Records and new species of *Pluteus* from Brazil based on morphological and molecular data

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Ten species of *Pluteus* are described and illustrated from specimens recently collected at three remnants of Atlantic forest in São Paulo State, Southeast Brazil. Two new taxa are proposed: *Pluteus aureovenatus* and *P. dominicanus* var. *hyalinus*, as well as a new status, *P. sublaevigatus* to *P. chrysophlebus* subsp. *sublaevigatus*. The occurrence of *P. fulgineonevosus*, *P. jamaicensis*, and *P. riberaletensis* var. *conquistensis* represent the first records from Brazil. *Pluteus albostipitatus*, *P. fluminesis*, *P. harrisii* and *P. xylophilus* are also described and illustrated. In addition, a molecular study was performed based on parsimony analyses of nLSU and ITS + 5.8S sequences of Brazilian and other *Pluteus* species. The generated phylogenetic trees revealed a well-supported clade with all *Pluteus* species. In the ITS + 5.8S analyses, it was possible to identify a clade with all species of section *Hispiderma* and another including members of both sections *Hispiderma* and *Celluloderma*. In the ITS + 5.8S analyses, it was possible to identify three major clades, each of them corresponding to the majority representatives of sections *Celluloderma*, *Hispiderma* and *Pluteus*.

**Keywords:** Agaricales; Basidiomycota; ITS; nLSU; Phylogeny; Pluteaceae; South America; Taxonomy

**Introduction**

*Pluteus* Fr. is a large and widely distributed genus of presumably saprophytic and non-ectomycorrhizal species (Singer 1986; Banerjee and Sundberg 1995). The genus as defined by Singer (1986) is characterised by free lamellae, pinkish spore print, absence of both annulus and volva, inamyloid basidiospores, cystidia metuloid or not and inverse hymenophoral trama. However, recently Minnis et al. (2006) and Corriol and Moreau (2007), supported by molecular and morphological data, transferred to *Pluteus* two annulate species previously classified in the genus *Chamaeota* (W.G. Sm.) Earle. Thus, the concept of *Pluteus* must be amended to also accommodate species with partial veil.

The infrageneric classification of *Pluteus* currently in use subdivides the genus into three sections (*Pluteus*, *Hispiderma* Fayod and *Celluloderma* Fayod) based on morphological features such as the structure of the pileipellis and characteristics of the pleurocystidia (Singer 1958, 1986). A hymeniform layer of spheropedunculate cells characterise the pileipellis of the section *Celluloderma*, while the other two sections exhibit pileipellis with elongate, pilose or hyphous elements. Members of the section *Pluteus* differ from those of section *Hispiderma* by the presence of metuloids and thin-walled pleurocystidia, respectively (Singer 1958, 1986). Singer (1956, 1958, 1986) also considered two subsections in section *Celluloderma*: Mixtini Singer and *Eucellulodermini* Singer, differed by a pileipellis composed of uniform or heteromorphic elements, respectively.

Vellinga and Schreurs (1985) also proposed an infrageneric classification for *Pluteus* that maintains the section *Pluteus* according to Singer’s classification and introduces the new section *Villosi* Schreurs & Vellinga to include the species with pileipellis differentiated as a cutis combined with thin-walled pleurocystidia. The section *Celluloderma* also was maintained but divided into three subsections according to the shape of the pileipellis cells. The two subsections, *Mixtini* and *Eucellulodermini*, proposed by Singer (1956, 1958, 1986), were maintained and a third subsection was proposed, *Hispidermini* (Fayod) Vellinga & Schreurs, which is characterised by a trichodermic pileipellis or by a hymeniderm with cylindrical to fusiform elements, grouping mostly members of section *Hispiderma sensu* Singer (Singer 1958, 1986).

The knowledge of *Pluteus* in Brazil started with Hennings (1900) with the description of *P. scruposus* Henm. from Mato Grosso State. Later, Hennings (1904a, b) described *P. cervinus* var. *griseoviridis* Henm. from São Paulo State and *P. termatum* Henm. from Amazonas State. Most of these early species described from Brazil were not preserved and may not be *Pluteus*, as mentioned by Saccardo and Trotter (1912), who recognised that *P. termatum* was a possible synonym of *Collybia eurhiza* (Berk.) Höhn., and by Singer (1958), who established *P. scruposus* as a synonym of *Oudemansiella canarii* (Jungh.) Höhn. and *P. termatum* as a probable Lepiota sp.

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Rick (1907, 1919, 1930, 1938, 1961) also described and recorded some problematic species. In total, 21 Pluteus taxa from Brazil (Rio Grande do Sul State), including six species (P. cristatusus Rick, P. fibrillosus Rick, P. leptonia Rick, P. sensitivus Rick, P. straminellus Rick, and P. velatus Rick) and two varieties [P. exigus var. venosus Rick and P. nanus var. podospileus (Sacc. & Cub.) Rick] with Brazilian types. However, Singer (1953, 1958) considered several of Rick’s collections as misidentifications, nomina dubia, synonyms, or species of other genera.

Another 10 Pluteus taxa described as new from Brazilian materials were described by Bresadola (1920) and Singer (1953, 1956, 1958, 1973, 1989): P. amazonicus Singer, P. cervinus var. brasiliensis Bres., P. fluminensis Singer, P. hylaeicola Singer, P. melanotomatus Singer, P. paraensis Singer, P. riograndensis Singer, P. subfibrillosus Singer, P. umbrinoalbidus Singer, and P. varzeicola Singer. Recently, Menolli and Capelari (2010) described two new species (P. densifibrillosus Menolli & Capelari and P. puttemansii Menolli & Capelari) from materials collected in the Atlantic forest in São Paulo State.

Grandi et al. (1984), Singer (1984, 1989), Raithelhuber (1991), Stijve and Meijer (1993), Stijve (1995), Pegler (1997), Meijer (2001, 2006, 2008), and Drechsler-Santos et al. (2007) also contributed to increasing the knowledge about Pluteus in Brazil. However, these works are just lists and do not include complete descriptions of the species.

Wartchow et al. (2004, 2006) recorded and provided a complete description of P. albotipitatus (Dennis) Singer, P. aquosus Singer, P. beniensis Singer, P. globiger Singer, P. nigrolineatus Murrill, and P. thomsonii (Berk. & Broome) Dennis for Rio Grande do Sul State. However, Rodriguez et al. (2008) considered that the European species P. thomsonii recorded by Wartchow et al. (2004) is probably P. neotropicalis Rodr.-Alcánt., which was recently described (Rodriguez et al. 2008) based on Mexican material previously misidentified as P. thomsonii (Rodriguez and Guzmán-Dávalos 1999).

Moreover, Meijer (2008) and Menolli and Capelari (2010) recently provided complete descriptions of one species [P. xylophilus (Speg.) Singer] from Paraná State and four [P. densifibrillosus, P. longistriatus (Peck) Peck, P. puttemansii and P. umbrinoalbidus] from São Paulo State, respectively. Meijer (2008) also mentioned that 34 species of Pluteus occur in Paraná State, but he did not mention the names of them. In addition, in his major papers including Pluteus (Stijve and Meijer 1993, Meijer 2001, 2006, 2008), it was only possible to localize about 24 Pluteus taxa. According to Meijer (2009, personal communication), the remaining 10 taxa mentioned are different from any other known Pluteus species and so far they have not been formally described.

All records of Pluteus from Brazil are very confusing and incomplete due to poor descriptions, synonyms, misidentifications, the lack of preserved material, and lists lacking descriptions. So far, 70 epithets have been recorded, distributed over nine States (Amazonas, Bahia, Mato Grosso, Pará, Paraná, Rio de Janeiro, Rio Grande do Sul, Rondônia, and São Paulo), with 23 of them represented by Brazilian types. However, only 23 are known for certain or are at least cited with a complete description. The remaining represent misidentifications, synonyms, species of other genera, unpreserved specimens, or are presented in lists.

Molecular studies involving Pluteus are restricted and they do not include South American species. Moncalvo et al. (2002) and Matheny et al. (2006) conducted a broad study of Agaricales, wherein the Pluteus clade was superficially discussed. Later, Minnis et al. (2006) added a Chamaeota sequence to the nLSU analysis done by Moncalvo et al. (2002) and proposed a new combination in Pluteus. Malysheva et al. (2009) and Rodriguez et al. (2009) performed analyses of the ITS + 5.8S region with the placement of new species or new records from Russia and Mexico, respectively.

Here, we report, describe and illustrate 10 species of Pluteus recently collected in the remnants of the Atlantic forest in Southeast Brazil. We proposed two new taxa, a new status and three new records for Brazil. Moreover, for the first time in Pluteus, molecular analyses with sequences of South American species based on nLSU and ITS + 5.8S data are presented.

**Material and methods**

**Sampling**

The studied materials were collected at the Parque Estadual da Cantareira, São Paulo city; Parque Estadual das Fontes do Ipiranga, São Paulo city; and Reserva Biológica de Paranapiacaba, Santo André city, all of them are remnants of the Atlantic forest in São Paulo State, Southeast Brazil. When necessary, materials from other localities were examined.

**Morphological study**

The macroscopic descriptions and illustrations of basidiomata were based on fresh material. Colour terms are according to Küppers (1979). For microscopic analyses, the dried materials were rehydrated in 70% ethanol followed by 5% KOH or Melzer’s reagent. All microscopic illustrations were made with the aid of a drawing tube. The notation “their collections” 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”. The basidiospores were measured in lateral view, always 20 basidiospores from each basidioma, and the terms denoting their shapes were according to Bas (1969). Q represents the range of the length/width quotient for all the measured spores, Qm represents the average of all
computed Q values for all the measured basidiospores and Lm (Wm) represents the average of all lengths (widths) of the measured basidiospores. The terms used to characterize the pleurocystidia as Cervinus- and Magnus-types are according to Singer (1958) and Banerjee and Sundberg (1995). For the pileipellis cells, the length of the pedicel was included in the measurement of the sphaeropedunculate cells, and its length is also reported separately. A separate measurement is given when an apical projection was present. The specimens and the voucher of the sequences are deposited at the herbarium SP. Generic and infrageneric concepts follow Singer (1986); for comparison, the classification proposed by Vellinga and Schreurs (1985) was also considered.

**Molecular study**

**DNA extraction**

Procedures for DNA extraction were done according to an adapted protocol by Zolan and Pukkila (1986) using lyophilised basidiomata previously ground to a fine powder in liquid nitrogen. The sample was resuspended in 50 μl of TE, incubated at 37 °C for 30 min after the addition of RNAsé (0.01 mg/μl), and stored at −20 °C.

**PCR amplification and DNA sequencing**

The ITS + 5.8S region was amplified using the primer set ITS1-F and ITS4 (Vilgalys and Hester 1990; White et al. 1990; Gardes and Bruns 1993), and the nLSU rDNA was amplified using the primer set LR0R and LR5 (Moncalvo et al. 2000). The PCR reaction, containing 2.0 μl of Platinum® Taq DNA Polymerase (Invitrogen), 0.2 mM of each dNTP, 1.5 mM of MgCl₂, and 0.2 μM of each primer of the selected region in a total of 100 μl, was performed in a Eppendorf thermocycler, using the following program: 94 °C for 5 min, 40 cycles at 94 °C for 40 s, 55 °C for 30 s, and 72 °C for 60 s, and then 72 °C for 5 min. Amplification products were purified using the PureLink PCR Purification Kit (Invitrogen). DNA sequencing reactions were performed with the DYEnamic ET Dye Terminator Kit in a MegaBACE 1000 DNA sequencer (GE Healthcare) according to the manufacturer’s instructions. The samples were sequenced in both directions. The sequences were deposited in GenBank (Table 1).

**Data analysis**

To elucidate the relationship of *Pluteus* species found in São Paulo State, Brazil, we conducted phylogenetic analyses using nLSU and ITS + 5.8S sequences determined in this study with sequences available in GenBank (Table 1). The sequences were automatically aligned using the Clustal W version (Thompson et al. 1994) in the BioEdit version 7.0.5.3 (Hall 1999). Parsimony analysis was performed with PAUP version 4.0b10 (Swofford 2003). Parsimony trees were obtained by heuristic searches with simple sequence addition in 1000 replicates, employing tree-bisection-reconnection (TBR) branch-swapping algorithm. Characters from the extreme 5' and 3' ends of the sequences were deleted from all taxa to obtain individual datasets that had identical start and end positions, gaps were treated as missing, all characters were unordered and equally weighted, and multistate taxa was interpreted as uncertainty. Starting trees were obtained via stepwise addition, with one tree held at each step during stepwise addition and the steepest descent option not in effect. Also, the initial MaxTrees were set to auto-increase, branches of zero length were collapsed (creating polytomies), and MulTrees options were in effect.

