
First records of *Hygrophoraceae* from Panama including a new species of *Camarophyllus* and a new veiled species in *Hygrocybe* section *Firmae*

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Six species of *Hygrophoraceae* were collected on Barro Colorado Island, representing the first fully documented records for the family from Panama. A species with a pink pileus and stipe, a glutinous partial veil, and dimorphic spores and basidia, *Hygrocybe roseopallida* Lodge & Ovrebo sp. nov. is described in *H.* section *Firmae* from Panama, and a more strongly pigmented form is also reported from Costa Rica. Hyphae of the outer veil are connected to the appendiculate pileipellis margin while those of the inner veil emanate from the lamellar edge. Partial veils have not been previously reported in *Hygrocybe* s.s. (*i.e.*, excluding *Camarophyllus*). Additionally, four other species of *H.* section *Firmae* are newly reported here from Panama: *Hygrocybe batistae*, *H. hypohaemacta*, *H. chloochlora* and *H. cf. earlei*. The latter species differs from the type of *H. earlei* by having a white stipe and larger spore Q. Finally, we describe a second new species, *Camarophyllus panamensis* Lodge & Ovrebo sp. nov., which resembles *C. ferrugineoalbus* (Singer) Singer, but differs in having an orange stipe and much larger spores.

Keywords: *Agaricales*, *Basidiomycota*, Central America, fungal taxonomy, neotropical fungi

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Introduction

The *Hygrophoraceae* can form a common mycological component of tropical regions, as extensively documented in the Greater and Lesser Antilles (Dennis, 1953; Pegler and Fiard, 1978; Pegler, 1983; Lodge, 1999; Lodge and Pegler, 1990; Cantrell and Lodge, 2000, 2001, 2004; Courtecuisse and Fiard, 2004). In this paper, we report on six species in the family that were collected by the second author from seasonally wet forest on Barro Colorado Island (BCI), Panama (previous studies see Desjardin and Ovrebo, 2006; Ovrebo and Baroni, 2007). Five species, one of them proposed as a new species, have dimorphic spores and basidia, and thus belong to *H.* section *Firmae*, with one proposed as a new species. The new species, *Hygrocybe roseopallida*, has a

fibrillose-glutinous partial veil, which is the first report of this feature in the genus *Hygrocybe sensu stricto*, though glutinous veils are found in species of *Hygro-phorus* and *Camarophyllus*. Re-examination of *Hygrocybe hypohaemacta*, also in section *Firmae* and reported here for the first time from Panama, suggests it may also bear a glutinous veil. The sixth species represents a new species of *Camarophyllus*, *C. panamensis*. The collections reported here represent the first fully documented records of *Hygrophoraceae* in Panama. Color photographs are provided for two of the species, *Hygrocybe batistae* Singer and *H. roseopallida* (Figs 1-2). Future collecting in Panama at different elevations should reveal how common the family is throughout the country. Information on BCI can be found in Buyck and Ovrebo (2002).



Figs 1-2. Color photographs of *H. roseopallida* and *Hygrocybe batistae*. 1. *Hygrocybe roseopallida* (Ovrebo 4053), basidiomes. 2. *Hygrocybe batistae* (Ovrebo 3903), basidiomes and inset of veil in exicati. Bars = 10 mm.

Table 1. Sources of collections used for molecular analyses of nuclear ribosomal DNA sequences (ITS and partial LSU.)

<i>Hygrocybe</i> species	Section	Genbank No.	Source	Collection
<i>H. coccinea</i> (Schaeff.) P. Kumm.	<i>Coccineae</i>	EU435146	Denmark	Boertmann 2002/8
<i>H. chloochlora</i> Pegler & Fiard, var. "microspora", nom. prov., ined.	<i>Firmae</i>	EU435147	Belize	DJL, BZ-3042
<i>H. chlorophana</i> (Fr.) Wünsche	<i>Chlorophanae</i>	EU435148	Denmark	Boertmann 2002/9
<i>H. glutinipes</i> var. <i>rubra</i> Bon	<i>Chlorophanae</i>	EU435149	USA (NC)	DJL-TN-9 2005 = CFMR db NC-9
<i>H. hypohaemacta</i> (Corner) Pegler	<i>Firmae</i>	EU435150	Belize	DJL, BZ-1903
<i>H. occidentalis</i> var. <i>scarletina</i> Pegler & Fiard	<i>Firmae</i>	EU435151	Puerto Rico	Cancerel, PR-6493
<i>H. roseopallida</i> Lodge & Ovrebo	<i>Firmae</i>	EU435152	Panama	Ovrebo 4073

Materials and Methods

Macroscopic observations on fresh basidiomes were made by CLO. Sections were cut by hand and mounted in 3% KOH or Melzer's reagent. Size ranges of spores for the new species were based on ocular micrometer measurements of 20 spores. Placement of *H. roseopallida* within *Hygrocybe* was explored using analyses of nuclear ribosomal DNA sequences. DNA was extracted from dried specimens using a modified CTAB extraction method and cleaned with glass milk. The ITS and an adjacent 322 bp fragment of the large subunit (LSU) of *H. roseopallida* were sequenced by J.-M. Moncalvo, an ITS sequence for *H. glutinipes* var. *rubra* from the Great Smoky Mountain National Park was obtained by DJL and K. Hughes, and the remaining reference sequences from *H. chloochlora*, *H. coccinea*, *H. hypohaemacta* and *H. occidentalis* var. *scarletina* (ITS plus partial LSU) were obtained by DJL (Table 1). Sequences were deposited in Genbank (Table 1). Sequences were edited with Sequencher 4.5 and then aligned using Clustal X followed by manual alignment in MacClade. Only 348 alignable bp surrounding four conserved motifs in the ITS were used. Although single bp deletions were recorded, most were excluded in analyses as they occurred in highly variable, parsimony-uninformative regions. PAUP was used to obtain Neighbor Joining trees and perform phylogenetic analyses. A heuristic search using Maximum Likelihood settings was used with TBR branch swapping (73 trees generated) followed by bootstrap analysis (1000 replicates) using the same parameters, first unrooted and then rooted with *H. coccinea*.

Results

Camarophyllus panamensis Lodge & Ovrebo, **sp. nov.** (Figs 3-8)

Mycobank: 511071

Etymology: for country of Panama.

