Mycologia, 107(6), 2015, pp. 1205–1220. DOI: 10.3852/14-312

Phylogeny of *Pluteus* section *Celluloderma* including eight new species from Brazil

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Abstract: A general phylogeny of *Pluteus* section *Celluloderma* based on nuc rITS1-5.8-ITS2 (ITS) barcode sequences is presented with description of eight new species from Brazil supported by morphological and molecular data: *P. brunneocrinitus*, *P. cebolinhae, P. crinitus*, *P. halonatus*, *P. hispidulopsis*, *P. karstedtiae*, *P. necopinatus* and *P. paucicystidiatus*.

Key words: Agaricales, biodiversity, Pluteaceae, rDNA ITS

Introduction

The historical subdivision of *Pluteus* into three sections (*Pluteus*, *Celluloderma* Fayod, *Hispidoderma* Fayod) has been supported by molecular phylogenetic studies (Menolli et al. 2010; Justo et al. 2011a, b) with some rearrangements. *Pluteus* sect. *Celluloderma*, as recognized by Singer (1959, 1986), includes species with non-metuloid pleurocystidia and pileipellis composed of an epitheliod hymeniform layer interrupted or not by elongate cystidioid bodies. Singer (1956, 1959, 1986) further subdivided *Pluteus* sect. *Celluloderma* into two subsections: *Mixtini* Singer, characterized by the presence of elongated elements in the pileipellis, and *Eucellulodermini* Singer, characterized by the lack of these elements.

Vellinga and Schreurs (1985) proposed a variation on this classification system subdividing *Pluteus* sect. *Celluloderma* into three subsections, *Mixtini*, *Eucelullodermini* and *Hispidodermini* (Fayod) Vellinga & Schreurs, with the latter characterized by a trichodermal pileipellis or by a euhymeniderm of cylindrical to fusiform elements that correspond to part of the members of *Pluteus* sect. *Hispidoderma* sensu Singer (1959, 1986). The species characterized by a cutis-like pileipellis and non-metuloid cystidia were accommodated in a new section, namely *Pluteus* sect. *Villosi* Schreurs & Vellinga, which was introduced for the remaining members of *Pluteus* sect. *Hispidoderma* sensu Singer (1959, 1986). However, molecular phylogenetic studies that include species of *Pluteus* sect. *Celluloderma* (Justo et al. 2011a, 2012) do not support any subsections proposed by Singer (1956, 1959, 1986) or Vellinga and Schreurs (1985).

Based on molecular data (Minnis et al. 2006; Menolli et al. 2010; Justo et al. 2011a, b; Vizzini and Ercole 2011), *Pluteus* sect. *Celluloderma* now includes species with non-metuloid pleurocystidia and a pileipellis as a euhymeniderm or an epithelioid hymeniderm composed of short elements (Qm < 3), intermixed or not with elongate cystidioid elements (corresponding to *Pluteus* sect. *Celluloderma* as defined by Singer 1956, 1959, 1986) and species with a cutis-like pileipellis and non-metuloid cystidia (corresponding to *Pluteus* sect. *Villosi* or *Hispidoderma* sensu Singer p.p.). The species with cutis-like pileipellis and possessing a partial veil, formerly placed in the genus *Chamaeota* (W.G. Sm.), also are included in *Pluteus* sect. *Celluloderma* based on molecular data (Minnis et al. 2006, Vizzini and Ercole 2011).

After a morphological and molecular study of new Brazilian collections of *Pluteus* sect. *Celluloderma* we provide a phylogenetic overview for this section with emphasis on species occurring in Brazil including the complete description of eight new species from that country.

Materials and methods

Sampling.—Materials studied in the morphological and molecular analyses include specimens recently collected in different areas in Brazil including fragments of Atlantic and Amazon forests. The terminology of vegetation types is according to Veloso et al. (1991). The herbarium acronyms follow Thiers (2015) and the Rede Brasileira de Herbários (www.botanica. org.br/rede.herbarios.php) for the herbarium from Passo Fundo University (RSPF).

Molecular study and phylogenetic analyses.—Methods for DNA isolation, PCR and sequencing follow Justo et al. (2011b). The nuc rDNA ITS1-5.8S-ITS2 (ITS) region was amplified with the primer pair ITS1-F and ITS4 (White et al. 1990, Gardes and Bruns 1993). The molecular analyses were conducted with existing DNA sequences used by Menolli et al. (2010), Justo et al. (2011a, b, c; 2012), Pradeep et al. (2012) and from newly collected sequences of

Submitted 21 Nov 2014; accepted for publication 2 Sep 2015.
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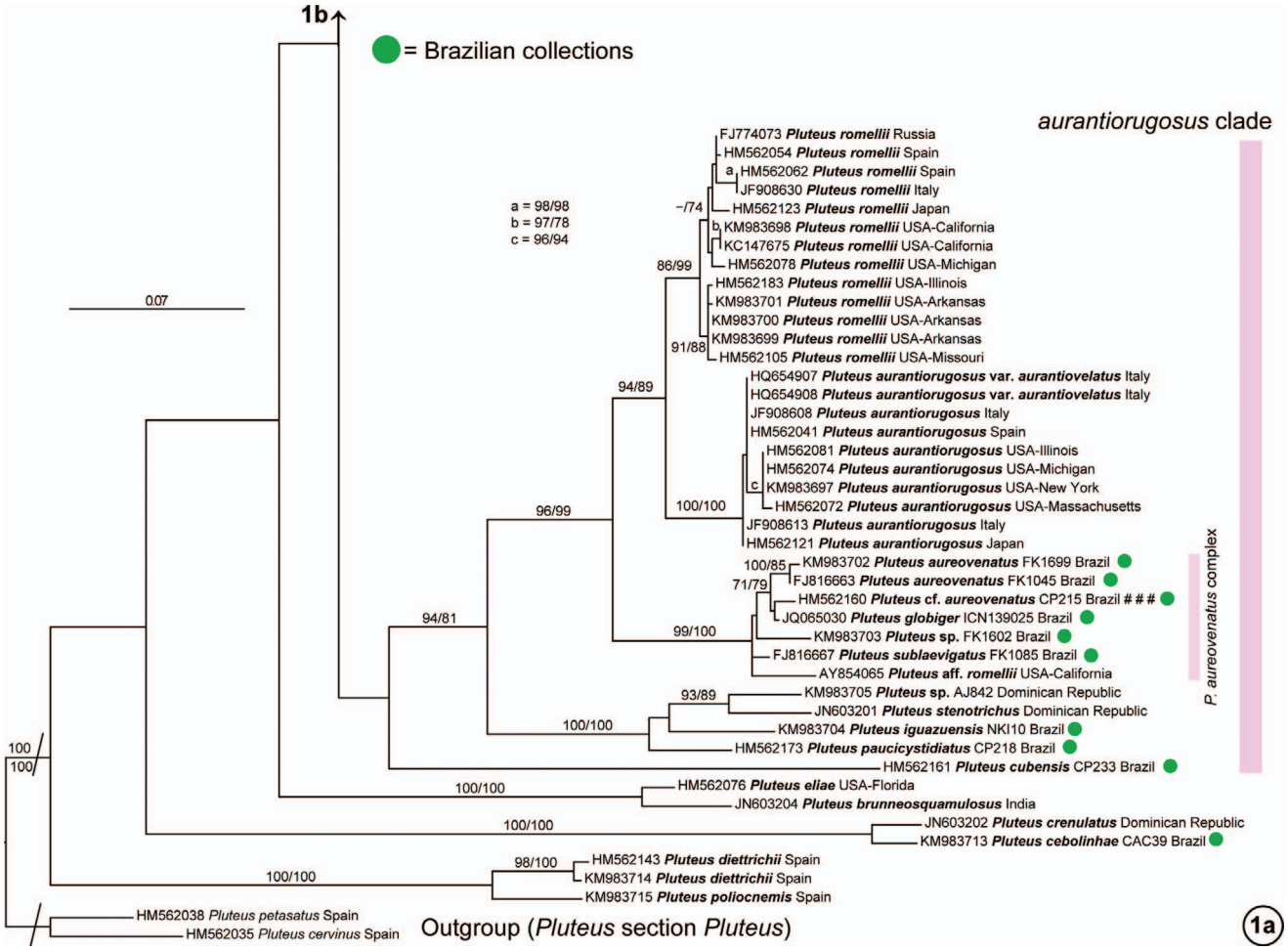

FIG. 1. Best tree from the maximum likelihood analysis for the ITS dataset of *Pluteus* sect. *Celluloderma*. Bootstrap values ≥70% are on branches (ML/MP). Root length has been reduced to facilitate graphical representation. Epithets in quotation marks represent names that need revision for correct identification. # # # Species names that were renamed (see DISCUSSION). a. aurantiorugosus clade and three outside lineages (*P. diettrichii* and *P. poliocnemis*; *P. crenulatus* and *P. cebolinhae*; *P. eliae* and *P. brunneosquamulosus*). b. ephebeus and podospileus clades. c. phlebophorus, thomsonii, hispidulus and cinereofuscus clades and an external branch including *P. hispidulus* var. *cephalocystis* and *Pluteus* sp. (*AJ588*).

materials representing species of *Pluteus* sect. *Celluloderma*. Newly obtained sequences were deposited in GenBank and accession numbers are provided (FIG. 1). Sequences were aligned with MAFFT 6 (http://mafft.cbrc.jp/alignment/server/; Katoh and Toh 2008) with the Q-INS-i option. The alignment was visually examined and manually corrected with MacClade 4.05 (Maddison and Maddison 2002). Maximum parsimony (MP) and maximum likelihood (ML) were performed with the parameters specified in Justo et al. (2011b) with PAUP *4.0.b10 (Swofford 2002) for MP and the RAxML servers (Stamatakis et al. 2008) for ML. Two representatives of *Pluteus* sect. *Pluteus*, namely *P. cervinus* (Schaeff.) P. Kumm. and *P. petasatus* (Fr.) Gillet, were used as outgroup taxa. The following abbreviations are used: most parsimonious trees (MPT) and bootstrap support (BS). Sequence divergence was calculated with MatGAT (Campanella et al. 2003).

