

New species of *Inocybe* from *Dicymbe* forests of Guyana

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Four new species of *Inocybe* (*Agaricales*) with pleurocystidia and nodulose spores are recorded from a remote region of rain forest in Guyana, in northeastern South America. All four species of *Inocybe* occur in association with the arborescent legume genus, *Dicymbe* (*Caesalpiniaceae*, tribe *Amherstieae*). This constitutes the first report of a legume host genus with *Inocybe* in the neotropics. The new species are *I. ayangannae*, *I. epidendron*, *I. lilacinosquamosa* and *I. pulchella*. A dichotomous key, morphological descriptions, illustrations, taxonomic commentary, and a discussion of *Inocybe* in the tropics, are provided.

INTRODUCTION

The systematics of *Inocybe* (*Agaricales*) have been investigated in temperate areas of South America such as the Tierra del Fuego region of the *Nothofagus* zone (Singer 1953a, 1954, 1969, Horak 1979a, Garrido 1988), and initial progress made in *Quercus* and *Pinaceae* forests of Mexico (Perez-Silva 1967). However, little work has been done to document *Inocybe* diversity from the vast neotropical regions of South and Central America aside from the scattered publications of Dennis (1953, 1970), Guzmán (1982), Murrill (1912), Pegler (1983), Rick (1920, 1930, 1938, 1961), Singer (1962), Singer, Araujo & Ivory (1983) and de Meijer (2001). In the preceding tropical treatments, most *Inocybe* taxa have been reported in association with *Quercus* (*Fagaceae*) that occur at low or high elevations, or putative hosts left unclear. Indeed, Singer (1962) had concluded that few species of *Inocybe* occur in lowland tropical rain forests, but the majority of those that do, remarkably, possess pleurocystidia and nodulose basidiospores (Singer *et al.* 1983). A survey of macrofungi in southern Brazil reaffirms Singer's observations of the presence of several nodulose-spored taxa and lack of smooth-spored taxa (de Meijer 2001). It remains both of phylogenetic and biogeographic interest why the rain forests of the neotropics host only a fraction of the diversity of *Inocybe* found in more northerly and southerly temperate areas and noteworthy that the four *Inocybe* species documented from Guyana under

Dicymbe (*Caesalpiniaceae*, tribe *Amherstieae*) all share affinities with sect. *Inocybe* (Singer 1986).

Dicymbe has previously been reported to host various ectomycorrhizal fungi of the *Boletaceae*, *Russulaceae*, *Amanitaceae*, *Cantharellaceae* and *Elaphomycetaceae* (*Ascomycota*) in South America (Henkel 1999, Henkel, Aime & Miller 2000, Miller, James & Henkel 2001, Henkel, Terborgh & Vilgalys 2002, Simmons, Henkel & Bas 2002). Singer & Araujo (1979) noted caesalpinoid legumes in the ectotrophic campinarana forests in Central Amazonia. This is consistent with findings that members of the caesalpinoid tribes *Amherstieae* and *Detarieae* form ectomycorrhizas (Malloch, Pirozynski & Raven 1980). To date, however, no *Inocybe* species have been documented in association with this family of arborescent legumes, although Singer (1962, 1978) first observed *I. matrisdei* in periodically inundated rain forests of Bolivia and *I. amazoniensis* in legume forests of Brazil (Singer *et al.* 1983). In fact, *Dicymbe* and *Macrolobium* are the sole neotropical genera of the tropical African-centered caesalpinoid tribe *Amherstieae*, many species of which have been shown to form ectomycorrhizas in rain forests of the Guinea-Congolian region (Alexander 1989). *Macrolobium*, however, appears not to be ectomycorrhizal in French Guiana (Béreau, Gazel & Garbaye 1997).

In this paper we present descriptions of four new species of *Inocybe* (subgen. *Inocybe*), associated with *Dicymbe* in Guyana. The discovery of these Guyanese taxa allied with sect. *Inocybe* reinforces the observations

of Singer *et al.* (1983) that the infrageneric diversity of *Inocybe* is limited in neotropical rain forests. The documentation of additional tropical species, however, merits phylogenetic and biogeographic attention.

METHODS AND MATERIALS

Basidiomata were collected during the rainy season (May–August) of 2000 and 2001 in the Pakaraima Mountains, 20 km east of Mt Ayanganna, near the confluence of the Potaro River and Alukyadongbaru Creek. The elevation and longitudinal/latitudinal positions of collecting sites include: base camp, 650 m elevation, N 5° 18.070' W 59° 54.668'; *Dicymbe* 1 plots (D-1), 850 m, N 5° 16.580' W 59° 54.966'; and *Dicymbe* 2 plots (D-2), 845 m, N 5° 16.463' W 59° 54.731'. GPS readings for *Dicymbe* 3 plots could not be made due to the dense canopy cover.

Gross morphological characters were noted in the field. Colours were documented with Kornerup & Wanscher (1967), for example, dark brown (5F6) refers to plate 5, column F, row 6. 'L' is the number of lamellae that extend from the pileal margin to the stipe. Basidiomata were dried slowly over charcoal (2000 field season) or in airtight containers by silica gel (2001 field season) and then stored with silica gel to prevent spoilage by excessive humid conditions.

Sections of dried material were mounted in 10% ammonium hydroxide (NH₄OH) or 3% potassium hydroxide (KOH). At least 20 basidiospores, ten pleurocystidia and ten basidia were measured to determine the range and mean of these cells per species. Means are italicized and reported within the range. Extreme basidiospore lengths and widths are placed in parentheses if those values constitute 5% or less frequency. The length/width ratio of basidiospores is presented as the *Q* value. The distribution of *Q* values is presented similarly to the length and width of spores. Spore pigmentation was observed under a light microscope. Terminology for cystidia follows that of Kuyper (1986). Scale bars in illustrations are equal to 10 µm for basidiospores and 25 µm for cystidia and basidia.

Collections are curated at the University of Guyana Herbarium (BRG), Virginia Polytechnic Institute (VPI), the University of Washington (WTU), or Duke University (DUKE).

TAXONOMY

Inocybe epidendron Matheny, Aime & T. W. Henkel, **sp. nov.** (Figs 1, 5)

Etym.: Refers to the habit of occurrence on sides of *Dicymbe* trunks and woody debris.

