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Molecular phylogeny and phylogeography of Holarctic species of *Pluteus* section *Pluteus* (Agaricales: Pluteaceae), with description of twelve new species

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Abstract

The taxonomy and phylogeography of *Pluteus* section *Pluteus* in the Holarctic region was investigated using morphological and molecular data. Over 300 specimens spanning the major areas of boreal and temperate forests of the Northern Hemisphere were studied and nrITS and *tef1* were obtained for phylogenetic analyses. In order to stabilize the taxonomy of the group all available type collections were studied and, if possible, sequenced. A total of 26 species occurring in Eurasia and North America were recovered in the phylogenetic analyses. Twelve species are described as new (*Pluteus rangifer*, *P. elaphinus*, *P. hibbettii*, *P. eos*, *P. orestes*, *P. methvenii*, *P. shikae*, *P. kovalenkoi*, *P. leucoborealis*, *P. sepiicolor*, *P. oreibatus*, *P. atrofibrillosus*), one is provisionally named (*P. parilis*) and one variety is raised to species rank (*P. americanus*). In many cases separation of the species based on morphology alone is challenging. In general, *tef1* distinguishes the species better than nrITS. Structured infraspecific genetic variation was detected in the nrITS phylogenies for five species (*P. atromarginatus*, *P. hibbettii*, *P. orestes*, *P. primus* and *P. shikae*) and in the *tef1* phylogenies for *P. cervinus*. Phylogeographic patterns are strikingly different among the species in this group and include widespread Holarctic species, exclusively Palearctic, putative disjuncts and endemics in each Holarctic subregion (Eastern/Western Palearctic and Nearctic). Identification keys are provided for each subregion.

Introduction

The taxonomy of the genus *Pluteus* Fr. has recently been revised using molecular phylogenies, which essentially upheld the morphologically recognized sections (*Pluteus*, *Celluloderma* Fayod and *Hispidoderma* Fayod) with minor rearrangements (Justo *et al.* 2011a, 2011b). Section *Pluteus* Fr. accommodates the species with metuloid hymenial cystidia and a pileipellis organized as a cutis, and includes the type species of the genus, *Pluteus cervinus* (Schaeffer) Kummer (1874: 138) or “deer mushroom”. *Pluteus cervinus* is commonly depicted in popular field guides (e.g. Bessette *et al.* 1997; Phillips 2010) and websites (e.g. <http://mushroomobserver.org/>; http://www.mushroomexpert.com/pluteus_cervinus.html) although it has been suspected for a long time to be a complex of several species (Singer 1956).

The questions about the actual number of species in section *Pluteus* that occur in the Northern Hemisphere, the morphological characters that might be used to separate them and the correct names that should be applied to these taxa have baffled mycologists for decades. Studies on section *Pluteus* in Europe (Kühner & Romagnesi 1953; Singer 1956; Orton 1986; Bonnard 1986, 1987, 2001; Vellinga 1990) have recognized around thirteen species, with numbers varying depending on taxonomic opinion, and with as many as seven described in the last three decades (Singer 1984; Bonnard 1986, 1987, 1991, 2001; Deparis 2003; Justo & Castro 2007a,b). In North America, section *Pluteus* has received considerable attention (Murill 1917; Singer 1956; Smith & Stuntz 1958; Banerjee & Sundberg 1993, 1995). A total of 18 species have been reported, again with discrepancies depending on the taxonomic concepts of the different authors. Furthermore, many species names based on European material (*P. atromarginatus*, *P. cervinus*, *P. pellitus*, *P. patricius*, *P. petasatus*, *P. pouzarianus*, *P. salicinus*) have been applied to North American collections (Banerjee & Sundberg 1995; Rodríguez 2013).

In the first comprehensive phylogenies of section *Pluteus* (Justo *et al.* 2011a, 2011b) 98 nrITS sequences, the fungal barcode (Schoch *et al.* 2012), were analyzed, with a focus on collections from western Europe and eastern North America with a few Asian, (sub-) tropical or Southern Hemisphere samples. Sixteen species or monophyletic species-complexes were recognized, but in many cases nrITS alone proved insufficient to reach a conclusion about the species diversity in section *Pluteus*. In addition, the difficulty in interpreting old names in the absence of molecular data became evident.