Morphological study.—The macroscopic descriptions are based on fresh specimens. Color terms are according to Küppers (1979) or Kornerup and Wanscher (1978) for *P. paucicystidiatus*. In microscopic analyses the dried material was wetted with 70% ethanol and rehydrated in 5% KOH or stained with Melzer's reagent to check for any basidiospore wall reactions. Descriptive terms for micromorphological features follow Vellinga (1988). The notation [a/b/c] at the beginning of a set of basidiospores data is to be read as "(a) basidiospores were measured from (b) basidiomata taken from (c) collections". Q represents the range of the length/width ratio for all measured spores, Qm represents the average of all calculated Q values for all measured basidiospores, and Lm (Wm) represents the average of all of the lengths (widths) of the measured basidiospores. At least 20 basidiospores from each basidioma were measured in lateral view, and the terms denoting basidiospore shape follow Bas (1969).

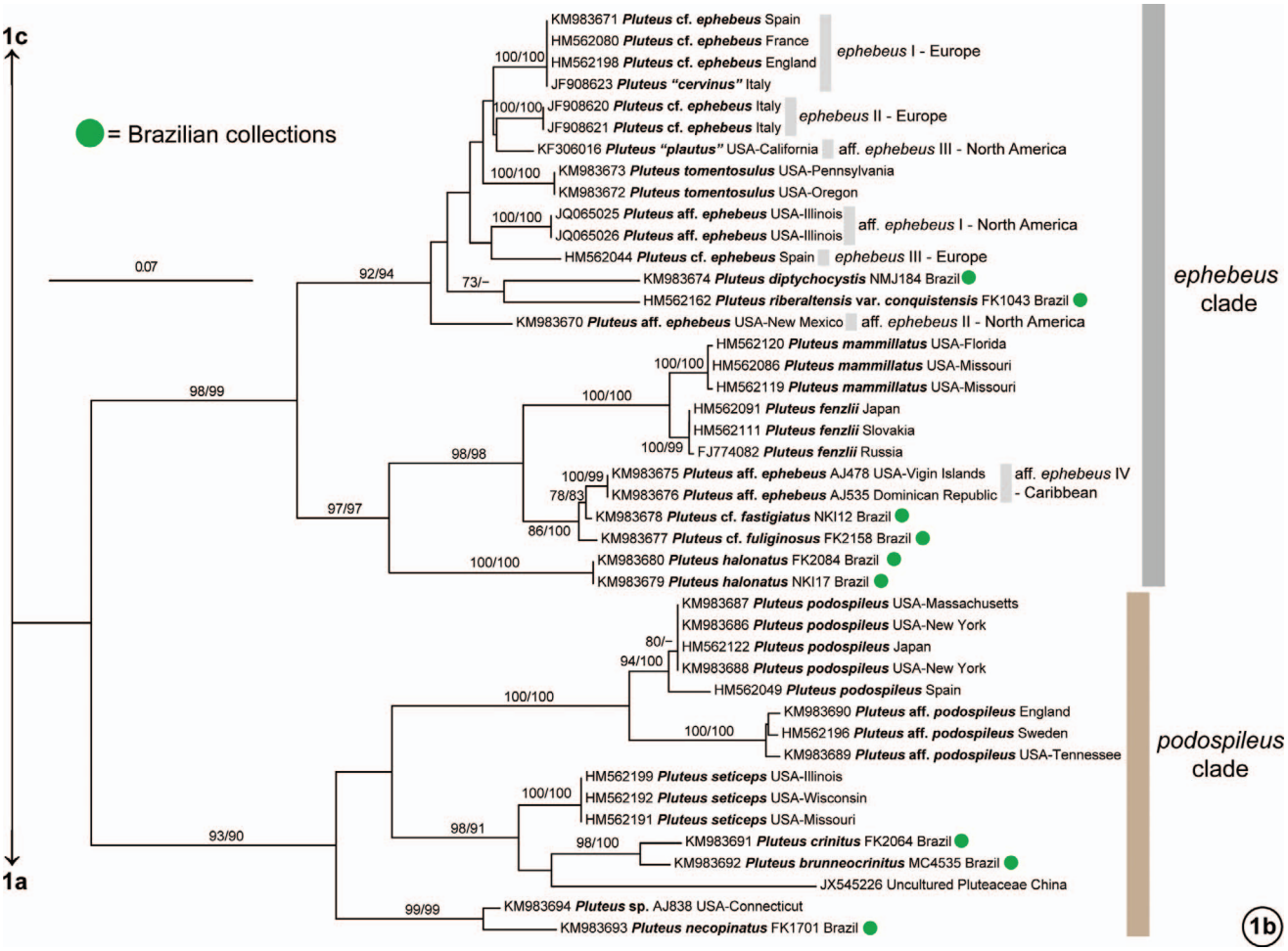

FIG. 1. Continued.

RESULTS

The final dataset consists of 159 ingroup sequences with a total of 828 characters (gaps included), of which 383 are parsimony informative. In the MP analysis 106 MPT were recovered (length = 2446, CI = 0.32, RI = 0.85). A general phylogeny of *Pluteus* sect. *Celluloderma* based on the best tree from the ML analysis is provided (FIG. 1). The alignment file was deposited in TreeBASE (S16548).

Six well-supported clades, already recognized in Justo et al. (2011b), were recovered in the ML and MP phylogenies (FIG. 1): aurantiorugosus, podospileus, ephebeus, cinereofuscus, thomsonii and phlebophorus clades. A seventh, not previously recognized group, the hispidulus clade, also was recovered with high support. Four species pairs fall out of these well-supported lineages: i. *Pluteus diettrichii* Bres. and *P. poliocnemis* Kühner, that appear as sister to all other *Celluloderma* species; ii. *P. cebolinhae* and *P. crenulatus* Justo, Battistin & Angelini; iii. *P. brunneosquamulosus* C.K. Pradeep & K.B. Vrinda and *P. eliae* Singer; iv. *P. hispidulus* var. *cephalocystis* Schreurs and *Pluteus* sp. (collection *AJ588*). None of the sister taxa relationships among the major clades or the isolated species pairs receive high support in the phylogenetic analyses and alternative topologies have been recovered in analyses of section *Celluloderma* (Justo et al. 2011a, b, c, 2012; Pradeep et al. 2012).

As cited by Justo at al. (2011a) and confirming the artificial status of the subsections proposed by Singer (1956, 1959, 1986), taxa with *Mixtini*-type pileipellis are grouped in the podospileus and thomsonii clades, which are formed primarily by species with this type of pileipellis (except by *P. dominicanus* var. *hyalinus* Menolli & Capelari, which has an epithelioid hymeniderm pileipellis, and by the voucher of JX545226 from which the morphological data are unavailable) but also present at least in three other clades: aurantiorugosus (*P. stenotrichus* Justo, Battistin & Angelini), cinereofuscus (*P. eludens* E.F. Malysheva, Minnis & Justo and *P. multiformis* Justo, A. Caball. & G. Muñoz) and phlebophorus (*P.* cf. *eugraptus*). Transitions between epithelioid hymeniderm and cutis-like pileipellis probably happened several times in the

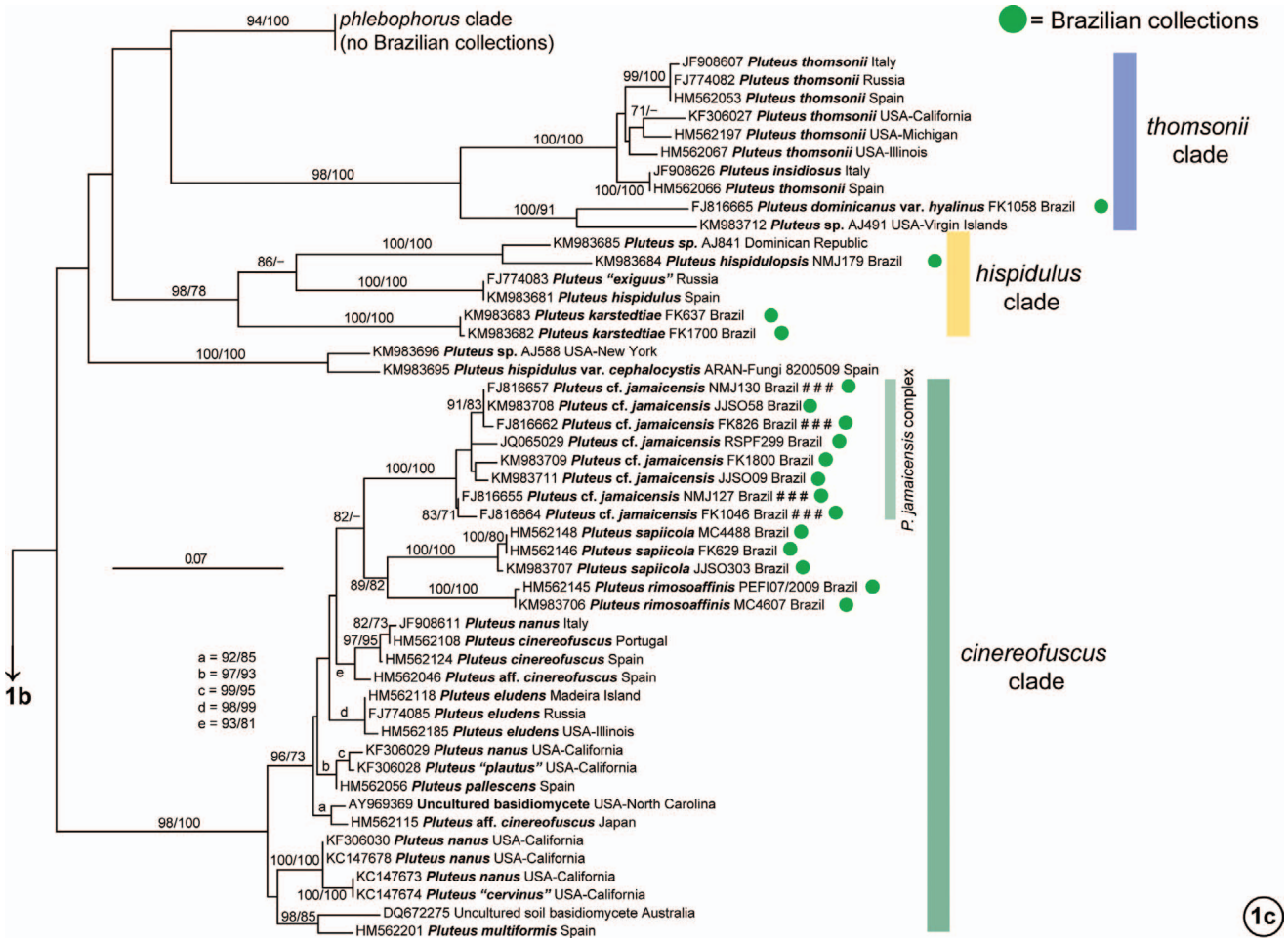

FIG. 1. Continued.

evolution of *Pluteus* sect. *Celluloderma* because taxa with a cutis appeared at least in three independent clades: aurantiorugosus (*P. cubensis* [Murrill] Dennis), ephebeus (all taxa) and hispidulus clade (all taxa).