Branch and branch node supports were determined using 1000 BS replicates. Estimated levels of homoplasy and phylogenetic signal (retention and consistency indexes) were determined. The generated trees were rooted to *Limacella illinita* (Fr.) Maire, *Auricularia polytricha* (Mont.) Sacc. and *Volvariella volvacea* (Bull.) Singer as the outgroup taxa for nLSU analysis following Minnis et al. (2006), and *V. gloiocephala* (DC.) Boekhout & Enderle and *V. volvacea* for the ITS + 5.8S analysis (Table 1).

**Results and discussion**

**Sequence data from the nLSU region**

In the nLSU analysis, 29 sequences of 26 taxa plus three outgroups were aligned. The alignment dataset consisted of 1304 characters, including gaps. Prior to analysis, 515 characters from 5' and 3' ends of the sequences were excluded. Of the 789 characters included in the analysis, 590 characters were constant, 109 variable characters were parsimony-uninformative and 90 were parsimony-informative.

The heuristic searches retained 24 equally most parsimonious trees resulting in a bootstrap 50% majority-rule consensus tree with the following scores: tree length = 380 steps, CI = 0.592, RI = 0.703, RC = 0.416, and HI = 0.408.

The MP tree generated from the nLSU sequence data (Figure 1) revealed a well-supported clade (89% BS) including all *Pluteus* species. Two clades can be distinguished with low BS support: one clade (58% BS) clustering species that belong to section *Pluteus*, and the other revealing a polytomy including members of sections *Hispidoderma* and *Celluloderma* (51% BS).

**Sequence data from the ITS + 5.8S region**

In the ITS + 5.8S analysis, 48 sequences of 31 taxa plus three outgroups were aligned. The alignment dataset consisted of 1397 characters, including gaps and portions of
Table 1. Collection data and GenBank accession number of the *Pluteus* and outgroups taxa analysed.

| Species                        | ITS + 5.8S | LSU    | Voucher/ Strain | Country   | Reference                                |
|--------------------------------|------------|--------|-----------------|-----------|------------------------------------------|
| *Auricularia polytricha*       | –          | AF261554 | HN4076          | –         | Moncalvo et al. 2002                     |
| *Limacella illinita*           | –          | AF261439 | VT8.96           | –         | Moncalvo et al. 2002                     |
| *Pluteus admirabilis*          | –          | AF261577 | DAOM193532      | –         | Moncalvo et al. 2002                     |
| *P. albostipitatus*            | FJ816656   | –      | NMJ128          | Brazil    | This paper                               |
| *P. albostipitatus var. poliobasis* | FJ816661   | FJ816647 | FK782           | Brazil    | This paper                               |
| *P. atromarginatus*            | DQ494687   | –      | Isolate 113     | Mexico    | Rodriguez et al. 2009                    |
| *P. aromarginatus*             | EF530926   | –      | UBC F16254      | Canada    | Denis et al. Not published               |
| *P. aurantiorugosus*           | –          | AF261579 | DAOM197369      | –         | Moncalvo et al. 2002                     |
| *P. brunneoradiatus*           | –          | AF261570 | JB97/19         | –         | Moncalvo et al. 2002                     |
| *P. cervinus*                  | FJ774088   | –      | LE217575        | Russia    | Malyshева et al. 2009                    |
| *P. cervinus var. cervinus*    | EU486448   | –      | UBC F16293      | Canada    | Denis and Beeree. Not published          |
| *P. christophlebius*           | AF261581   | –      | DAOM190194      | Canada    | Moncalvo et al. 2002                     |
| *P. diverticulatus*            | FJ375247   | –      | Isolate 242     | France    | Rodriguez et al. 2009                    |
| *P. dominicanus var. hyalinus* | FJ816665   | FJ816651 | FK1058          | Brazil    | This paper                               |
| *P. ephbeus*                   | –          | AF261574 | JB97/23         | –         | Moncalvo et al. 2002                     |
| *P. exigus*                    | FJ774074   | –      | LE227554        | Russia    | Malyshева et al. 2009                    |
| *P. fenzlii*                   | FJ774082   | –      | LE246083        | Russia    | Malyshева et al. 2009                    |
| *P. flavinensis*               | FJ816655   | –      | NMJ1127         | Brazil    | This paper                               |
| *P. fuligineovenosus*          | FJ816662   | –      | FK826           | Brazil    | This paper                               |
| *P. granulatus*                | FJ774086   | –      | LE212990        | Russia    | Malyshева et al. 2009                    |
| *P. harrisii*                  | FJ816654   | FJ816644 | NMJ122          | Brazil    | This paper                               |
| *P. horakianus*                | FJ816666   | FJ816652 | FK1066          | Brazil    | This paper                               |
| *P. jamaicensis*               | FJ816657   | –      | NMJ1130         | Brazil    | This paper                               |
| *P. leoninus*                  | FJ774079   | –      | LE212090        | Russia    | Malyshева et al. 2009                    |
| *P. mammillatus*               | –          | DQ451549 | ASM 7916        | –         | Minnis et al. 2006                      |
| *P. namus*                     | FJ774081   | –      | LE213093        | Russia    | Malyshева et al. 2009                    |
| *P. nigrolineatus*             | FJ375245   | –      | Isolate 114     | Mexico    | Rodriguez et al. 2009                    |
| *P. pallidus*                  | –          | AF261569 | JB97/27         | –         | Moncalvo et al. 2002                     |
| *P. petalatus*                 | –          | FJ816571 | JB93/3          | –         | Moncalvo et al. 2002                     |
| *P. plautus*                   | FJ774078   | –      | LE217548        | Russia    | Malyshева et al. 2009                    |
| *P. primus*                    | FJ375243   | –      | Isolate 222     | Mexico    | Rodriguez et al. 2009                    |
| *P. petasatus*                 | –          | AF042611 | JB91/21         | –         | Moncalvo et al. 2000                     |
| *P. plautus*                   | FJ375242   | –      | Isolate 100     | Mexico    | Rodriguez et al. 2009                    |
| *P. plautus*                   | FJ774076   | –      | LE213024        | Russia    | Malyshева et al. 2009                    |
| *P. podospileus*               | FJ774085   | –      | LE213015        | Russia    | Malyshева et al. 2009                    |
| *P. pouzarianus*               | –          | AF261568 | JB94/26         | –         | Moncalvo et al. 2002                     |
| *P. primus*                    | –          | AF042610 | JB94/24         | –         | Moncalvo et al. 2000                     |
| *P. riberaaltensis var. conquistensis* | FJ816648   | –      | FK1043          | Brazil    | This paper                               |
| *P. romellii*                  | –          | AF261575 | JB97/26         | –         | Moncalvo et al. 2002                     |
| *P. salicinus*                 | FJ774087   | –      | LE215427        | –         | Malyshева et al. 2009                    |

(Continued)
nLSU and/or nLSU. Prior to analysis, 898 characters from the 5′ and 3′ ends of the sequences were excluded. Out of the 499 characters included in the analysis, 153 variable characters were parsimony-uninformative and 244 were parsimony informative.

The heuristic searches retained two equally most parsimonious trees resulting in a bootstrap 50% majority-rule consensus tree with the following scores: tree length = 1425 steps, CI = 0.451, RI = 0.711, RC = 0.321, and HI = 0.549.

The MP tree generated from the ITS + 5.8S sequence data also revealed a well-supported clade (82% BS), including all *Pluteus* species, divided into three major clades (Figure 2). Species from sections *Pluteus* and *Celluloderma* are clustered into two sister-clades with 85 and 73% BS support, respectively. In an external branch of these clades there is a third clade that groups the majority species from section *Hispidoderma* with 64% BS support.

**Phylogenetic analyses from the rDNA sequence data**

It was possible to confirm the monophyletic origin of *Pluteus* from both analyses (nLSU and ITS + 5.8S), as also shown by Moncalvo et al. (2002) and Matheny et al. (2006). Moreover, especially in the ITS + 5.8S (Figure 2) it was possible to recognize three major clades, each one corresponding to the sections proposed by Singer (1958, 1986).

All species from section *Pluteus* clustered in the same clade (Figures 1 and 2), forming a well-supported group in accordance with the infrageneric classification of Singer (1958, 1986).

The clustering of species from section *Celluloderma* in one clade was observed in both analyses (Figures 1 and 2). The nLSU analysis for section *Celluloderma* (Figure 1) showed a polytomy within a clade with low BS support (51%) including members of section *Hispidoderma*, such as *P. umbrosus* (PERS.) P. Kumm. and *P. riberaaltensis* var. *conquisitensis* Singer, and also including members of the section *Villosi*, viz. *P. ephebeus* (Fr.) Gillet, and species with partial veil traditionally classified in the genus *Chamaeota*, viz. *P. mammillatus* (Longyear) Minnis, Sundb. & Methven. The relationship between members of section *Celluloderma* and section *Hispidoderma* was also demonstrated by Moncalvo et al. (2002) in a well-supported clade (92% BS).

In the ITS + 5.8S analysis (Figure 2), the majority members of the section *Celluloderma* are clustered in a branch connected to section *Pluteus* clade, while the members of the section *Hispidoderma* are mostly in an external branch from the clades with members of the sections *Pluteus* and *Celluloderma*. Some species formerly classified in the section *Hispidoderma*, such as *P. ephebeus*, *P. exigus* (Pat.) Sacc. and *P. fenzlii* (Schulzer) Corriol & P.-A. Moreau (an annulated species), formed a clade with all species of section *Celluloderma*.

For the members of the section *Hispidoderma* (including *Villosi* and *Chamaeota* members), it will be necessary to perform a detailed study to elucidate the evolutionary history of the group and to find characters that are shared with other members of section *Celluloderma* (or also of section *Pluteus*, if the position of *P. albostipitatus* and *P. nigrolineatus* are considered, as discussed below). Until now, it has not been possible to recognize the monophyly of the section *Hispidoderma* as proposed by Singer (1958, 1986), and perhaps this represents an artificial group delimited by morphological characters. However, one should not disregard the possibility that the section *Hispidoderma* is a subsection of *Celluloderma*, as proposed by Vellinga and Schreurs (1985).

Table 1. (Continued)

| Species                | ITS + 5.8S | LSU       | Voucher/ Strain | Country | Reference                        |
|------------------------|------------|-----------|-----------------|---------|----------------------------------|
| *P. semibalbosus*      | FJ774080   | –         | LE227534        | Russia  | Malysheva et al. 2009           |
| *P. sublaevigatus*     | FJ816667   | FJ816535  | FK1805          | Brazil  | This paper                      |
| *P. thomsonii*         | FJ774084   | –         | LE234787        | Russia  | Malysheva et al. 2009           |
|                        | FJ737525   | –         | Isolate 85      | France  | Rodríguez et al. 2009           |
|                        | FJ7375253  | –         | Isolate 155     | Spain   | Rodríguez et al. 2009           |
| *P. umbrosus*          | –          | AF261580  | NMJ143          | Brazil  | This paper                      |
| *P. xylophilus*        | FJ816659   | FJ816645  | AF042612        | Brazil  | This paper                      |
|                        | FJ816660   | FJ816646  | NMJ147          | Brazil  | This paper                      |
| *Pluteus* sp.          | –          | AF2361576 | JMCR.124        | –       | Moncalvo et al. 2002           |
|                        | –          | AF042612  | JM96/28         | –       | Moncalvo et al. 2000           |
| *Volvariella gloiocephala* | FJ375254 | –         | NMJ132          | Brazil  | This paper                      |
|                        | DQ494701   | –         | PMB2272         | USA     | Matheny et al. 2006             |
| *Volvariella volvacea* | –          | AF261531  | Jmleg.SRL       | –       | Moncalvo et al. 2002           |
|                        | –          | –         | OE-140          | –       | Singh et al. 2003               |

*Voucher material misidentified as *P. pallidus* (LAU!), see discussion in the text.*
In the ITS +5.8S analysis (Figure 2), it is possible to observe the presence of two species currently classified in section *Hispidoderma* (*P. albostipitatus* and *P. nigrolineatus*) but positioned in the section *Pluteus* clade. Rodríguez et al. (2009) had already demonstrated the affinities between section *Pluteus* and section *Hispidoderma* (89% BS) due to the presence of these species in the same clade with other representative species of section *Pluteus*. Morphological characters, such as the presence of a slightly thick-walled pleurocystidia and sometimes with poorly developed prongs and/or a repent epicutis, could be used to make assumptions about the position of *P. albostipitatus* and *P. nigrolineatus* in the section *Pluteus* (Figure 2) and to consider that these species probably represent a transition between sections *Hispidoderma* and *Pluteus* (see discussion under *P. albostipitatus*). However, it is not possible to confirm this assumption with ITS + 5.8S analysis because the internal structure of the section *Pluteus* is unresolved. A molecular study is necessary.