Pileo 0.5–1.5 cm lato, convexo demum plano, saepe exumbonato, squarroso vel squamuloso-fibrilloso, ad marginem fibrilloso, umbrino, hygrophano, odore inconspicue, carne inmutabili. Lamellis adnatis, confertis, subbrunneolis demum brunneis. Stipite 1.5–3.5 cm × 0.75–1.5 mm, aequali, vinacea brunnea vel avellanea, cortina praedita probabiliter. Basidiosporis 6.5–8 × 5–6 µm, gibbosis, 9–12 gibberibus obtusis, ochraceis. Basidiis 19–25 × 7–10 µm, quattuor sterigmatibus. Pleurocystidiis 45–53 × 11–15 µm, fusiformibus vel subutriformibus, membrana crassiuscula praedita, haud cum crystallis, hyalinis, apicibus obtusis. Cheilocystidiis similibus pleurocystidiis. Caulocystidiis nullis. Hyphis fibulatis.

Dispersa, in arborum truncis *Dicymbae* vel ad lignum cariosum sub *Dicymbe*.

Typus: **Guyana**: *Potaro-Siparuni*: Pakaraima Mountains, 10 km east of base of Mt Ayanganna, 'D-1 plot', 20 May 2001, *M. C. Aime MCA 1473* (BRG – holotypus).

Pileus 0.5–1.5 cm diam, convex with a decurved margin expanding to plane, infrequently with a slight obtuse umbo; center with upright squamules that are often pronounced, at times fibrillose-squamulose or appressed-squamulose, towards the margin radially fibrillose, at times splitting, or translucent-striate; edge of margin at times appendiculate with whitish fibrils; colour of surface umber brown (5E8-5E7), hygrophanous; context very thin, 0.5 mm diam, concolourous with pileus surface, no colour changes where cut or bruised; odour indistinct to faintly spermatic, taste not remarkable. *Lamellae* narrowly adnate to adnate, moderately close, about 25 L, with two tiers of lamellulae, very pale brown (4B3) when young, brown (5D6-5D8) in age, 1.5–2 mm broad, edges faintly fimbriate. *Stipe* 1.3–3.5 cm × 0.75–1.5 mm, even; cortina fugacious; stipe surface silky-fibrillose, nowhere pruinose, vinaceous brown with a silvery white superficial covering to light greyish vinaceous or avellaneous (9D4-8D5-7B2); context loosely stuffed to hollow. *Basidiospores* 6.5–7.2–8 × 5–5.8–6 (6.5) µm; *Q* = 1.1–1.2–1.4 (*n* = 20), nodulose and at times coarsely so, often subelliptic in outline with 9–12 obtuse nodules, infrequently with one blunt-shaped

Key to nodulose-spored *Inocybe* species with a cortina and pleurocystidia in Guyana

- 1 Pleurocystidia thick-walled, walls 3.0–4.0 µm thick; pileus scaly; frequently on sides of *Dicymbe* trunks or woody debris **epidendron**
- Pleurocystidia thin-walled, at most only slightly thick-walled proximally, but not as above; on soil and root mats; if on sides of *Dicymbe* trunks, then pileus not scaly 2
- 2(1) Basidiomes minute, habit like a mycenoid *Galerina*; pileus silky-fibrillose to subglabrous, to 6 mm diam; on trunks of *Dicymbe* **pulchella**
- Basidiomes small to medium sized, habit inocyboid, pileus scaly, 10–40 mm diam; on soil under *Dicymbe* 3
- 3(2) Basidiomes brown or dark brown; pileus 10–40 mm diam **ayanganna**
- Basidiomes cream or pale yellowish with lilac-tipped squamules; pileus up to 20 mm diam **lilacinosquamosa**

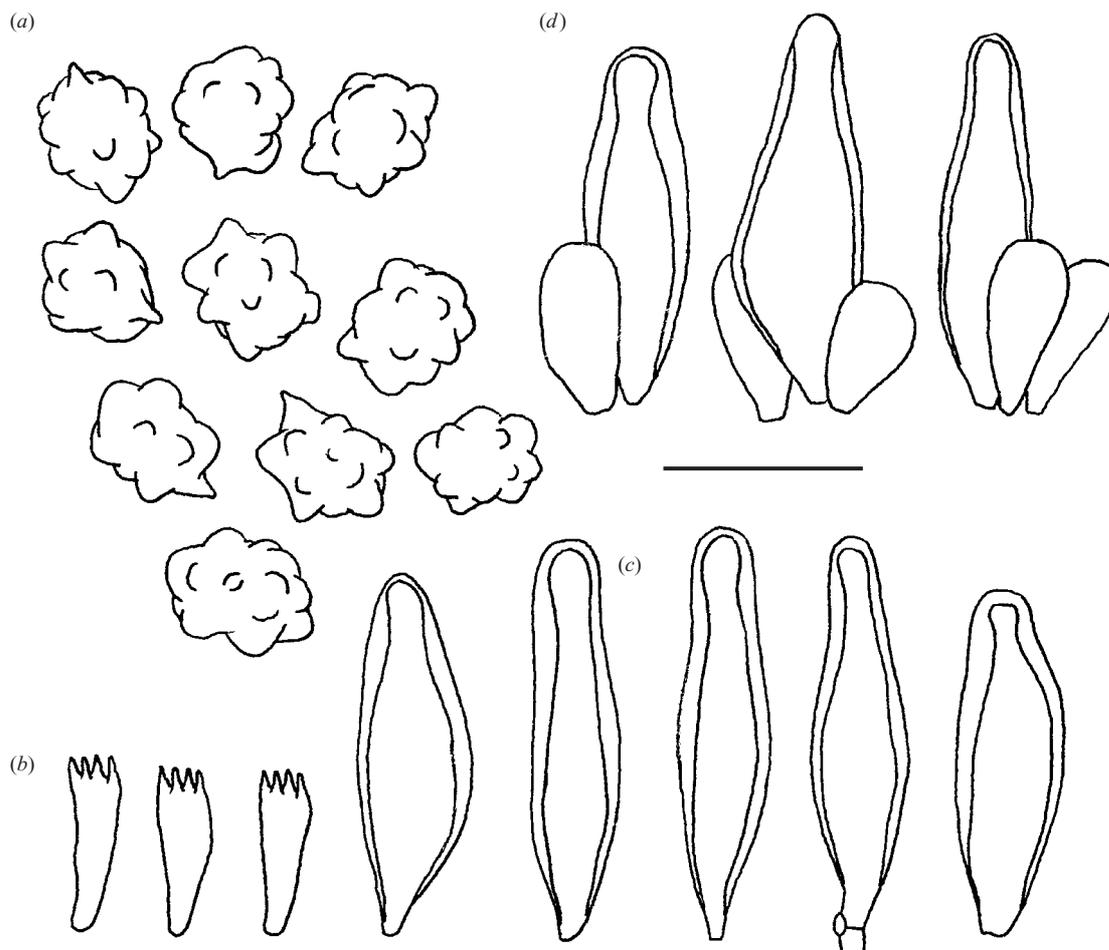


Fig. 1. *Inocybe epidendron* (holotype). (a) Basidiospores; (b) basidia; (c) pleurocystidia; and (d) cheilocystidia and paracystidia.