The ITS sequences within the *P. aureovenatus* complex (FIG. 1a) are 95–99% identical, suggesting the presence of multiple taxa. Current studies using combined analyses of ITS plus sequences of the *tef1* gene (data not shown) revealed the existence of at least four species in this complex from tropical areas. Thus for now we confirm the occurrence of *P. aureovenatus* Menolli & Capelari (*FK1045*, *FK1699*), *P. globiger* Singer (ICN139025) and *P. sublaevigatus* (Singer) Menolli & Capelari (*FK1085*) in Brazil, but the status of the remaining collections in this clade needs further study. A similar case is the *P. jamaicensis* complex (FIG. 1c), which awaits additional collection and molecular data to identify the species present in this clade. Some collections in this complex were identified as *P. fluminensis* Singer (*FK1046*, *NMJ127*), *P. fuligineovenosus* E. Horak (*FK826*) and *P. jamaicensis* Murrill (*NMJ130*) by Menolli et al. (2010). However, a recent morphological reexamination (Menolli et al. 2015) of the specimens of this complex revealed that they are characterized by a rugose-venose pileus and both pigmented and colorless cheilocystidia. Following Menolli et al. (2015) we now prefer to maintain all collections in this complex as *P.* cf. *jamaicensis*.

Species concepts of many taxa are still in flux and many names of the included non-Brazilian sequences need to be reconsidered, but that falls outside the scope of this paper. For these sequences the epithet appears in quotation marks (e.g. "exiguus") (FIG. 1). Some taxa from Brazil are newly sampled in molecular studies, and they also are highlighted on the tree (viz. *P. diptychocystis* Singer, *Pluteus* cf. *fastigiatus* Singer, *Pluteus* cf. *fuliginosus* Murrill, *P. iguazuensis* Singer and *P. rimosoaffinis* Singer).

Considering the fact that this phylogeny is based only on ITS data, the actual relationships or the position of the sampled taxa might be different, suggesting that additional data will be necessary to assess limits of *Pluteus* species. Genes for translation elongation factor 1-α such as *tef1*, which were used to resolve species

limits in the *Pluteus* complexes (Menolli et al. 2014, Justo et al. 2014), also may prove informative in *Pluteus* sect. *Celluloderma*.

TAXONOMY

Based on morphological and molecular data we here propose eight new species: *P. brunneocrinitus, P. cebolinhae, P. crinitus, P. halonatus, P. hispidulopsis, P. karstedtiae, P. necopinatus* and *P. paucicystidiatus*.

Pluteus brunneocrinitus Menolli, Justo & Capelari, sp. nov. FIGS. 2c, f, 3

MycoBank MB810812

Diagnosis: Similar to *P. crinitus* but differing in the presence of brownish fibrils on stipe, colored lamellar edges with pigmented cheilocystidia and by longer caulocystidia and the narrowly clavate cheilocystidia.

Typification: BRAZIL. SÃO PAULO: São Paulo, Parque Estadual da Cantareira, Núcleo Engordador, 25 Nov 2009, *M. Capelari & L.A.S. Ramos MC4535* (**holotype** SP417458).

Etymology: brunneus (L.) means brown and *crinitus* (L.) means having tufts of long weak hairs, and this name refers to the brown hairy pileus surface and its resemblance to *P. crinitus*.

Pileus 6–12 mm diam, convex then applanate, dark brown ($N_{80}Y_{90}M_{60}$) and darker at center or in mature specimens, covered by brownish erect fibrils, densely tomentose-fibrillose to spinulose, sometimes cracking and revealing the whitish context; margin not striate or sulcate but with tooth-shaped scales hanging over the edge. Lamellae free, pinkish, subdistant, ventricose, with brown lamellar edges and 1–3 lamellulae for each series of lamellae. Stipe 12–25 × <1(apex)–1(base) mm, slightly attenuated upward; with a small subbulbous base; central; surface translucent-white, covered by small brownish fibrils overall, apparently without basal mycelium. Odor, flavor and context color not recorded.

Basidiospores [20/1/1] 4.5–5.5 × 4.5(–5.0) μm (Q = 1.00–1.16[–1.30]); Qm = 1.13; Lm = 5.0 μm; Wm = 4.4 μm), globose to broadly ellipsoid, inamyloid, hyaline, smooth, thick-walled, guttulate. Basidia 20–26 × 6.0–8.5 μm, clavate to narrowly clavate, thin-walled, four-spored. Pleurocystidia absent. Cheilocystidia 41–66 × 13.5–16.0(–22) μm, narrowly clavate, filled with evenly dissolved brownish intracellular pigment, thin-walled, numerous. Lamellar edges sterile. Lamellar trama inverse, up to 31 μm wide, composed of thin-walled hyphae, 2.5–10.5 μm diam, hyaline. Pileus context undifferentiated, approx. 31 μm thick, composed of thin-walled hyphae, 2.5–12.5 μm diam, hyaline. Pileipellis a transition between hymeniderm and ephitelium, intermixed by cystidioid elements, composed of one layer of broadly lageniform to clavate or subglobose to spheropedunculate cells, 33–54 × 13.0–31 μm, with narrowly fusiform to filiform cystidioid elements, 70–182 × 13.5–26 μm, thin-walled, mostly with condensed brownish intracellular pigment or rarely with dissolved content. Caulocystidia 62–96 × 7.5–18.5 μm, narrowly clavate to narrowly fusiform or filiform, thin-walled, filled with brownish content, moderately numerous. Clamp connections absent in all parts examined.

Habit and habitat: In groups of up to three basidiomata on decayed wood. In a fragment of seasonal semideciduous forest, part of the Atlantic Forest domain.

Comments: Pluteus brunneocrinitus is morphologically close to *P. crinitus*, *P. necopinatus*, *P. seticeps* (G.F. Atk.) Singer and *P. thomsonii* (Berk. & Broome) Dennis, which also are characterized by the absence of pleurocystidia and a strict cellulodermal pileipellis composed of short cells intermixed by cystidioid elements. *Pluteus brunneocrinitus* appears in the podospileus clade (FIG. 1b) forming a well-supported clade with *P. crinitus* from Brazil, *P. seticeps* from USA and an uncultured *Pluteus* from China (JX545226).

The close relationship between *P. brunneocrinitus* and *P. crinitus* is evident in both morphological and molecular data. However, *P. crinitus* is morphologically different because of the absence of brownish fibrils on the stipe, the presence of concolorous lamellar edges, the shape, size and pigmentation of the cheilocystidia 25–34(–49) × 12.5–21(–26) μm, colorless and broadly clavate to broadly utriform or subglobose to sphaeropedunculate and the shape and size of the caulocystidia (37–75 × 8.5–21 μm, narrowly clavate to narrowly fusiform).

Pluteus necopinatus differs from *P. brunneocrinitus* in a less fibrillose pileus that is brownish pink, concolorous lamellar edges, broader cheilocystidia, non-filiform and shorter cystidioid elements in the pileipellis and distinct and thick-walled terminal members of the stipitipellis hyphae.

Pluteus seticeps differs morphologically from *P. brunneocrinitus* mainly by the absence of a pileus fully covered by brownish erect fibrils with tooth-shaped scales hanging over the edge, the presence of concolorous lamellar edges and the shape and pigmentation of the cheilocystidia (colorless and subglobose to sphaeropedunculate to pyriform to clavate-cylindrical) (Minnis and Sundberg 2010), which apparently are more similar to those of *P. crinitus*.

In addition to the phylogenetic position of *P. brunneocrinitus* and *P. thomsonii* in different clades (FIG. 1b, c), they also are separated by morphology because *P. thomsonii* is characterized by a gray to dark gray and usually highly reticulate-veined pileus, the concolorous lamellar edges and the colorless cheilocystidia with an apical projection; pleurocystidia are normally absent in

FIG. 2. a, b. *P. brunneocrinitus* (*MC4535* – holotype). c, d. *P. cebolinhae* (*CAC39* holotype). e, f. *P. crinitus* (*FK2064* holotype). g, h. *Pluteus halonatus* (*FK2084* holotype). i, j. *P. hispidulopsis* (*NMJ179* holotype). k, l. *P. karstedtiae* (*FK1700* holotype). m, n. *P. necopinatus* (*FK1701* holotype). o–s. *P. paucicystidiatus* (*CP218* holotype); o. Basidiomata; p. Lamellar section showing the absence of cystidia; q. Lamellar section of the only pleurocystidium seen (black arrow); r. Pleurocystidium; s. Cheilocystidium. Bars: a, e–f, i–l = 5 mm; b = 1 mm; c, d, g, h, m–o = 1 cm, p, q = 50 µm; r, s = 10 µm.