In the present article we focus on the taxonomy and biogeography of *Pluteus* section *Pluteus* in the forested areas (temperate and boreal) of the northern Hemisphere, which roughly corresponds to the Holarctic region as commonly defined (Kreft & Jetz 2010) with the exception of northern Africa. To overcome the limitations of prior studies we have: (i) expanded the sampling with more collections, especially from eastern Eurasia and western North America; (ii) obtained molecular data from the protein-coding gene *tefl* (translation-elongation factor 1- α), which has proved to be a valuable alternative to nrITS for species delimitation in other groups of mushroom-forming fungi (e.g. Buyck & Hofstetter 2011); and (iii) studied available type collections of previously described holarctic taxa, and generated molecular data from them when possible.

Material and Methods

Fungal collections:—Three hundred and forty five fresh or dried collections of *Pluteus* section *Pluteus* were used for both the morphological and molecular studies. These include (i) 70 collections, mostly from western Europe and eastern North America, studied by Alfredo Justo and Drew Minnis, previously sampled for nrITS in the study of Justo *et al.* (2011a) (ii) 104 collections from all over the Russian territory studied by Ekaterina Malysheva and Tatiana Bulyonkova (iii) 46 collections from California (USA) studied by Else C. Vellinga, Gerry Cobian and Nhu Nguyen (mostly from Point Reyes National Seashore and Yosemite National Park) and (iv) 125 collections, mostly from eastern North America, with a few from Europe or western North America, including new collections sampled for this project and 14 type specimens, studied by Justo and Minnis. In addition, twelve type collections were examined morphologically but no molecular data could be obtained from them. Some of the Iberian collections of section *Pluteus* listed in Justo & Castro (2007c) were used for the elaboration of some descriptions and they are listed in the respective “collections examined” sections.

Collections were studied using standard procedures for morphological examination of section *Pluteus* (Justo & Castro 2007a). The term “intermediate cystidia” refers to the pleurocystidia situated near the lamella edges, which are described separately from the rest (Bonnard 1988). Descriptive terms for morphological features follow Vellinga (1988). The notation [60, 3, 2] indicates that measurements were made of 60 basidiospores, from 3 samples in 2 collections. Color codes are from Munsell Soil Color Charts (Munsell Color 2009). The following abbreviations are used in the descriptions: avl for average length, avw for average width, Q for quotient of length and width and avQ for average quotient. Herbarium acronyms follow Thiers (2014).

Molecular data:—Protocols for DNA extraction, PCR and sequencing were the same as those outlined in Justo & Hibbett (2011). PCR amplification and sequencing of the ITS region was performed using primers ITS1F and ITS4 (White *et al.* 1990; Gardes & Bruns 1993). Primers EF1-983F and EF1-1567R were used to amplify approximately 500bp of *tefl* (Rehner & Buckley 2005), using the touchdown PCR protocol described in Justo & Hibbett (2011). Raw sequence data were edited and assembled in Sequencher 4.7 (Gene Codes Corporation) and MEGA 5 (Tamura *et al.* 2011).

Phylogenetic analyses:—In addition to the sequences generated here, 29 nrITS sequences were retrieved from GenBank (Benson *et al.* 2011) and their accession numbers are given in the corresponding figures. The taxonomic identities of these sequences are given as they appear on GenBank. Both the nrITS and *tefl* sequences were aligned using MAFFT version 7.110 (Kato & Toh 2008) and the strategy FFT-NS-i was selected. The alignments were manually corrected using MacClade 4.08 (Maddison & Maddison 2002). For the combined datasets the individual alignment files were concatenated in MacClade. Three different datasets were assembled for the phylogenetic analyses: nrITS, *tefl* and combined (nrITS + *tefl*). In all datasets two representatives of *Pluteus* section *Celluloderma*, *Pluteus* aff. *romellii* (nrITS AY854065, *tefl* AY883433) and *Pluteus aureovenatus* Menolli & Capelari (Menolli *et al.* 2010: 139; nrITS FJ816663, *tefl* KJ010056), were used as outgroup taxa.

