletize debris, and the supernatant was transferred to a new tube and brought to 500 μL with CTAB. Eight hundred microliters chloroform was added and the tubes inverted for 1 min before centrifuging at full speed 10 min. The supernatant was removed and extracted in 800 μL chloroform. DNA was precipitated with two volumes of 100% isopropanol and 1/10 volume ammonium acetate at −20 C overnight. DNA was pelleted by centrifugation at full speed for 10 min. The DNA pellet was washed in 70% ethanol and resuspended in 1× TE buffer.

PCR reactions were performed with 1 μL DNA diluted 1:10, 0.4 μM primer and 12.5 μL EconoTaq Plus 2× Mastermix as per manufacturer's recommendations (Lucigen Corp., Middleton, Wisconsin). Cycling temperatures were: initial denaturation at 94 C for 10 min; cycle 35 times at 94 C for 30 s, 54 C for 30 s and 72 C for 30 s.

PCR products were sent to Sequetech (Mountain View, California; http://www.sequetech.com/) for sequencing. Sequences were processed and assembled using CodonCode Aligner 3.5.7 (CodonCode Corp., Dedham, Massachsetts; http://www.codoncode.com/). For the new sequences, assembled sequence contigs of ITS were used in preliminary blastN queries of the GenBank (http://www.ncbi.nlm.nih.gov/) database to confirm generic affinities and indicate the most similar described and sequenced species.

Manual alignment for ITS sequences of all species included 767 characters, of which 511 nucleotide characters were included in the analysis, while 256 were excluded because they constituted gaps or were in areas that were too variable to align. The alignment is available at TreeBASE at: http://purl.org/phylo/treebase/phylows/study/TB2:S16770. Maximum parsimony (MP) analysis was completed with default settings in PAUP* 4.0 (Swofford 2003). A maximum likelihood (ML) search was run in GARLI (Zwickl 2006) with the GTR+I+G model. Support for phylogenetic relationships was assessed based on 500 bootstrap replicates in PAUP (for MP) and Garli (for ML).

RESULTS

blastN queries and phylogenetic analysis.—blastN queries for ITS sequences of the four new species reported here produced best matches to species of *Sarcodon*, but none exceeded 95% similarity. The MP search found only one most parsimonious tree with a score of 384 steps. The ML tree, with a likelihood score of −ln 2448.83248, had an identical topology to that of the MP tree (data not shown). These analyses demonstrated that the four new Neotropical *Sarcodon* species described here are phylogenetically distinct and are nested within a well-supported clade that also includes the north temperate species *S. atroviridis* (FIG. 1; 100% ML and MP support). A midpoint rooted tree is shown and no outgroup was used for this analysis because ITS sequences from other genera of Thelephorales were too distant to be reliably aligned in the ITS region with species of *Sarcodon*. Therefore, our analysis necessarily focused on the placement of the Neotropical species and could not resolve other phylogenetic relationships within the genus or address the position of *Sarcodon* within the Bankeraceae or Thelephorales. Among the four new species, *S. quercophilus* and *S. portoricensis* had the closest affinity with *S. atroviridis*, with the three species occurring in a well-supported subclade (FIG. 1; 96% ML, 99% MP support). *Sarcodon umbilicatus* and *S. pakaraimensis* lay in a sister relationship to the rest of the taxa of this clade in a well-supported subclade (FIG. 1; 89% ML, 86% MP support). The remaining north temperate *Sarcodon* species included in the analysis were resolved outside the *S. atroviridis* clade (FIG. 1).

TAXONOMY

Sarcodon pakaraimensis A. Grupe & T.W. Henkel, sp. nov. FIGS. 2, 3, 4

MycoBank MB809566

Diagnosis: Sarcodon pakaraimensis differs from other species of *Sarcodon* in its combination of pinkish gray, smooth to pitted, black-staining pileus, hollow stipe with internal squamules at maturity, pink staining of exposed trama, basidiospores that are 5−7 µm long, and its unique ITS sequence.

Typification: GUYANA: REGION 7 CUYUNI-MAZARUNI: Pakaraima Mountains, Upper Mazaruni River Basin, within 0.5 km of base camp at 5°26′21.3″N; 60°04′43.1″W; ~ 800 m; vicinity of base camp, 22 Dec 2010, *Henkel 9513* (holotype BRG; isotypes NY 02329648; HSU). GenBank accession: ITS KC155390.

Pileus initially conic, broadly conic to plano-convex with age, 21−74 mm broad, 3−18 mm tall, predominantly pinkish gray (7B2−7C2) throughout initially, with irregular darker purplish spots, with age developing irregular black auto-oxidative patches, these occasionally coalescing throughout, bruising similarly; surface glabrous macroscopically with irregular fine pits, under hand lens a densely interwoven, repent mat; margin entire, slightly incurved when young, becoming irregularly wavy with age; trama cream (5A2), staining slowly to light pink (11A2−11B2) upon exposure. Hymenophore dentate, adnate; teeth crowded, 0.5−1.0 mm long at margin, 1.0−2.0 mm centrally, 2.0−3.0 mm at stipe, subacuminate, cream-colored throughout in young specimens (4A3−4A4), staining dark brown (6F5) upon pressure, becoming mottled brown with age with tips remaining cream. Stipe subequal, 22−58 × 3−19 mm, tapering slightly at the base, glabrous, grayish cream (7A2−7B2) when young, later concolorous with pileus; somewhat purplish toward apex, black at base; trama substuffed initially, later hollow with internal black erect squamules, concolorous with pileus trama, staining light pink (11A2−11B2) initially upon exposure, darkening to burgundy with time. Odor somewhat citrus-like or of conifer sap; flavor mildly bitter. Macrochemical reactions: all tissues staining dark blue to black with KOH and NH_4OH on dried basidiomata. Dried pileus olive-gray (3E2−3E3) with bluish gray (23F3) spots; context yellowish gray (2C2−2C3). Basidiospores dark reddish brown (9E4−9F4) in fresh deposit, more yellowish brown (5E4) when dried; 5−7(−8) × 5−9(−10) µm including ornamentation (mean = 6.4 × 7.6 µm; n = 40), Q range = 0.71–1.2, Q mean = 0.84, suboblate, tuberculate, light brown in H_2O, pale golden brown in KOH, inamyloid; tubercle apices mostly rounded, rarely exsculpate, also evident under SEM; hilar appendage 1−2 µm long. Basidia 27−47(−54) × 7−13 µm wide apically, 5−7 µm wide centrally, 2−3 µm at basal septum, clavate, somewhat curving subcentrally, with numerous small guttules, hyaline in H_2O and KOH; basal septum with clamp connection; sterigmata (2−)3−4, curved, (4−)5−6(−7) µm long. Hymenial cystidia absent. Hymenophoral trama of parallel to slightly interwoven hyphae, diverging slightly immediately below subhymenium, in mass light gray to light