or bifid nodule, ochraceous buff. *Basidia* 19–22–25 × 7–8–10 μm ($n=10$), 4-sterigmate, clavate, hyaline. *Pleurocystidia* 45–48–53 × 11–13–15 μm ($n=10$), fusiform to narrowly utriform with obtuse apices, tapered below to a short pedicel; thick-walled, walls 3.0–4.0 μm thick, hyaline; apices lacking crystals. *Cheilocystidia* similar to pleurocystidia; paracystidia clavate, hyaline, thin-walled. *Caulocystidia* absent; superficial hyphae on stipe minimal at apex, more dense below, cylindrical, hyaline, irregular mostly 5–10 μm diam, thin-walled; stipe hyphae cinnamon to yellowish brown in mass. *Lamellar trama* regular, compact; hyphae pale yellowish brown in mass, 5–25 μm diam, composed chiefly of inflated to subsodiametric cells; subhymenium a narrow pseudoparenchymatous layer. *Pileipellis* a trichoderm of scattered broad fascicles of hyphae tapering upwards, brown or tawny in mass, cylindrical, inflated to isodiametric, the terminal cells of which are often cylindrical, 5–12 μm diam, and tapered, lightly incrustated with pigment although the terminal cells appear smooth; walls thin- to slightly thick-walled; tramal hyphae pale yellowish in mass, cylindrical to inflated; tissues not exuding any pigments in 10% ammonia solution. *Clamps* present.

Habitat: Scattered singly on sides of *Dicymbe corymbosa* in *Dicymbe*-dominated woods, on woody debris, on humus layer of a dead *Dicymbe* stump, and one collection on a root mat; known only from the type locality along the Upper Potaro River in the Pakaraima Mountains, Guyana, fruiting during rainy season, May to June.

Notes: *Inocybe epidendron* is characterized by its small inocyboid habit and frequent occurrence on the sides of *Dicymbe* trunks and woody debris. It is distinguished from the similarly sized *I. pulchella* mainly by its umber brown pileus with often upright scales on the center and consistently thick-walled pleurocystidia. MCA 1880 is somewhat noteworthy due to its olive brown (olive tints near 3E7) pileus but is otherwise similar to the other umber brown collections cited here.

After having studied the holotype of *I. amazoniensis* (B11019; INPA), we determined the collections of *I. epidendron* as a separate species based chiefly on two differences: (1) the squamulose covering of the pileus that when sectioned reveals a trichoderm in contrast to the cutis of *I. amazoniensis*; and (2) the ecology of *I. epidendron*, in which it often occurs on sides of *Dicymbe* trunks or on woody debris. Singer *et al.* (1983)

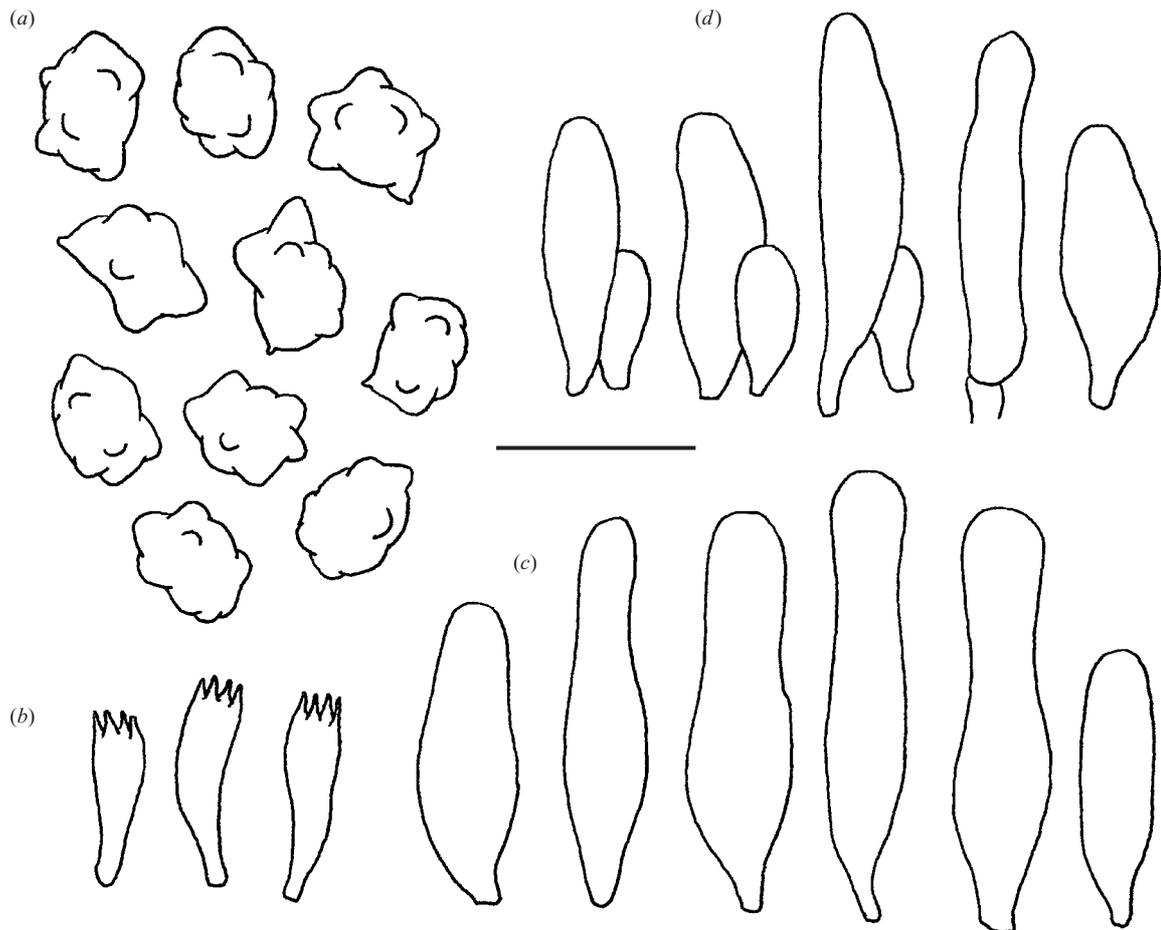


Fig. 2. *Inocybe pulchella* (holotype). (a) Basidiospores; (b) basidia; (c) pleurocystidia; and (d) cheilocystidia and paracystidia.

mentioned three collections of *I. amazoniensis* with an occurrence on humus and among superficial roots in campinarana vegetation. Both species, however, do share similar thick-walled pleurocystidia, similar sized basidiospores with 9–11 distinct nodules, and association with leguminous hosts.