Three different phylogenetic analyses were performed for all the datasets: (i) Maximum likelihood (ML)

analyses were run in the RAxML servers, version 7.2.8 (Stamatakis & *et al.* 2008), under a GTR model with one hundred rapid bootstrap (BS) replicates (ii) equally weighted parsimony analyses were performed using PAUP *4.0.b10 (Swofford 2002). One thousand heuristic search replicates were performed with starting trees generated by stepwise addition with random addition sequences followed by tree bisection reconnection branch swapping. Up to two trees were kept in each replicate. Parsimony BS analysis was performed with 1000 replicates, each with 10 random taxon addition sequences and branch swapping set to subtree pruning and regrafting; (iii) Bayesian (BY) analyses were run using MrBayes (Ronquist & Huelsenbeck 2003) at the Cipres Science Gateway (Miller & *et al.* 2010; MrBayes version 3.2.2) for 10 million generations, under a GTR model, with four chains, and trees sampled every 1000 generations. The initial burn-in phase was set to 2.5 million generations after examining the graphic representation of the likelihood scores of the sampled trees which confirmed that this is an adequate value for all datasets. A fifty percent majority rule consensus tree was computed using the remaining trees. A node is considered to be strongly supported if it receives support in at least two of the three analyses by a BS value equal or greater than 70% and/or a posterior probability (PP) equal or greater than 0.95. A search for potential conflicts between the nrITS and *tefl* datasets was performed by comparing the resulting trees for each dataset and looking for strongly supported positive conflict.

Characterization of Single Nucleotide Polymorphisms (SNPS):—We visually inspected the nrITS and *tefl* alignments to search for SNPS that characterized putative infraspecific lineages in each of the 26 species studied here. Apparently heterozygous positions (Y, R, W, etc.) were verified by visual inspection of the electropherograms using Sequencher 4.7 (Gene Codes Corporation) and MEGA 5 (Tamura *et al.* 2011). All nucleotide position numbers used in the results section refer to the individual nrITS and *tefl* alignments deposited in TreeBASE (S15767).

Results

New Sequences and alignments:—Five hundred and twenty seven new sequences were generated for this study: 275 nrITS and 252 *tefl*. GenBank accession numbers are given for each studied collection after the herbarium number. Alignments have been deposited in TreeBASE (S15767).

Combined dataset:—The dataset includes 376 isolates of *Pluteus* section *Pluteus*: 248 are represented by both nrITS and *tefl* sequence data, 126 only by nrITS data and two have only *tefl* data. The final dataset consists of 1279 characters (gaps included): 762 constant, 69 parsimony uninformative and 448 parsimony informative. In the MP analyses 422 most parsimonious trees were recovered (Length = 1263; CI = 0.60, RI = 0.97).

The overall topologies of the MP, ML and BY trees are very similar, with six major clades recovered (Fig. 1a): *cervinus*, *pouzarianus*, *brunneidiscus*, *petasatus*, *salicinus* and *atromarginatus*. All these clades and their backbone relationships are supported, with the exception of the *pouzarianus* clade (only supported in the ML analysis) and the grouping of the *cervinus*, *pouzarianus* and *brunneidiscus* clades (only supported in the MP analysis).

The *cervinus* clade (Fig. 2a) includes six species (*P. cervinus*, *P. exilis*, *P. rangifer*, *P. hongoi*, *P. elaphinus* and *P. alniphilus*), all supported as monophyletic except *P. rangifer*. The isolates of *P. rangifer* appear as a non-monophyletic assemblage in a supported clade that also includes *P. exilis*. All sister-clade relationships are supported.

The *pouzarianus* clade (Fig. 3a) includes seven species (*P. pouzarianus*, *P. hibbettii*, *P. eos*, *P. parilis*, *P. orestes*, *P. primus* and *P. methvenii*), all supported as monophyletic. The isolates of *P. hibbettii* appear as two distinct subclades according to their geographic origin (Eurasian vs. North American). The sister taxon relationship of *P. primus* and *P. methvenii* and the grouping of *P. pouzarianus*, *P. hibbettii* and *P. eos* in one clade are supported but other sister-clade relationships receive no statistical support.

The *brunneidiscus* clade (Fig. 4a) includes three species (*P. brunneidiscus*, *P. shikae* and *P. kovalenkoi*), all supported as monophyletic. The isolates of *P. brunneidiscus* and *P. shikae* appear as two distinct subclades. All sister-clade relationships are supported.

The *petasatus* clade (Fig. 5a) includes three species (*P. petasatus*, *P. pellitus* and *P. leucoborealis*), all supported as monophyletic. Some internal subclades in *P. petasatus* and *P. pellitus* receive good statistical support. The sister-taxa relationships between these three species are not supported.