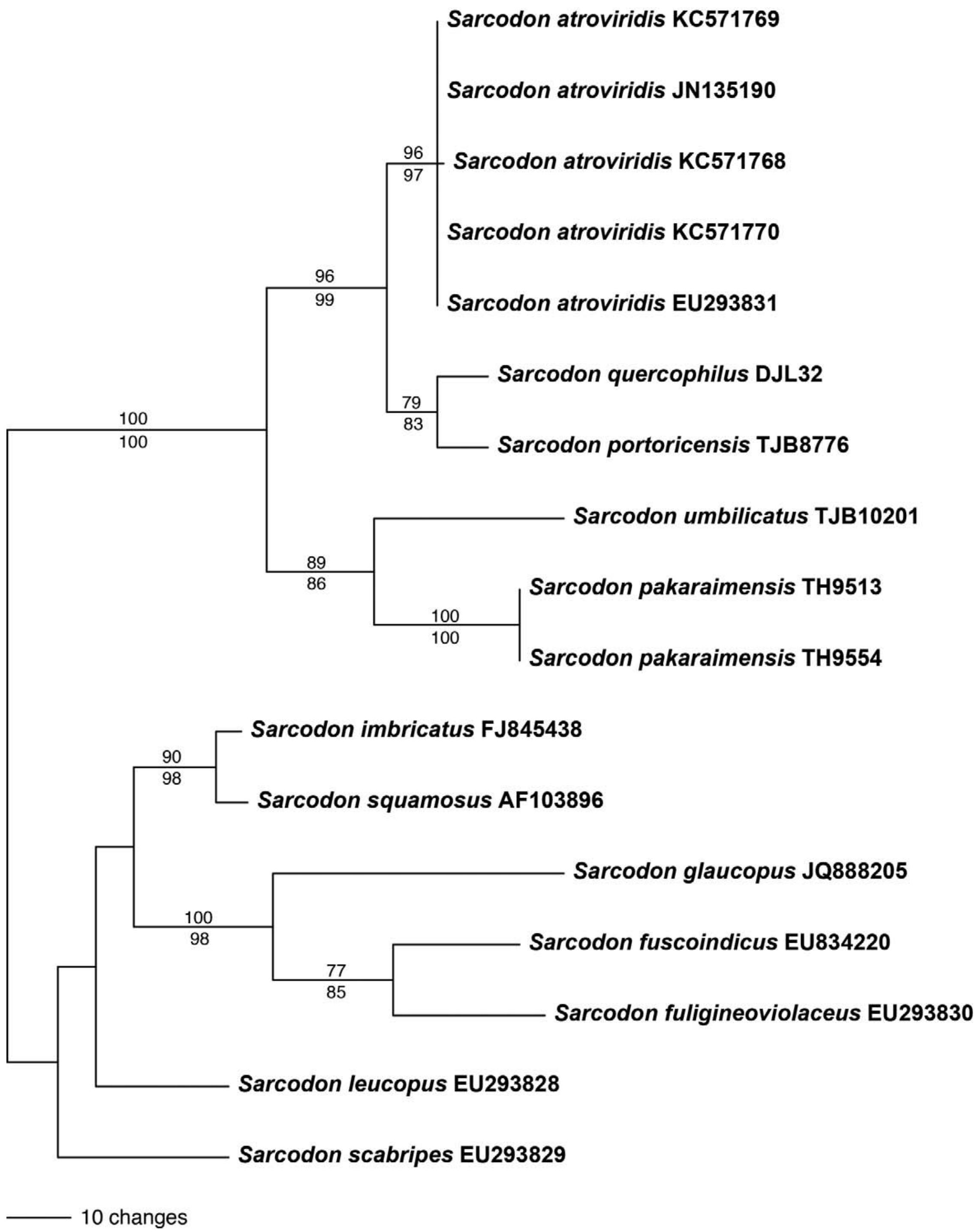

FIG. 1. Most parsimonious phylogram (384 steps; mid-point rooted) based on internal transcribed spacer (ITS) ribosomal DNA sequences depicting phylogenetic relationships of Neotropical *Sarcodon* species. Support values above the nodes are maximum likelihood bootstrap support values, whereas values below the nodes are maximum parsimony support values. Nodes with bootstrap support values less than 75 are not shown. Sequences for all *Sarcodon* species found outside the Neotropics were obtained from GenBank with numbers next to species epithets.

orange-brown in H_2O, faint tan to light blue-green in KOH; individual hyphae faint gray in H_2O, faint green-blue in KOH, 3−6 μm wide, with densely clustered 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, suffused from suprapellis downward to 133−180 μm into subpellis with dense masses of