Camarophyllo ferrugineoalbo similis, sed pileo colore aurantiaco magis vivido, *stipite* aurantiaco-rubro (non albo), *quoad* formam fusiformi (non cylindrico atque ad apicem sursum patenti), *basidiosporis* majoribus, 9-10.6 × 6.2-8 (non 4.2-6.3 × 3.2-5 μm) differt.

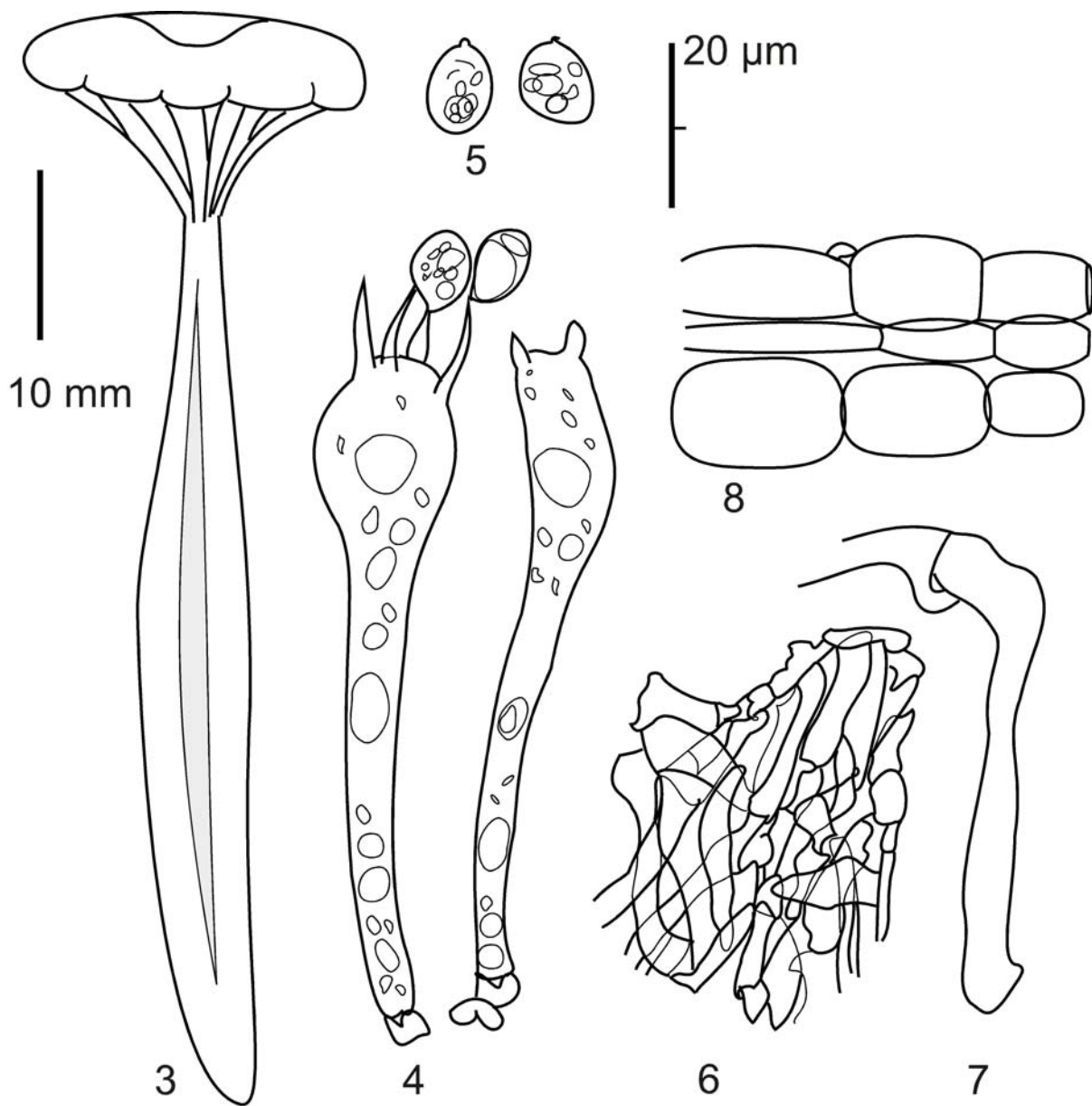
Holotypus: Ovrebo 4102, Insula Barro Colorado, Panama (PMA).

Pileus 20 mm diam, slightly depressed at center, margin inrolled and scalloped, sulcate-striate, orange, opaque, not viscid. *Lamellae* white, decurrent, thick, forked, distant. *Stipe* 50 × 6 mm in dried specimen, orange-red in middle, yellow at apex and base, flattened, subfusiform, dry.

Spores 9-10.6 × 6.2-8 μm (\bar{x} = 9.9 × 7.2 μm, Q = 1.23-1.54, mean Q = 1.4), broadly ellipsoid. *Basidia* 63-76 × 10-15 μm, 2- or 4-sterigmate. *Hymenial cystidia* absent. *Lamellar edge* fertile or sterile (basidioles). *Hymenophoral trama* of highly interwoven hyphae of 3-7 μm diam., with a central strand of parallel or subparallel hyphae of 4.5-7 μm diam. *Pileipellis* with chains of short broad hyphae 12-22 × 4-11 μm. Hypodermium with subglobose or broadly ellipsoid elements 13-20 × 10-15 μm. *Stipitipellis* composed of hyphae 2-3 μm wide, appressed, slightly interwoven, smooth, thin-walled, hyaline. *Clamp connections* found throughout, often of the medallion type.

Habit, habitat and distribution: solitary, on soil. Known only from the type locality.

Specimen examined: PANAMA: Province of Panama, Gatun Lake, Barro Colorado Island, Wheeler Trail, 15 August 2001, Ovrebo 4102 (PMA).



Figs 3-8. *Camarophyllus panamensis* (Ovrebo 4102, from **holotype**). 3. Basidiome. 4. Basidia. 5. Basidiospores. 6. Lamellar trama. 7. Lamellar trama hypha near central strand. 8. Pileipellis.