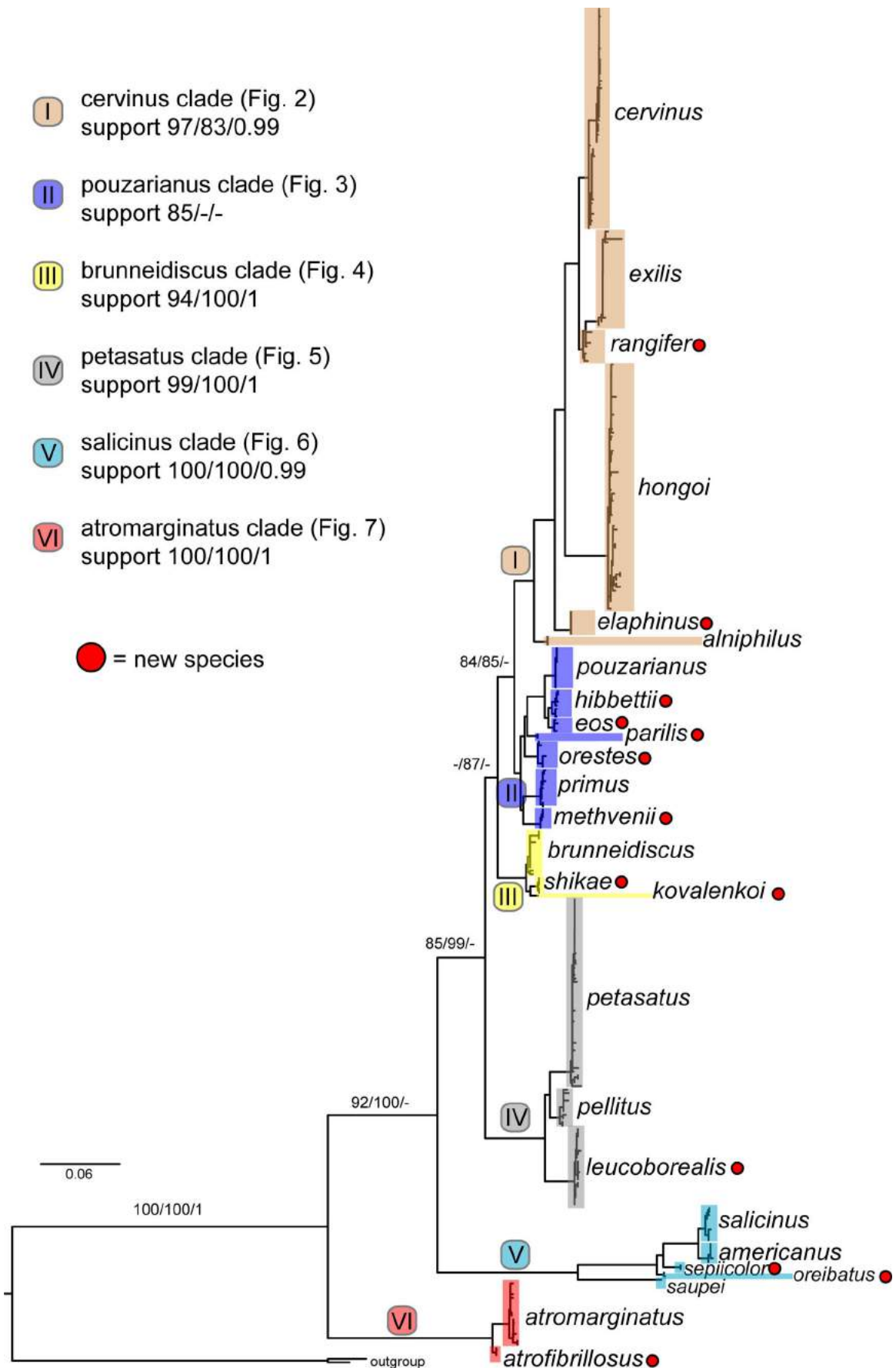


FIGURE 1. Best tree from the ML analyses of the combined dataset. Support Values (ML/MP/BY) are given on or below the branches.