Figure 1. Phylogenetic tree generated by MP analysis of partial LSU sequences. The tree is rooted using *Auricularia polytricha*, *Limacella illinita* and *Volvariella volvacea*. The BS numbers are shown before the nodes. *Voucher material misidentified as *P. pallidus*, see discussion in the text.
which would show a well-resolved topology for section *Pluteus*, placing these species as sister group of all other species in section *Pluteus*, to confirm this phylogenetic relation (Justo 2009, personal communication).

In both analyses, it is possible to recognize some species or species_complexes that need revision to confirm the scope and/or the monophyly of the section. The nLSU analysis showed the presence of *P. pallidus* Homola, a species of section *Celluloderma*, in the section *Pluteus* clade (Figure 1). This fact was also observed by Moncalvo et al. (2002) but the authors did not comment the position of *P. pallidus* and considered the section *Pluteus* as a well-supported group. However, a re-examination of the voucher material, demonstrated that it actually represents a species of section *Pluteus* because it has the typical horned and metuloidal pleurocystidia. This was confirmed by Bonnard...
In the clade including members of the Cervinus group (section Pluteus clade), based on the ITS + 5.8S analysis (Figure 2), there is also some species for which identification must be revised. Two sequences of P. cervinus (Schaeff.) P. Kumm., representative (EU486448 and FJ774088) of different countries (USA and Russia, respectively), clustered in a well-supported clade (84% BS), while the Mexican material of P. cervinus (FJ375241) also clustered in a well-supported clade (90% BS), but with sequences of P. pellitus (Pers.) P. Kumm. and P. petasatus (Fr.) Gillet, both from Mexico (FJ375243 and FJ375242, respectively), and with another sequence of P. petasatus from the Czech Republic (AF085495, origin of voucher strain CBS441.85 obtained at http://www.cbs.knaw.nl/databases/). Rodríguez et al. (2009) already reported molecular affinities (96% BS) between their sequences of P. cervinus, P. pellitus and P. petasatus, and also mentioned macroscopic similarities between them. Previous morphological relations between P. pellitus and P. petasatus were indicated by Vellinga and Schreurs (1985) and Rodríguez and Guzmán-Dávalos (2000). The sequence of P. pellitus from Russia (FJ774078), which probably represents this species, formed a separate branch from the Mexican sequence of P. pellitus. The sequences of P. petasatus clustered in a well-supported clade (90% BS), despite their origins being from different regions of the world (Mexico and Czech Republic).

Considering these data, it is probable that the Mexican materials forming the P. cervinus/pellitus/petasatus complex could represent only one species, most likely P. petasatus. Thus, the collections of all P. cervinus, P. pellitus and P. petasatus present in the analysis must be revised because sequences from different collections around the world and with the same identification are not grouped together or species with different names clustered in the same clade. Moreover, many species of the Cervinus group most likely represent a complex of species with morphological similarities, which means that different worldwide species are erroneously named with the same epithet, e.g. P. cervinus.

For the Celluloderma and Hispidoderma clades (Figure 2) some collections of P. romelli (Britzelm.) Sacc. and P. aurantiogrus (Trog) Sacc. also need revision to confirm their GenBank identification. The sequences of P. romelli (FJ774073, FJ375246 and AY854065) from different countries (Russia, Mexico and USA, respectively) were grouped in the same clade with P. aurantiogrus, P. aureovenatus Menolli & Capelari and P. sublaevigatus (Singer) Menolli & Capelari (both of the latter herein described) but in different branches. The three sequences of P. romelli need revision, especially the material from the USA (California), which segregated from the other P. romelli sequences and clustered, despite the low support (53% BS), with the morphologically different P. aureovenatus and P. sublaevigatus (see discussion under P. aureovenatus and P. sublaevigatus).

The Russian collection of P. aurantiogrus (FJ774077) also needs revision because it grouped with 100% BS with P. leoninus (Schaeff.) P. Kumm. in the section Hispidoderma clade (Figure 2). Both species, despite some ecological and macromorphological similarities pointed out by Malysheva et al. (2009), have different pileipellis structures and are consequently traditionally classified in different sections, Hispidoderma and Celluloderma, respectively. Malysheva et al. (2009) obtained the same support (100% BS) for these species groupings. However, considering this high support and that the other sequences of P. aurantiogrus (FJ375249 and FJ375246) from different countries clustered in another clade with all species of the section Celluloderma, it is likely that the Russian collection named as P. aurantiogrus in the GenBank actually represents P. leoninus.

The presence of P. semibulbosus (Lasch) Quél. in the section Hispidoderma clade and the clustering with P. plautus (Weinm.) Gillet (52% BS) should also be regarded with caution, because Singer (1986) considered the first as a member of section Hispidoderma, while Orton (1986) classified it in the section Celluloderma. These data are in accordance with Malysheva et al. (2009), whom already reported molecular affinities (96% BS) between them, and with Vellinga and Schreurs (1985), whom considered P. semibulbosus sensu Singer as synonymous of P. plautus, a member of section Hispidoderma. In addition, Vellinga and Schreurs (1985) considered P. semibulbosus sensu Orton as a P. inquilinus Romagn., which in fact is a member of section Celluloderma.

**Taxonomy**

*Pluteus alhostipitatus* (Dennis) Singer, *Lloydia* **21**: 240 (1959) (Figure 3).

≡ *Pluteus spilopus* var. *alhostipitatus* Dennis, Bull. Soc. Mycol. Fr. 69: 195, 1953.

Pileus 34–37 mm diam, plane, slightly to deeply umbo nate, light brown to greyish brown (N₉₀A₅₀M₄₀ to N₉₀A₅₀M₅₀), darker with coffee shades at the centre (N₉₀A₅₀M₆₀), covered by appressedly and radially arranged fibrils, more concentrated at the centre and dissolving outside of the central disc, finely pruinose at the centre, margin sulcate-striate. Lamellae free, white then pinkish, crowded, with lamellulae. Stipe 35–54 × 2(apex)-4(base) mm, slightly tapering towards the apex, central, occasionally flexuous, white to pale cream, with greyish to slightly silver base, slightly longitudinally striate, with scanty basal mycelium. Odour, taste, and flesh colour not recorded.
Basidiospores [40/2/2] (6.2–)7.5–10.0(−11.2) × 6.2–7.5 (−8.7) μm [Q = 1.00–1.29(−1.40); Qm = 1.14; Lm = 8.4 μm; Wm = 7.4 μm], globose to broadly ellipsoid, occasionally subglobose or ellipsoid, widely variable in form, especially among different collections, inamyloid, hyaline, smooth, thick-walled, sometimes guttulate. Basidia (20–)25–31(−35) × 8.7–12.5 μm, versiform to clavate, thin-walled, four-spored, sometimes with small scattered guttules. Pleurocystidia (39–)50–83(−92) × (11.2–)15.0–24 μm, slightly ventricose with a rounded to subcapitate apex or slightly strangled at the apex, thin- to relatively thick-walled, sometimes confused with a metuloid with a evenly thickened wall up to 1 μm wide, colourless, hyaline and moderately numerous. In some cases a second and rare type of pleurocystidia is observed, with two short lateral prongs, almost similar in size to the most common type, but rarely shorter in length with approximately 27 μm high. Cheilocystidia (25–)31–52(−55) × (6.2–)8.7–13.7(−15.0) μm, clavate, rarely slightly ventricose, sometimes with a well developed pedicel at the base, colourless, hyaline, thin-walled, abundant. Lamellar edge sterile. Lamellar trama inverse, up to 62 μm wide, composed of thin or slightly thick-walled hyphae, 2.5–10.0(−12.5) μm diam, hyaline. Pileus context undifferentiated, thin, approximately 38 μm thick, composed of thin- or slightly thick-walled hyphae, 3.7–10(−18.7) μm diam, hyaline. Pileipellis a repent epicutis up to 62 μm thick, composed of thin or slightly thick-walled hyphae, 2.5–6.2 μm diam, elongated, septe, with brown vacuolar content. Clamp connections absent in all parts examined.

Habitat and habit: Solitary, on wood.

Material examined: BRAZIL, São Paulo State, São Paulo city, Parque Estadual da Cantareira, Núcleo Engordador, 24 Apr. 2007, Menolli Jr. et al. NMJ128 (SP); 23 Oct. 2006, F. Karstedt & M. Capelari FK782 (SP).

Comments: Pluteus albostipitatus was described from Trinidad (Dennis 1953 as P. spilopus var. albostipitatus Dennis), and since then, it was also reported for several countries: Argentina (Singer 1956, 1958, Horak 1964), Bolivia (Singer 1958), Martinique (Pegler 1983), Galapagos Islands (Reid et al. 1981) and the French Guiana (Courtecuisse 1991). For Brazil, this species was already recorded from Paraná (Stijve and Meijer 1993 as P. cf. albostipitatus; Meijer 2001, 2006), Rio Grande do Sul (Wartchow et al. 2006) and São Paulo States (Pegler 1997).

The two materials herein studied differ themselves in basidiospore, pleuro- and cheilocystidia shapes (Figure 3). The collection Menolli Jr. et al. NMJ128 has predominantly globose basidiospores, pleurocystidia with evenly thickened walls up to 1.0 μm and rarely with two subacute lateral prongs, and cheilocystidia usually clavate and without a long pedicel at the base. On the other hand, the collection F. Karstedt & M. Capelari FK782 has usually slightly ellipsoid basidiospores, pleurocystidia that sometimes have two rounded lateral prongs and with thin to slightly thickened walls but that are not distinctly thick, and cheilocystidia frequently with a well developed pedicel at the base. These morphological differences observed in our two collections probably represent intraspecific variations, and it will be necessary to study more materials to determine the frequency of these characters and to or not attribute a varietal status to them.

Pluteus albostipitatus is probably a taxon with wide micromorphological variations, especially regarding the basidiospore, pleuro- and cheilocystidia shapes. Singer (1958) observed a variation in the basidiospore shape from subglobose to broad ellipsoid, but never globose, and

Figure 3. Pluteus albostipitatus. A. Basidioma (Menolli Jr. et al. NMJ128). B. Basidiospores; B1. F. Karstedt & M. Capelari FK782; B2. Menolli Jr. et al. NMJ128. C. Basidia (Menolli Jr. et al. NMJ128). D. Pleurocystidia; D1. F. Karstedt & M. Capelari FK782; D2. Menolli Jr. et al. NMJ128. E. Cheilocystidia; E1. F. Karstedt & M. Capelari FK782; E2. Menolli Jr. et al. NMJ128. Bars (A) = 1 cm; (B–E) = 10 μm.
recorded the presence of short obtuse or subacute small prongs in the pleurocystidia, in accordance with our material, except for the absence of globose basidiospores. Pegler (1983) also observed a variation in basidiospore shape from subglobose to ellipsoid and recorded the presence of a narrow pedicelate base in the cheilocystidia, but observed pleurocystidia without prongs. Horak (1964) and Courtecuisse (1991) described pleurocystidia with rounded or truncate apex, without mention of the presence or absence of prongs and cheilocystidia with a long basal pedicel. However, Horak (1964) recorded basidiospores as round-oval to almost globose as shown in the illustrations presented, like those observed in our collections. Courtecuisse (1991) recorded small basidiospores (5.5–6.5 × 4.5–5.2 μm), but had performed their measurements in an immature material.

Moreover, the materials herein analysed have minor differences when compared to the Brazilian collections studied by Wartchow et al. (2006). They recorded P. albostipitatus with a larger pileus (50–55 mm) and basidiospores varying from subglobose to broad ellipsoid, but never globose or ellipsoid, as observed in our collections. The pleuro- and cheilocystidia are also moderately longer [56.7–97.6 (−113) × 12–24 μm and 35.2–71.2 × 8–18.4 μm, respectively], and for the pleurocystidia, there is no mention of the two short lateral prongs and either the wall is slightly thickened and not relatively thick (nearly to metuloidal), as observed in our materials. Wartchow et al. (2006) did not describe, but illustrated a different shape of pleurocystidia, with round and small several finger-like protuberances at the apex.