Additional specimens examined: **Guyana:** Region 8, Potaro-Siparuni: Pakaraima Mountains, upper Potaro River, 10 km east of base of Mt Ayanganna, near base camp on east bank of Potaro River, on root mat under *Dicymbe*, 6 June 2000, *M. C. Aime MCA 1137* (BRG, VPI); D-1 plot, 30 May 2001, *M. C. Aime MCA 1498* (BRG); D-1 plot, on trunk of *Dicymbe*, 5 June 2001, *M. C. Aime MCA 1880* (BRG, WTU).

Inocybe pulchella Matheny, Aime & T. W. Henkel, **sp. nov.** (Figs 2, 6)

Etym.: So-named due to the beautiful colour and exquisitely small size.

Pileo diminuto, 2–6 mm lato, convexo, fissili, roseo-lavandulaceo, hygrophano, carne inmutabili. Lamellis adnatis, subconfertis, albis tinctisque roseo. Stipite 1.5 cm × 1 mm, gracili, centrali, aequali, fibrillosa, concolora cum pileo, cortina fugaci. Basidiosporis 6–8 × 4.5–5.5 μm, gibbosis, 6–10 gibberibus parvis obtusis vel rotundatis, ochraceis. Basidiis 18–25 × 7–10 μm, quattuor sterigmatibus. Pleurocystidiis 40–62 × 10–15 μm, lageniformibus, fusiformibus raro cylindricis,

membrana tenui praedita, haud cum crystallis, hyalinis. Cheilocystidiis similibus pleurocystidiis. Caulocystidiis nullis. Hyphis fibulatis.

Gregaria ad truncos *Dicymbae*.

Typus: **Guyana:** Potaro-Siparuni: Pakaraima Mountains, 10 km east of base of Mt Ayanganna, 'D-1 plot', 4 June 2000, *M. C. Aime MCA 1879* (BRG – holotypus).

Pileus 0.2–0.6 cm diam, conical to convex, surface with cottony to silky tomentum, in age glabrous, often with a tiny acute umbo, margin splitting in age; colour with pinkish lavender tints (12D4) when fresh, fading to light brown or tan (5C3–5D5), umbo often darker than margin; context extremely thin, odour and taste not recorded. *Lamellae* adnate, close, 13–14 L, white with a subtle pinkish cast. Stipe 1–1.5 cm × 0.5–1 mm, even or a little swollen at the base; cortina fugacious; stipe surface with silvery white to silvery pinkish appressed fibrils; concolourous with pileus or lighter. *Basidiospores* (5.5–)6–6.8–8 × 4.5–5.1–5.5 μm; $Q = (1.1)–1.2–1.3–1.5(–1.6)$ ($n = 54$), angular-nodulose with 6–10 small obtuse to hemispherical nodules around a trapeziform, polygonal or subelliptic outline, wall only slightly thickened, ochraceous buff. *Basidia* 18–21–25 × 7–9–10 μm ($n = 20$), 4-sterigmate, clavate to sphaeropedunculate, hyaline or on occasion ochraceous. *Pleurocystidia* 40–51–62 × 10–12–15 μm ($n = 30$),