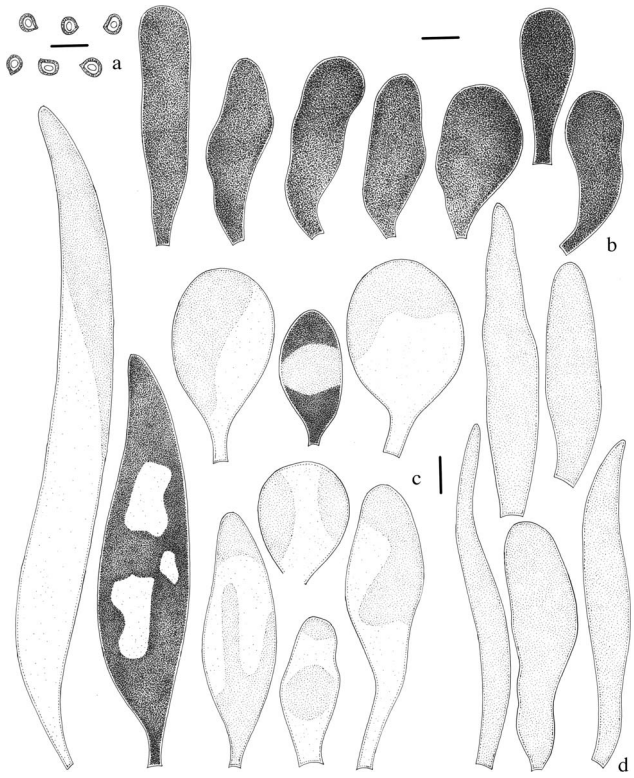

FIG. 3. *Pluteus brunneocrinitus* (*MC4535* holotype). a. Basidiospores. b. Cheilocystidia. c. Pileipellis elements. d. Caulocystidia. Bars = 10 μm.

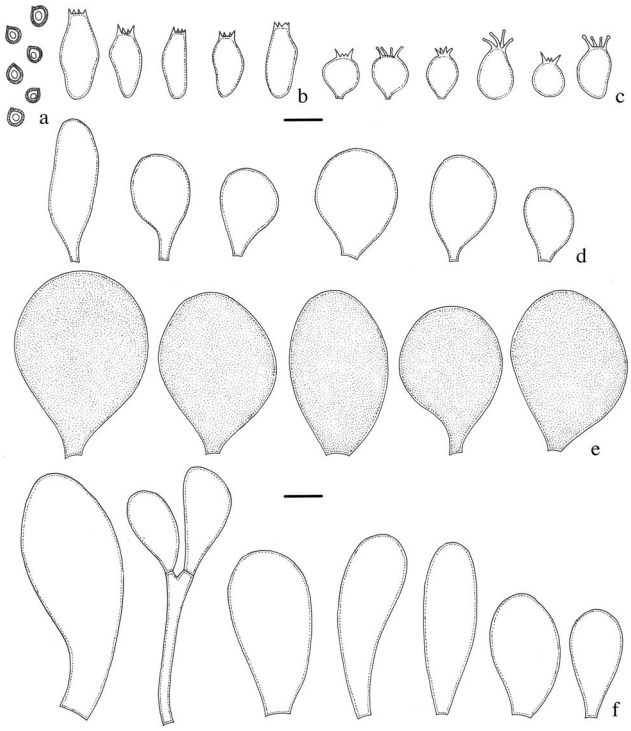

FIG. 4. *Pluteus cebolinhae* (*CAC39* holotype). a. Basidiospores. b. Basidia type I. c. Basidia type II. d. Cheilocystidia. e. Pileipellis elements. f. Caulocystidia. Bars = 10 μm.

that species but if present have also an apical projection (Homola 1972, Orton 1986, Minnis and Sundberg 2010).

Pluteus cebolinhae Menolli, Justo & Capelari FIGS. 2d, e, 4

MycoBank MB810813

Diagnosis: Similar to *P. crenulatus* by the deeply sulcate pileus and the absence of pleurocystidia but differing in the non-crenulate pileus margin, shape and size of the basidia, rare cheilocystidia, and shape of the pileipellis elements and caulocystidia.

Typification: BRAZIL. SÃO PAULO: São Paulo, Reserva Biológica do Alto da Serra de Paranapiacaba, 20 Jun 2007, *C.A. Canavese & F. Karstedt CAC39* (**holotype** SP417455).

Etymology: Named in honor of the Brazilian comic character Cebolinha (http://turmadamonica.uol.com.br/personagem/cebolinha/), who has a few strands of hair on his head that are arranged like the sterigmata of the unusual basidia present on the lamellar edges of the new species. Moreover, in Portuguese cebolinha means chive or small onion, and the basidia of *P. cebolinhae* also resemble the small bulb and the short roots of chives or onions.

Pileus 20 mm diam, convex, brown, darker at center ($N_{80}A_{99}M_{60}$) and paler towards the margin ($N_{60}A_{99}M_{60}$) to pure white alternating to the brownish tones on the insertion points of lamellae; center veined-rugulose; margin deeply plicate-sulcate. Lamellae free, pinkish ($N_{10}Y_{50}M_{40}$), crowded, ventricose, ≤4 mm broad, with concolorous edges and lamellulae of different lengths, 1–3 for each lamella. Stipe 15 × 2(apex)–3(base) mm, attenuated upwards; central; surface white, pruinose or with very small punctation overall, with scanty basal mycelium. Odor, taste and context color not recorded.

Basidiospores [20/1/1] (3.7–)4.5–5.0(–5.5) × 3.5–4.5 μm (Q = [1.00–]1.16–1.35; Qm = 1.24; Lm = 4.8 μm; Wm = 3.9 μm), broadly ellipsoid to ellipsoid, rarely globose, inamyloid, hyaline, smooth, thick-walled, guttulate. Basidia dimorphic: i. 16.0–23 × 7.5–10.0 μm, clavate to lageniform, frequent on lamellar sides, thin-walled, four-spored; ii. 8.5–13.5 × 8.0–10.0 μm, ovoid to balloon-shaped, present on lamellar edges, thin-walled, four-spored. Pleurocystidia absent. Cheilocystidia 20–37 × 12.5–22 μm, broadly clavate to subglobose or spheropedunculate, colorless and hyaline, thin-walled, rare. Lamellar edges heteromorphous. Lamellar trama inverse, up to 31 μm wide, composed of thin-walled hyphae, up to 7.5 μm diam, hyaline, interwoven by oleiferous hyphae up to 2.5 μm diam. Pileus context undifferentiated, approx. 45

μm thick, composed of thin-walled hyphae, up to 7.5 μm diam, hyaline, interwoven by oleiferous hyphae up to 2.5 μm diam. Pileipellis an epithelioid hymeniderm up to 50 μm thick, composed of one layer of subglobose to spheropedunculate cells, 40–50 × 27–37 μm, thin-walled, filled with evenly dissolved brownish intracellular pigment or almost colorless and hyaline for those near the pileus margin. Caulocystidia 22–68 × 12.5–27 μm, narrowly clavate, thin-walled, mostly colorless and hyaline or rarely with pale yellowish content. Clamp connections absent in all parts examined.

Habit and habitat: Solitary on decayed wood. In a fragment of dense ombrophilous submontane forest, part of the Atlantic Forest domain.

Comments: Pluteus cebolinhae is characterized by a veined and deeply plicate-sulcate pileus with the extreme margin with alternating shades of brown and white, absence of pleurocystidia, the rare cheilocystidia and the narrowly clavate caulocystidia. In addition, the short ovoid to balloon-shaped basidia are also commonly observed on lamellar edges. Some of these characters are shared with *P. crenulatus*, a species recently described from Dominican Republic (Justo et al. 2012) and phylogenetically close to *P. cebolinhae* (FIG. 1a). The deeply sulcate pileus with the margin alternating brown and whitish shades and the absence of pleurocystidia are the main characteristics for both species. However, their ITS sequences are only 95.9% identical and *P. crenulatus* has a pileus with a crenulate margin, basidia evenly clavate to narrowly utriform and crowded, narrowly clavate cheilocystidia forming a well-developed strip (Justo et al. 2012).

The phylogenetic position of *P. crenulatus* and *P. cebolinhae* is still unresolved based only in ITS data. Justo et al. (2012) showed the isolated placement of *P. crenulatus* as sister of all taxa in *Pluteus* sect. *Celluloderma* except for *P. diettrichii*, although with no statistical support. In our analyses *P. crenulatus* and *P. cebolinhae* appear with no strong support as the sister clade of all taxa in *Pluteus* sect. *Celluloderma* except for *P. diettrichii* and *P. poliocnemis* (FIG. 1a).

Pluteus cebolinhae differs remarkably in the macroscopic aspect, mainly in the deeply plicate-sulcate pileus margin, from the other species of *Pluteus* sect. *Celluloderma* that are lacking pleurocystidia and with a strict cellulodermal or a euhymenidermal pileipellis (*P. diettrichii*, *P. insidiosus* Vellinga & Schreurs, *P. paucicystidiatus* and *P. poliocnemis*). These taxa also differ from *P. cebolinhae* in shape and size of the basidiospores, cheilocystidia and caulocystidia (Kühner and Romagnesi 1956, Vellinga and Schreus 1985, see *P. paucicystidiatus* for full description). *Pluteus diettrichii*, *P. paucicystidiatus* and *P. poliocnemis* appear separate from *P. cebolinhae* in the ML tree (FIG. 1a).

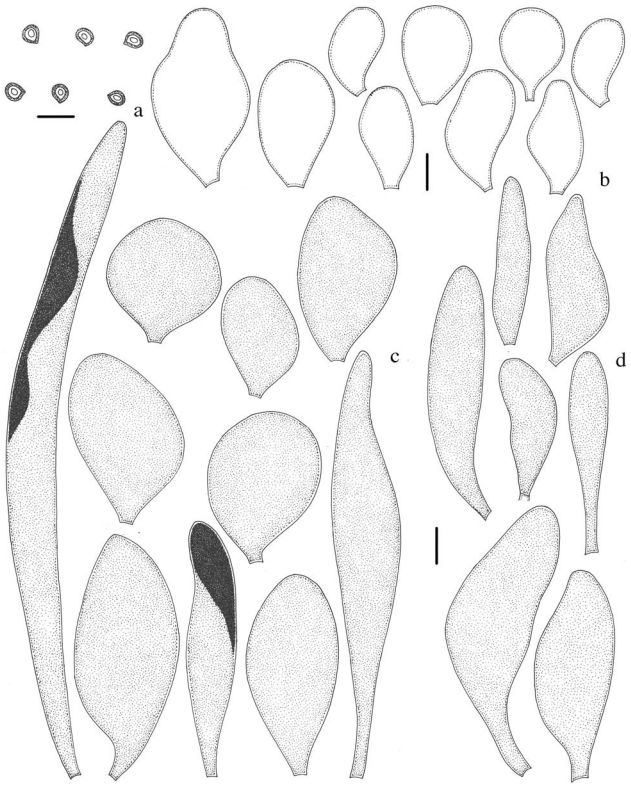

FIG. 5. *Pluteus crinitus* (*FK2064* holotype). a. Basidiospores. b. Cheilocystidia. c. Pileipellis elements. d. Caulocystidia. Bars = 10 μm.