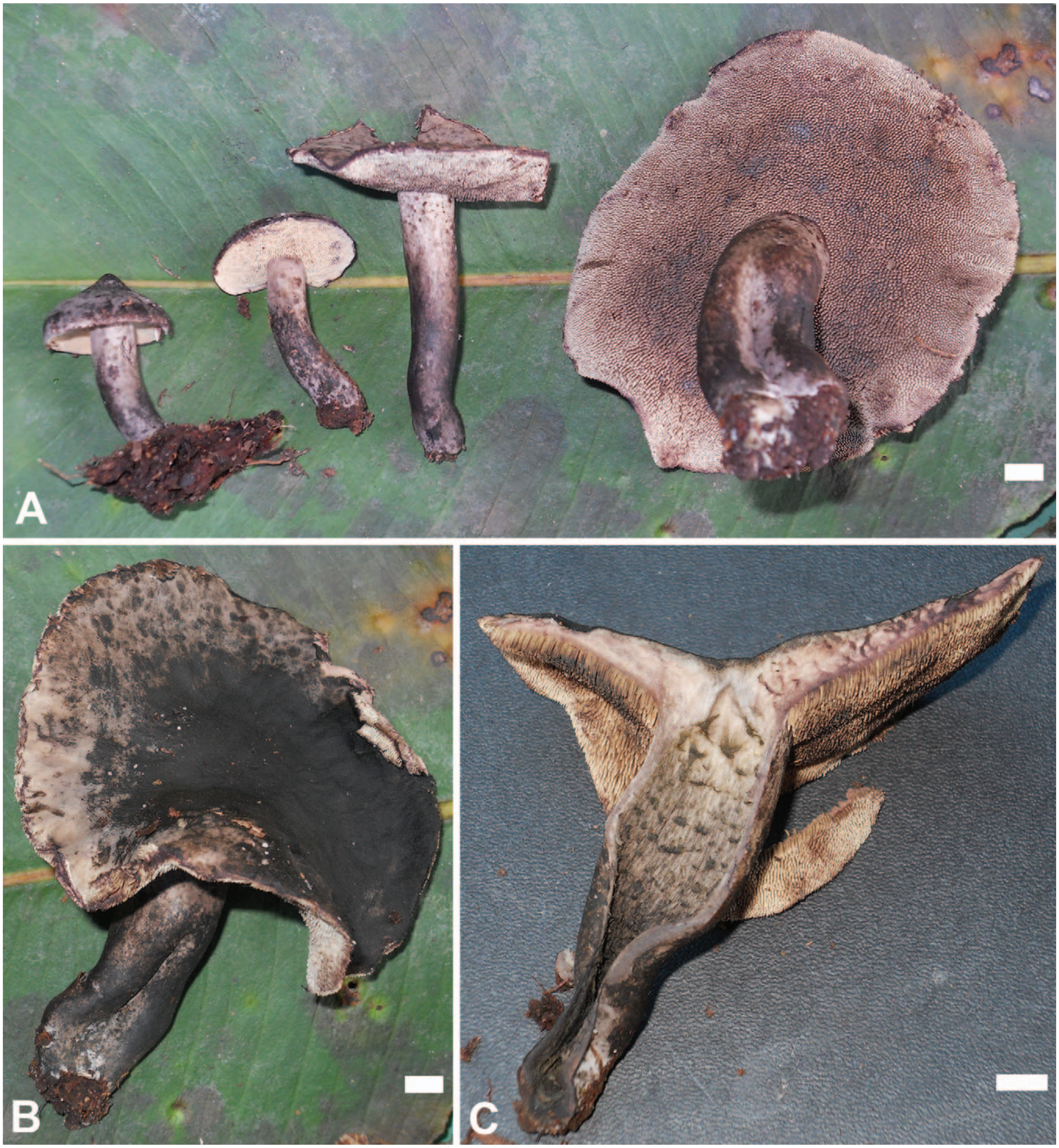

FIG. 2. Basidiomata of *Sarcodon pakaraimensis* (HOLOTYPE; *Henkel 9513*). A. Developmental series. B. Basidioma with black auto-oxidation and staining reaction on the pileus. C. Longitudinal section with pink staining of the exposed pileus trama and hollow stipe with internal squamules. Bar = 10 mm.

irregularly shaped, extracellular, granular pigment bodies, these black in H_2O, bluish green in KOH and eventually dissolving and leaching into solution; individual hyphae light gray-green in H_2O, faintly gray-brown to light gray in KOH, 4−6(−12) μm wide, irregularly bulging and constricting; 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 in H_2O, faint gray in KOH, occasionally branching, most

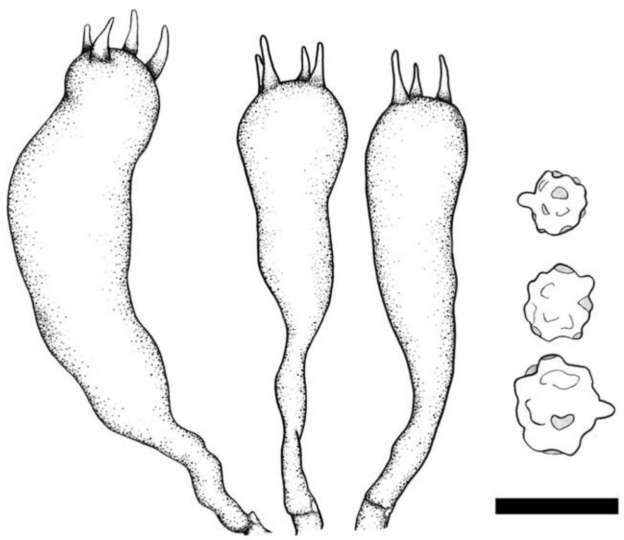

FIG. 3. Basidia and basidiospores of *Sarcodon pakaraimensis* (HOLOTYPE; *Henkel 9513*). Bar = 10 μm.

irregularly bulging and constricting, some cylindrical, (2−)6−11 μm wide. Stipitipellis a cutis of largely repent hyphae, grading inward to a more anticlinally interwoven subpellis, in mass gray in H_2O, variably gray-blue in KOH, with scattered extracellular granular pigment bodies, these dark blue to nearly black in H_2O, dark bluish green in KOH; individual hyphae light gray in H_2O, faint gray to faint gray-blue in KOH, isodiametric or frequently with irregular bulges and constrictions, 3−8(−10) μm wide; terminal cells undifferentiated. Stipe trama interwoven, in mass light gray-tan in H_2O and KOH, with frequent irregularly shaped pockets devoid of hyphae, these (20−)30−47(−91) μm wide across longest axis; individual hyphae faint gray in H_2O and KOH, isodiametric to frequently with irregular bulges and constrictions, 5−10 μm wide, slightly constricted at septa. Inner surface of hollow stipe an interwoven mass of subanticlinal hyphae continuous with the stipe trama, interspersed with fascicles of massed anticlinal hyphae corresponding to inner stipe squamules; fascicle hyphae in mass gray in H_2O, grayish brown in KOH. Clamp connections abundant on hyphae of all tissues.

Habit, habitat and distribution. Scattered to gregarious on humic substrata on the forest floor in mixed *Pakaraimaea/Dicymbe* forest; known only from the type locality in the Upper Mazaruni River Basin of Guyana.

Etymology. Pakaraimensis (-ensis Latin adj. B) = adjectival suffix indicating origin or place, referring to the type locality of the species in the Pakaraima Mountains of Guyana.

Other specimen examined. GUYANA: REGION 7 CUYUNI-MAZARUNI: Pakaraima Mountains, Upper Mazaruni River Basin, ~1 km SW of base camp, 29 Dec 2010, *Henkel 9554* (BRG; HSU). GenBank accession: ITS KM668103.

Commentary. *Sarcodon pakaraimensis* is recognized in the field by its pileate-stipitate, determinate basidioma with pinkish gray, smooth, black-staining pileus with dentate hymenophore, concolorous subequal stipe that is hollow with internal squamules when mature, and the pink staining of exposed trama. *Sarcodon pakaraimensis* can be differentiated from each of the other new Neotropical species described here based on key features of the pileus surface, staining reactions of the exposed trama, stipe trama, basidiospore ornamentation and stipitipellis (TABLE I).

Sarcodon pakaraimensis is similar to the north temperate *S. atroviridis* in that both have pits or ridges on the otherwise smooth pileus that stains black when bruised (Morgan 1895, Banker 1906, Coker and Beers 1951). *Sarcodon pakaraimensis* is distinguished from *S. atroviridis* by its pink-staining reaction of the exposed trama, lack of an olive cast to the dried basidioma, internal squamules within the hollow stipe, and shorter basidiospores (5−7 vs. 7.2−9 μm) (Morgan 1895, Banker 1906, Coker and Beers 1951, Baird et al. 2013). In addition, ITS sequences of *S. pakaraimensis* are only ~ 86% similar to sequences of *S. atroviridis* from the USA and so these two species are distinct in the phylogenetic analysis (FIG. 1).

Sarcodon pakaraimensis is similar to the paleotropical *S. thwaitesii* in basidioma color and black staining of the pileus, and the hollow stipe at maturity, but differs in its densely interwoven, matted pileipellis (vs. an erect tomentum); in addition, the interior stipe squamules and pink-staining reaction of the exposed trama are lacking in *S. thwaitesii* (Berkeley and Broome 1873, Maas Geesteranus 1964, 1971, 1974a).