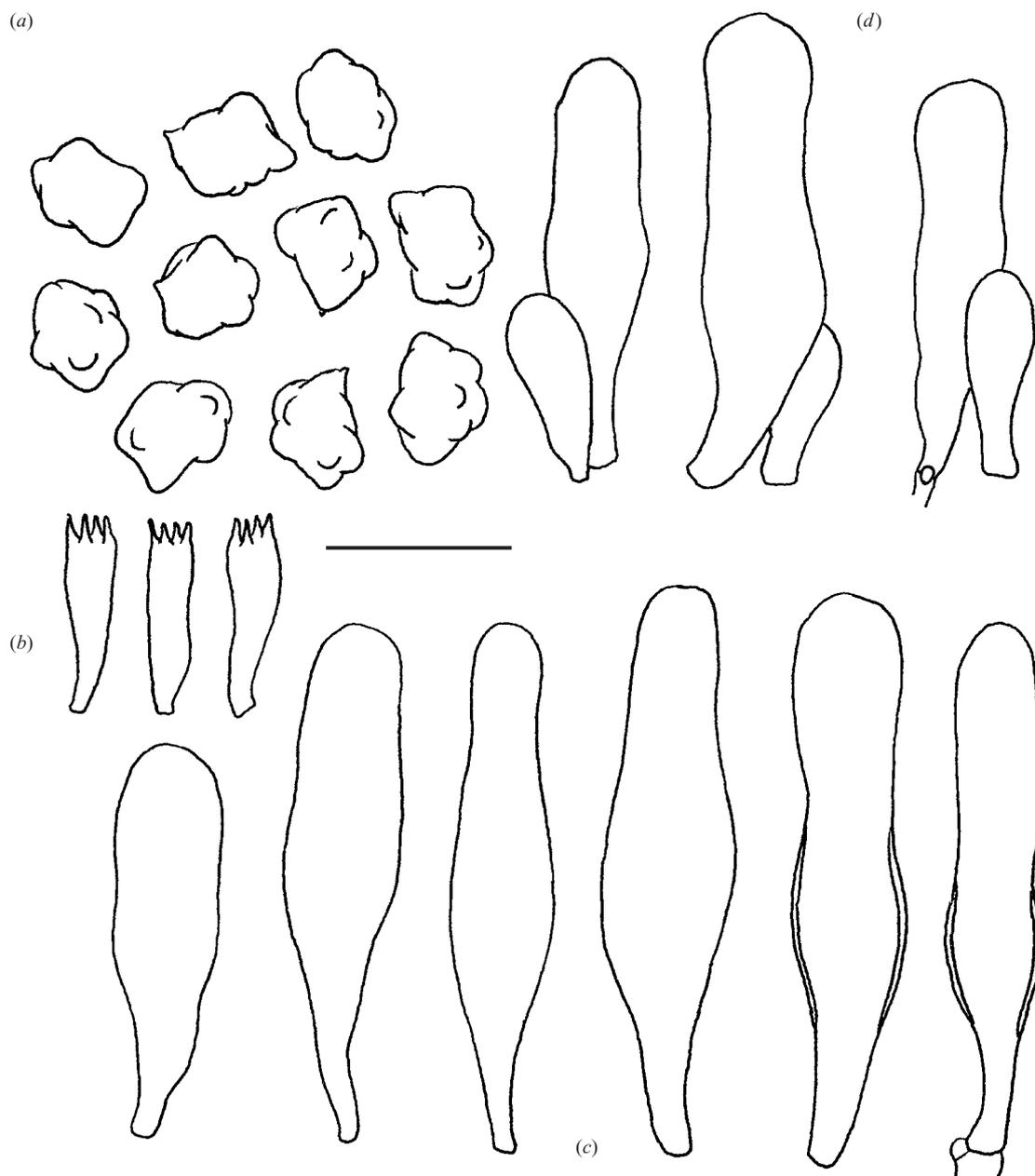


Fig. 3. *Inocybe ayangamae* (holotype, and *MCA 1465*). (a) Basidiospores; (b) basidia; (c) pleurocystidia; and (d) cheilocystidia. The basidia, cheilocystidia, and pleurocystidia with slightly thickened walls (two at far right) are from *MCA 1495*.

lageniform, fusiform to occasionally cylindric, thin-walled, hyaline; apices obtuse to subcapitate, bare (lacking crystals); necks differentiated, base with pedicel. *Cheilocystidia* similar to pleurocystidia; paracystidia clavate, thin-walled, hyaline, like basidioles. *Caulocystidia* absent; superficial hyphae on stipe irregular to regular, descending to base of stipe, hyphae smooth, cylindric, 5–10 μm diam, hyaline in mass, thin-walled but thickened at septa, at times thick-walled elsewhere, terminal cells tapered towards apices but otherwise undifferentiated; stipe hyphae cinnamon brown in mass, to 15 μm diam, with faint incrusted walls. *Lamellar trama* regular, pale yellowish to subhyaline in mass; hyphae 3–10 μm diam. *Pileipellis* composed of a superficial layer of irregular to regular hyphae, at times scattered upwards, cylindric, 4–15 μm

diam, walls slightly thickened to thin, often thickened at septa, hyaline in mass, subtending cells of this layer often inflated to isodiametric, to 25(–35) μm diam; subpellis cinnamon brown in mass transitioning into paler tramal hyphal zone of cylindric to inflated hyphae; refractive hyphae not observed. *Clamps* present.

Habitat: Fruiting singly to scattered on and inside hollow of trunks of living *Dicymbe corymbosa*, known only from type locality along the Upper Potaro River in the Pakaraima Mountains, Guyana, May to July.

Notes: The combination of the very small size, purplish to pinkish tones of the silky-tomentose to subglabrous pileus, the thin-walled pleurocystidia, and consistent occurrence on trunks of *Dicymbe* in the neotropics certainly make *I. pulchella* unique. Very few diminutive *Inocybes* from the northern hemisphere

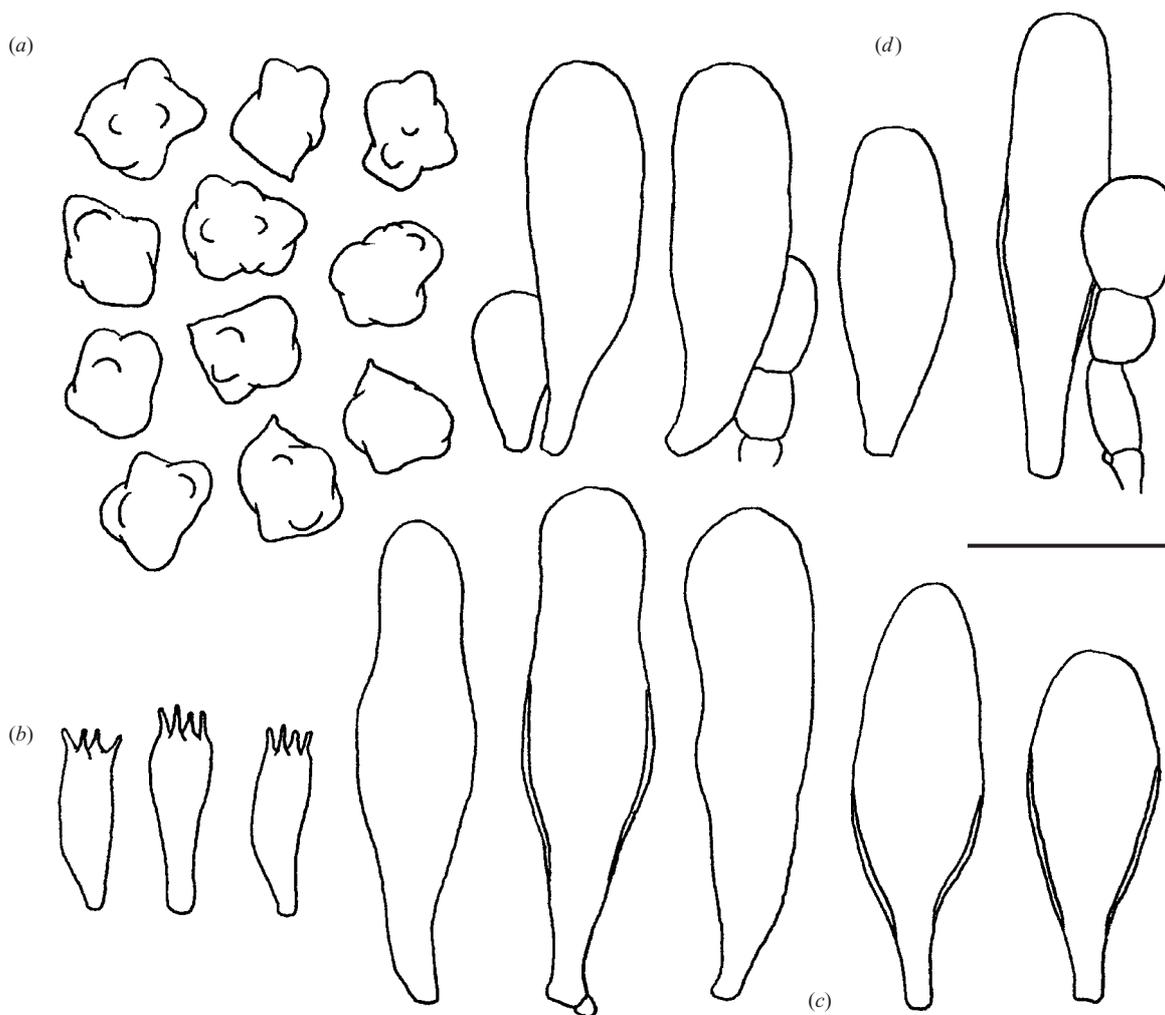


Fig. 4. *Inocybe lilacinosquamosa* (holotype, and *MCA 1460*). (a) Basidiospores; (b) basidia; (c) pleurocystidia; and (d) cheilocystidia and paracystidia. The cheilocystidium and paracystidium at far right are drawn from *MCA 1460*.