Singer (1973) described P. albostipitatus var. poliobasis from Mexico (Veracruz State), which differs from the type variety only by the pearl-grey colour (griseo) of the stipe base. Regarding this variety characterization, Singer (1956, 1958) described the stipe of P. albostipitatus as “white, towards the base mostly pale sordid greyish” or “white, finally becoming somewhat silvery-white to glassy-cinereous”, respectively. The stipe colour of our material resembles the descriptions of Singer (1956, 1958), and the stipe base of P. albostipitatus var. poliobasis probably has a darker grayish shade, as mentioned by Rodriguez and Guzmán-Dávalos (2000, 2001) from material recollected in Jalisco State, Mexico.

Pluteus albostipitatus is close to P. melanopotamicus Singer described from Amazonas State, Brazil (Singer 1989). The latter species is macroscopically the same as P. albostipitatus, and according to the protologue, the main differences between them are the dimorphic basidiospores of P. melanopotamicus, which for us is irrelevant, because type 2 are only 0.5 μm longer than type 1 and there can be a gradual variation in size as observed in P. albostipitatus. The pleurocystidia of P. melanopotamicus were described (Singer 1989) as non-metuloidal, with wall thicknesses varying from 0.3 to 0.6 μm, and with round and small several finger-like protuberances at the apex. In our collections of P. albostipitatus, a relatively thickened wall, up to 1.0 μm, was observed which could be compared to those of P. melanopotamicus. On the other hand, the pleurocystidia with apical ornamentation of P. melanopotamicus were not found, but they were observed in the P. albostipitatus collections studied by Wartchow et al. (2006). Probably, either P. melanopotamicus is a later synonym of P. albostipitatus or the material identified by Wartchow et al. (2006) as P. albostipitatus is actually P. melanopotamicus. These materials should be revised to solve this question.

In the ITS + 5.8S analysis (Figure 2), P. albostipitatus clustered (68% BS) in a clade with P. nigrolineatus, P. albostipitatus var. poliobasis, P. harrisi and Pluteus sp. (section Pluteus). The molecular relation of P. albostipitatus with P. nigrolineatus and P. harrisi may indicate the transitional position of P. albostipitatus between section Pluteus and section Pluteus, because P. nigrolineatus belongs to section Hispidoderma, and P. harrisi, although classified in section Pluteus, has pleurocystidia with poorly developed prongs. Pegler (1983) also observed this intermediary position for P. albostipitatus, due to the unusual pleurocystidia shape as reported by Singer (1958), which could indicate an intermediate relationship with the metuloidal pleurocystidia of the section Pluteus.

In the nLSU analysis (Figure 1), P. albostipitatus clustered (82% BS) with P. salicinus. Despite the results of the molecular analyses, P. albostipitatus is considered distinct from all these species because, among other characteristics, P. harrisi has a glabrous pileus without appressedly fibrils and metuloidal pleurocystidia (Murrill 1911; Singer 1956, 1958; Pegler 1983; Banerjee and Sundberg 1995), P. nigrolineatus is a clamped species (Singer 1956, 1961; Wartchow et al 2006), and P. salicinus is also clamped and has characteristically metuloidal pleurocystidia (Singer 1956; Orton 1986; Banerjee and Sundberg 1995).

Pluteus aureovenatus Menolli & Capelari, sp. nov. (Figure 4) MycoBank: MB 513078

Etym.: The name refers to the colour and ornamentation of the pileus surface.

Pileus 22 mm diam, conicus vel convexus, aureoflavus, hygrophanus, venosus ad rugulosum, venae rubro-luteae, margo leviter sulcata, striata et leviter erosa. Lamellae subliberae, luteae. Stipes 30 × 1( apex)–3(basis) mm, curvus, leviter compressus, subbuliformis in basi, centralis, luteus. Basidiosporae 6.2 (−7.5) × (5.0)–6.2 (−7.5) μm, globoseae, hyalinae, inamiloideae, laeves, crassis parietibus. Pleurocystidia (50)–56–68 (−64) × (12.5)–15.0–22 (−31) μm, clavata, hyalina, cum parietibus tenuibus. Cheilocystidia (25)–31–49 (−61) × (8.7)–10.0–17.0 (−21) μm, clavate vel versiformi-clavata, interdum leviter verrucosa,
hyalina, cum parietibus tenuibus. Pileipellis cellularis a strato unico composita ex cellulis subglobosis, 54–70 × (36–)46–58 μm, hyalineis, incoloratis, absque pedicellis, interdum papilla apicali munitis. Fibulae absentes.

**Holotypus:** BRAZIL, São Paulo State, São Paulo city, Parque Estadual das Fontes do Ipiranga, 24 Jan. 2008, F. Karstedt & L.A.S. Ramos FK1045 (SP—holotype).

**Pileus** 22 mm diam, conic to convex, deep yellowish-orange, hygrophanous, veined-rugulose all over except at the margin, vein reddish-orange, margin slightly sulcate, translucently striate and slightly eroded. **Lamellae** sub-free, yellow, crowded, with lamellulae. **Stipe** 30 × 1 (apex)–3 (base) mm, curved, slightly compressed, with a subbulbous base, central, yellow, smooth, slightly longitudinally striate. **Odour, taste, and flesh colour** not recorded. **Basidiospores** [20/1/1] 6.2(–7.5) × (5.0–)6.2(–7.5) μm [Q = 1.00(–1.24); Qm = 1.03; Lm = 6.4 μm; Wm = 6.2 μm] globose, rarely broadly ellipsoid, inamyloid, hyaline, smooth, thick-walled, guttulate. **Basidia** 27–36 × 7.5–8.7 μm, clavate, slim, thin-walled, four-spored. **Pleurocystidia** (50–)56–64(–68) × (12.5–)15–22(–31) μm, clavate, sometimes slightly fusoid, frequently with apical mucilage in KOH, colourless, hyaline, thin-walled, moderately abundant. **Cheilocystidia** (25–)31–49(–61) × (8.7–)10–17(–21) μm, clavate to versiform-clavate, sometimes slightly ventricose, colourless, hyaline, thin-walled, moderately abundant. **Lamellar edge** heteromorphous. **Lamellar trama** inverse, up to 44 μm wide, composed of thin-walled hyphae, some commonly inflated, 2.5–10.0(–18.7) μm diam, hyaline, septate, sometimes with oleiferous hyphae up to 3.7 μm diam. **Pileus context** undifferentiated, up to 230 μm thick, composed of thin-walled hyphae, 3.7–8.7 μm diam, hyaline, septate. **Pileipellis** cellular approximately 56 μm, composed of one layer of subglobose cells, 54–70 × (36–) 46–58 μm, non-pediculate, thin-walled, colourless, hyaline, occasionally with an apical extension digitate to papillate up to 20 μm long. **Clamp connections** absent in all parts examined.

**Habitat and habit:** Solitary, on wood.

**Material examined:** BRAZIL, São Paulo State, São Paulo city, Parque Estadual das Fontes do Ipiranga, 24 Jan. 2008, F. Karstedt & L.A.S. Ramos FK1045 (SP—holotype).

**Comments:** *Pluteus aureovenatus* is characterised by a deep yellowish-orange and veined pileus, conic to convex and margin translucently striate, sub-free and yellow lamellae, globose basidiospores, large non-pedicelate pileipellis cells, and frequently clavate pleuro- and cheilocystidia.

This species is closely related to *P. aurantiorugosus* Murrill, *P. aurantiacus* Berk. & Curt., and *P. laetifrons* (Berk. & Curt.) Sacc. However, according to the type description (Murrill, 1917) and Smith and Stuntz (1958), *P. aurantiorugosus* is different because the pileus is convex umbonate, the basidiospores are subglobose to broadly ellipsoid, the pleuro- and cheilocystidia are similar and slightly shorter [28–38 (–50) × 9–14 × 5–10 μm] when compared to *P. aureovenatus*, and the cells of the pileipellis are clavate-pedicellate and much smaller (15–33 μm). Singer (1956) considered *P. aurantiorugosus* as a synonym for *P. aurantiorugosus*. However, Smith and Stuntz (1958) recognised them as distinct species, since *P. aurantiacus* has an orange stipe and slightly longer and more elongated basidiospores. Regardless, *P. aurantiacus* differs from *P. aureovenatus* because, according to Homola (1972), *P. aurantiacus* has a whitish to yellowish stipe at first and then orange to red tints at the base, an orange to yellowish-orange pileus in the dried specimens instead of beige-straw for *P. aureovenatus*, basidiospores that are not predominantly globose (6–7 × 4.5–5 μm), and cells of the pileipellis that are vesiculose, clavate, or occasionally

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Figure 4. *Pluteus aureovenatus* (holotype). A. Basidioma. B. Basidiospores. C. Basidia. D. Pleurocystidia. E. Cheilocystidia. F. Pileipellis cells. Bars (A) = 1 cm; (B–F) = 10 μm.
subfuscoid-ventricose and much shorter (22–39 × 22–31 μm) than *P. aureovenatus*.

*Pluteus laetifrons* is another species with orange-red pileus related to *P. aureovenatus*. However, Dennis (1953) and Singer (1958) described *P. laetifrons* with slightly smaller basidiospores (spheric with 5–6 μm and 4.5–5.5 × 4.3–5.3 μm, respectively) and according to Dennis (1953) much smaller cells of the pileipellis (20–35 μm). Singer (1958) described a new variety of *P. laetifrons* from Bolivia, viz. *P. laetifrons* var. *bolivianus* Singer, that differs from the type variety due to its larger and almost geometrically globose basidiospores (5.3–6.8 × 5.3–6.8 μm) and its darker, deeply coloured spots on the pileus that consist of pigmented pileipellis cells. Nevertheless, *P. aureovenatus* has pileipellis cells that are always colourless and basidiospores that are occasionally broadly ellipsoid and slightly longer than those described for *P. laetifrons* var. *bolivianus*. Moreover, Singer (1958) did not mention the size of pileipellis cells for *P. laetifrons* var. *bolivianus*, which are approximately 20–35 μm, as described in the type variety and they are, therefore, much shorter than those observed for *P. aureovenatus*.

The relationship of *P. aureovenatus* with *P. aurantiacrus*, *P. aurantiorugosus* and *P. laetifrons* is probably comparable to the relation between *P. chrysophlebius* and *P. sublaevigatus* (see discussion under *P. chrysophlebius*), where these species are separated by molecular data and have some morphological differences such as pileipellis cell size and basidiospores that differ slightly in size and shape.

In the molecular analyses (Figures 1 and 2), *P. aureovenatus* clustered in the clade with all species of section *Celulodermata* and together with *P. romellii* (from USA – California) and *P. sublaevigatus*. However, *P. romellii* is described to have a different pileipellis colour (date-brown, umber or snuff-brown), much longer pleuro- and cheilocystidia [52–100 × (16–)20–40 μm and 30–80 × 12–40(–53) μm, respectively] and pedicelate pileipellis cells with brownish vacuolar contents (Orton 1986). *Pluteus sublaevigatus* differs from *P. aureovenatus* because it has a yellow pileus that is slightly rugulose just at the centre and without orange tints or reddish-orange veins all over, a sterile lamellar edge and shorter [(35–)44–51(–55) × (22–)29–34 μm] pedicelate pileipellis cells (see description under *P. sublaevigatus*). *Pluteus aureovenatus* belongs to section *Celuloidea*

**Pluteus dominicanus** var. *hyalinus* Menolli & Capelari, var. nov. (Figure 5)

Mycobank: MB 513080

Etym.: The varietal name refers to the hyaline and colourless pileipellis cells.

Similis *Pluteus dominicanus* var. *dominicanus* Singer sed cellulis hyalinis et achoromaticis pileipellis differt.

Holotypus: BRAZIL, São Paulo State, São Paulo city, Parque Estadual da Cantareira, Núcleo Engordador, 2.1.2008, F. Karstedt et al. FK1058 (SP).

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**Figure 5.** *Pluteus dominicanus* var. *hyalinus* (holotype). A. Basidioma. B. Basidiospores. C. Basidia. D. Pleurocystidia. E. Cheilocystidia. F. Pileipellis cells. Bars (A) = 1 cm; (B–F) = 10 μm.