Both *S. pakaraimensis* and the Neotropical *S. bambusinus* have non-decurrent teeth, a similar pileus shape, and similar stipe lengths, but *S. pakaraimensis* differs from *S. bambusinus* in its pileus surface of an interwoven, repent mat, pink trama-staining reaction, hollow stipe with internal squamules, and basidiospore length (5−7 vs. 6.5−9 μm) (Baker and Dale 1951, Maas Geesteranus 1974b).

Sarcodon portoricensis A. Grupe & T.J. Baroni, sp. nov. FIGS. 4, 5, 6

MycoBank MB809567

Diagnosis: Sarcodon portoricensis differs from other species of *Sarcodon* in its combination of grayish brown, black-staining, matted fibrillose pileus with an areolate disk at maturity, black staining trama, basidiospores that are 8−9 μm wide, and unique ITS sequence.

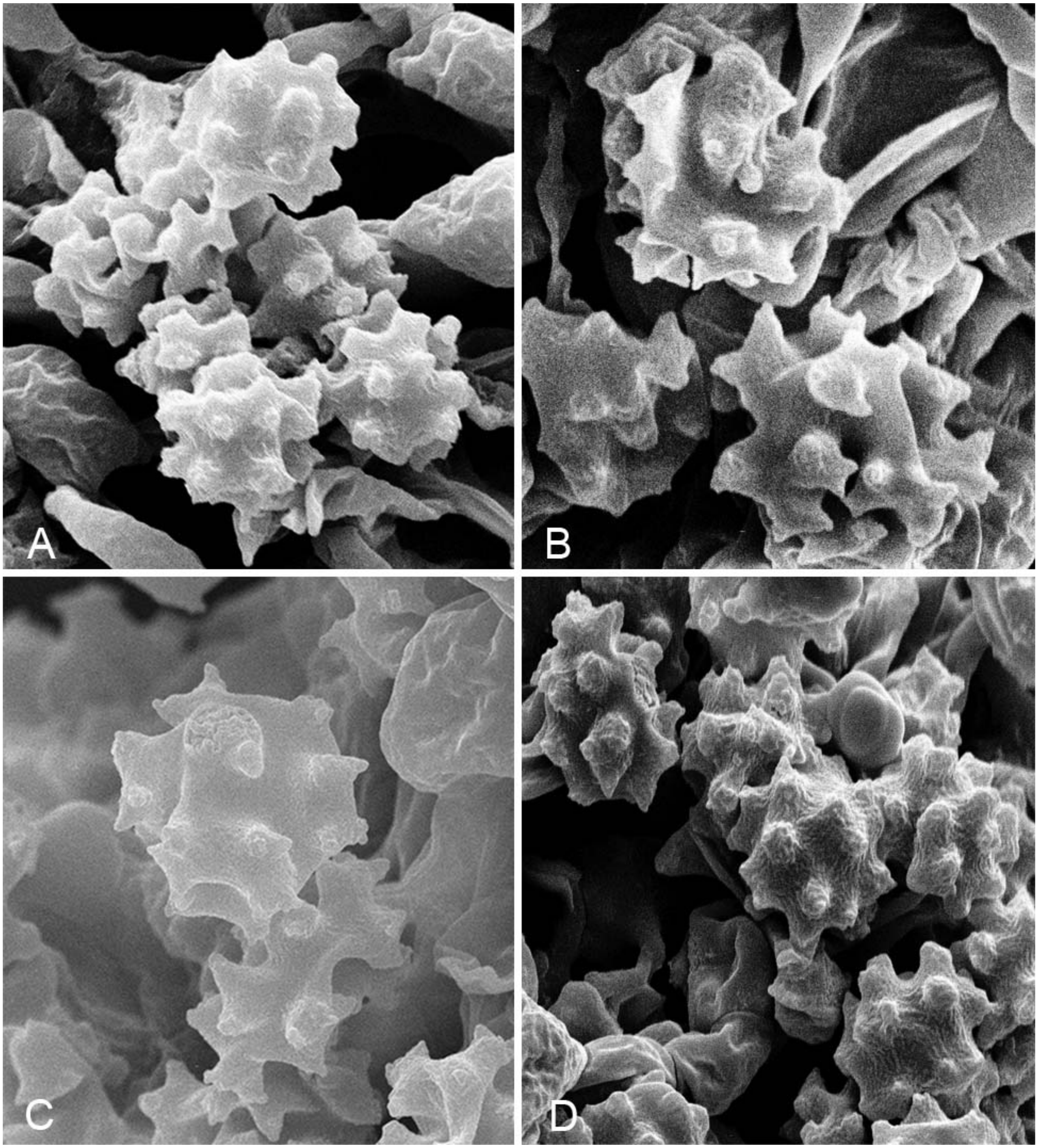

FIG. 4. Scanning electron micrographs of basidiospores of new Neotropical *Sarcodon* species. A. *Sarcodon pakaraimensis* (HOLOTYPE; *Henkel 9513*). B. *Sarcodon portoricensis* (HOLOTYPE; *Baroni 8776*). C. *Sarcodon quercophilus* (HOLOTYPE; *CFMR-BZ-3833*). D. *Sarcodon umbilicatus* (HOLOTYPE; *Baroni 10201*). 4000×.

Typification: PUERTO RICO: MUNICIPALITY CANOVANAS: El Yunque National Forest; El Toro Trail, 18°16′51.4″N; 65°51′31.3″W, ~ 710 m; 5 Jun 1998, *Baroni 8776* (holotype: NY 02329649; isotype: CORT 011998). GenBank accession: ITS KM668100.

Pileus initially conic with broad umbo, becoming planate or with an uplifted, broadly wavy margin, 12−30 mm wide, 8−12 mm tall, grayish brown (5D4), somewhat lighter near margin, staining black upon pressure, matted fibrillose throughout; disk finely

TABLE I. Diagnostic morphological characters of new *Sarcodon* species from Guyana, Puerto Rico and Belize