have been described, but these are quite dissimilar to *I. pulchella*. These include the smooth-spored *I. comatella* (Peck 1885) and the nodulose-spored *I. diminuta* (Matheny & Kropp 2001) and *I. petiginosa* (Stangl 1989). Although the mycorrhizal status of *I. pulchella* (and *I. epidendron*, see above) might be questioned, it should be pointed out that certain species of *Russula* and *Lactarius* occur on trunks of saplings and larger trees in *Dicymbe*-dominated rain forests and have been shown to be ectomycorrhizal (Henkel *et al.* 2000). *Inocybe epidendron*, which also may occur on trunks of *Dicymbe*, can be distinguished despite its small size by the squamulose pileus and thick-walled pleurocystidia. On rare occasions pale violate cytoplasmic pigments were observed in sections of the pileus and stipe of *I. pulchella*, but most collections reveal essentially hyaline superficial hyphae.

Additional specimens examined: **Guyana:** *Region 8, Potaro-Siparuni:* Pakaraima Mountains, upper Potaro River, 10 km east of base of Mt Ayanganna, near base camp on east bank of Potaro River, on *Dicymbe* trunk, 4 June 2000, *M. C. Aime MCA 1122* (BRG, VPI); 31 May 2000, on *Dicymbe* trunk, *M. C. Aime MCA 1090* (BRG, VPI); 14 July 2000, *T. W.*

Henkel TH 7602 (DUKE); D-3 plot, on *Dicymbe* trunk, 18 May 2001, *M. C. Aime MCA 1465* (BRG, WTU); D-1 plot, 25 May 2001, *M. C. Aime MCA 1488* (BRG); near base camp, 2 June 2001, sheltered in humus on *Dicymbe* trunk, *M. C. Aime MCA 1872* (BRG).

***Inocybe ayangannae* Matheny, Aime & T. W. Henkel, sp. nov.** (Figs 3, 7)

Etym.: Named to indicate the locality of this species near Mt Ayanganna.

Pileo 2–4 cm lato, conico, umbonato, squamuloso-fibrilloso, rimuloso, brunneo vel umbrino, carnosus, sapore et odore nullo, carne immutabili. Lamellis adnatis, confertis, pallidis demum brunneis, acie cum fimbriis. Stipite usque ad 8.0 cm × 4 mm, aequali, cortina fugaci, fibrilloso-squamuloso, concolora cum pileo. Basidiosporis 6.0–7.5 × 4.5–6.0 μm, gibbosis, 5–8 gibberibus obtusis, ochraceis. Basidiis 21–28 × 6–8 μm, quattuor sterigmatibus. Pleurocystidiis 58–106 × 15–20 μm, cylindricis vel subfusiformibus vel utrififormibus, membrana tenui praedita, haud cum crystallis, hyalinis. Cheilocystidiis similibus pleurocystidiis. Caulocystidiis nullis. Hyphis fibulatis.

Dispersa, humi, sub *Dicymbe*.



Figs 5–8. New species of *Inocybe* from Guyana. **Fig. 5.** *I. epidendron* (holotype). **Fig. 6.** *I. pulchella* (MCA 1122). **Fig. 7.** *I. ayangannae* (holotype). **Fig. 8.** *I. lilacinosquamosa* (holotype). Bar = 1 cm.

Typus: **Guyana:** Potaro-Siparuni: Pakaraima Mountains, 10 km east of base of Mt Ayanganna, 1.5 h walk N of base camp, 4 June 2000, M. C. Aime MCA 1232 (BRG – holotypus, WTU – isotypus).

Pileus 2–4 cm diam, broadly conical, with a large umbo; surface dry, squamulose-fibrillose, center with raised

brown squarreae, margin shaggy-fibrillose, finely rimose; brown to dark brown throughout (5E6–5F6), where squarreae have been weathered showing smooth pale yellowish cuticle (~3A4); context pale yellowish (3A4), hygrophanous, 1.5 mm thick, no colour changes when cut or bruised, odor and taste indistinct. *Lamellae* adnate, close, pallid (3A3) becoming brown (5E7–6E8),

no olivaceous tones, narrow, to 2.5 mm broad, even, edges fimbriate. Stipe to 8 cm × 4 mm, even, neither bulbous nor tapered; apex concolourous with lamellae, minutely floccose at apex, remainder appressed fibrillose-squamulose, concolourous with pileus or slightly lighter; cortina fugacious; context pallid, solid, lacking any colour changes where cut or bruised. *Basidiospores* 6–6.8–7.5 × 4.5–5.2–6(–6.5) μm; $Q = 1.1–1.2–1.4$ ($n=60$), angular-nodulose with 5–8 obtuse nodules around a polygonal outline, ochraceous buff, wall only slightly thickened. *Basidia* 21–24–28 × 6–7–8 μm ($n=10$), 4-sterigmate, slenderly clavate, hyaline. *Pleurocystidia* 58–73–106 × 15–16–20 μm ($n=23$), cylindrical to subfusiform or utriform, thin-walled, at times thick-walled basally, wall here to 2.5 μm thick, hyaline, apices well-rounded to obtuse, at times indistinctly subcapitate, lacking crystals, with basal pedicel. *Cheilocystidia* similar to pleurocystidia but shorter, more often utriform; paracystidia clavate, thin-walled, hyaline. *Caulocystidia* not observed; apex of stipe with undifferentiated hyphal end cells that are faintly incrustated, cylindrical and thin-walled, with a well-developed superficial layer of tangled hyphae over the stipe surface. *Lamellar trama* regular, compact, hyphae cylindrical to inflated, 5–18 μm diam, pale yellow to hyaline in mass; subhymenium pseudoparenchymatous. *Pileipellis* composed of trichodermial fascicles of hyphae at center, more regularly arranged towards margin, hyphae cylindrical to inflated, 5–24 μm diam, thin-walled or with slightly thickened walls, incrustated, tawny in mass; tramal hyphae regular, pale yellowish to subhyaline in mass, cylindrical to inflated, smooth; refractive hyphae present. *Clamps* present.

Habitat: Solitary to scattered on root mat of forests dominated by *Dicymbe corymbosa*, known only from type locality along Upper Potaro River in Pakarima Mountains, Guyana, fruiting during heavy rainy season, May to July.