**Pileus** 31 mm diam, plane-convex, slightly umbrone, beige to light brown, slightly rugose at the centre, margin translucently striate, slightly sulcate or sometimes eroded. **Lamellae** free, pinkish, subdistant, with lamellulae. **Stipe** 54 × 2(apex)–5(base) mm, tapering towards the apex, central, whitish to beige, smooth. **Odour, taste, and flesh colour** not recorded. **Basidiospores** [20/1/1] 6.2–7.5(–8.7) × 5.0–6.2(–7.5) μm [Qm = 1.16–1.24(–1.40); Qm = 1.22; Lm = 7.3 μm; Wm = 6.0 μm], broadly ellipsoid, rarely ellipsoid, inamyloid, hyaline, smooth, thick-walled, sometimes guttulate. **Basidia** 20–29(–34) × 7.5–8.7 μm, clavate to versiform, thin-walled, four-spored. **Pleurocystidia** (35–)42–61(–69) × (10.0–)11.2–16.2(–17.5) μm, slightly ventricose, lancelate or sometimes fusiform-clavate, colourless, hyaline, sparse and few seen, thin-walled. **Cheilocystidia**, like the pleurocystidia, but smaller and very rare, (20–)29–43(–45) × (8.7–)10.0–14.0 μm. **Lamellar edge** heteromorphous. **Lamella trama** inverse, up to 50 μm wide, composed of thin- or slightly thick-walled hyphae, 2.5–7.5(–15.0) μm diam, hyaline. **Pileus context** undifferentiated, approximately 280 μm thick, composed of thin- or slightly thick-walled hyphae, 3.7–7.5(–18.7) μm diam, hyaline. **Pileipellis** cellular up to 44 μm thick, composed of one layer of clavate to spheropedunculate cells, (26–)32–47(–53) × (13.7–)16.2–21(–25) μm, with a short to
Pluteus dominicanus var. hyalinus is proposed as a variety of *P. dominicanus* especially because of the presence of hyaline and colourless pileipellis cells. *P. dominicanus* is known only from its type locality (Venezuela) in its original description (Singer 1961) and was subsequently recorded by Dennis (1970) based on the same material. Singer (1961) established *P. dominicanus* as “cheilocystidia not seen” and having pileipellis cells “with deep brownish-melleous dissolved intracellular pigment”, instead of the Brazilian material in which the cheilocystidia are rarely seen and the pileipellis cells are hyaline and colourless. The re-examination of the type of *P. dominicanus* (K!) demonstrated that the major difference of the new variety is, in fact, regarding the colour of the pileipellis cells. The type of *P. dominicanus* (Figure 6) has broadly ellipsoid or rarely subglobose basidiospores [20/1/1] 7.5–8.7(−10.0) × 6.2–7.5(–8.7) μm [Q = (1.15–) 1.16(–1.21); Qm = 1.17; Lm = 8.7 μm; Wm = 7.4 μm]; slightly lanceolate to ventricose pleurocystidia, 44–55 × 15.0–19.0 μm; cheilocystidia present, 36–55 × 12.5–20(−24) μm, like the pleurocystidia, but that are very rare and only possible to see in tangential view; and pileipellis composed of vesiculose to espheropedunculate cells, 37–48(−57) × 22–34(−39) μm, with a short to medium pedicel (2.5–10.0 μm long) and condensed or dissolved brownish pigment.

*Pluteus dominicanus* var. *hyalinus* is also related to the North American species *P. pallidus* and *P. umbrinodiscus*, but it differs from these especially in the pileus colour and the frequency of pleuro- and cheilocystidia.

*Pluteus dominicanus* belongs to section *Celluloderma* and clustered with all other species from section *Celluloderma* in both molecular analyses (Figures 1 and 2).

**Pluteus fluminensis** Singer, *Lloydia* 21: 292 (1959).

(Figure 7)

*Pileus* 27–31 mm diam, plane-convex, eventually slightly depressed at the centre or concave, not umbonate, deep sepia (N80A90M60) to porphyry brown, darker brown and rugose to venose at the centre, slightly paler towards the margin, margin sulcate or finely cracking and showing the white flesh. *Lamellae* free to sub-free, white then pinkish, close, with lamellulae.* Stipe* 30–38 × 2–3(apex)–5(base) mm, tapering towards the apex, with or without a small bulb, central, hollow, pale cream slightly greyish or translucent, finely pruinose and with finely brownish fibrils at base, slightly longitudinally striate, with scanty basal mycelium. *Odour, taste, and flesh colour* not recorded. *Basidiospores* [80/4/4] 6.2–7.5 × 5.0–6.2 μm (Q = 1.21–1.24; Qm = 1.23; Lm = 6.8 μm; Wm = 5.5 μm), broadly ellipsoid, inamyloid, hyaline, smooth, thick-walled, guttulate. *Basidia* 21–37 × 7.5–8.7(−10.0) μm, clavate to versiform, sometimes more slender, thin-walled, four-spored. *Pleurocystidia* (41–)47–65(–69) × 12.5–21(–25) μm, ventricose or slightly ventricose to lageniform, rarely vesiculose-saccate, colourless, hyaline, thin-walled, sparse, moderately abundant to scattered. *Cheilocystidia* (25–)32–50(–56) × (10.0–)11.2–18.7(–22)μm, like the pleurocystidia or rarely subclavate to clavate, difficult to see, moderately numerous. *Lamellar edge* heteromorphous. *Lamellar trama* inverse, up to 62 μm wide, composed of thin- or slightly thick-walled hyphae,
1.2–8.7(−15.0) μm diam, hyaline, septate. Pileus context undifferentiated, up to 125 μm thick, composed of thin or slightly thick-walled hyphae, 3.7–5.0 μm diam, hyaline, septated, sometimes with oleiferous up to 3.7 μm diam. Pileipellis cellular approximately 45 μm thick, composed of one layer of subglobose, vesiculose or subclavate cells, (20–)25–46(−52) × (17.5–)20–32(−37) μm, frequently non-pedicellate, often with a short to medium pedicel (1.2–7.5 μm long), thin-walled, with condensed or dissolved brown pigment. Clamp connections absent in all parts examined.

Habitat and habit: Solitary or in pairs, on wood.

Material examined: BRAZIL, São Paulo State, Cananéia city, Ilha do Cardoso, between Morro Três Irmãos and Sítio Grande, 23 Oct. 1984, M. Capelari MC164 (SP); near Morro Três Irmãos, 18 Dec. 1984, M. Capelari & R. Maziero MC212 (SP); São Paulo city, Parque Estadual da Cantareira, Núcleo Engordador, 24 Apr. 2007, Menolli Jr. et al. NMJ127 (SP); 24 Jan. 2008, F. Karstedt & L.A.S. Ramos FK1046 (SP).

Additional specimen examined: BRAZIL, Rio de Janeiro State, Angra dos Reis, 31 Sep. 1953, R. Singer B432 (F—holotype).

Comments: Pluteus fluminensis was described from Brazil (Rio de Janeiro State) and was also reported for Bolivia and USA (Florida) in its original description (Singer 1958). Later, Pegler (1997) reported it for São Paulo State and Stijve and Meijer (1993) and Meijer (2006) for Paraná State as P. cf. fluminensis. The basidiospores of P. fluminensis were described in the protologue (Singer, 1958) as “subglobose or rarely a few piriform, (4.5–)5–6.3(–7) × (4–)4.3–5.3(–5.8) μm”; however, upon re-examination of the type material (F!), it was demonstrated that the basidiospores are broadly ellipsoid, [20/1/1] 6.2–7.5 × 5.0–6.2 μm (Q = 1.21–1.24; Qm = 1.23; Lm = 6.8 μm; Wm = 5.5 μm). The pleuro- and cheilocystidia of the type are probably ventricose, but they had collapsed and it was not possible to confirm their size and shape. The pileipellis cells of the type are subglobose to vesiculose and slightly longer [(37–)41–57(−61) × (29–)31–38(−42) μm] than those of the other collections herein studied.

Pluteus jamaicensis is closely related to P. fluminensis, but, according to Singer (1958), the first has epicuticular elements with dissolved internal pigment instead of the pigmented condensations observed in P. fluminensis. The occurrence of pileipellis cells with condensed brown pigment was confirmed in the re-examination of the type and in additional collections of P. fluminensis herein examined. Singer (1958) also considered a future possibility of a subspecies status for P. fluminensis in P. jamaicensis, but herein they are considered as two distinct species.
**Pluteus fluminensis** belongs to section *Celluloderma* and clustered with all other species from section *Celluloderma* in both molecular analyses (Figures 1 and 2).

**Pluteus fuligineovenosus** Horak, *Nova Hedwigia* 8: 190 (1964). (Figure 8)

*Pileus* 14–38 mm diam, plane to slightly conic, apparently subumbonate, dark brown, slightly paler towards the margin and darker to blackish at the centre, veined all over especially around the centre then radially arranged towards the margin, vein darker, margin apparently neither sulcate nor striate. *Lamellae* free to slightly sinuate, white then pinkish, subdistant, with few lamellulae. *Stipe* 8–31 × 1–4 mm, slightly tapering towards the apex, central to slightly excentric, slightly flexuous, apparently hollow, translucent white, slightly longitudinally striate, with scanty basal mycelium. *Odour*, *taste*, and *flesh colour* not recorded. *Basidiospores* [20/1/1] 6.2–7.5 × (5.0–)6.2–7.5 μm [Q = 1.00(−1.24); Qm = 1.06; Lm = 6.5 μm; Wm = 6.2 μm], globose, occasionally broadly ellipsoid, inamyloid, hyaline, smooth, thick-walled, guttulate. *Basidia* 18.7–21(−25) × 6.2–7.5 μm, clavate to versiform, thin-walled, 4-spored. *Pleurocystidia* (51–)57–77 × 11.2–18.7 μm, fusoid-ventricose to lancelate, colourless, hyaline, thin-walled, sparse and moderately abundant. *Cheilocystidia* (37–)45–63 × (12.5–)15.0–20 μm, clavate to elongate-clavate, colourless, hyaline, thin-walled, not numerous. *Lamellar edge* apparently sterile. *Lamellar trama* inverse, up to 31 μm wide, composed of thin- or slightly thick-walled hyphae, 3.7–11.2 μm diam, hyaline, few septa seen, with oleiferous hyphae up to 5.0 μm diam. *Pileus context* undifferentiated, approximately 47 μm thick, composed of thin or slightly thick-walled hyphae, 5.6–7.5 μm diam, hyaline, few septa seen. *Pileipellis* cellular up to 100 μm thick, composed of one layer of vesiculose to spheropedunculate cells, (32–)39–50(−62) × (17.5–)20–32 (−39) μm, with a short to long pedicel (2.5–23 μm long), thin-walled, with condensed or dissolved brown to chestnut-brown pigment. *Clamp connections* absent in all parts examined.

**Habitat and habit**: Gregarious to disperse, on wood.

**Material examined**: BRAZIL, São Paulo State, São Paulo city, Parque Estadual da Cantareira, Núcleo Engordador, 12 Dec. 2006, F. Karstedt & M. Capelari MC826 (SP).

**Comments**: *Pluteus fuligineovenosus* is characterised by a brown and veined pileus, with darker to blackish centre and veins, globose basidiospores, and spheropedunculate cells of the pileipellis with condensed or dissolved brown to chestnut-brown pigment.

This species is known from Chile where it was originally described (Horak 1964), and later from Argentina (Singer 1969). The Brazilian collection has basidiospores that are slightly bigger than those mentioned in the original description (5.6–6.6 × 5.2–5.6 μm), but more similar in size [5.8–7(−7.8) × 5–6.2 μm] to those from the Argentinean collections (Singer 1969), pleurocystidia that are more frequently fusoid ventricose, and stipe that is apparently hollow and with scanty mycelium at the base, instead of solid stipe and a lack of basal micelium as described from the Chilean material (Horak 1964). This work reports for the first time *P. fuligineovenosus* from Brazil, and it is the second collection since its description.

In the ITS + 5.8S analyses (Figure 2), *P. fuligineovenosus* clustered in the clade with other species from section *Celluloderma*, forming a well-supported clade (99% BS) with *P. fluminensis* and *P. jamaicensis*. However, *P. fuligineovenosus* can be distinguished from *P. fluminensis* and *P. jamaicensis* by the basidiospore shape (preponderantly globose in *P. fuligineovenosus* instead of mostly broadly ellipsoid in *P. fluminensis* and *P. jamaicensis*) and the
pileus ornamentation, because *P. fuligineovenosus* is characterised by a pileus with a darker to blackish centre and veins all over, especially around the centre and then radially arranged towards the margin.