Species	Pileus surface	Pileus staining	Hymenophore attachment	Trama staining	Stipe	Basidiospore ornamentation	Basidia	Stipitipellis terminal cells
S. pakaraimensis	glabrous, pitted	black	adnate	pink	hollow	rounded, rarely exsculpate	clavate 27–47 × 5–7 µm	undifferentiated, 3–9 µm wide
S. portoricensis	fibrillose, areolate over disc	black	adnate	black	solid	exsculpate, rounded corners	clavate 33–44 × 7–12 µm	subclavate to subcapitate, 2–3 µm wide
S. querophilus	appressed felt-like, substriate at margin	none	adnate	absent	hollow	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	grayish brown	hollow	rounded, rarely exsculpate	clavate 32–38 × 5–7 µm	undifferentiated, subcapitate, or subclavate, 2–5 µm wide

areolate with age; trama 1–2 mm thick, creamy gray, blackening upon exposure. Hymenophore dentate, adnate; teeth 1–2 mm long, light grayish brown (5C4), somewhat flattened over distal one-third; tips bluntly acuminate, frequently bifurcate under hand lens. Stipe equal, 22–48 × 5–7 mm, rounded at extreme base, matted fibrillose over lower three-quarters, more glabrous at apex, grayish brown (~ 5D3), somewhat lighter near apex and base, staining black upon pressure, solid; trama grayish brown, staining black slowly upon exposure. Odor none; flavor bitter from dried specimen. Macrochemical reactions: all tissues dark blue to black with KOH and NH_4OH on dried basidiomata. Dried pileus olive gray (3E2–3E3), with bluish gray spots (21F3–21F4); context light brown (6D4–6E4). Basidiospores 7–9 × 8–9 µm with ornamentation included (mean = 8.7 × 8.6 µm; n = 20), Q range = 0.77–1.13, Q mean = 1.0, subglobose to globose, strongly tuberculate, faint tan in H_2O and KOH, inamyloid; tubercle apices mostly exsculpate with rounded corners, occasionally flat or rounded, also evident under SEM; hilar appendage 1–2 µm long. Basidia (30–)33–44(–48) × 8–13 µm apically, (5–)7–12 µm wide centrally, 2–4 µm at basal septum, clavate, curving centrally, with globular contents, faint gray in H_2O and KOH; basal septum with clamp connection; sterigmata 4, (5–)6–7(–8) µm long. Hymenial cystidia absent. Hymenophoral trama parallel, in mass light gray-tan to green-blue in H_2O, light red-brown in KOH; individual hyphae light gray in H_2O and KOH; extracellular, granular dark blue-green pigment bodies numerous, these partially soluble in KOH; cells 3–5(–6) µm wide. Pileipellis a cutis of largely repent hyphae, in mass light gray to green-blue in H_2O, dark gray-blue in KOH, with abundant irregularly-shaped dark gray-blue extracellular pigment bodies in H_2O, these only partially soluble in KOH; individual hyphae faint gray-green in H_2O, faint gray to gray-blue in KOH, commonly with irregular bulges and constrictions, occasionally cylindrical; terminal cells undifferentiated, (5–)7–12 µm wide. Pileus trama in mass light tan to brown-orange in H_2O, light green-blue in KOH; individual hyphae faint tan-gray in H_2O, faint gray in KOH, cylindrical, rarely with irregular bulges and constrictions, (3–)5–10(–12) µm wide. Stipitipellis a cutis of largely repent hyphae, in mass light gray-green in H_2O, dark gray-blue in KOH; individual hyphae light gray in H_2O, light gray-blue in KOH; terminal cells 2–3 µm wide, subclavate to subcapitate, with inflated tips 3–4 µm wide. Stipe trama in mass orange-brown in H_2O, light orange-brown to light green-blue in KOH; individual hyphae faint tannish orange in H_2O, faint tan to faint green-blue in KOH, (4–)6–7(–8) µm wide. Clamp connections abundant on hyphae of all tissues.

FIG. 5. Basidiomata of *Sarcodon portoricensis* (HOLOTYPE; *Baroni 8776*). Bar = 10 mm.

Habit, habitat and distribution. Scattered on clay soils of forest floor in a lower montane wet forest; known only from the type locality in the El Yunque National Forest, Puerto Rico.

Etymology. Portoricensis (-ensis Latin adj. B) = adjectival suffix indicating origin or place, referring to the type locality of the species in Puerto Rico.

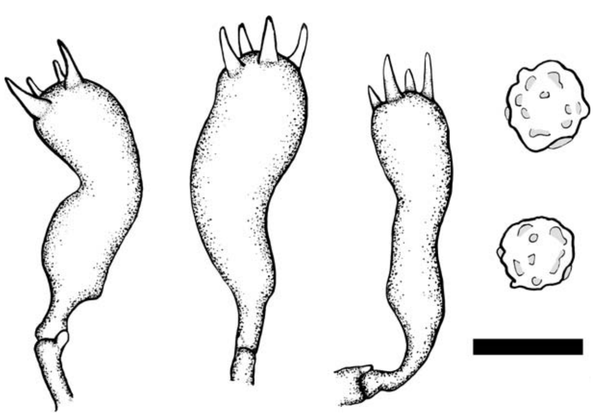

FIG. 6. Basidia and basidiospores of *Sarcodon portoricensis* (HOLOTYPE; *Baroni 8776*). Bar = 10 μm.

Other specimen examined. PUERTO RICO: MUNICIPALITY CANOVANAS: El Toro Trail, 18°17′0″N, 65°51′15″W, 650 m; 2 Jul 1998, coll. N. Pérez, S.A. Cantrell & J. Ramírez, *CFMR-PR-5421* (UPRRP).

Commentary. *Sarcodon portoricensis* is recognized in the field by its initially conic pileus becoming plane with an uplifted margin, grayish brown, black-staining and matted fibrillose pileus surface with a finely areolate disk at maturity, concolorous stipe, black-staining trama, and relatively long, grayish brown, frequently apically bifurcate teeth. *Sarcodon portoricensis* can be differentiated from each of the other new Neotropical species described here based on key features of the pileus surface, staining reactions of the exposed trama, stipe trama, basidiospore ornamentation and stipitipellis (TABLE I).

Sarcodon portoricensis is similar to *S. atroviridis* in its patch-like blackening of the pileus, non-decurrent hymenophore, glabrous stipe and basidiospore dimensions. *Sarcodon portoricensis* is distinguished from *S. atroviridis* by its pileus surface that is matted fibrillose and areolate over the disk (vs. tomentose to felt-like and non-areolate), black trama-staining reaction (vs. lilac to bluish gray), and matted fibrillose stipe surface (vs. glabrous to pubescent) (Morgan 1895, Banker 1906, Coker and Beers 1951, Maas

Geesteranus 1971, Baird et al. 2013). In addition, the ITS sequence of *S. portoricensis* is only ~ 87% similar to sequences of *S. atroviridis* from southeastern USA, and so these two species are distinct in the phylogenetic analysis (FIG. 1).

Sarcodon portoricensis is similar to *S. thwaitesii* in its pileus shape, areolation and black staining but differs in its grayish brown pileus and stipe, and wider basidiospores (8–9 vs. 5.4–7.2 μm) (Berkeley and Broome 1873; Maas Geesteranus 1964, 1971, 1974a).

Both *S. portoricensis* and *S. bambusinus* have a grayish brown stipe with similar dimensions, and similar basidiospore and basidium lengths, but *S. portoricensis* differs from *S. bambusinus* in its pileus surface that is matted fibrillose and finely areolate over the disk (vs. villose to subfurfuraceous), black staining trama (vs. slowly fuliginous to fuscous), and basidiospore width (8–9 vs. 5–7 μm) (Baker and Dale 1951, Maas Geesteranus 1974b).