Notes: *Inocybe ayangannae* shares similarities with *I. longicystis* from temperate North America (Atkinson 1918, Grund & Stuntz 1968), for which the correct name is *I. stellatospora* (Matheny & Kropp 2001). This new species differs from *I. stellatospora* by the much smaller basidiospores and legume ectomycorrhizal host. Grund & Stuntz (1977) describes the north temperate *I. parcecoacta*, which shares similar cystidia and spore characters as *I. ayangannae*, but differs by the nonsquamulose covering of the pileus and stipe. *I. cerasphora* has larger spores than *I. ayangannae* and occurs on rotten *Nothofagus* wood near Tierra del Fuego (Singer 1953a). *I. paracerasphora* has larger spores with pronounced nodules and occurs on rotten wood of *Nothofagus* in New Zealand and Indomalaya (Horak 1979b). *I. gibbosula* has larger spores, metuloid cystidia, and is not shaggy-squamulose (Horak 1979a, Garrido 1988). Lastly, a species described from xerophytic forests in Guadeloupe in the Lesser Antilles, *I. viridiumbonata* (Pegler 1983), differs by the dark brown pileus with greyish green tints and absence of

shaggy squamules; putative ectomycorrhizal host(s) were not specified for this species.

Inocybe ayangannae might be classified in sect. *Inocybe* (Singer 1986), however, this section is not monophyletic (Matheny *et al.* 2002).

Additional specimens examined: **Guyana**: *Region 8, Potaro-Siparuni*: Pakaraima Mountains, upper Potaro River, 10 km east of base of Mt Ayanganna, 1.5 h walk N of base camp, on ground, 28 May 2000, *M. C. Aime MCA 1046* (BRG, VPI); east bank Potaro River, 0.5 km east of base camp, on ground, 8 June 2000, *T. W. Henkel TH 7451* (DUKE); east bank Potaro River, 4 km upstream from Ayanganna airstrip, on slope along 'Benny's Ridge', 22 July 2000, *T. W. Henkel TH 7952*; (DUKE); base camp on trail to molecular plots, 17 May 2001, *M. C. Aime MCA 1463* (BRG); Palluway plot 2, on ground, 20 May 2001, *M. C. Aime MCA 1472* (BRG); D-3 plot, on ground, 28 May 2001, *M. C. Aime MCA 1495* (BRG); D-1 plot, on ground, 25 May 2001, *M. C. Aime MCA 1633* (BRG); D-3 plot, on ground, 2 June 2001, *M. C. Aime MCA 1873* (BRG).

***Inocybe lilacinisquamosa* Matheny, Aime & T. W. Henkel, sp. nov.** (Figs 4, 8)

Etym.: Refers to the lilac coloured tips of the squamules.

Pileo 0.7–1.2 cm lato, convexo demum subconico, squamuloso-fibrilloso, ad marginem furfuraceo-fibrilloso, cremoricolori, extremitatibus squamularum lilacinis, odore nullo, carne inmutabili. Lamellis adnatis, confertis, subolivaceis demum isabellinis, acie cum fimbriis. Stipite 2.5–5.5 cm × 1–2 mm, aequali, cremoricolori, squamulis lilacinis, ad basem ochracea, cortina praedita. Basidiosporis 5.5–6.5 × 4.5–5.5 μm, gibbosis, 6–8 gibberibus obtusis, ochraceis. Basidiis 20–26 × 6–8 μm, quattuor sterigmatibus. Pleurocystidiis 42–59 × 15–18 μm, subcylindricis vel utriformibus, membrana tenui vel crassiuscula praedita, haud cum crystallis, hyalinis, apicibus rotundatis. Cheilocystidiis similibus pleurocystidiis. Caulocystidiis nullis. Hyphis fibulatis.

Dispersa, humi, sub *Dicymbe*.

Typus: **Guyana**: *Potaro-Siparuni*: Pakaraima Mountains, near Ayanganna airstrip, 20 May 2000, *M. C. Aime MCA 976* (BRG – holotypus, VPI – isotypus).

Pileus 0.7–1.2 cm diam, convex to subconical, margin inrolled when young, surface deeply cracked into projecting matted squamules at the center, appressed squamulose-fibrillose to scurfy-fibrillose towards margin; creamy coloured (3A3) but tips of squamules lilac (18D4); context thin, pallid or pale yellowish (2A2), unchanging, without odor. *Lamellae* adnate, close to subcrowded, with pallid olivaceous (2B3) tint when immature, to isabelline (3B4), finally pale yellowish brown (~4B4), to 2.5 mm broad, edges fimbriate. Stipe 2.5–5.5 cm × 1–2 mm, even; yellowish like pileus but mostly cloaked in lilac squamules, base ochraceous; partial veil formed by squamulose fibrils at margin of pileus. *Basidiospores* 5.5–6.0–6.5 × 4.5–4.9–5.5 μm; $Q = 1.1–1.2–1.3$ ($n=30$) angular-nodulose, generally pentagonal to subtrapeziform in outline with 6–8 obtuse nodules, at times with one blunt or wedge-shaped nodule, ochraceous buff, slightly thick-walled.

Basidia 20–24–26 × 6–7–8 µm ($n = 10$), 4-sterigmate, clavate, hyaline. *Pleurocystidia* 42–50–59 × 15–16–18 µm ($n = 10$), subcylindric to utriform or subfusiform with well-rounded apices, at times subcapitate; thin-walled, at times proximally thickened, to 2.5 µm thick, hyaline to pale yellow, at times opaque, pedicel short; apices lacking crystals. *Cheilocystidia* similar to pleurocystidia; paracystidia abundant, clavate, hyaline, thin-walled, 15–24 × 10–16 µm, at times concatenated. *Caulocystidia* absent; terminal cells at apex undifferentiated, thin-walled, lilac pigments not observed; stipe hyphae pale yellowish brown in mass. *Lamellar trama* regular, compact; hyphae pale yellow in mass, 5–20 µm diam; subhymenium a narrow pseudoparenchymatous layer. *Pileipellis* a trichoderm of broad fascicles of hyphae, ochraceous in mass; hyphae cylindric to inflated, incrustations not evident, walls thin- to slightly thickened; tramal hyphae pale yellowish to hyaline, cylindric to inflated; tissues not exuding any pigments in 10% ammonia solution. *Clamps* present.

Habitat: Single to scattered on root mat under *Dicymbe corymbosa* in *Dicymbe*-dominated woods on sandy soils; known only from the type locality along the Upper Potaro River in the Pakaraima Mountains, Guyana, fruiting during rainy season, May to June.