Pluteus crinitus Menolli & Capelari, sp. nov. FIGS. 2g, h, 5 MycoBank MB810814

Diagnosis: Similar to *P. brunneocrinitus* but differing in the absence of brownish fibrils on stipe, concolorous lamellar edges and by shorter caulocystidia and colorless, smaller and differently shaped cheilocystidia.

Typification: BRAZIL. AMAZONAS: Manaus, Instituto Nacional de Pesquisas da Amazônia (INPA), Campus Aleixo I, 27 Jun 2011, *F. Karstedt FK2064* (**holotype** INPA241254, **isotype** SP445855).

Etymology: crinitus (L.) means having tufts of long weak hairs and refers to the hairy pileus surface.

Pileus 7–16 mm diam, convex then applanate, slightly depressed at center, chestnut brown ($N_{80}Y_{60}M_{30–40}$) and darker at center, covered by brownish erect fibrils, densely tomentose-fibrillose to spinulose, sometimes cracking, revealing the whitish flesh; margin not striate or sulcate but with tooth-shaped scales hanging over the edge. Lamellae free, pinkish, subdistant, ventricose, ≤3.5 mm broad, with concolorous edges and 1–3 lamellulae for every one series of lamellae. Stipe 12–18 × < 1 (apex)–1 (base) mm, slightly attenuated upward; with a small subbulbous base; central; surface translucent-white, covered by small and dispersed whitish fibrils at

base, with scanty tomentose basal mycelium. Odor, flavor and context color not recorded.

Basidiospores [20/1/1] (4.0–)5.0 × 4.5 µm (Q = [1.00–]1.16; Qm = 1.15; Lm = 4.9 µm; Wm = 4.3 µm), subglobose, rarely globose, inamyloid, hyaline, smooth, thick-walled, guttulate. Basidia 21–23 × 6.2–7.5 µm, clavate to broadly lageniform, thin-walled, four-spored. Pleurocystidia absent. Cheilocystidia 25–34(–49) × 12.5–21(–26) µm, broadly clavate to broadly utriform or subglobose to sphaeropedunculate, colorless and hyaline, thin-walled, not numerous. Lamellar edges heteromorphous. Lamellar trama inverse, up to 37 µm wide, composed of thin-walled hyphae, 2.5–12.5 µm diam, hyaline. Pileus context undifferentiated, approx. 31 µm thick, composed of thin-walled hyphae, 2.5–12.5 µm diam, hyaline. Pileipellis a transition between hymeniderm and epithelium, intermixed by cystidioid elements, composed of one layer of subglobose, spheropedunculate or clavate to narrowly clavate cells, 32–67 × 20–29 µm, with narrowly fusiform to filiform cystidioid elements, 70–180 × 12.5–22 µm, thin-walled, mostly with evenly dissolved brownish intracellular pigment or sometimes with few condensations. Caulocystidia 37–75 × 8.5–21 µm, narrowly clavate to narrowly fusiform, thin-walled, filled with light brown content, rare and sparse. Clamp connections absent in all parts examined.

Habit and habitat: Gregarious to scattered, in groups of up to 10 basidiomata, on decayed wood. In an anthropogenic fragment of secondary forest (capoeira) from an original dense ombrophilous forest, part of the Amazon Forest domain.

Comments: Pluteus crinitus is one of the few species without pleurocystidia and with a strict cellulodermal pileipellis with cystidioid elements. Despite its molecular closeness with *P. brunneocrinitus* (FIG. 1b), their morphology differs considerably (see *P. brunneocrinitus* comments).

Pluteus crinitus is also closely related to *P. necopinatus* and *P. seticeps*. However, *P. necopinatus* has a less fibrillose and pinkish brown pileus, slightly broader basidiospores, broader and differently shaped cheilocystidia, non-filiform and shorter cystidioid elements in the pileipellis and distinct thick-walled hyphae of the stipitipellis (see *P. necopinatus* for full description). *Pluteus seticeps* differs from *P. crinitus* mainly in the macroscopic appearance of the pileus that is not fully covered by brownish erect fibrils and by the presence of dark brown fibrils all over the stipe (Minnis and Sundberg 2010). In addition, the sequences of *P. necopinatus* from Brazil and those of *P. seticeps* from USA are placed on separate branches from *P. crinitus* and *P. brunneocrinitus* (FIG. 1b).

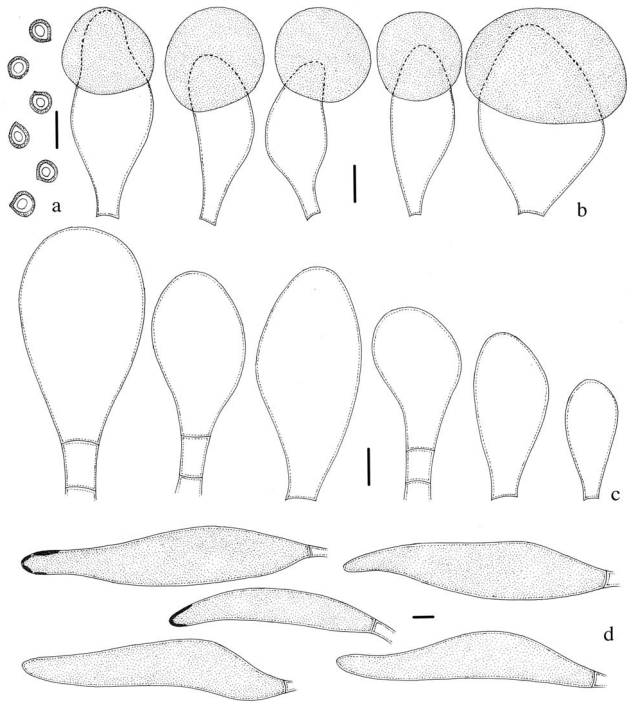

FIG. 6. *Pluteus halonatus* (*FK2084* holotype). a. Basidiospores. b. Pleurocystidia. c. Cheilocystidia. d. Pileipellis elements. Bars = 10 µm.

Pluteus halonatus Menolli, Justo & Capelari, sp. nov. FIGS. 2a, b, 6

MycoBank MB810811

Diagnosis: Similar to *P. riberaltensis* and its varieties but distinguished by the combination of a terrestrial habitat, brownish stipe covered by fibrils overall and pleurocystidia covered by an apical yellowish resinous encrustation forming a rigid spherical outline at the tip.

Typification: BRAZIL. AMAZONAS: Manaus, Instituto Nacional de Pesquisas da Amazônia (INPA), Campus Aleixo I, 29 Jun 2011, *F. Karstedt FK2084* (**holotype** INPA241273).

Etymology: halonatus (L.) means surrounded by an outer circle, in reference to the apical cover present on the pleurocystidia that resembles the representation of the golden halos of saints and angels.

Pileus 29–30 mm diam, plane to finally plano-concave, with a distinct umbo, surface brown ($N_{80}Y_{50}M_{40}$) covered by appressed and radially arranged fibrils, sometimes exposing at margin the pinkish and translucent background between the fibrils; margin not striate or sulcate. Lamellae free, pinkish ($N_{10}Y_{50}M_{40}$), close to subdistant, ventricose, approx. 4 mm broad, with concolorous edges and few lamellulae. Stipe 40–43 × 3–4 (apex)–5–6(base) mm, attenuated upward; base sometimes clavate to subbulbous; central; surface brownish concolorous with pileus, covered by brown fibrils

overall on pale background, with or without scanty basal mycelium. Odor, flavor and context color not recorded.

Basidiospores [40/2/2] 5.5–6.0 × 5.5–6.0 µm (Q = 1.00–1.11; Qm = 1.03; Lm = 6.1 µm; Wm = 5.9 µm), globose to subglobose, inamyloid, hyaline, smooth, thick-walled, guttulate. Basidia 18.7–26 × 7.5–8.5 µm, clavate to narrowly lageniform, thin-walled, four-spored. Pleurocystidia 42–55 × 13.5–21(–32) µm, narrowly fusiform to broadly utriform, colorless and without internal content, hyaline, thin-walled, mostly with an apical yellowish resinous encrustation forming a rigid spherical outline at the tip, moderately abundant. Cheilocystidia (32–)42–58 × 13.5–34 µm, similar to the pleurocystidia but mostly without the apical cover and frequently cylindrical to broadly clavate or with basal septum, colorless and hyaline, thin-walled, numerous. Lamellar edges sterile. Lamellar trama inverse, up to 31 µm wide, composed of thin-walled hyphae, up to 10.0 µm diam, hyaline. Pileus context undifferentiated, approx. 150 µm thick, composed of thin-walled hyphae, 2.5–15.0 µm diam, hyaline. Pileipellis a cutis up to 125 µm thick, composed of parallel chains of cylindrical and thin-walled hyphae, individual terminal elements 112–126 × 20–26 µm, sometimes a few elongated, ascendant and conspicuous subradial elements, mostly with rounded apex or gradually attenuated toward the apex (6.0–10.0 µm broad), sometimes with encrusted wall at the apex, filled with evenly dissolved brownish intracellular pigment or rarely with colorless terminal elements. Caulocystidia absent. Stipitipellis composed of thin- to thick-walled hyphae, 6.0–18.5 µm diam, yellowish or with brownish content mainly in the terminal elements. Clamp connections absent in all parts examined.

Habit and habitat: Solitary on soil. In an anthropogenic fragment of secondary forest (capoeira) from an original dense ombrophilous forest, part of the Amazon Forest domain.

Other specimen examined: BRAZIL. AMAZONAS: Manaus, Instituto Nacional de Pesquisas da Amazônia (INPA), Campus Aleixo I, 9 Feb. 2011, *N.K. Ishikawa & D. Komura NKI7* (INPA239965).

Comments: Pluteus halonatus is characterized by the brownish stipe covered with fibrils over entire length, globose to subglobose basidiospores, pleurocystidia covered by an apical yellowish resinous encrustation forming a rigid spherical outline at the tip, the cutis-like pilepellis, and the humicolous habitat.