Commentary: This species resembles *Camarophyllus ferrugineoalbus* (Singer) Singer, (an earlier name for *Camarophyllus umbrinus* var. *clarofulvus* Lodge & Pegler) in having an orange pileus and white decurrent lamellae, but it is readily distinguished by having a reddish yellow instead of a white stipe, brighter pigments in the pileus, a fusiform stipe and much larger spores ($9\text{-}10.6 \times 6.2\text{-}8$ vs. $4.2\text{-}6.3 \times 3.2\text{-}5$ μm). The bright pigments of the basidiome are more typical of the genus *Hygrocybe*, but the highly interwoven trama (Fig. 6) that gives rise to the opaque appearance, and the long narrow basidia (Fig. 4) clearly place *C.*

panamensis in *Camarophyllus* (the DNA analysis has not yet been done). The structure of the pileipellis (Fig. 8) and the presence of a medial strand of nearly parallel hyphae in the lamellar context (Fig. 7) are similar to those found in *C. ferrugineoalbus* and *C. umbrinus*. *Camarophyllus panamensis* has a more gracile aspect than *C. ferrugineoalbus*, with a pileus diameter to stipe ratio near 1:2 versus 1:1 for *C. ferrugineoalbus*. Although some specimens of *Cuphophyllus neopratenis* Courtec. & Fiard (2004) are gracile with pileus colors similar to those of the new species, *C. neopratenis* differs from *C. panamensis* in lacking chains of short

broad hyphal elements in the pileipellis, the presence of encrustations on the pileipellis hyphae, and smaller spores ($5\text{-}7 \times 4.5\text{-}5.5 \mu\text{m}$). While only a single basidiome of *C. panamensis* was found, the species is so distinct that it should be easily recognized among subsequent collections.

Hygrocybe batistae Singer, Atas do Instituto de Micologia 2: 20. (1965). (Fig. 2)

Habit, habitat and distribution: subcaespitose, on soil in wet and seasonally wet forests. Reported from Brazil, Colombia, Puerto Rico, and Panama; probably widespread.

Specimens examined: PANAMA: Province of Panama, Gatun Lake, Barro Colorado Island, Wheeler Trail, 11 August 1999, Ovrebo 3733; 26 May, 2000, Ovrebo 3903 (PMA, CSU).

Commentary: *Hygrocybe batistae* is characterized macroscopically by the non-perforate, often rugulose to rugose, reddish orange or yellow pileus, white lamellae and caespitose fruiting habit; microscopically by the coralloid hyphae in the pileipellis and dimorphic basidia and spores. It was originally described from Brazil and is also known from Colombia and Puerto Rico (Lodge and Pegler, 1990; Cantrell and Lodge, 2001).

Hygrocybe chloochlora Pegler & Fiard, Kew Bulletin 32: 303. (1978).

Habit, habitat and distribution: Solitary, on soil. Apparently widespread in the Caribbean Basin, including northern South America.

Specimen examined: PANAMA: Province of Panama, Gatun Lake, Barro Colorado Island, Lake Trail, 28 May 2000, Ovrebo 3919 (PMA).

Commentary: This species is distinguished by the smooth green to yellowish green pileus and stipe, pale green to yellowish green lamellae, and the dimorphic spores and basidia that place it in *H.* section *Firmae*. It is the only all-green species in this section. This taxon was originally described from Martinique (Pegler, 1983) and has also been reported from Guadeloupe and Puerto Rico (Lodge and Pegler, 1990; Cantrell and Lodge, 2001) in the Caribbean, and Veracruz in southeastern Mexico (Montoya *et al.*, 2005). The sizes of the basidiomes and macro- and micro-spores of collections from Panama and the Antilles (Lodge and Pegler, 1990) were similar. Additional records on the internet from northern South America include a collection from Cauca,

Colombia (A.E. Franco Molano 417, 6 May 1990, NY 34684), and an annotated photograph from Saül, French Guyana.

Hygrocybe cf. earlei (Murrill) Pegler, Kew Bulletin 42(4): 873. (1987). (Figs 9-24)

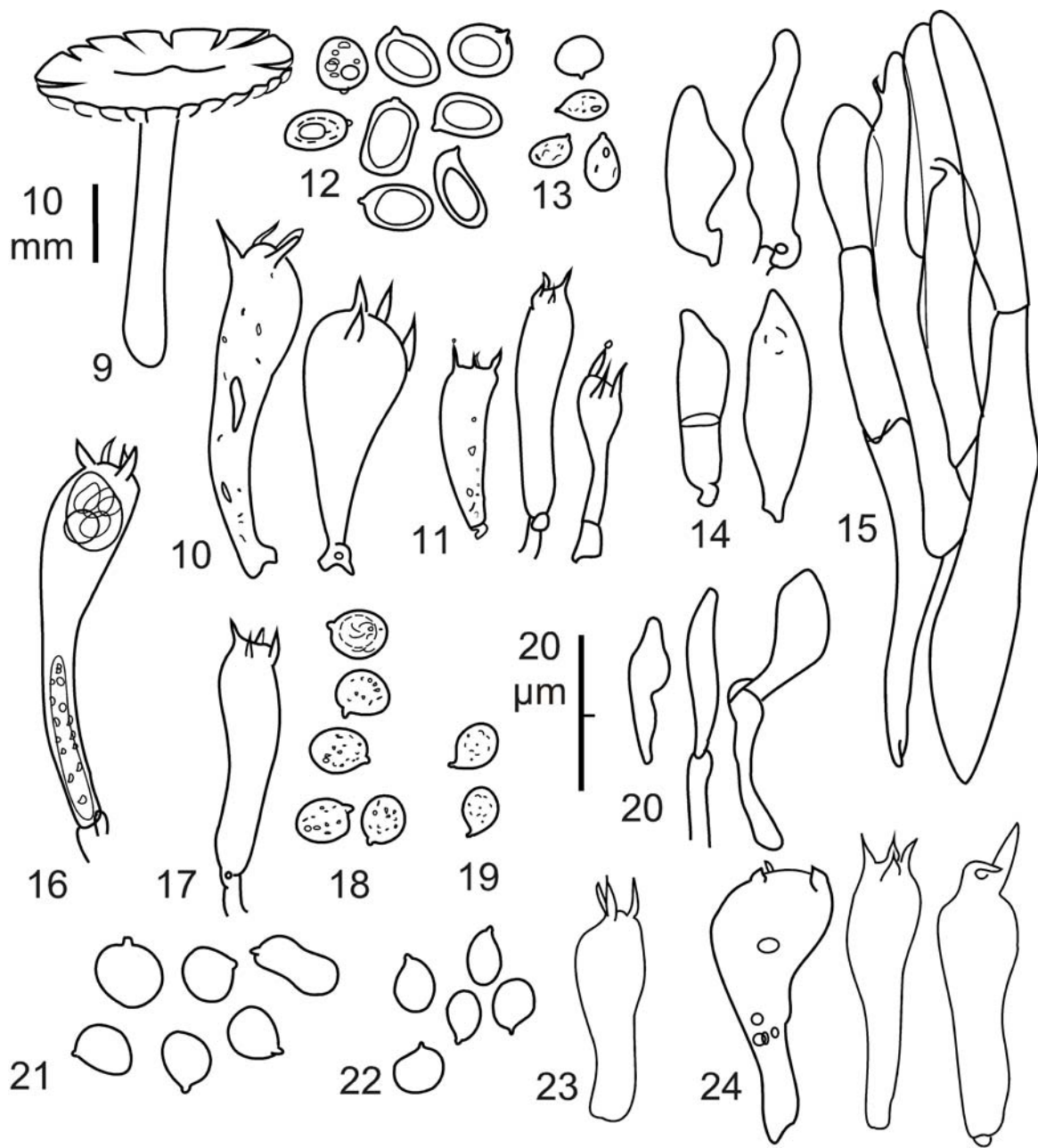
Pileus 30 mm diam, umbonate with an uplifted margin, pale reddish yellow, orange, or orange-yellow; surface smooth, shiny. *Lamellae* pale yellow, with a white edge, adnexed, nearly free. *Stipe* $40 \times 4\text{-}5$ mm, flared slightly at apex and base, pure white, smooth, silky.