**Pluteus harrisii** Murrill, *Mycologia* 3: 277 (1911).

(Figure 9)

*Pileus* 20–33(−55) mm diam, conic to convex, slightly umbonate, hazel (N<sub>60</sub>A<sub>30</sub>M<sub>70</sub>) to brown or with coffee shades, slightly darker at the centre, with or without finely white punctuation especially at the centre, margin finely sulcate to sulcate-striate. *Lamellae* free, white then pinkish, attachment partially unequal, crowded, with lamellulae. *Stipe* 30–48(−62) × 2(apex)–5(base) mm, subequal, central, occasionally flexuous, apparently hollow, white to whitish grey, slightly pruinose at the apex, longitudinally striate, with basal mycelium. *Odour*, *taste*, and *flesh colour* not recorded. *Basidiospores* [80/4/4] 7.5–8.7(−10.0) × (5.0–)6.2–7.5(−8.7) μm [Q = (1.15–)1.16–1.21(−1.50); Qm = 1.23; Lm = 8.2 μm; Wm = 6.7 μm], broadly ellipsoid, occasionally ellipsoid or rarely subglobose, inamyloid, hyaline, slightly pinkish in KOH, smooth, thick-walled, sometimes guttulate. *Basidia* 24–30 × 7.5–10.0 μm, versiform to clavate, thin-walled, four-spored, sometimes with small scattered guttules. *Pleurocystidia* (40–)52–82(−91) × 15.0–24 μm, fusoid-ventricose, colourless, hyaline, sparse, moderately numerous to abundant, moderately thick-walled, wall usually uniform up to 1.2 μm.

![Figure 9. *Pluteus harrisii*. A–C. Menolli Jr. et al. NMJ122. A. Basidiomata. B. Basidiospores. C. Basidia. D. Pleurocystidia; D<sub>1</sub>. Menolli Jr. et al. NMJ122; D<sub>2</sub>. F. Karstede et al. FK1066. E. Cheilocystidia; E<sub>1</sub>. Menolli Jr. et al. NMJ122; E<sub>2</sub>. F. Karstede et al. FK1066. Bars (A) = 1 cm; (B–E) = 10 μm.](image-url)
wide or sometimes thinner towards the base and thickening up to 2.5 μm wide at the apex, apices usually with two to four versiform lateral prongs (up to 5.0 μm long), prongs rarely with a secondary bifurcation, occasionally without prongs and with a rounded or deformed apex, sometimes a colourless internal condensed content is present. *Cheilocystidia* (31–36–59 × 8.7–15(–17.5) μm, clavate to versiform-clavate, usually with a moderately long pedicel, colourless, hyaline, moderately abundant, thin-walled. *Lamellar edge* sterile. *Lamellar trama* inverse, up to 62 μm wide, composed of thin or slightly thick-walled hyphae, 2.5–13.7 μm diam, sometimes branched or with terminal elements slightly inflated up to 17.5 μm diam, hyaline, septate. *Pileus context* undifferentiated, up to 200 μm thick, composed of thin- or slightly thick-walled hyphae, 3.7–8.7 μm diam, sometimes inflated up to 25 μm diam, hyaline, septate. *Pileipellis* a repent epicutis, up to 100 μm thick, composed of thin- to slightly thick-walled hyphae, 5.0–12.5 μm diam, elongated, septate, with light to dark brown content, sometimes with terminal elements slightly inflated. *Clamp connections* absent in all parts examined.

**Habitat and habit:** Solitary, on leaf of palm tree or decaying wood.

**Material examined:** BRAZIL, São Paulo State, São Miguel Arcanjo city, Parque Estadual Carlos Botelho, 25 Apr. 1986, *M. Capelari & V.L.R. Bononi MC10* (SP); Santo André city, Reserva Biológica de Paranapiacaba, 11 Apr. 1990, *M. Capelari et al. MC3282* (SP); 22 Mar. 2007, *Menolli Jr. et al. NMJ122* (SP); São Paulo city, Parque Estadual da Cantareira, Núcleo Engordador, 31 Jan. 2008, *F. Karstedt et al. FK1066* (SP).

**Comments:** *Pluteus harrisii* is characterised by a dark brown pileus, a white stipe with greyish tones, and metuloid with a moderately long pedicel, colourless, hyaline, moderately abundant, thin-walled. *Pleurocystidia* 5.0–12.5 μm diam, hyaline, septate. *Pleurocystidia* 3.7–13.7 μm diam, clavate to versiform, thin-walled, four- or six-spored, *Pleurocystidia* (46–)50–56 × 10.0–13.7–(17.5) μm, fusoid-ventricose to lancelate, colourless, hyaline, thin-walled, sparse and not abundant. *Cheilocystidia* (25–)31–45(–50) × (7.5–)10.0–12.5 μm, clavate to elongate-clavate, colourless, hyaline, thin-walled, numerous. *Lamellar trama* inverse, up to 62 μm wide, composed of thin- or slightly thick-walled hyphae, 3.7–13.7 μm diam, hyaline. *Pileus context* undifferentiated, approximately 62 μm thick, composed of thin- or slightly thick-walled hyphae, 3.7–10.0 μm diam, shiny, smooth, thick-walled, sometimes guttulate. *Basidium* 25–29(–31) × 6.2–8.7 μm, clavate to versiform, thin-walled, four-spored. *Cheilocystidia* 31–62 μm, clavate to elongate-clavate, colourless, hyaline, thin-walled, sparse and not abundant. *Cheilocystidia* (25–)31–45(–50) × (7.5–)10.0–12.5 μm, clavate to elongate-clavate, colourless, hyaline, thin-walled, numerous. *Lamellar trama* inverse, up to 62 μm wide, composed of thin- or slightly thick-walled hyphae, 3.7–13.7 μm diam, hyaline. *Pileus context* undifferentiated, approximately 62 μm thick, composed of thin- or slightly thick-walled hyphae, 3.7–10.0 μm diam. *Pileipellis* cellular up to 125 μm, composed of one or more layers of spheropedunculate cells, (37–)45–54 × (31–)37–42 μm, with a short pedicel (5.0–10.0 μm long), thin-walled, with dissolved brown cytoplasmic content. *Clamp connections* absent in all parts examined.

**Habitat and habit:** Gregarious, on wood.

**Material examined:** BRAZIL, São Paulo State, São Paulo city, Parque Estadual da Cantareira, Núcleo Engordador, 24 Apr. 2007, *Menolli Jr. et al. NMJ130* (SP).

*Pluteus jamaicensis* Murrill, *Mycologia* 3: 278 (1911) (Figure 10)

*Pileus* 17–34 mm diam, campanulate-convex, sometimes slightly umbonate, dark beige to dark brown (N70A80M70), slightly paler towards the margin, finely rivulose all over, rugose to rivulose at the centre, margin slightly sulcate and sometimes finely cracking and showing the white flesh. *Lamellae* free to sinuate-remote, white then pinkish, with numerous lamellulae. *Stipe* 20–30 × 1–2 mm, equal, central, hollow, cream to translucent white, slightly greyish at base. *Odour, taste* and *flesh colour* not recorded. *Basidiospores* [20/1/1] 6.2(–7.5) × 5.0(–6.2) μm [Q = (1.21–)1.24; Qm = 1.24; Lm = 6.4 μm; Wm = 5.2 μm], broadly ellipsoid, inamyloid, hyaline, smooth, thick-walled, sometimes guttulate. *Basidia* 25–29(–31) × 6.2–8.7 μm, clavate to versiform, thin-walled, four-spored. *Cheilocystidia* (46–)50–56 × 10.0–13.7–(17.5) μm, fusoid-ventricose to lancelate, colourless, hyaline, thin-walled, sparse and not abundant. *Cheilocystidia* (25–)31–45(–50) × (7.5–)10.0–12.5 μm, clavate to elongate-clavate, colourless, hyaline, thin-walled, numerous. *Cheilocystidia* (25–)31–45(–50) × (7.5–)10.0–12.5 μm, clavate to elongate-clavate, colourless, hyaline, thin-walled, numerous. *Lamellar trama* inverse, 62 μm wide, composed of thin- or slightly thick-walled hyphae, 3.7–13.7 μm diam, hyaline. *Pileus context* undifferentiated, approximately 62 μm thick, composed of thin- or slightly thick-walled hyphae, 3.7–10.0 μm diam. *Pileipellis* cellular up to 125 μm, composed of one or more layers of spheropedunculate cells, (37–)45–54 × (31–)37–42 μm, with a short pedicel (5.0–10.0 μm long), thin-walled, with dissolved brown cytoplasmic content. *Clamp connections* absent in all parts examined.

**Habitat and habit:** Gregarious, on wood.

**Material examined:** BRAZIL, São Paulo State, São Paulo city, Parque Estadual da Cantareira, Núcleo Engordador, 24 Apr. 2007, *Menolli Jr. et al. NMJ130* (SP).
Comments: *Pluteus jamaicensis* was described from Jamaica (Murrill 1911), and since then, it was reported from Trinidad (Dennis 1953 as *P. aethalus var. jamaicensis*; Pegler 1983), Argentina (Singer and Digilio 1951 as “*P. phlebophorus var.?*”; Singer 1956, 1958), Venezuela (? (Dennis 1970), and Martinique and Guadalupe (Pegler 1983). Moreover, according to Singer (1958), *P. phlebophorus* (Ditmar) P. Kumm. *sensu* Rick (1938) reported from São Leopoldo, Rio Grande do Sul State, Brazil, is perhaps *P. jamaicensis*. This species was originally described without cystidia (Murrill 1911), but posterior revisions of the type confirmed the presence of marginal and facial cystidia (Singer 1958; Smith and Stuntz 1958; Pegler 1983; Banerjee and Sundberg 1993). The Brazilian collection has a slightly sulcate pileus margin, as reported by Singer (1956, 1958) from Argentinean materials; preponderantly clavate cheilocystidia, as described by Pegler (1983); and broadly ellipsoid basidiospores that are slightly longer than those described by Smith and Stuntz (1958) in the revision of the type specimen (subglobose, 5–6 × 5–5.5 μm).

In the ITS + 5.8S analysis (Figure 2), *P. jamaicensis* clustered with *P. fluminensis* and *P. fuligineovenosus*. However, they are morphologically distinct (see discussion under *P. fluminensis* and *P. fuligineovenosus*). This work reports *P. jamaicensis* for the first time from Brazil. As supported by the molecular (Figure 2) and the morphological data, *Pluteus jamaicensis* belongs to section *Celluloderma*.

*Pluteus riberaltensis var. conquistensis* Singer, *Lloydia* **21**: 255 (1959). (Figure 11)

*Pileus* 27–53 mm diam, campanulate when young, then convex, umbo-nate, dark brown, slightly darker in the centre, slightly radially coloured, finely pruinose all over and finely cracking especially around the centre, margin not striate and showing the whitish flesh between the fibrils. *Lamellae* free, pinkish, moderately crowded, with lamellulae. *Stipe* 53–65 × 4–9 mm, slightly tapering towards the apex, base subbulbous, central to slightly eccentric, white-cream with brown fibrils over the surface especially when young, then brownish and slightly longitudinally striate, with scanty mycelium at base. *Odour*, *taste*, and *flesh colour* not recorded. *Basidiospores* [20/1/1] 6.2–7.5 × 6.2 μm (Q = 1.00–1.21; Qm = 1.08; Lm = 6.7 μm;
the stipe surface, especially when young, as described for this variety. Also, there are some cavities on the pileus surface showing the flesh, probably caused by insects. However, our material has moderately longer pleurocystidia than those described for *P. riberaltensis* var. *conquistensis* (38–41 × 14–22.5 μm), and these are more similar to those of the type variety (41–86 x 12.5–39 μm), as described in the protologue (Singer 1958).

Singer (1961) described another variety, viz. *P. riberaltensis* var. *missionensis* Singer, based on an Argentinian specimen that has a white stipe similar to the type variety but that differs from the latter by the conspicuous incrustation of the cystidia, and the missing differentiation in size of cheilo- and pleurocystidia. *Pluteus riberaltensis* and its varieties were described based on single collections and no other records have been reported. This work is the first to mention *P. riberaltensis* var. *conquistensis* from Brazil and reports the first collection since its description.

*Pluteus riberaltensis* var. *conquistensis*, as well as other species formerly classified in the section *Hipidoderma* (*P. ephbeus*, *P. exigus*, *P. umbrosus*), clustered in the clade including members of the section *Celluloderma*. As discussed above, these species probably share morphological similarities, and the scope of the section *Hipidoderma* must be revised. For now, *Pluteus riberaltensis* var. *conquistensis* has been classified in the section *Hipidoderma*.