Sarcodon portoricensis resembles *Sarcodon quietus* Maas G. from the Congo in its solid stipe, black staining trama and exsculpate basidiospore ornamentation, but differs in it grayish brown (vs. distinctly olivaceous) basidioma color, adnate (vs. decurrent) hymenophore, and areolate (vs. squamulose) pileus disc (Maas Geesteranus 1967).

Sarcodon quercophilus A. Grupe & D.J. Lodge, sp. nov. FIGS. 4, 7, 8

MycoBank MB 809568

Diagnosis: Sarcodon quercophilus differs from other species of *Sarcodon* in its combination of felty matted, dull violet pileus with substriate margin, hollow stipe with internal squamules, non-staining trama, basidia that are 22–30 × 11–16 μm, basidiospores that are 5−7 μm long, and unique ITS sequence.

Typification: BELIZE: TOLEDO, CAYO DISTRICT: Chiquibul National Park, Maya Mountains, Doyle's Delight, 1070 m; East Trail, 12 Aug 2004, coll. *Lodge, CFMR-BZ-3833* (holotype: NY 02329783; isotype: HSU). GenBank accession: ITS KM668101.

Pileus convex, 18–33 mm broad, 40–74 mm tall, dull violet (15E4–15F4) throughout; surface an appressed felt-like mat, lighter concolorous and substriate at margin; trama tan, 4 mm thick above stipe, unchanging. Hymenophore dentate, adnate; teeth blunt-acuminate, pale yellow when young (3A2–4A2), browning slightly with age. Stipe subclavate, somewhat flattened, 40–75 × 4–8 mm, broadening over basal one-quarter to 5.7–11.5 mm wide; surface a submoist, felt-like mat, dull violet (15E4–15F4); trama substuffed to hollow, with internal stipe squamules observable in sections of the dried stipe (not noted in field), unchanging; basal mycelium lighter concolorous, matted. Odor none; flavor bitter. Macrochemical reactions: all tissues staining dark blue to black with KOH and NH_4OH on dried basidiomata. Dried pileus grayish green (1D3−1D4) over disk, with bluish gray spots (22F3−22F4); context grayish yellow (3C2−3C3). Basidiospores 5–7 × 7–9 μm including ornamentation (mean = 5.7 × 8 μm; n = 40), Q range = 0.63–0.88, mean Q = 0.71, oblate, tuberculate, tan in H_2O, lighter concolorous in KOH, inamyloid; tubercles tall, appearing flat in polar view, in side view exsculpate with two prominent, rounded or finely pointed to mammillate apices, these projecting outward, also evident under SEM; hilar appendage 1–2 μm long. Basidia 22–30(−36) × 10–16 μm apically, 5–10 μm centrally, 2–3 μm basally, clavate, occasionally curved near center, faint gray in H_2O and KOH; sterigmata four, curved, 4–7 μm long. Hymenial cystidia absent. Hymenophoral trama of parallel, slightly interwoven hyphae, in mass gray in H_2O and KOH; individual hyphae light gray in H_2O and KOH, cylindrical, (2−)3–5 μm wide. Pileipellis a cutis of largely repent hyphae, in mass dark yellow-green in H_2O, faint tan in KOH; individual hyphae faint gray to faint yellow-green in H_2O, faint gray-blue in KOH, mostly cylindrical, infrequently with irregular bulges and constrictions, 4–7 μm wide, sometimes branching in subpellis; terminal cells undifferentiated. Pileus trama in mass light gray-green to brown-green in H_2O, light gray-blue overall in KOH, blue-green where granular pigment bodies present, light brown-orange where pigment bodies absent; extracellular pigment bodies in KOH irregularly shaped, granular, blue-green, solubilizing gray-blue into solution; individual hyphae faint gray-tan in KOH, faint gray-green in H_2O, cylindrical or often with irregular bulges and constrictions, frequently branching, 5–10 μm wide. Stipitipellis a cutis of strongly interwoven repent hyphae, in mass gray-green in H_2O, blue-green in KOH; extracellular pigment bodies abundant, of two types, some amber and irregularly shaped, these persistent in KOH and H_2O, others irregularly shaped, small, granular, blue-green, solubilizing gray-blue into solution in KOH and staining trama hyphae; individual hyphae faint gray-green in H_2O, faint gray to gray-blue in KOH, mostly cylindrical; 2–4 μm wide; terminal cells with slightly inflated apex and 2–8 irregular serpentine undulations. Stipe trama in mass light gray-green in H_2O, light gray-tan in KOH; individual hyphae faint gray or tan in H_2O and KOH, mostly cylindrical, infrequently with irregular bulges and constrictions, infrequently branching, (4–)5–7(−9) μm wide. Clamp connections abundant on hyphae of all tissues.

FIG. 7. Basidiomata of *Sarcodon quercophilus* (HOLOTYPE; *CFMR-BZ-3833*). A. Dorsal view. B. Ventral view, showing pale hymenophore. Bars = 10 mm.

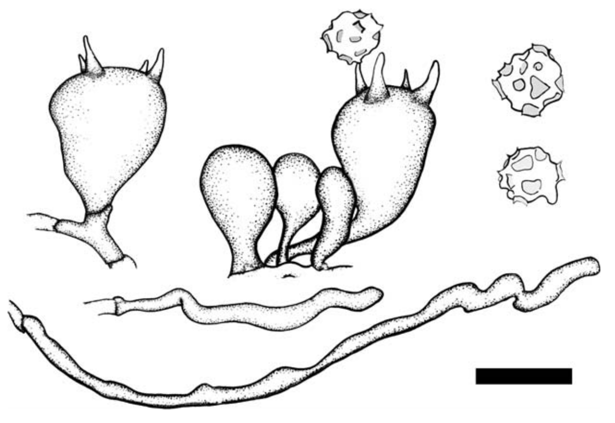

FIG. 8. Basidia, basidiospores and stipitipellis terminal cells of *Sarcodon quercophilus* (HOLOTYPE; *CFMR-BZ-3833*). Bar = 10 µm.

Habit, habitat and distribution. Scattered on soil in montane cloud forest under *Quercus*; known only from the type locality in the Maya Mountains of Belize.

Etymology. Quercophilus (-philus in Greek comp.) = *Quercus* (oak) loving; referring to occurrence of the species in *Quercus*-dominated forests.

Other specimen examined. BELIZE: TOLEDO, CAYO DISTRICT: North Ridge Trail, 16°29″N, 89°02′W, 1100 m, 19 Aug 2004, coll. *Lodge, CFMR-BZ-3928* (NY 02329784; BRH).