Spores vaguely dimorphic, macrospores broadly ellipsoid, few subglobose or ellipsoid and slightly constricted, $7\text{-}9\text{-}(10) \times (4.5\text{-})5\text{-}7 \mu\text{m}$, [$\bar{x} = 7.6 \times 5.6 \mu\text{m}$, $Q = 1.1\text{-}1.6\text{-}(1.9)$, mean $Q = 1.46$]; microspores broadly ellipsoid, $5.8\text{-}7 \times (3.2\text{-})4\text{-}5 \mu\text{m}$ ($\bar{x} = 6.4 \times 4.4 \mu\text{m}$, $Q = 1.2\text{-}2.1$, mean $Q = 1.5$). *Basidia* dimorphic, 4-sterigmate: macrobasidia $24\text{-}46 \times 6.8\text{-}10\text{-}(15) \mu\text{m}$; microbasidia $22\text{-}30 \times 5\text{-}6.2\text{-}(7) \mu\text{m}$. *Hymenial cystidia* absent; lamellar edge fertile but basidia mixed with sterile elements (hyphal end-cell type) with medallion basal clamp connections, rarely with secondary septum. *Hymenophoral trama* of parallel hyphae $23\text{-}105 \times 6\text{-}15 \mu\text{m}$, septa oblique on tapered ends or right-angled on non-constricted septa. *Pileipellis* with an intermittent thin gelatinous coating over hyphae $(2\text{-})6\text{-}10\text{-}(12) \mu\text{m}$ diam. *Clamp connections* found throughout, often of the medallion type.

Habit, habitat and distribution: Solitary, on soil. A rare fungus known previously only from Cuba and Trinidad.

Specimens examined: CUBA: Santiago de las Vegas, Herradura, 16 June 1907, F.S. Earle 562 (TYPE, K). PANAMA: Province of Panama, Gatun Lake, Barro Colorado Island, near intersection of Miller and Barbour-Lathrop trails, 13 August 1997, Ovrebo 3623 (PMA). TRINIDAD: Sangre Grande, soil under *Theobroma*. R.W.G. Dennis 161 (K).

Commentary: *Hygrocybe earlei* appears to be a cryptic member of *H.* section *Firmae* in which dimorphism of the basidia and spores is subtle. *Hygrocybe earlei* was described from Cuba by Murrill, and has also been reported from Trinidad by Dennis (1953). *Hygrocybe earlei* resembles two other species in this complex, *H. laboyi* S.A. Cantrell & Lodge and especially *H. flavocampanulata* S.A. Cantrell & Lodge, but differs from both in having a pale reddish yellow or orange-yellow rather than



Figs 9-24. *Hygrocybe earlei*. **9-15.** *Hygrocybe* cf. *earlei* (Ovrebø 3623). **9.** Basidiome. **10.** Macrobasidia. **11.** Microbasidia. **12.** Macrospores. **13.** Microspores. **14.** Cheilocystidia. **15.** Lamellar trama. **16-20.** *Hygrocybe earlei* (Earle 562 from Cuba, Holotype). **16.** Macrobasidium. **17.** Microbasidium. **18.** Macrospores. **19.** Microspores. **20.** Cheilocystidia. **21-24.** *Hygrocybe earlei* (R.W.G. Dennis 161 from Trinidad). **21.** Macrospores. **22.** Microspores. **23.** Microbasidium. **24.** Macrobasidia.

spectrum yellow pileus, and shorter macrospores [6.8-9(-11) vs 11.2-16.8 μm]. The collection from Panama is atypical, and differs from the type in having a white rather than a cream or pale yellow stipe and macrospores that are narrower and slightly longer [7-9(-10) × 5-6.2(-7) vs 6.8-8.4 × 5.8-7.2] with a larger *Q* (1.1-1.92 vs 1-1.38; mean 1.46 vs. 1.14). Macrospores in Dennis' collection 161 from Trinidad

(Fig. 21) were intermediate between the type from Cuba and the Panama collection [Figs 18 and 12, respectively; RWG Dennis 161 from Trinidad macrospores 6.8-9.5(-11) × 5.6-5.7(-7), *Q* = 1.01-1.66, mean *Q* = 1.23]. Hesler and Smith (1963) indicated that both of Dennis' collections from Trinidad (*i.e.*, RWG Dennis 50 and 161) were better referred to *H. subflavida* (Murrill) Pegler. The type of *H.*

subflavida however, has broadly adnate lamellae with a decurrent tooth rather than adnexed to nearly free lamellae. Furthermore, the annotations by Hesler (1 July 1960) of RWG Dennis 161 at Kew indicated the spores were $9\text{-}14 \times 7\text{-}9$ rather than $5\text{-}9.5 \times 4.4\text{-}7$ μm in measurements by DJL. The spore dimensions in Hesler's annotation match those for RWG Dennis 50 that was mounted on the same page and was originally determined as *H. earlei*, (Dennis, 1953), but is referable instead to *Hygrocybe konradii* var. *antillana* Lodge & S. A. Cantrell (Cantrell and Lodge, 2000). We therefore surmise that Hesler accidentally annotated RWG Dennis 50 twice, labeling one set of notes as belonging to RWG Dennis 161.