**Pluteus sublaevigatus** (Singer) Menolli & Capelari, stat. nov. (Figure 12)

MycoBank: MB 513081
Basionym: *Pluteus chrysophlebius* subsp. *sublaevigatus* Singer, *Lloydia* **21**: 278 (1959).

**Pileus** 11–28 mm diam, campanulate when young, then convex to plane, not umbonate, sometimes slightly depressed at the centre, yellow (N00A30M40 to N00A80M30), hygrophanous, slightly rugulose at the centre, margin translucently striate, sometimes eroded. *Lamellae* free to subfree, close, yellowish, moderately crowded, with lamellulae. *Stipe* 28–33 × 1–4 mm, curved, cylindric with a subbulbous base, central, whitish yellow, more yellowish at the base, surface smooth, sometimes with white punctuations and white pruinose mycelium at the base. *Odour*, *taste*, and *flesh colour* not recorded. *Basidiospores* [40/2/1] (5.0–)6.2–7.5 × 5.0–6.2(–7.5) μm (Q = 1.00–1.21(–1.24); Qm = 1.08; Lm = 6.5 μm; Wm = 6.1 μm), preponderantly globose, sometimes broadly ellipsoid, inamylold, hyaline, smooth, thick-walled, guttulate, sometimes with small scattered guttules. *Basidioceps* [40/2/1] (5.0–)6.2–7.5 × 5.0–6.2(–7.5) μm (Q = 1.00–1.21(–1.24); Qm = 1.08; Lm = 6.5 μm; Wm = 6.1 μm), preponderantly globose, sometimes broadly ellipsoid, inamylold, hyaline, smooth, thick-walled, guttulate, sometimes with small scattered guttules. *Basidia* (20–)22–27 (–30) × 7.5–8.7(–10.0) μm, clavate, thin-walled, four-spored. *Pleurocystidia* (34–)36–50(–65) × 12.5–17.5(–25) μm, clavate to vesiculose, sometimes slightly ventricose, very translucent and difficult to see in KOH, sparse and very rare, thin-walled.

**Cheilocystidia** (22–)31–49(–54) μm, globose or occasionally broadly ellipsoid, inamylold, hyaline, smooth, thick-walled, guttulate. *Basidia* 21–27(–31) × (7.5–)8.7–10.0 μm, clavate, thin-walled, four-spored, with small scattered guttules. *Pleurocystidia* (44–)48–69(–78) × (15.0–)17.5–28(–35) μm, slightly ventricose to lageniform, sparse and not abundant. *Cheilocystidia* (27–)30–47(–57) × (12.5–)17.7–27 μm, like pleurocystidia, but very rooting on the hymenium and hard to see. *Lamellar edge* heteromorphous with abundant basidia. *Lamellar trama* inverse, up to 37 μm wide, composed of thin- or thick-walled hyphae, 3.7–10.0 μm diam, hyaline, few septa seen, with oleiferous hyphae up to 3.7 μm diam. *Pileus context* undifferentiated, approximately 125 μm thick, composed of thin- or thick-walled hyphae, 3.7–7.5 μm diam, hyaline, septate. *Pileipellis* a cutis, approximately 100 μm thick, composed of thin-walled hyphae, 10–20 μm diam, elongated, septate, with dissolved brown vacuolar content, sometimes with the terminal elements slightly inflated and often ascendant. *Clamp connections* absent in all parts examined.

**Habitat and habit:** In pairs on wood.

**Material examined:** BRAZIL, São Paulo State, São Paulo city, Parque Estadual das Fontes do Ipiranga, 24 Jan. 2008, F. Karstedt & L.A.S. Ramos FK1043 (SP).

**Comments:** This variety was described from Bolivia (Singer 1958) and differs from the type variety almost exclusively by the umber-grey fibrils on the stipe. The Brazilian specimen is characterised by brown fibrils over the stipe surface, especially when young, as described for this variety. Also, there are some cavities on the pileus surface showing the flesh, probably caused by insects. However, our material has moderately longer pleurocystidia than those described for *P. riberaltensis* var. *conquistensis* (38–41 × 14–22.5 μm), and these are more similar to those of the type variety (41–86 x 12.5–39 μm), as described in the protologue (Singer 1958).
Figure 12. *Pluteus sublaevigatus* (F. Karstedi et al. FK1085). A. Basidioma. B. Basidiospores. C. Basidia. D. Pleurocystidia. E. Cheilocystidia. F. Pileipellis cells. Bars (A) = 1 cm; (B–F) = 10 μm.

× (7.5–)10.0–21(–26) μm, like the pleurocystidia, clavate to vesiculose, very translucent, abundant, thin-walled. Lamellar edge sterile. Lamellar trama inverse, up to 62 μm wide, composed of thin- or slightly thick-walled hyphae, 3.7–10 μm diam, hyaline, septate. Pileus context undifferentiated, up to 187 μm thick, composed of thin- or slightly thick-walled hyphae, 2.5–6.2(–16.2) μm diam, hyaline, septate. Pileipellis cellular up to 50 μm thick, composed of one layer of clavate, vesiculose or subglobose cells, (35–) 44–51(–55) × (22–)29–34 μm, with a short pedicel (2.5–7.5 μm long), thin-walled, colourless, hyaline. Clamp connections absent in all parts examined.

Habitat and habit: Gregarious on decaying wood.

Material examined: BRAZIL, São Paulo State, São Paulo city, Parque Estadual da Cantareira, Núcleo Engordado, 19 Feb. 2008, F. Karstedi et al. FK1085 (SP).

Additional specimen examined: BOLIVIA, Dpto La Paz, Prov. Nor-Yungas, Charobamba, 13 Feb. 1956, R. Singer 1147 (LIL—holotype).

Comments: The frequently globose basidiospores and the large subglobose cells of the pileipellis, along with the results of the molecular analyses, are the basis to propose the new status for *P. chrysophlebius ssp. sublaevigatus*.

Singer (1958) used the frequently globose basidiospores as the distinctive character to propose *P. chrysophlebius ssp. sublaevigatus* based on material collected in Bolivia. The Brazilian collection is slightly different because it has a pileus slightly rugose at the centre and pleurocystidia predominantly clavate to vesiculose and slightly longer than those described for *P. chrysophlebius ssp. sublaevigatus*, which has a pileus with “the disc seemingly smooth when wet, but in dry or dried condition becoming rugulose” and cystidia “about 35 × 15 μm if vesiculose, about 53 × 9.5 μm if ampullaceous” (Singer, 1958). These are minor differences that we consider intraspecific variations between the two collections. Moreover, the re-examination of the type of *P. sublaevigatus* (LIL!) demonstrated that it has basidiospores that are preponderantly globose and rarely broadly ellipsoid, [20/1/1] 6.2–7.5 × 6.2–7.5 μm [Q = 1.00(−1.21); Qm = 1.01; Lm =7.0 μm; Wm = 7.0 μm], as well as a pileipellis composed of vesiculose or subglobose cells, 35–54 × 21–37 μm, characterised as thin-walled, colourless, hyaline, and by have a short pedicel (2.5–7.5 μm long). The pleuro- and cheilocystidia of the type are collapsed and it was not possible to confirm their size and shape.

*Pluteus sublaevigatus* is close to *P. chrysophlebius* and *P. admirabilis* in morphology, but the molecular analysis of the nLSU gene (Figure 1) showed that they clustered in separated clades, with *P. chrysophlebius* and *P. admirabilis* in one clade and *P. sublaevigatus* in another clade with the Brazilian yellow species *P. aureovenatus*.

The morphological re-examination of the three collections (DAOM!) of *P. admirabilis* and *P. chrysophlebius* used in the molecular analyses showed some differences in microcharacters among themselves and when compared to *P. sublaevigatus* (F. Karstedi et al. FK1085), especially in the pileipellis cells (Figures 13–15). The pileipellis cells from these collections are usually clavate-vesiculose to subglobose, ranging in size and in the presence or absence of apical projections (Table 2). Moreover, the size and shape of basidiospores are a constant character; the pleurocystidia are constantly slightly ventricose with few differences in size; and the cheilocystidia are frequently clavate-vesiculose to slightly ventricose (Table 2). These microcharacters partly agree with the type study results presented by Banerjee and Sundberg (1993) and Singer (1956) for *P. admirabilis* and *P. chrysophlebius*, and they differ from those observed in the Brazilian collection of *P. sublaevigatus* (Table 2).

These differences are probably due to intraspecific variations because in our analysis, the nLSU sequences of *P. chrysophlebius* and *P. admirabilis* from GenBank clustered in a clade with 99% BS. This relationship between the sequences was already reported by Moncalvo et al.
N. Menolli Jr. et al. (2002) and Minnis et al. (2006). Then, if these collections really are representatives of *P. chrysophlebius* and *P. admirabilis*, according to the morphological and molecular data presented, they cannot be considered independent species. This fact is in accordance with Murrill (1917) and Singer (1956), who already considered them as synonyms.

The study of the voucher collections from the GenBank sequences was important for establishing the morphological

Figures 13–15. 13. *Pluteus admirabilis* (DAOM193532). 14. *P. admirabilis* (DAOM197226). 15. *P. chrysophlebius* (DAOM190194). A. Basidiospores. B. Basidia. C. Pleurocystidia. D. Cheilocystidia. E. Pileipellis cells. Bars = 10 μm.

Table 2. Micromorphological comparison between collections of *Pluteus admirabilis*, *P. chrysophlebius* and *P. sublaevigatus*.

| Characters                        | *P. admirabilis* DAOM193532 | *P. admirabilis* DAOM197226 | *P. chrysophlebius* DAOM190194 | *P. sublaevigatus* F. Karstedt et al. 1085 |
|----------------------------------|-------------------------------|-----------------------------|--------------------------------|-------------------------------------------|
| Basidiospores                    | 7.5 × 6.2 μm, broadly ellipsoid | 7.5 × 6.2 μm, broadly ellipsoid | 7.5 × 6.2 μm, broadly ellipsoid | 6.2–7.5 × 5.0–6.2 μm, preponderantly globose |
| Pleurocystidia                   | 47–71 × 16.2–21 μm, slightly ventricose, with apical mucilage | 50–81 × 17.5–25 μm, slightly ventricose | 41–52 × 10.0–18.7 μm, slightly ventricose | 36–50 × 12.5–17.5 μm, clavate to vesculos |
| Cheilocystidia                   | 21–38 × 7.5–12.5 μm, clavate-vesiculose to slightly ventricose | 26.2–50 × 10.0–18.7 μm, clavate-vesiculose to slightly ventricose | 30–40 × 10.0–11.2 μm, clavate-vesiculose to slightly ventricose | 31–49 × 10.0–21 μm, clavate to vesculos |
| Pileipellis cells                | 16.2–51 × 12.5–25 μm, with or without a medium pedicel up to 12.5 μm long, frequently with a short to long apical projection approximately 5.0–25 μm long | 35–49 × 13.7–25 μm, with a short to medium pedicel up to 13.7 μm long, without apical projections, and sometimes with a broadly obtuse apex | 26–37.5 × 12.5–17.5 μm, with a short to medium pedicel approximately 2.5–15.0 μm long, and rarely subventricose with a broadly obtuse apex up to 5.0 μm long | 44–51 × 29–34 μm, with a short pedicel approximately 2.5–7.5 μm long |
differences between them and the Brazilian collections, as well as for supporting the results obtained with the molecular analysis. *Pluteus sublaevigatus* differs from the vouchers of *P. chrysophlebius* and *P. admirabilis* because it has close and not remote lamellae, basidiospores that are frequently globose, larger pileipellis cells, and similar pleuro- and cheilocystidia that are predominantly clavate-vesiculose (Table 2).

In the ITS + 5.8 analyses (Figure 2), *P. sublaevigatus* clustered with low BS support (53%) together with *P. aureovenatus* and *P. romelli*. However, as to *P. aureovenatus*, *P. romelli* can be distinguished from *P. sublaevigatus* by the pileus colour and the size of the pleuro- and cheilocystidia. *Pluteus aureovenatus* can also be separated from *P. sublaevigatus* as discussed under the description of *P. aureovenatus*.

Stijve and Meijer (1993) and Meijer (2006) recorded in a checklist the occurrence of *P. chrysophlebius* subsp. *bruchii* Singer from Paraná State, Brazil, which probably represents *P. sublaevigatus*. The records of *P. chrysophlebius* for Martinique and Guadeloupe by Pegler (1983) also probably represent *P. sublaevigatus*, due to the description and illustrations presented. Supported by the molecular (Figures 1 and 2) and the morphological data, *Pluteus sublaevigatus* belongs to section *Celluloderma*.