Commentary. *Sarcodon quercophilus* is recognized in the field by its convex, felt-like matted pileus that is dull violet throughout with lighter concolorous, substriate outer margin, adnate hymenophore of pale yellow teeth and concolorous, relatively long, subclavate, laterally compressed, hollow stipe with internal squamules. *Sarcodon quercophilus* can be differentiated from the other new Neotropical species described here based on key features of the pileus surface, staining reactions of the exposed trama, stipe trama, basidiospore ornamentation and stipitipellis (TABLE I).

Sarcodon quercophilus is similar to *S. atroviridis* in the dark, somber colors of the fresh basidiomata and felt-like matted pelli. *Sarcodon quercophilus* can be distinguished from *S. atroviridis* by its substriate pileus margin (vs. smooth), grayish green to bluish gray dried pileus (vs. olivaceous), shorter basidia (22–30 vs. 31−42 µm), shorter basidiospores (5−7 vs. 7.2−9 µm) and stipitipellis terminal cells with serpentine undulations (Morgan 1895, Banker 1906, Maas Geesteranus 1971, Baird et al. 2013). In addition, the ITS sequence of *S. quercophilus* is only ∼ 95% similar to sequences of *S. atroviridis* from southeastern USA, and so these two species are distinct in our phylogenetic analysis (FIG. 1).

Sarcodon quercophilus is similar to *S. thwaitesii* in overall basidioma colors, the long, hollow stipe, and basidium length, but differs in its appressed felt-like, marginally substriate pileus (vs. short erect tomentum throughout), appressed felt-like stipe (vs. tomentose to glabrescent) and narrower basidia (5–10 vs. 10–13 µm) (Berkeley and Broome 1873; Maas Geesteranus 1964, 1971, 1974a).

Sarcodon quercophilus and *S. bambusinus* have similar basidioma shapes, dimensions and basidium lengths, but *S. quercophilus* differs from *S. bambusinus* in its appressed felt-like, marginally substriate pileus, non-staining trama, wider basidium apices (11−16 vs. 8−11 µm), and wider basidiospores (7−9 vs. 5−7 µm) (Baker and Dale 1951, Maas Geesteranus 1974b).

Sarcodon quercophilus resembles *Sarcodon procerus* Maas G. from the Congo in its basidioma colors, striate pileal margin, hollow stipe and lack of trama staining upon exposure, but differs in its narrower pileus (18–33 vs 40–60 mm), adnate (vs. decurrent) hymenophore, shorter, broader basidiospores (5–7 × 7–9 vs. 6.7–8 × 4.5–5.4 µm) with strongly exsculpate (vs. rounded) ornamentation (Maas Geesteranus 1967).

Sarcodon umbilicatus A. Grupe, T.J. Baroni & D.J. Lodge, sp. nov. FIGS. 4, 9, 10
MycoBank MB809569

Diagnosis: Sarcodon umbilicatus differs from other species of *Sarcodon* in its combination of grayish brown to fuscous, rugulose, umbilicate, brown staining pileus, adnexed hymenophore, hollow stipe with internal squamules, grayish brown staining trama, basidiospores that are 6–7 × 7–8 µm, and unique ITS sequence.

Typification: BELIZE: TOLEDO, CAYO DISTRICT: Chiquibul National Park, Maya Mountains, Doyle's Delight, North East Trail to creek, 16°29′42,0″N, 89°02′37.3″W, 1038 m; 26 Aug 2007, *Baroni 10201* (holotype: NY 02329650; isotype: CORT 011996). GenBank accession: ITS KM668102.

Pileus convex to broadly convex and umbilicate, 20–60 mm wide, 13–16 mm tall, initially grayish brown (6C2), Dark Drab in center, Natal Brown or Army Brown on margin, with age to dark brown (7F3), Sepia, margin sometimes concentrically banded; umbilicus deep, occasionally perforate and continuous with the hollow stipe; surface rugulose, matted fibrillose under hand lens, staining darker brown when handled; trama light brown (5D4), staining fuscous slowly upon exposure, 6 mm thick above stipe. Hymenophore dentate, adnexed; teeth 3–4 mm long centrally, 2–3 mm near margin, 1 mm near stipe, acuminate, grayish orange (5B3; 5D4 in side view), Straw Yellow, becoming Drab Gray. Stipe equal, 20–55 × 4–6 mm, slightly tapered at base, concolorous with

FIG. 9. Basidiomata of *Sarcodon umbilicatus* (HOLOTYPE; *Baroni 10201*). Bar = 10 mm.

pileus, darkening to fuscous with handling, subglabrous, hollow, with minute internal squamules; basal mycelium a low grayish mat. Odor indistinct; flavor bitter. Macrochemical reactions: all tissues dark blue to black with KOH and NH_4OH on dried basidiomata. Dried pileus yellowish gray to olive (3C2−3D2); context yellowish gray (2B2−2C2). Basidiospores (5–)6–7 × (6–)7–8(−9) μm including ornamentation, (mean = 6 × 7.6 μm; n = 40), Q range = 0.63–1.0, mean Q = 0.83, oblate, tuberculate, faint brown in H_2O and KOH, inamyloid; tubercles short, apices usually rounded, occasionally flattened, rarely exsculpate, also evident under SEM; hilar appendage 1–1.2 μm long. Basidia (30–)32–38(−40) × 9–10 μm apically, 5–7 μm centrally, (2–)3–4 μm basally, clavate, regularly curved centrally, faint tan in H_2O, gray in KOH; sterigmata four, barely curving, 5–6 μm long. Hymenial cystidia absent. Hymenophoral trama of parallel, slightly interwoven hyphae, diverging slightly at subhymenium, in mass light gray in H_2O, faint tan in KOH; individual hyphae light gray in H_2O, faint gray in KOH, with two types of irregularly shaped extracellular pigment bodies, some of which are large, amber and non-soluble in H_2O and KOH, others that are small, granular, blue-green and solubilizing gray-blue into solution in KOH; cells (2–)3–5(−6) μm wide. Pileipellis a cutis, in mass overall light brown-green in H_2O, dark blue-green or faint tan in KOH depending on concentration of pigment bodies; individual hyphae faint tan in H_2O, with scattered light blue-green internal granulose pigments, faint gray-blue in KOH; terminal cells undifferentiated, 4–7 μm wide. Pileus trama in mass light gray or light tan in H_2O, light tan or gray-blue in KOH; individual hyphae faint gray in H_2O, faint gray-blue or faint tan in KOH, frequently with irregular bulges and constrictions, occasionally cylindrical, (3–)5–7(−8) μm wide, with rare hyphal cells containing copious intracellular, evenly dispersed pigments, these uniformly dark gray-blue in KOH, not evident in H_2O. Stipitipellis a cutis of largely repent, interwoven hyphae, difficult to separate, in mass light