None of the species with a cutis-like pileipellis and cystidia with an apical cover grows on soil. *Pluteus halonatus* is close morphologically to *P. circumscissus* Singer, *P. glyphidatus* (Berk. & Broome) Sacc. and *P. riberaltensis* var. *missionensis* Singer. *Pluteus circumscissus* is distinguished by the presence of a narrow volval belt at the stipe base, the broadly ellipsoid and non-globose basidiospores and by the shape (mucronate and narrowly lageniform) and pigmentation of the pleuro- and cheilocystidia (Singer 1959). *Pluteus glyphidatus* from Sri Lanka has a whitish to pale yellow and glabrous stipe and caespitose clusters of dermatocystidioid elements on the cutis pileipellis (Pegler 1986). Finally *P. riberaltensis* var. *missionensis*, which probably is morphologically closest to *P. halonatus*, has a pure white stipe without any dark fibrils (Singer 1962) and a lignicolous habitat. In addition to the type variety of *P. riberaltensis* Singer, Singer (1959, 1962) described two varieties (viz. *P. riberaltensis* var. *conquistensis* Singer and *P. riberaltensis* var. *missionensis*). The first differs from the type variety by the presence of black stripes on the stipe (Singer 1959, Menolli et al. 2010) and the second due to the apical resinous encrustation on cystidia (Singer 1962).

Despite the morphological similarities between the two varieties of *P. riberaltensis* and *P. halonatus*, the latter is proposed as a new species because of the combination of two distinctive characters (brownish stipe covered by fibrils and pleurocystidia covered by an apical yellowish resinous encrustation) plus its terrestrial habitat. Molecular analyses based on ITS (FIG. 1b) showed that within the ephebeus clade *P. halonatus* is phylogenetically closer to *P. mammillatus* (Longyear) Minnis, Sundb. & Methven, *P. fenzlii* (Schulzer) Corriol & P.-A. Moreau and related taxa than, for instance, another Brazilian sequence belonging to a specimen identified as *P. riberaltensis* var. *conquistensis* by Menolli et al. (2010).

Pluteus hispidulopsis Menolli, Justo & Capelari, sp. nov. FIGS. 2m, n, 7
MycoBank MB810815

Diagnosis: Similar to *P. hispidulus* but differing in the globose to subglobose basidiospores and the versiform cheilocystidia.

Typification: BRAZIL. RIO GRANDE DO NORTE: Baía Formosa, Reserva Particular do Patrimônio Natural Mata Estrela, 14 Jul 2010, *Menolli Jr. et al. NMJ179* (**holotype** SP417459).

Etymology: hispidulopsis from the composition of the Latin *hispidulus*, which is diminutive of *hispidus* and means covered with coarse rigid erect hairs or bristles harsh to the touch, and the Greek *opsis*, which indicates resemblance; the name refers to the morphological and phylogenetic relationship with *P. hispidulus*.

Pileus 12 mm diam, convex, not umbonate, brownish black at center ($N_{90}A_{99}M_{30}$) and grayish brown ($N_{80}A_{99}M_{35}$) toward the margin; surface covered by brownish or grayish appressed fibrils, densely tomentose-fibrillose with blackish and spinulose squamules at center; margin not striate or sulcate but slightly fringed with some long whitish fibrils. Lamellae free,

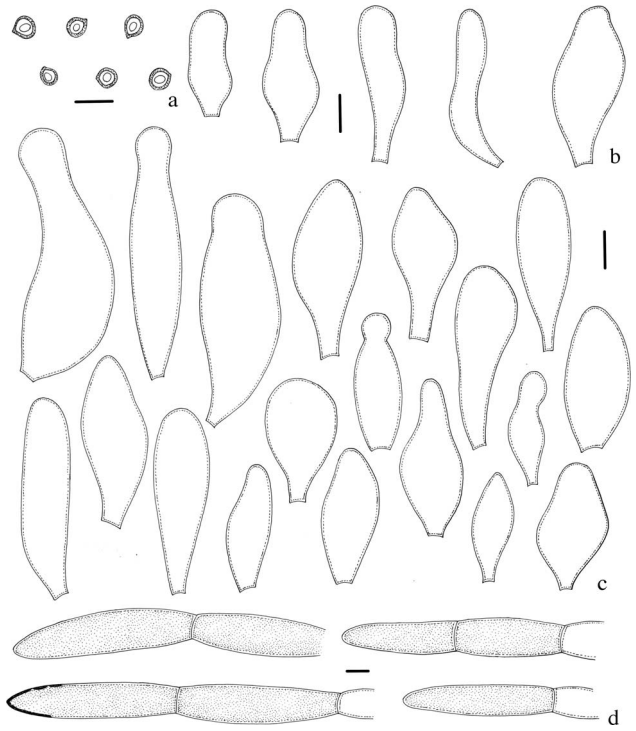

FIG. 7. *Pluteus hispidulopsis* (*NMJ179* holotype). a. Basidiospores. b. Pleurocystidia. c. Cheilocystidia. d. Pileipellis elements. Bars = 10 μm.

pinkish, crowded, with concolorous edges and one lamellula for every 1–2 lamellae. Stipe 24 × 1(apex)–2(base) mm, slightly attenuated upward; with a small subbulbous base; central; surface white and entirely covered by whitish fibrils mainly at base, slightly longitudinally striate at apex, with scanty tomentose basal mycelium. Odor, flavor and context color not recorded.

Basidiospores [20/1/1] 5.0–5.5 × (4.5–)5.0(–5.5) μm (Q = 1.00–1.12[–1.16]; Qm = 1.04; Lm = 5.2 μm; Wm = 5.0 μm), globose to subglobose, rarely broadly ellipsoid, inamyloid, hyaline, smooth, thick-walled, guttulate. Basidia 20–26 × 7.5–8.5 μm, clavate, thin-walled, four-spored. Pleurocystidia 27–41 × 7.5-17.5 μm, lageniform to utriform or narrowly clavate, colorless and hyaline, thin-walled, rare or apparently absent in some slices. Cheilocystidia 29–64 × 8.5–21 μm, variable in shape, clavate, lageniform, utriform, fusiform, capitate or spheropedunculate, colorless and hyaline, thin-walled, moderately numerous. Lamellar edges heteromorphous. Lamellar trama inverse, up to 31 μm wide, composed of thin-walled hyphae, 2.5–10.0 μm diam, hyaline. Pileus context undifferentiated, approx. 81 μm thick, composed of thin-walled hyphae, 2.5–10.0 μm diam, hyaline. Pileipellis a cutis, approx. 100 μm thick, composed of parallel chains of cylindrical and thin-walled hyphae, with short individual terminal elements 42–76 × 12–18 μm, sometimes with ascendant and suberect elements mainly at pileus center, mostly with rounded apex or gradually attenuated toward the apex (6.0–10.0 μm broad), sometimes with encrusted wall at apex, filled with evenly dissolved brown intracellular pigment. Caulocystidia absent. Stipitipellis composed of thin-walled hyphae, 2.5–11.0 μm diam, colorless and hyaline. Clamp connections absent in all parts examined.

Habit and habitat: Solitary on decayed wood. In a fragment of dense ombrophilous forest, part of the Atlantic Forest domain.

Comments: Pluteus hispidulopsis is characterized by a blackish and densely tomentose-fibrillose pileus, globose to subglobose basidiospores, the rarely present pleurocystidia and the variously shaped cheilocystidia.

The current molecular analyses (FIG. 1c) show that *P. hispidulopsis*, and *P. hispidulus* (Fr.) Gillet and *P. karstedtiae*, two species that also lack pleurocystidia and have a cutis-like pileipellis, belong to the same clade.

Pluteus hispidulus is a rarely recorded species that seems to be restricted to Europe (Kühner and Romagnesi 1956, Orton 1986, Justo and Castro 2007); it is morphologically different from *P. hispidulopsis* by the non-globose basidiospores and the narrowly to broadly clavate cheilocystidia (Kühner and Romagnesi 1956, Vellinga and Schreus 1985). Vellinga and Schreurs (1985) presented *P. hispidulus* var. *cephalocystis* Schreurs as different from the type variety by the presence of subcapitate to capitate narrowly utriform to narrowly clavate cheilocystidia and by few subglobose basidiospores as illustrated by them (Q ≅ 1.06–1.38; Qm ≅ 1.17). A French collection fitting the description of *P. hispidulus* var. *cephalocystis* (*ARAN-Fungi 8200509*) described in full by Arrillaga et al. (2011) has been sampled for molecular data (KM9836695) and appears (FIG. 1c) separate from collections identified as *P. hispidulus* (KM983681). Orton (1986) also reported for one collection of *P. hispidulus* more versiform cheilocystidia, varying from clavate or fusiform to lageniform, utriform or capitate lageniform, with transitional characteristics between *P. hispidulus* var. *hispidulus* and *P. hispidulus* var. *cephalocystis*. The species complex around *P. hispidulus* obviously needs more work, but that falls outside the scope of the present paper.

Pluteus karstedtiae differs from *P. hispidulopsis* in the chestnut brown but not dark or blackish pileus, the sulcate striate pileus margin, the translucent and less fibrillose stipe and rare or apparently absent cheilocystidia (see *P. karstedtiae* for full description).

The collection *AJ841* (KM983685) from the Dominican Republic appears as the sister taxon of *P. hispidulopsis* in the phylogenies but morphologically it

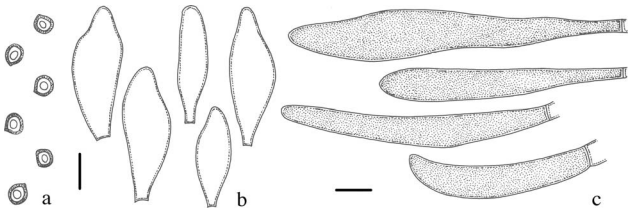

FIG. 8. *Pluteus karstedtiae* (*FK1700* holotype). a. Basidiospores. b. Cheilocystidia. c. Pileipellis elements. Bars = 10 μm.

differs, among other characters, in the abundant pleurocystidia (A. Justo unpubl).

Pluteus karstedtiae Menolli, Justo & Capelari, sp. nov. FIGS. 2o, p; 8
MycoBank MB810816

Diagnosis: Similar to *P. hispidulus* but differing in the globose to subglobose basidiospores and fusoid-ventricose to slightly lageniform and rare or apparently absent cheilocystidia.