**Pluteus xylophilus** (Speg.) Singer, *Lilloa* 22: 405 (1951). (Figure 16)

≡ *Entoloma xylophilum* Speg., Bol. Ac. Nac. Cord. 28: 305, 1926.

**Pileus** 30–70 (−110) mm diam, plane-convex, occasionally slightly concave, sometimes slightly umbonate, light brown (N₁₆₀A₆₀M₅₀ to N₁₆₀A₄₀M₄₀), darker at the centre (N₈₀A₅₀M₅₀), paler and discolouring radially towards the margin, margin sometimes splitting and apparently not sulcate or striate. *Lamellae* remote, slightly pinkish to pinkish, crowded, with lamellulae. *Stipe* 35–60 (−120) × 3–10 (−apex)–9–20 (−base) mm, tapering towards the apex, rarely equal with 3 mm diam, central, sometimes flexuous, cream with brown fibrils over the surface and especially at base, longitudinally striate, with scant mycelium at base. *Odour*, *taste*, and *flesh colour* not recorded. *Basidiospores* [160/8/7] (5.0–)6.2–7.5 (−8.7) × 3.7–6.2 μm [Q = (1.21–)1.24–1.68 (−1.74); Qm = 1.38; Lm = 6.7 μm; Wm = 4.9 μm], broadly ellipsoid to ellipsoid, occasionally elongate, inamylody, hyaline, smooth, thick-walled, guttulate. *Basidia* (18.7–)21–26 × 6.2–8.7 μm, clavate or versiform, thin-walled, four-spored, with small scattered guttules. *Pleurocystidia* of three types: (I) the normal *Cervinus*-type, (46–)52–75 (−87) × 12.5–23 (−25) μm, fusoid-ventricose, colourless, hyaline, apices usually with two to six lateral prongs, moderately thick-walled especially in the apical region and tapering towards the base, sparse, and abundant to very abundant, frequently with adhered basidiospores on many pleurocystidial apices; (II) the modified *Cervinus*-type as found in *P. harrisii*, usually without prongs and subcapitate or slightly strangled at the apex, or sometimes with two short lateral prongs, size similar to type I; (III) preponderantly of the *Magnus*-type, usually shorter especially in length, 38–62 × (8.7–)11.0–28 μm, lageniform to fusoid, with acute apex or rarely with a rounded apex, colourless, hyaline, thin- to moderately thick-walled, rare. *Cheilocystidia* dimorphic, not abundant, very rooting on hymenium, and hard to see: (I) short vesiculose, clavate to subclavate, 21–37 × 8.7–15 μm; (II) long-cylindrical-clavate, sometimes with a moderately long pedicel, 40–69 × 10.0–15.0 μm; sometimes transitions between the two extreme forms are found that are usually slightly ventricose or versiform and moderately deformed. *Lamellar trama* heteromorphous. *Lamellar trama* inversus, up to 62 μm wide, composed of thin or slightly thick-walled hyphae, sometimes moderately inflated, 1.2–13.7 μm diam, hyaline, septate. *Pileus* context undifferentiated, approximately 187 μm thick, occasionally very thick more than 1,000 μm thick, composed of slightly thick-walled hyphae, sometimes inflated, 3.7–21 μm diam, hyaline, septate. *Pileipellis* a repent epicutis up to 125 μm thick, composed of thin- to slightly thick-walled hyphae, 3.7–6.2 μm diam, elongated, septate, with dissolved brown vacuolar content. *Clamp connections* absent in all parts examined.
Habitat and habit: Solitary to scattered on wood.

Material examined: BRAZIL, São Paulo State, São Paulo city, Parque Estadual das Fontes do Ipiranga, 10 Nov. 1982, G. Guzmán 22986 (SP); 16 Jan. 1987, Pegler et al. 3712 (SP); 20 June 2006, F. Karstedt et al. FK683 (SP); 30 May 2007, Menolli Jr. et al. NMJ138 (SP); 18 Oct. 2007, Menolli Jr. & F. Karstedt NMJ150 (SP); Parque Estadual da Cantareira, Núcleo Engordador, 21 Aug. 2007, Menolli Jr. et al. NMJ143 (SP); 23 Oct. 2008, M. Capelari & L.A.S. Ramos MC4397 (SP).

Comments: Pluteus xylophilus is characterised by a moderately large pileus, three types of pleurocystidia, and two types of cheilocystidia. The specimens herein studied have surfaces usually with some cavities, probably caused by insects, showing the white flesh.

Singer (1958) described two varieties, viz. P. xylophilus var. tucumanensis Singer and P. xylophilus var. major Singer, based on the size and pigmentation differences of the pileus and the predominance of each cheilocystidia type. However, he emphasises that it is necessary to check whether each of these characters remains constant in successive fruitings and to verify if these morphological variations constitute a form, varieties, or independent microspecies. Singer’s varieties are not considered in this work because considerable morphological variations were not observed.

Singer (1956, 1958) accepted two varieties of P. cervinus, viz. P. cervinus var. brasiliensis and P. cervinus var. tucumanensis Singer, as synonyms of P. xylophilus, and also considered P. cervinus sensu Rick (1938), which was recorded for Brazil, as a probable P. xylophilus.

The geographic distribution of P. xylophilus includes Argentina (Spegazzini 1925 as Entoloma xylophilum; Singer and Digilio 1951 as P. cervinus var. tucumanensis and P. cervinus var. brasiliensis; Singer 1958), Bolivia (Singer 1958), Brazil (Bresadola 1920 as P. cervinus var. brasiliensis; Grandi et al. 1984; Stijve and Meijer 1993 as P. xylophilus and P. xylophilus var. tucumanensis; Pegler 1997; Meijer 2006, 2008) and Peru (Singer 1958).

The molecular analyses (Figures 1 and 2) confirm the position of P. xylophilus in the section Pluteus and relate it with the other species of the Cervinus-group, forming a well-supported clade (86% BS, Figure 2).

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References

Baker REP, Dale WT. 1951. Fungi of Trinidad and Tobago. Mycol Pap. 33:1–123.
Banerjee P, Sundberg WJ. 1993. Reexamination of Pluteus type specimens: types housed at the New York Botanical Garden. Mycotaxon 49:413–435.
Banerjee P, Sundberg WJ. 1995. The genus Pluteus section Pluteus (Pluteaceae, Agaricales) in the Midwestern United States. Mycotaxon 53:189–246.
Bas C. 1969. Morphology and subdivision of Amanita and a monograph on its section Lepidella. Persoonia 5:285–579.
Bonnard J. 2001. Pluteus albinus sp. nov. (Agaricales, Basidiomycetes). Mycol Helv. 11:131–136.
Bresadola G. 1920. Selecta mycologica. Ann Mycol. 18: 26–70.
Corriol G, Moreau P-A. 2007. Agaricus (Annularia) fenzlii redécouvert das les Pyrénées. Notes sur le genre Chamaeota en Europe. Persoonia 19: 233–250.
Courtecuisse R. 1991. Éléments pour un inventaire mycologique des environs du saut Pararé (Arataye) et de L’Inselberg des Nouragues, (Guyane française) V. Pluteaceae. (Pluteales, Basidiomycota). Cryptogam Bot. 2:136–152.
Dennis RWG. 1953. Les Agaricales de L’Ile de la Trinité: Rhodosporea-Ochromyceae. Bull Soc Mycol Fr. 69:145–198.
Dennis RWG. 1970. Fungus flora of Venezuela and adjacent countries. Kew Bull Addit Ser. 3:1–531.
Drechsler-Santos ER, Pastorini LH, Putzke J. 2007. Primeiro relato de fungos Agaricales em fragmento de mata nativa em Frederico Westphalen – RS. Rev Bras Bioc. 5:471–473.
Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for Basidiomycetes – application to the identification of mycorrizae and rusts. Mol Ecol. 2:113–118.
Grandi RAP, Guzmán G, Bononi VL. 1984. Adições às Agaricales (Basidiomycetes) do Parque Estadual das Fontes do Ipiranga, São Paulo, SP, Brasil. Rickia 11:27–33.
Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser. 41:95–98.
Hennings P. 1900. Fungi mottogrossenses a Dr. R. Pilger collecti 1899. Hedwigia 39:134–139.
Hennings P. 1904a. Fungi amazoniconi I. a cl. Ernesto Ule collecti. Hedwigia 43:154–186.
Hennings P. 1904b. Fungi S. Paulenses III a cl. Puttemans collect. Hedwigia 43:197–209.
Homola RL. 1972. Section Cellisiderina of the genus Pluteus in North America. Mycologia 64:1211–1247.
Horak E. 1964. Fungi austroamericani II. Pluteus Fr. Nova Hedwigia 8:163–199.
Kölppers H. 1979. Atlas de los colores. Barcelona: Editorial Blume. Lim YW, Jung HS. 1998. Phylogenetic relationship of Amanita species based on ITS1–5.8S rDNA–ITS2 region sequences. J Microbiol. 36:203–207.
Källersjö M, Nylund J, Stenlid J, Sundberg P. 2000. Molecular and morphological approaches to study the genus Pluteus Fr. Mikol Fitopatol. 43:216–231.
Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo J-M, Ge ZW, Yang ZL, Sot JC, Ammirati J, Baroni TJ, Bouguer NL, Hughes KW, Lodge DJ, Kerrigan RW, Seidl MT, Aanen DK, DeNritis M, Daniele GM, Desjardin DE, Kropp BR, Norvell LL, Parker A, Vellinga EC, Völglyás R, Hibbett DS. 2006. Major clades of Agaricales: a multilocus phylogenetic overview. Mycologia 98:982–995.
Meijer AAR de. 2001. Mycological work in the Brazilian State of Paraná. Nova Hedwigia 72:105–159.
Meijer AAR de. 2006. Preliminary list of the macromycetes from the Brazilian State of Paraná. Bol Mus Bot Munic. 68:1–55.
Meijer AAR de. 2008. Notable macrofungi from Brazil’s Paraná Pine forest. Colombo: Embrapa Florestas.
Menolli Jr N, Capelari M. 2010. Notes on Pluteus (Pluteaceae, Agaricales) from Brazil including two new species and a new record. Mycologia 102:697–707.
Minnis AM, Sundberg WJ, Methven AS, Sipes SD, Nickrent DL. 2006. Annulate Pluteus species: a study of the genus Chamaeota in the United States. Mycologia 96:31–45.
Moncalvo J-M, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R. 2000. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. Syst Biol 49:278–305.
Moncalvo J-M, Vilgalys R, Redhead SA, Johnson JE, James TY, Arne MC, Hofstetter V, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsen S, Clémenton H, Miller Jr OK. 2002. One hundred and seventeen clades of euagarcas. Mol Phylogenet Evol. 23:357–400.
Murrill WA. 1911. The Agaricaeae of tropical North America. Mycologia 3:271–282.
Murrill WA. 1917. Agaricales Agaricaeae (pars) Agaricales (pars). North Am Flora 10:77–144.
Murrill WA. 1939. Additions to Florida Fungi - I. Bull Torrey Bot Club 66: 29–37.
Orton PD. 1986. British Fungus Flora Agarics and Boleti 4—Pluteaceae: Pluteus & Volvariella. Edinburgh: Royal Botanic Garden.
Pegler DN. 1983. Agaric flora of the Lesser Antilles. Kew Bull Addit Ser. 9:1–668.
Pegler DN. 1997. The agarics of São Paulo. Kew: Royal Botanic Gardens.
Raithelhuber J. 1991. Flora Mycologica Argentina. Hongos III. Buenos Aires: Stuttgart.
Rick J. 1907. Contributivo ad monographiam Agaricarum et Polyporacearum Brasiliensium. Broteria 6:65–92.
Rick J. 1919. Contributivo II ad monographiam Agariciniornus brasieliniun. Broteria 17:101–111.
Rick J. 1930. Contributo IV ad monographiam Agaricarum Brasiliensium. Broteria 24:97–118.
Rick J. 1938. Agarici riograndenses. Lilloa 3:399–455.
Rick J. 1961. Basidiomycetes ebusadiis in Rio Grande do Sul – Brasil. 5. Agaricaeae. Iheringia Ser Bot. 8:296–450.
Rodriguez O, Galván-Corona A, Villalobos-Arámbula AR, González-Juárez LA, Ramírez MD, Vázquez-López. 2015. Contribution towards a monograph of the genus Pluteus (Pluteaceae, Agaricales). mycotaxon 129:273–278.
Saccardo PA, Trotter A. 1912. Sylloge Fungorum XXI. Padua: Edwards.