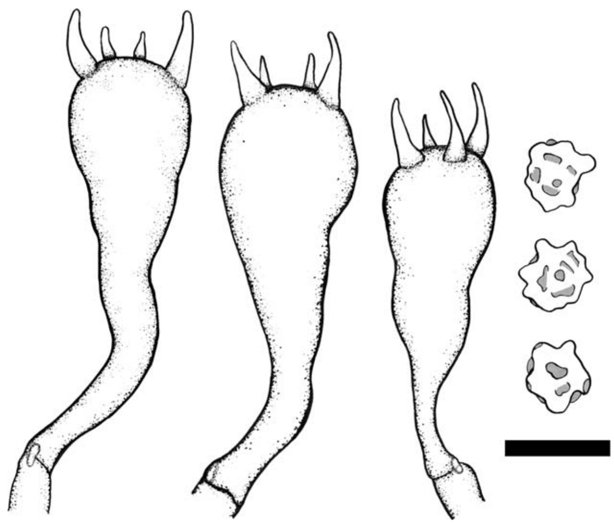

FIG. 10. Basidia and basidiospores of *Sarcodon umbilicatus* (HOLOTYPE; *Baroni 10201*). Bar = 10 μm.

gray-green in H_2O, light grayish to greenish blue in KOH; individual hyphae faint gray in H_2O, faint green-gray in KOH, mostly cylindrical with undifferentiated terminal cells, 2–3(−5) μm wide, interspersed with scattered hyphae with subclavate to subcapitate terminal cells, these (2–)3–5 μm wide. Stipe trama in mass light brown-orange in H_2O, lighter in KOH, with pockets devoid of hyphae, these (7–)12–114(−156) μm across longest axis; individual hyphae faint gray in H_2O and KOH, irregularly bulging, occasionally cylindrical, sometimes branching, (4–)7–12 μm wide. Clamp connections abundant on hyphae of all tissues.

Habit, habitat and distribution. Scattered on soil in montane cloud forest under *Quercus*; known only from the type locality in the Maya Mountains of Belize.

Etymology. Umbilicatus (Latin adj. A) = navel-like, having a small central depression; referring to the umbilicate pileus of the species.

Other specimens examined. BELIZE: TOLEDO, CAYO DISTRICT: Chiquibul National Park, Maya Mountains, Doyle's Delight, North East Trail to creek, 16°29′42.0″N, 89°02′37.3″W, 1131 m; 20 Aug 2007, *Baroni 10113* (CORT 011997); Doyle's Delight, North Ridge Trail, 16°30′14.3″N, 89°03′04.3″W, elevation 1100 m, 24 Aug 2007, coll. *S. Matola, CFMR-BZ-4332* (NY 02329785; HSU); 1100 m, 26 Aug 2007, coll. *Lodge, CFMR-BZ-4382* (NY 02329786; HSU).

Commentary. *Sarcodon umbilicatus* is recognized in the field by its convex to broadly convex, umbilicate pileus with a rugulose surface that is initially grayish brown to fuscous at maturity, the dark brown to fuscous staining of the various tissue layers upon pressure or exposure, and hollow stipe with internal squamules. *Sarcodon umbilicatus* can be differentiated from each of the other new Neotropical species described here based on key features of the pileus surface, staining reactions of the exposed trama, stipe trama, basidiospore ornamentation, and stipitipellis (TABLE I).

Sarcodon umbilicatus is similar to *S. atroviridis* in its convex to broadly convex pileus and basidiospore widths. *Sarcodon umbilicatus* can be distinguished from *S. atroviridis* by its pileus that is consistently fuscous (7F3) at maturity (vs. brownish gray [5D3–5E3], grayish violet [15F3] or black), matted fibrillose to rugulose, umbilicate pileus (vs. tomentose to felted/glabrous and lacking an umbilicus), dark staining reactions with pressure or exposure, concolorous stipe, and shorter basidiospores (5–7 vs. 7.2–9 μm) (Morgan 1895, Banker 1906, Maas Geesteranus 1971, Baird et al. 2013). Additionally, the ITS sequence of *S. umbilicatus* is only ~82% similar to sequences of *S. atroviridis* from the southeastern USA and so these two species are distinct in the phylogenetic analysis (FIG. 1).

Sarcodon umbilicatus is similar to *S. thwaitesii* in its hollow mature stipe, basidium lengths, and basidiospore dimensions, but differs in its umbilicate pileus with a rugulose surface (vs. short tomentose), and longer teeth (3–5 vs. 1–3 mm) (Berkeley and Broome 1873; Maas Geesteranus 1964, 1971, 1974a).

Sarcodon umbilicatus and *S. bambusinus* have initially grayish brown pilei and concolorous stipes, a grayish brown trama-staining reaction, and teeth up to 5 mm long, but *S. umbilicatus* differs from *S. bambusinus* in its matted fibrillose to rugulose pileus (vs. villose to subfurfuraceous), presence of an umbilicus, and wider basidiospores (7–8 vs. 5–7 μm) (Baker and Dale 1951, Maas Geesteranus 1974b).

KEY TO NEOTROPICAL *SARCODON* SPECIES, WITH SELECTED EXTRALIMITAL TAXA

1. Pileus pinkish gray, with scattered darker purplish spots, with age developing irregular black patches, or grayish lilac or dark purple when young 2

1. Pileus color not as above, some shade of grayish, orangish or yellowish brown 4

2(1). Pileus surface irregularly pitted; a densely interwoven mat under hand lens; trama slowly staining pink upon exposure; Guyana, in *Pakaraimaea* (Dipterocarpaceae) forests. . . . . *Sarcodon pakaraimensis*

2. Pileus surface not as above; trama unchanging or not staining as above 3

3(1). Pileus surface appressed, felt-like; substriate at margin; stipitipellis terminal cells with 2–8 serpentine undulations; Belize, in montane *Quercus* forests . . . . *Sarcodon quercophilus*

3. Pileus surface erect tomentose or velutinous, eventually areolate; stipitipellis terminal cells

undifferentiated; Malaysian Archipelago and New Guinea (Dipterocarpaceae and Fagaceae), New Zealand in *Nothofagus* forests . . . *Sarcodon thwaitesii*

4(1). Pileus surface tomentose, felted or pubescent, eventually glabrous; basidioma some shade of orangish to olivaceous brown to sepia; drying olivaceous; teeth up to 16 mm long; eastern North America, Europe, eastern Asia . . . *Sarcodon atroviridis*

4. Pileus surface not as above, or not with those combinations; basidioma some shade of grayish brown or fuscous; not drying olivaceous; teeth not exceeding 6 mm 5

5(4). Pileus regularly with a deep umbilicus; Belize, in montane *Quercus* forests . . . *Sarcodon umbilicatus*

5. Pileus without an umbilicus 6

6(5). Pileus surface matted fibrillose throughout, with age finely areolate over disk; all tissues quickly staining black upon pressure or exposure; Puerto Rico, in lower montane wet forests . . . *Sarcodon portoricensis*

6. Pileus surface villose or subfurfuraceous, more repent fibrillose near margin; stipe staining slowly fuliginous to fuscous with pressure or age; Trinidad, Brazil, in lowland tropical rainforests. . . . . *Sarcodon bambusinus*

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