Typification: BRAZIL. RIO DE JANEIRO: Guapimirim, Parque Nacional Serra dos Órgãos, Sede Guapimirim, Poço da Ponte Velha, 6 Jan 2011, *F. Karstedt et al. FK1700* (**holotype** SP445828).

Etymology: The name is in honor of Fernanda Karstedt for her contribution of more than 40 specimens of *Pluteus* collected 2006–2012 in Brazil. F. Karstedt is the collector of almost 12% of all Brazilian material of *Pluteus* studied by the first author since 2007. Moreover, the collection *FK637* of *P. karstedtiae* is probably one of the first *Pluteus* specimens collected by her.

Pileus 13–22 mm diam, convex to plane-convex, sometimes subumbonate and slightly depressed around the umbo, chestnut brown to coffee brown, darker at center and paler toward the margin; surface fibrillose-squamulose, covered by brownish fibrils, punctate-squamulose to spinulose at center with the fibrils appearing split outside the central disk and sometimes concentrating on the insertion points of lamellae, with the brown and pale cream alternate; margin sulcate-striate over half of the radius, sometimes exposing the whitish background, with some long brownish fibrils at margin. Lamellae free, cream to pinkish, close but not crowded, with concolorous edges and short lamellulae for each series of lamellae. Stipe 15–23 × 1–1.5(apex)–1.5–2(base) mm, slightly attenuated upwards; central; translucent to grayish white, covered by small whitish fibrils at base, with scanty tomentose basal mycelium. Odor, flavor and context color not recorded.

Basidiospores [40/2/2] 5.0–5.5(–6.0) × 4.5–5.5 μm (Q = 1.00–1.12[–1.16]; Qm = 1.05; Lm = 5.2 μm; Wm = 5.0 μm), globose to subglobose, rarely broadly ellipsoid, inamyloid, hyaline, smooth, thick-walled, guttulate. Basidia 20–27 × 7.5–8.5 μm, clavate to ventricose, thin-walled, four-spored. Pleurocystidia absent. Cheilocystidia 26–37 × 7.5–13.5 μm, narrowly clavate to narrowly lageniform, rare or apparently absent in some mounts. Lamellar edges heteromorphous. Lamellar trama inverse, up to 37 μm wide, composed of thin-walled hyphae, 2.5–8.5 μm diam, hyaline. Pileus context undifferentiated, approx. 42 μm thick, composed of thin-walled hyphae, 1.2–6.0 μm diam, sometimes interwoven by inflated hyphae up to 20 μm diam, hyaline. Pileipellis a cutis, approx. 100 μm thick, composed of parallel chains of cylindrical and thin-walled hyphae, with short individual terminal elements 48–92 × 7.5–12.5 μm, sometimes with ascendant and suberect elements mainly at pileus center, mostly with rounded apex or gradually attenuated toward the apex (4.0–7.0 μm broad), filled with evenly dissolved brown intracellular pigment. Caulocystidia absent. Stipitipellis composed of thin-walled hyphae, 2.5–7.5 μm diam, colorless and hyaline. Clamp connections absent in all parts examined.

Habit and habitat: Solitary on decayed unidentified wood or on decayed caudex of *Dicksonia* sp. in fragments of dense ombrophilous and seasonal semideciduous forests, part of the Atlantic Forest domain.

Other specimen examined: BRAZIL. SÃO PAULO: São Paulo, Parque Estadual da Cantareira, Núcleo Engordador, 27 Apr 2006, *F. Karstedt* & *M. Capelari* FK637 (SP417456).

Comments: Pluteus karstedtiae is characterized by a chestnut brown and fibrillose-squamulose pileus, globose to subglobose basidiospores and a cutis-like pileipellis; pleurocystidia are absent and cheilocystidia are rarely present.

Pluteus karstedtiae is morphologically and phylogenetically close to *P. hispidulus* and *P. hispidulopsis*, two species also characterized by the absent to rare pleurocystidia and a cutis-like pileipellis (FIG. 1c). However, *P. hispidulus* can be distinguished by the (subglobose) broadly ellipsoid to ellipsoid basidiospores and the clavate and numerous cheilocystidia (Kühner and Romagnesi 1956, Vellinga and Schreurs 1985). *Pluteus hispidulopsis* differs from *P. karstedtiae* by the blackish pileus and the numerous and versiform cheilocystidia. In the molecular phylogenies (FIG. 1c) *P. karstedtiae* appears in the same clade as *P. hispidulus*, *P. hispidulopsis* and *Pluteus* sp. (*AJ841*) but is clearly different from all of these species by the morphological characters given above.

Pluteus necopinatus Menolli & Capelari, sp. nov. FIGS. 2q, r, 9
MycoBank MB810817

Diagnosis: Similar to *P. crinitus* but differing in the pinkish brown and less fibrillose pileus, slightly

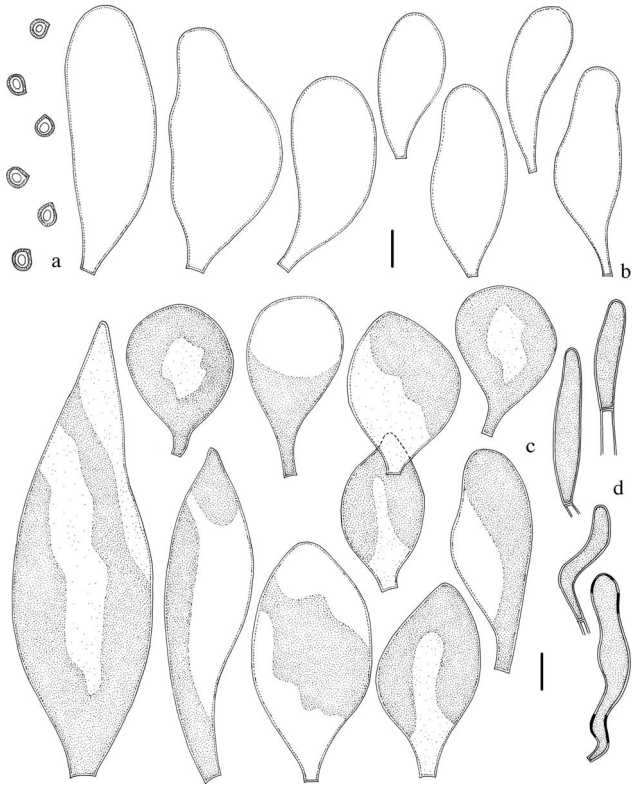

FIG. 9. *Pluteus necopinatus* (*FK1701* holotype). a. Basidiospores. b. Cheilocystidia. c. Pileipellis elements. d. Terminal elements in the stipitipellis. Bars = 10 μm.

broader basidiospores, broader and differently shaped cheilocystidia, non-filiform and shorter cystidioid elements in the pileipellis and distinct thick-walled hyphae of the stipitipellis.

Typification: BRAZIL. RIO DE JANEIRO: Teresópolis, Parque Nacional Serra dos Órgãos, Sede Teresópolis, 6 Jan 2011, *F. Karstedt et al. FK1701* (**holotype** SP445830).

Etymology: necopinatus (L.) means unexpected, surprising, in reference to the fact that the type material was found growing attached to a concrete wall.

Pileus 14 mm diam, convex to applanate, depressed at center, pinkish brown ($N_{40}A_{20}M_{30}$) and distinctly brownish at center ($N_{50}A_{60}M_{50}$); fully covered by small brownish fibrils; center entire and densely punctate-fibrillose, with the fibrils dissociating outside the central disk and exposing the pinkish background, finely punctate-fibrillose overall; margin slightly sulcate-striate with few short scales hanging over the edge. Lamellae free, pinkish ($N_{20}A_{30}M_{30}$), subdistant, ventricose, ≤3 mm broad, with concolorous edges and 1–2 lamellulae for every series of lamellae. Stipe 12 × 1(apex)–1.2(base) mm, slightly attenuated upward; with a small subbulbous base; central; surface translucent-pink ($N_{10}A_{20}M_{10}$), covered by small and dispersed brownish fibrils overall. Odor, flavor and context color not recorded.

Basidiospores [20/1/1] 5.0–5.5 × 5.0–5.5 μm (Q = 1.00–1.12; Qm = 1.05; Lm = 5.5 μm; Wm = 5.2 μm), globose to subglobose, inamyloid, hyaline, smooth, thick-walled, guttulate. Basidia 16.0–21 × 6.0–8.5 μm, clavate to ventricose-clavate, thin-walled, four-spored. Pleurocystidia absent. Cheilocystidia 37–74 × 12.5–30 μm, clavate to broadly lageniform or utriform, colorless and hyaline, thin-walled, moderately abundant. Lamellar edges sterile. Lamellar trama inverse, up to 25 μm wide, composed of thin-walled hyphae, 1.0–3.5 μm diam, interwoven by oleiferous hyphae up to 3.5 μm diam, hyaline. Pileus context undifferentiated, approx. 31 μm thick, composed mostly of oleiferous hyphae up to 3.5 μm diam, and thin-walled hyphae, 1.0–3.5 μm diam, hyaline. Pileipellis a transition between hymeniderm and epithelium, intermixed by cystidioid elements, composed of one layer of subglobose, spheropedunculate or clavate to broadly fusiform cells, 39–65 × 24–32 μm, with narrowly fusiform cystidioid elements, 72–125 × 20–37 μm, thin-walled, mostly with evenly concentrated brownish intracellular pigment or sometimes almost colorless. Caulocystidia apparently absent but with some distinct terminal members of the stipitipellis organized in fascicles of irregular and slightly to moderately thick-walled hyphae, 28–50 × 3.5–8.5 μm, filled with evenly dissolved brownish intracellular pigment and sometimes with encrusted wall in some points. Clamp connections absent in all parts examined.

Habit and habitat: Solitary on a concrete wall, within a fragment of dense ombrophilous forest, part of the Atlantic Forest domain.

Comments: Pluteus necopinatus is morphologically related to a few other species characterized by the absence of pleurocystidia and a truly hymeniform or a strict cellulodermal pilepellis that are intermixed with cystidioid elements (viz. *P. brunneocrinitus*, *P. crinitus*, *P. seticeps*, *P. thomsonii*).