Notes: This small slender squamulose species is remarkable in the possession of a number of interesting characters. The spores are small and nodulose like those of *I. relicina* (Moser 1978) and *I. tahquamenonensis* and possess, at times, a blunt-shaped nodule as in *I. tahquamenonensis* (Stuntz 1954, Matheny & Kropp 2001). Remarkably, the tips of the squamules are lilac, an unusual character that is not retained after drying. The hymenial cystidia are thin-walled but at times thickened proximally, and subcylindric with well-rounded to subcapitate apices similar in shape to *I. tahquamenonensis*, the latter a species restricted in its distribution to eastern North American hardwood forests (Matheny & Kropp 2001). However, DNA sequence data suggest *I. lilacinosquamosa* is closely related to *I. ayangannae* (Matheny, unpubl.).

Another interesting species worthy to note is *I. magnifica* described from Papua New Guinea under *Nothofagus* (Horak 1979b). This outstanding species contains wine red-brown pigments that are exuded in solution of alkali mounts (as in *I. tahquamenonensis*). However, no pigments of *I. lilacinosquamosa* tissues dissolve in alkaline solutions. *Inocybe magnifica* differs from its North and South American counterparts by the absence of pleurocystidia.

Additional specimens examined: **Guyana**: Region 8, Potaro-Siparuni: Pakaraima Mountains, upper Potaro River, 10 km east of base of Mt Ayanganna, at Ayanganna airstrip, 21 May 2000, M. C. Aime MCA 1000 (BRG, VPI); 30 May 2000, M. C. Aime MCA 1088 (BRG, VPI); Ayanganna airstrip, singly on exposed roots of *Dicymbe corymbosa*, on trail, 16 May 2001, M. C. Aime MCA 1460 (BRG, WTU); on base camp trail to molecular plots, 17 May 2001, M. C. Aime MCA

1464 (BRG); D-1 plot, solitary, 25 May 2001, M. C. Aime MCA 1634 (BRG); near base camp, solitary, 10 June 2001, M. C. Aime MCA 1863 (BRG).

DISCUSSION

Rick (1919, 1920, 1930, 1938, 1961) documented many agarics from South America in Brazil, but the evident misapplication of several European names to these taxa, non-extant type collections, and terse descriptions largely make application of Rick's concepts problematic (Singer 1953b). Because most of Rick's Brazilian collections are of uncertain status, only about 25 species of *Inocybe* are sufficiently well-documented from the neotropics to date. This figure is a remarkably small percentage of taxa (7–10%) that occur worldwide as extrapolated from Kuyper (1986). Of the 25 neotropical species, most are described from the Lesser Antilles, primarily in degraded xerophytic forests (Pegler 1983), or under *Quercus* at high to low elevations from Costa Rica to Colombia (Singer 1962, 1963, Singer *et al.* 1983). Nishida (1989) comments on some of the problems encountered historically to document fleshy fungi from the tropics.

It is noteworthy that of the higher infrageneric taxa in subgen. *Inocybe* (Kühner & Romagnesi 1953, Singer 1986), all four Guyanese species documented here share affinities with sect. *Inocybe* of Singer (1986), a group, however, that does not appear to be monophyletic (Matheny *et al.* 2002). Additionally, Singer (1983), reported *I. matrisdei*, sect. *Marginatae*, from periodically inundated rain forest in Bolivia, although host associates were not specified. *I. matrisdei* shares similarities with north and south temperate species that possess an entirely pruinose stipe with a marginate basal bulb. In any event, the phylogeny of the four Guyanese species is currently under study.

Both Guzmán (1982) and Pegler (1983) have described single species from sect. *Rimosae* in the neotropics. *I. tropicalis* is recorded from a tropical rain forest (host not specified) on the Yucatan Peninsula of Mexico, whereas *I. ingae* is described in association with the arborescent legume *Inga* (*Mimosaceae*) on Martinique, in the Lesser Antilles. At least six species of sect. *Rimosae* are recorded from the neotropics, several in association with *Quercus*. In contrast, no members of subg. *Mallocybe* or sect. *Cervicolores* have yet to be reported from the neotropics, or from the *Nothofagus* zone of South America (Singer 1986). Cladistic analyses of *Inocybe* from Europe indicate that these two higher level taxa, *Mallocybe* and *Cervicolores*, are monophyletic groups basal to the remainder of *Inocybe* (Kuyper 1986). The basal positions of exemplar taxa from subgen. *Mallocybe* and sect. *Cervicolores* are also supported by phylogenetic analyses of DNA sequences (Matheny *et al.* 2002). Given these positions, one might hypothesize that the species of *Inocybe* that occur in the neotropics are of more recent descent, as is suggested by Kuyper (1986). Extraordinarily, only two

smooth-spored cortinate species of subgen. *Inocybe* (*sensu* Kuyper 1986), the most species-rich infrageneric taxon, have been documented in the neotropics (Dennis 1970, Singer *et al.* 1983).

Two previously described neotropical species of *Inocybe* have been reported in association with legumes (Pegler 1983, Singer *et al.* 1983), *I. ingae* and *I. amazoniensis*. *I. ingae* has the unusual reputation of association with *Inga*, however, Alexander (1989) noted the lack of evidence supporting *Inga* as an ectomycorrhizal associate. Furthermore, species of *Inga* recently have been found to form arbuscular mycorrhizas in French Guiana (Béreau *et al.* 1997) and Guyana (McGuire & Henkel, unpubl.). The report here of four newly described species associated with the confirmed ectomycorrhizal host genus, *Dicymbe*, should bring attention to the likelihood that neotropical *Caesalpinaceae* harbour additional inocyboid taxa. Five unclarified species of *Inocybe*, all with nodulose-spores, are recorded from southern Brazil by de Meijer (2001), but ectomycorrhizal hosts are not specified.

Results from paleotropical studies generally indicate the lack of cystidiate smooth-spored species as well. Heim (1968) recorded the nodulose-spored *I. scleroticola* from Gabon, but associated vegetation was not mentioned in either case. Buyck & Eyssartier (1999) mention several other species associated with tropical African vegetation, including two new species with nodulose spores and pleurocystidia, one of which occurs under *Uapaca* (*Phyllanthaceae*). Watling (2001), however, has documented a paleotropical member of subgen. *Mallocybe*, *I. aureophumosa*, in association with leguminous hosts. De Seynes (1897) described *I. erythroxa* (subgen. *Mallocybe*) from the former French Congo. Interestingly, *Mallocybe* species have yet to be recorded from the neotropics.

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