Hygrocybe hypohaemacta (Corner) Pegler, Kew Bulletin 32: 299. (1978).

Habit, habitat and distribution: Solitary, on soil in wet and seasonally dry forests. In Singapore and Korea in SE Asia; widespread in the neotropics in the Caribbean and northern South America.

Specimen examined: PANAMA: Province of Panama, Gatun Lake, Barro Colorado Island, Balboa Trail, 14 August 1997, Ovrebo 3637 (PMA).

Commentary: *Hygrocybe hypohaemacta* is characterized by the glutinous pileus and stipe, scarlet pileus, white, free lamellae and dimorphic basidia and spores with globose or subglobose macrospores. It was originally described from Singapore (Corner, 1936) and has been reported in the neotropics from Puerto Rico (Lodge and Pegler, 1990), Jamaica and the US Virgin Islands (Cantrell and Lodge, 2001) in the Greater Antilles, Martinique in the Lesser Antilles (Pegler and Fiard, 1978; Pegler 1983), and Colombia (Franco-Molano and Uribe-Calle, 2000), French Guyana (Courtecuisse, 1989) and Venezuela (Dennis, 1961) in northern South America. Systematists have so far been unable to distinguish disjunct populations of *H. hypohaemacta* in the neotropics and SE Asia based on morphology. *Hygrocybe hypohaemacta* var. *boninensis* (Hongo) Hongo from Japan differs substantially from the original concept and should probably be considered as a separate species. Molecular comparisons with sequences from SE Asian material are necessary for resolving both of these issues. Some recent collections from Puerto Rico (Lodge, unpublished) appear to have a glutinous partial veil,

originating as a break between the glutinous layers of the pileipellis and stiptipellis. Courtecuisse (1989) noted the appendiculate pileus margin (denticulée festonnée) in *H. hypohaemacta* from French Guyana. The appendiculate gelatinous margin and possible points of former attachment on the glutinous layer on the stipe may be seen in several specimens in a photograph from French Guyana posted on a web site (<http://jlcheype.free.fr/classification/Guyane/Guyane.htm>).

Hygrocybe roseopallida Lodge & Ovrebo, **sp. nov.** (Figs 1, 25-33)

Mycobank: 511072

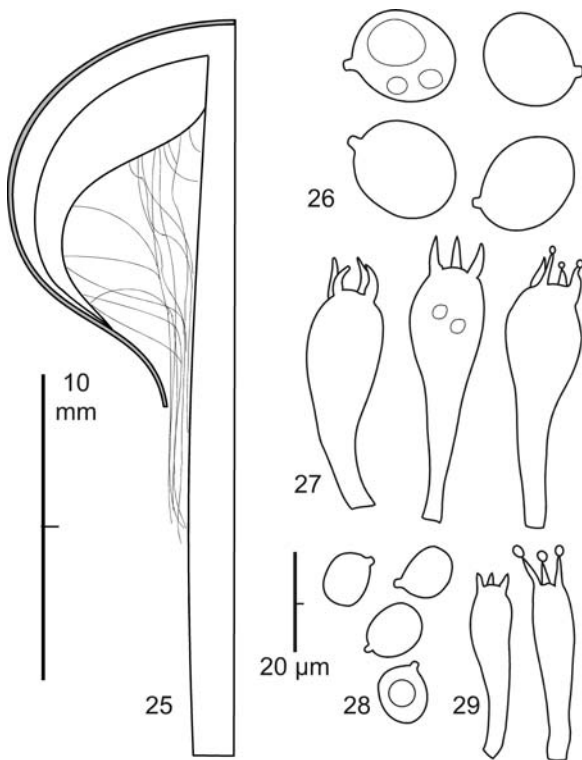
Etymology: *roseus* (L.) – rose-colored; *pallidus* (Latin) – pale colored; referring to pileal color.

Species haec in combinatione unica pileo roseolo, volva partiali praesenti, basidiis dimorphis, basidiosporis subglobois vel late ellipsoideis procreantibus, macrosporis $1\text{-}12 \times 8\text{-}9$ μm , microsporis $6\text{-}7 \times 5\text{-}5.5$ μm imprimis distinguitur.

Holotypus: Ovrebo 4053, Insula Barro Colorado, Panama (PMA).

Pileus 15-30 mm wide; buttons hemispheric, expanding to plane, often slightly depressed and occasionally perforated at the center; surface dull and waxy-greasy feeling when dry, apparently viscid when wet, often with debris clinging, glabrous, faintly translucent-striate at very edge, dull light pink overall when young, at maturity light pink with white margin, slightly hygrophanous and drying lighter, not discoloring; context 1-2 mm thick, translucent dull pink, young specimens with watery context when cut; odor and taste nondescript. *Lamellae* 1-3 mm wide, adnexed, white, not discoloring, crowded; edge often uneven or eroded; lamellulae numerous but not in distinct tiers. *Stipe* 20-70 \times 2-6 mm, equal or tapered in lower third to a rounded base, terete or slightly flattened, occasionally with a longitudinal groove, glabrous, slightly greasy feeling, probably viscid when wet, translucent white, occasionally light pink at the apex, hollow. *Partial veil* fibrillose-membranous, probably also viscid or glutinous when fresh, leaving an annulus composed of a low ridge of remnants near stipe apex, white.

Spores dimorphic; macrospores $10\text{-}12 \times 8\text{-}9$ μm ($\bar{x} = 10.7 \times 8.7$ μm , $Q = 1.17\text{-}1.28$, mean $Q = 1.23$), subglobose or broadly ellipsoidal in profile and face view; microspores $6\text{-}7 \times 5\text{-}5.5$ μm ($\bar{x} = 6.5 \times 5.2$ μm , $Q = 1.09\text{-}1.4$, mean



Figs 25-29. *Hygrocybe roseopallida* (Ovrebø 4053, from holotype). **25.** Basidiome longitudinal section. **26.** Macrospores. **27.** Macrobasidia. **28.** Microspores. **29.** Microbasidia.