Pluteus brunneocrinitus and *P. crinitus* are morphologically different from *P. necopinatus* by all characteristics discussed (see discussion under these species). *Pluteus seticeps* differs by the pileus color (dark brown), the shorter cheilocystidia (18–50 × 11–35 μm), which are subglobose to sphaeropedunculate to pyriform to clavate-cylindrical, and the absence of distinct thick-walled terminal elements in the stipitipellis (Minnis and Sundberg 2010). *Pluteus thomsonii* differs by the highly reticulate-veined pileus and the presence of a long apical projection on the pleuro- and cheilocystidia and the pileipellis elements (Homola 1972, Orton 1986, Minnis and Sundberg 2010, Menolli et al. 2015).

The ITS sequence of *Pluteus* sp. *AJ838* (New Haven, Connecticut) is 96.9% identical to that of *P.*

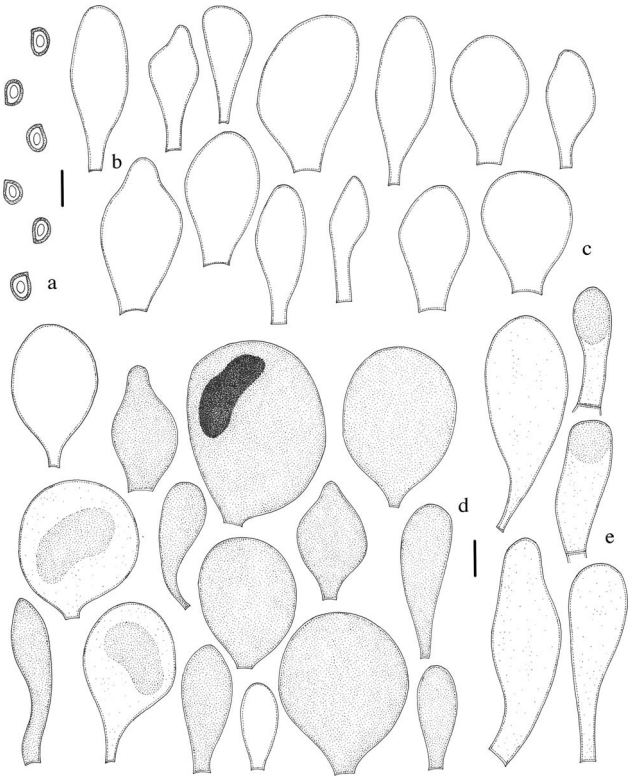

FIG. 10. *Pluteus paucicystidiatus* (*CP218* holotype). a. Basidiospores. b. Pleurocystidium. c. Cheilocystidia. d. Pileipellis elements. e. Caulocystidia. Bars = 10 μm.

necopinatus. Morphologically *AJ838* differs in the presence of pleurocystidia, differently shaped and more variable pileipellis elements and longer terminal elements in the stipitipellis (A. Justo unpubl). *Pluteus necopinatus* and *Pluteus* sp. (*AJ838*) appear in the podospileus clade (FIG. 1b) and are not closely related to the thomsonii clade (FIG. 1c).

Pluteus paucicystidiatus, Menolli, Justo & Capelari, sp. nov. FIGS. 2a–e, 10
MycoBank MB810818

Diagnosis: Similar to *P. insidiosus* in the pileus color and size and shape of the basidiospores and pileipellis cells but differing in the distinctly sulcate-striate and rugose-venose pileus and the absence of long apical projections on the cheilocystidia.

Typification: BRAZIL. SÃO PAULO: Iporanga, Parque Estadual Turístico do Alto Ribeira, Núcleo Ouro Grosso, 21 Mar 2007, *C. Puccinelli et al. CP218* (**holotype** SP394383).

Etymology: pacicystidiatus from the composition of the Latin words *pauci*, *cystidia* and the suffix *atus* that means having few cystidia; the name refers to the paucity of pleuro- and cheilocystidia.

Pileus 10–20 mm diam, shallowly and broadly obtusely conical to broadly convex then applanate, dark brown (6F6-8) on disk, slightly paler toward the margin and sometimes splitting, rugose to venose at center; margin brown to light brown (6E7-8) and sulcate-striate over at least one-third of the radius. Lamellae free, white then pinkish grayish orange (6A-B3), close to crowded, with concolorous edges and 1–3 lamellulae for each lamella. Stipe 20–30 × 1.5–2 mm, almost equal; central; white to translucent, finely pruinose mainly on the lower half. Odor, flavor and context color not recorded.

Basidiospores [20/1/1] 6.0–7.5 × 5.0–6.0 μm (Q = 1.21–1.24; Qm = 1.22; Lm = 6.9 μm; Wm = 5.7 μm), broadly ellipsoid, inamyloid, hyaline, smooth, thick-walled, guttulate. Basidia 17.5–24 × 6.0–6.5 μm, versiform, thin-walled, four-spored. Pleurocystidia almost absent, only one single clavate element (44 × 15.0 μm) was found in one of many mounts. Cheilocystidia, 31–45 × 10.0–25 μm, clavate to narrowly fusiform or narrowly lageniform to almost utriform, colorless and hyaline, thin-walled, rare to almost absent in some mounts. Lamellar edges subheteromorphous with few basidia and many basidioles but not differentiated in cystidioid elements. Lamellar trama inverse, approx. 12.5 μm wide, composed of thin-walled hyphae, 3.5–8.5(–11.0) μm diam, interwoven by oleiferous hyphae up to 5.0 μm diam, hyaline. Pileus context undifferentiated, up to 75 μm thick, composed predominately of oleiferous hyphae up to 6.0 μm diam and intermixed with thin-walled hyphae, 3.5–8.5 μm diam, hyaline. Pileipellis a transition between hymeniderm and epithelium up to 50 μm thick, individual elements (23–)30–50 × 10.0–37 μm, mostly sphaeropedunculate but a few resemble the cheilocystidia, clavate to narrowly fusiform or almost utriform, filled with dissolved or sometimes condensed brownish intracellular pigment. Caulocystidia 22–68 × 12.5–27 μm, clavate or broadly lageniform, thin-walled, filled with condensed or dissolved pale yellow content. Clamp connections absent in all parts examined.

Habit and habitat: Solitary to subcespitose in clusters of two or three basidiomata on rotten hardwood logs. In a fragment of dense ombrophilous montane forest, part of the Atlantic Forest domain.

Comments: Pluteus paucicystidiatus is characterized by the almost complete absence of cystidia and by the centrally rugose to venose pileus with a sulcate-striate margin. It resembles some species in stirps *longistriatus* (Singer 1986) including *P. longistriatus* (Peck) Peck, *P. neophlebophorus* Singer, *P. sanctixaverii* Singer, *P. variipes* Singer and *P. oligocystis* Singer. However, all these taxa, including *P. neophlebophorus* and *P. sanctixaverii* that are most similar to *P. paucicystidiatus* due to the rugose-venose pileus, have abundant cystidia and a pileipellis intermixed with cystidioid elements (Singer 1959).

Furthermore, *P. longistriatus* is now accepted in *Pluteus* sect. *Hispidoderma* (Justo et al. 2011a, b).

Other species without cystidioid elements in the pileipellis and absent to rare pleurocystidia invited comparison to *P. paucicystidiatus* (viz. *P. crenulatus*, *P. diettrichii*, *P. insidiosus*, *P. poliocnemis*, *P. cebolinhae*).

Pluteus crenulatus clearly differs from *P. paucicystidiatus* by the deeply sulcate pileus with a crenulate margin and the globose basidiospores. *Pluteus crenulatus* is closest to *P. cebolinhae* on an external branch to all other taxa in *Pluteus* sect. *Celluloderma* (except *P. diettrichii*, *P. poliocnemis*) in the phylogenetic analyses (FIG. 1a).

Pluteus diettrichii and *P. poliocnemis* have longer, ellipsoid to oblong basidiospores (Vellinga and Schreurs 1985). They are commonly found on soil and are apparently restricted to Europe (Kühner and Romagnesi 1956, Vellinga and Schreurs 1985, Orton 1986, Justo and Castro 2007). In the molecular phylogenies both taxa appear in an isolated position, as sister of all other species in section *Celluloderma* (FIG. 1a).

Pluteus insidiosus is likely the species morphologically closest to *P. paucicystidiatus* due to the pileus color and size and shape of the basidiospores and pileipellis cells (Vellinga and Schreurs 1985). However, according to Vellinga and Schreurs (1985), *P. insidiosus* has characteristic cheilocystidia with a long apical projection and in addition the pileus is not distinctly sulcate or rugose-venose as in *P. paucicystidiatus*. Finally *P. cebolinhae* has a deeply plicate-sulcate pileus and dimorphic basidia that differ from *P. paucicystidiatus* and they are distantly related (FIG. 1a).

In the phylogenetic analyses of Justo et al. (2011b), *P. paucicystidiatus* (as *Pluteus* sp. IV SP394383) was included in the romelli/aurantiorugosus clade as sister of all species with yellow-orange basidiomata and also separate from other species with a pileipellis truly hymeniform or a strict celluloderm and that are lacking cystidia, such as *P. diettrichii*. This position was confirmed in the analysis of Justo et al. (2012) that showed the relationship of *P. paucicystidiatus* with *P. stenotrichus* and now, based on the current analyses (FIG. 1a), we also reveal a relationship with *P. iguazuensis* from Amazonas (Brazil) and an unidentified collection (*AJ842*) from the Dominican Republic.

ACKNOWLEDGMENTS

The authors thank the curators of INPA, RSPF and SP for the loan of the specimens studied; Patrick Leacock for the presubmission review; Noemia Kazue Ishikawa and Iuri Goulart Baseia for helping and all assistance during the expeditions to Manaus and Natal, respectively; N.K. Ishikawa and I.G. Baseia, as well as Fernanda Karstedt Carla Puccinelli, Adriana M. Gugliotta and Dennis E. Desjardin, also are thanked for photographs and/or collecting some specimens used in this study; David S. Hibbett for receiving N. Menolli Jr in his lab and for allowing the generation of some sequences; Flávia Ribeiro Santos for helping with DNA extraction of some samples; Klei R. Sousa for inking the line drawings; Francisco Kuhar for helping with the suggestions and composition of the new names. N. Menolli Jr. and M. Capelari thank Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP grants 04/04319-2, 09/53272-2), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES-PNADB grant 23038.000043/2010-43) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq fellowships) for financial support. A. Justo acknowledges support from the National Science Foundation grant DEB 0933081.

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