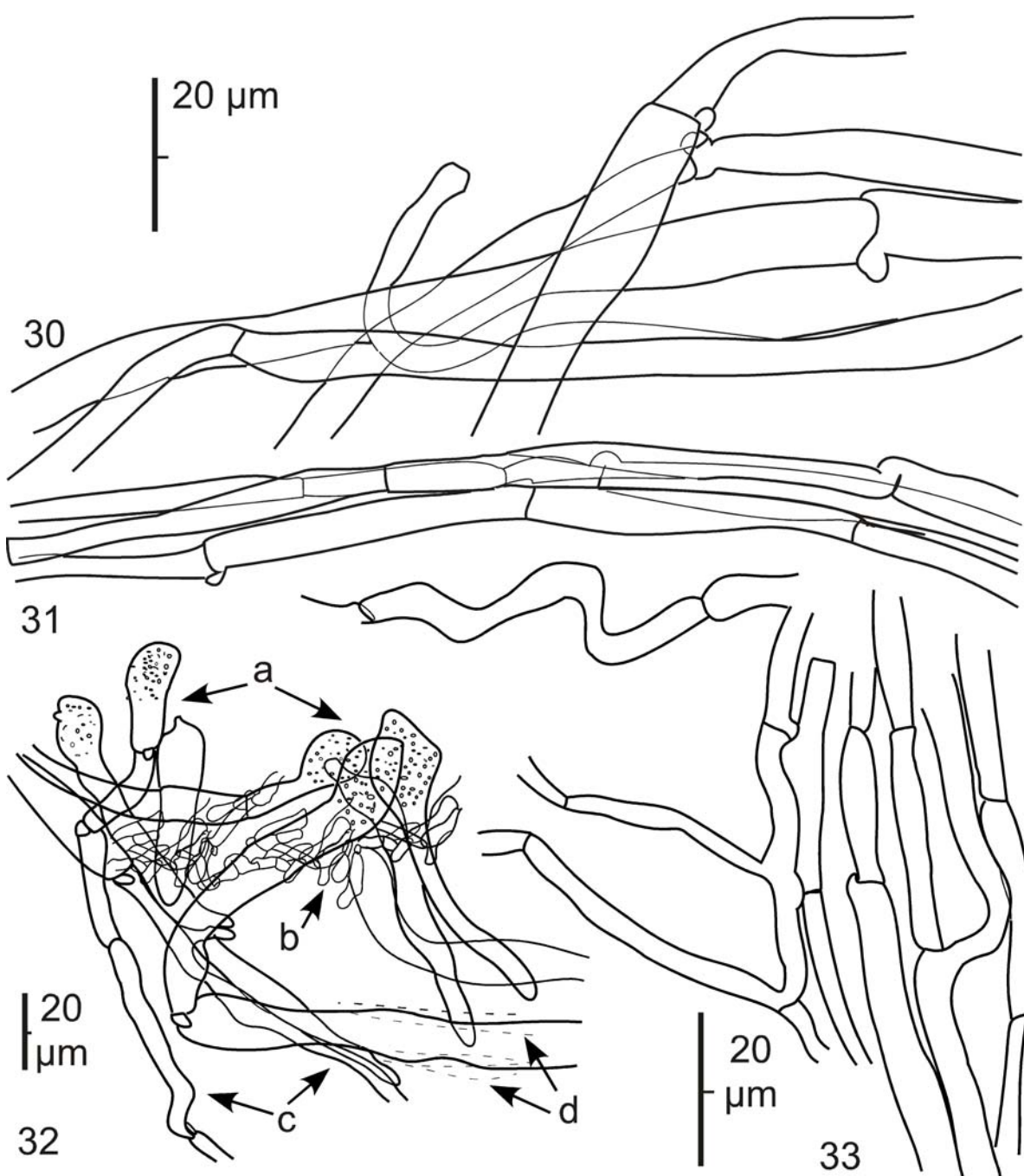
$Q = 1.26$), elliptic, broadly elliptic or subglobose in profile and face view, smooth, thin-walled, hyaline, uni- or pluriguttulate, inamyloid, acyanophilic. *Basidia* dimorphic: macrobasidia $41-48 \times 12-17 \mu\text{m}$, 4-sterigmate, clavate, hyaline, guttulate; microbasidia $31-38 \times 7-8.5 \mu\text{m}$ 4-sterigmate, clavate, hyaline, guttulate. *Hymenial cystidia* absent. *Lamellar trama* not gelatinized, composed of long parallel hyphae with tapered ends, cells $(32-130-260 \times 4-19(-22) \mu\text{m})$, mixed with some disorganized narrow hyphae ($2-3 \mu\text{m}$); hyphae hyaline, inamyloid. *Subhymenium* of interwoven hyphae $3-4 \mu\text{m}$ wide. *Pileipellis* an ixocutis $160-170 \mu\text{m}$ deep, of parallel or interwoven hyphae $4-7 \mu\text{m}$ wide, cylindrical, often wavy, smooth, hyaline, thin-walled, with a thick gelatinous coating. *Hyphae of pileus trama* up to $17 \mu\text{m}$ wide, hyaline. *Stipitipellis* $10-15 \mu\text{m}$ thick, composed of a thin ixocutis $5-15 \mu\text{m}$ deep, of cylindrical, hyaline hyphae that are $2-7 \mu\text{m}$ wide, appressed and parallel or occasionally interwoven (from veil?); caulocystidia not seen. *Hyphae of stipe trama* $3-15 \mu\text{m}$ wide, cylindrical or swollen, hyaline,

occasionally faintly incrustated. *Hyphae of partial veil* $4-12 \mu\text{m}$ wide, outer ones thickly coated with gel, cylindrical, hyaline, smooth, thin-walled, arranged parallel to one another or in places twisted and interwoven; inner veil elements arising from context hyphae near the lamellar edge and having an expanded base and conspicuous vacuoles (Figs 25, 32). *Clamp connections* large, of the medallion type, abundant throughout.

Habit, habitat and distribution: scattered, gregarious, occasionally subcaespitose, on soil. Known in Central America from Costa Rica and Panama.

Specimens examined: COSTA RICA: Osa Peninsula, Puntarenas, 24 August 1936, coll. R. Sándola, Dodge & Goerger (FH); *ibid.*, 27 August 1936, coll. R. Sándola 10612, Dodge & Goerger (FH); same location, 1 Sept 1936, coll. R. Sándola, Dodge & Goerger (FH). PANAMA: Province of Panama, Gatun Lake, Barro Colorado Island, Miller Trail, 28 May 2000, Ovrebø 3912 (PMA); Fausto Trail, 8 August 2001, Ovrebø 4053 (Holotype, PMA: Isotype, NY); same location, 11 August 2001, Ovrebø 4073 (PMA); same location, 15 August 2001, Ovrebø 4101 (PMA); Fairchild Trail, 14 August 2001, Ovrebø 4087 (PMA); Donato Trail, 16 August 2001, Ovrebø 4105 (PMA, CSU).

Commentary: The presence of dimorphic basidiospores and basidia and the molecular analyses are consistent with the placement of *H. roseopallida* in *Hygrocybe* section *Firmae*. The glutinous pileus and subglobose basidiospores suggest an affinity of *H. roseopallida* with *H. hypohaemacta*, though it differs from the latter in having a pink rather than scarlet pileus and an obvious annulus. In analyses of all seven taxa in Table 1, *H. roseopallida* and *H. hypohaemacta* were placed together in the Neighbor Joining trees for alignable parts of ITS sequences and for combined ITS and LSU sequences (Figs 34 and 35, respectively). Unrooted trees and trees rooted with *H. coccinea* had the same topology, and only a single tree was retained in each analysis. Phylogenetic analysis of the combined ITS and LSU fragment (102 parsimony informative characters among 677 bp) produced a single tree that had 52% bootstrap support for the clade representing Section *Firmae*, which was comprised of two clades, one with *H. occidentalis* and *H. chloochlora* (100% bootstrap support), and the other with *H. roseopallida* and *H. hypohaemacta* (76% bootstrap support). The molecular analyses are therefore consistent



Figs 30-33. *Hygrocybe roseopallida* sections, all in their natural orientation. **30.** Ixocutis of pileipellis. **31.** Pileipellis. **32.** Lamellar edge showing partial veil elements emanating from the edge: a. Expanded and vacuolated basal cells of the fibrous veil elements originating in the lamellar context. b. Hymenium overlying the velar hyphae at the lamellar edge. c. Multiseptate hyphae of fibrous veil elements. d. Gelatinized veil elements, whose origin could not be traced. **33.** Veil elements from annulus. (Fig. 30 from Ovrebo 3912; Figs 31-33 from Ovrebo 4053).

with a monophyletic Section *Firmae* that includes *H. roseopallida*.

Hygrocybe roseopallida is unique to *H.* section *Firmae* in having a pink pileus and in possessing an obvious annulus, although a re-evaluation of *H. hypohaemacta* suggests it may also possess a glutinous partial veil (see

comments under *H. hypohaemacta*). The combination of pink basidiomes with a glutinous annulus and subglobose basidiospores is new for the section. Previously described species of Section *Firmae* are red, orange, yellow, green, purple, brown or gray in color, and none are pink. Material collected by R. Sándola in the

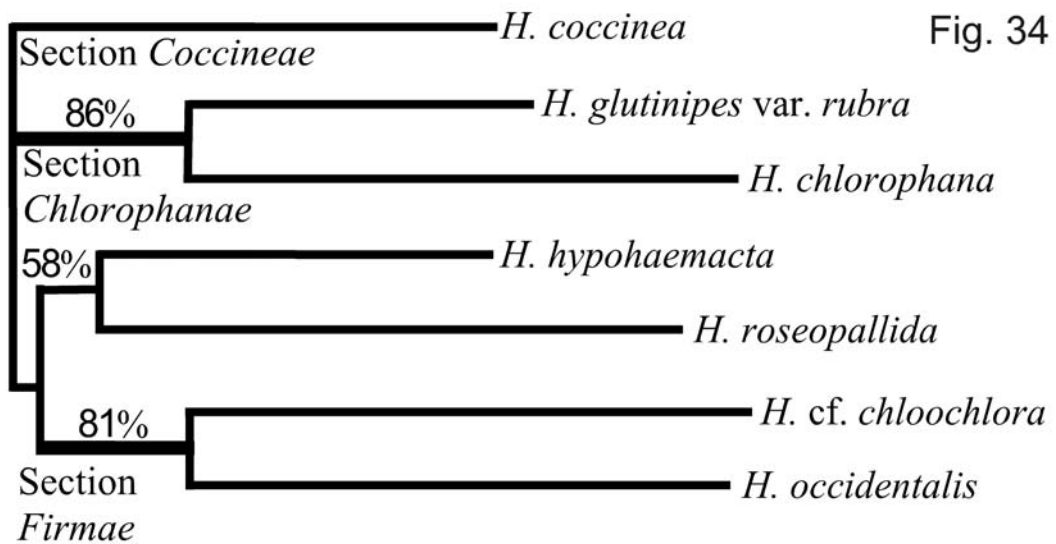


Fig. 34

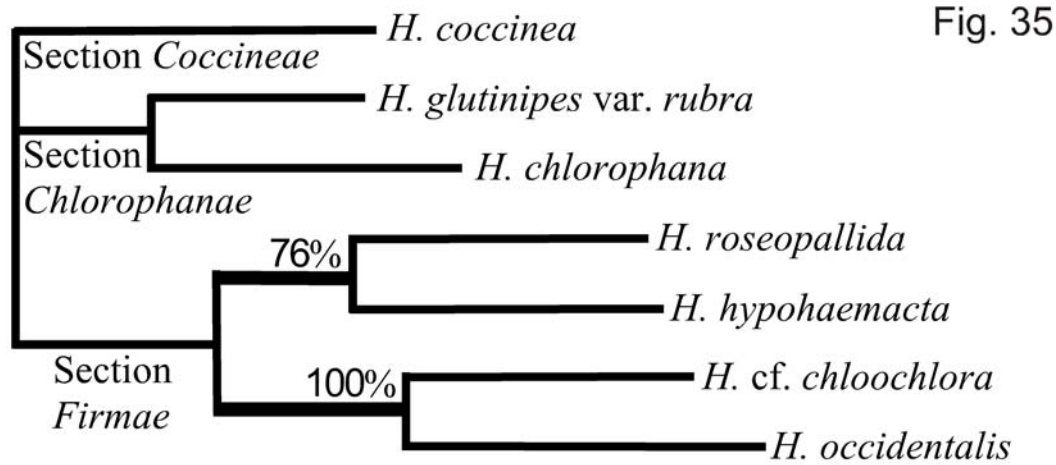


Fig. 35

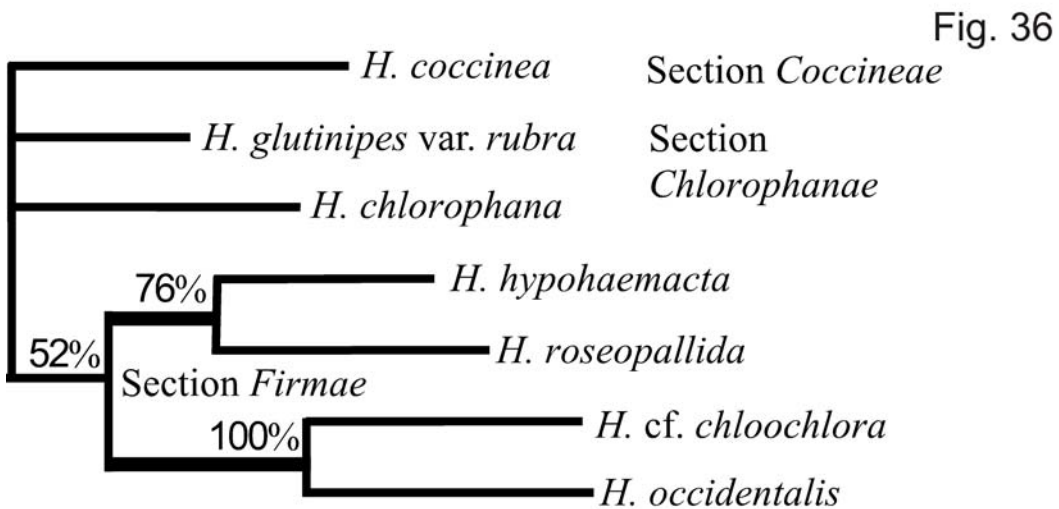


Fig. 36

Figs 34-36. Trees showing placement of *Hygrocybe roseopallida* based on nrDNA analyses (bootstrap values are shown at the nodes; branches with values above 80% bolded). **34.** Neighbor Joining tree obtained from ITS sequences. **35.** Consensus tree generated by Branch & Bound search of ITS sequences. **36.** Phylogram of the most parsimonious tree from the Branch & Bound analysis based on sequences of the ITS and a partial LSU fragment.

Osa Peninsula of Costa Rica and deposited at the Farlow Herbarium by Dodge and Goerger resembles collections from Panama in all respects except for stronger pigmentation, with colors near the center of the pileus described as Corinthian Red to Corinthian Pink or Coral Pink, and fading to white at the margin.

The origin of the veil material is interesting. The inner velar hyphae that extend from the lamellar edge are perhaps analogous to the hyphae that separate the lamellae from the partial veil in some species of *Amanita*. Veil hyphae originated in the lamellar context (Fig. 32a), parting the hymenium at the lamellar edge (Fig. 32b) and protruded beyond the edge (Fig. 32c). Similar veil hyphae were found in the collection of *H. hypohaemacta* that was sequenced (Table 1) but these differed from corresponding hyphae of *H. roseopallida* in lacking a guttulate expanded base, and consisting of single cells rather than chains of cells. The origin of the outer, gelatinous veil material in *H. roseopallida* is apparently an extension of the thick, gelatinous ixocutis of the pileipellis (Fig. 25), and might represent a portion of a peronate universal veil. Gelatinized hyphae were found in a section through the veil (Fig. 32d) but their origin could not be traced. While the original notes on the collections from Panama did not indicate they were viscid, the presence of a thick gelatinized ixocutis of the pileipellis and the thin ixocutis of the stipitipellis indicates they may have been viscid at some time; notes on the Costa Rican collections indicated they were viscid.

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References

- Buyck, B. and Ovrebo, C.L. (2002). New and interesting species of *Russula* species from Panama. *Mycologia* 94: 888-901.
- Cantrell, S.A. and Lodge, D.J. (2000). *Hygrophoraceae* of the Greater Antilles: *Hygrocybe* subgen. *Hygrocybe*. *Mycological Research* 104: 873-878.
- Cantrell, S.A. and Lodge, D.J. (2001). *Hygrophoraceae* (*Agaricales*) of the Greater Antilles: *Hygrocybe* subgenus *Pseudohygrocybe* section *Firmae*. *Mycological Research* 105: 215-224.
- Cantrell, S.A. and Lodge, D.J. (2004). *Hygrophoraceae* of the Greater Antilles: Section *Coccineae*. *Mycological Research* 108: 1301-1214.
- Corner, E.J.H. (1936). *Hygrophorus* with dimorphous basidiospores. *Transactions of the British Mycological Society* 20: 157-184.
- Courtecuisse, R. (1989). Eléments pour un inventaire mycologique des environs du Sau Pararé (Arataye) et de l'inselberg des Nourages (Guyane Française). I. Introduction. II. *Hygrophoraceae*. *Cryptogamie Mycologie*. 10: 181-216.
- Courtecuisse, R. and Fiard, J.P. (2004). *Cuphophyllus neoprattensis* un nouvel *Hygrophore* des Antilles. *Bulletin de la Societe Mycologique de France* 120: 441-462.
- Dennis, R.W.G. (1953). Some West Indian collections referred to *Hygrophorus* Fr. *Kew Bulletin* 2: 253-267.
- Dennis, R.W.G. (1961). Fungi venezuelani: IV *Agaricales*. *Kew Bulletin* 15: 67-156.

- Franco-Molano, A.E. and Uribe-Calle, E. (2000). Hongos *Agaricales* y *Boletales* de Colombia. *Biota Colombiana* 1: 25-43.
- Hesler, L.R. and Smith, A.H. (1963). *North American Species of Hygrophorus*. University of Tennessee Press, Knoxville.
- Lodge, D.J. (1999). *Cuphophyllus pegleri* sp. nov. (*Hygrophoraceae*) from the Lesser Antilles. *Kew Bulletin* 54: 805-810.
- Lodge, D.J. and Pegler, D.N. (1990). *Hygrophoraceae* of the Luquillo Mountains of Puerto Rico. *Mycological Research* 94: 443-456.
- Montoya, L., Bandala, V.M. and Jarvio, D. (2005). New records of *Hygrocybe* from the Gulf of Mexico area. *Mycotaxon* 91: 471-480.
- Pegler, D.N. (1983). 668 pp. *Agaric Flora of the Lesser Antilles*. Royal Botanic Gardens, Kew, *Kew Bulletin Additional Series IX*, HMS, London.
- Pegler, D.N. and Fiard, J.P. (1978). *Hygrocybe* sect. *Firmae* (*Agaricales*) in tropical America. *Kew Bulletin* 32: 297-322