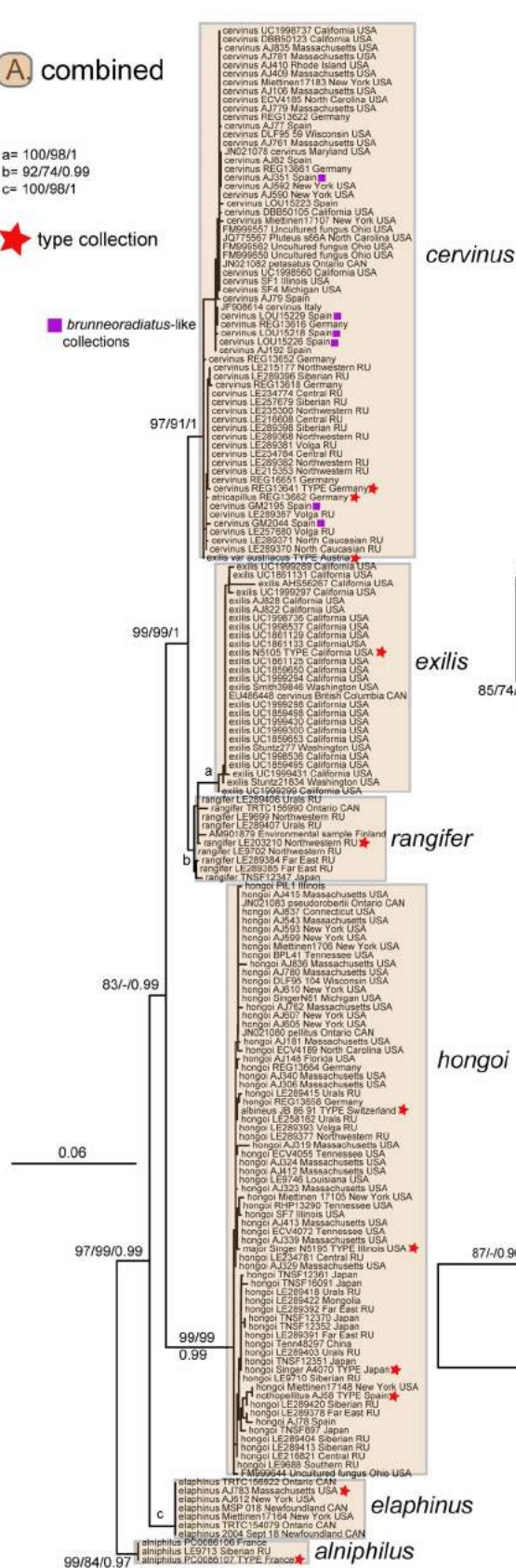
I cervinus clade

A. combined

a= 100/98/1
b= 92/74/0.99
c= 100/98/1

★ type collection

■ brunneoradiatus-like collections



B. nrITS

a= 87/73/-

cervinus

exilis

rangifer

hongoi

alniphilus

elaphinus

alniphilus

-85/0.99

cervinus

rangifer I

exilis

rangifer II

hongoi

alniphilus

elaphinus

C. tef1

hongoi

alniphilus

elaphinus

alniphilus

99/98/1

cervinus

rangifer TRTC156990 Ontario CAN

rangifer LE289384 Far East RU

rangifer LE9699 Northwestern RU

rangifer LE289385 Far East RU

rangifer LE289407 Urals RU

rangifer LE289406 Urals RU

rangifer LE9702 Northwestern RU

rangifer LE203210 Northwestern RU

rangifer TNSF12347 Japan

exilis

exilis AJ828 California USA

exilis AJ822 California USA

exilis UC1861131 California USA

exilis Stuntz21834 Washington USA

elaphinus

hongoi

alniphilus

99/100/1

100/100

93/84/0.92

87/-/0.96

99/99/1

99/99/1

99/99/1

99/99/1

99/99/1

99/99/1

99/99/1

99/99/1

99/99/1

99/99/1

99/99/1

FIGURE 2. Detail of the best trees from the ML analyses of the combined (a), nrITS (b) and *tef1* datasets (c) focusing on the cervinus clade. Support Values (ML/MP/BY) are given on or below the branches. For each collection the collection number and country information are given. In the case of Canada (CAN), Russia (RU) and the United States of America (USA), the name of the province/federal district/state is also included.

II pouzarianus clade

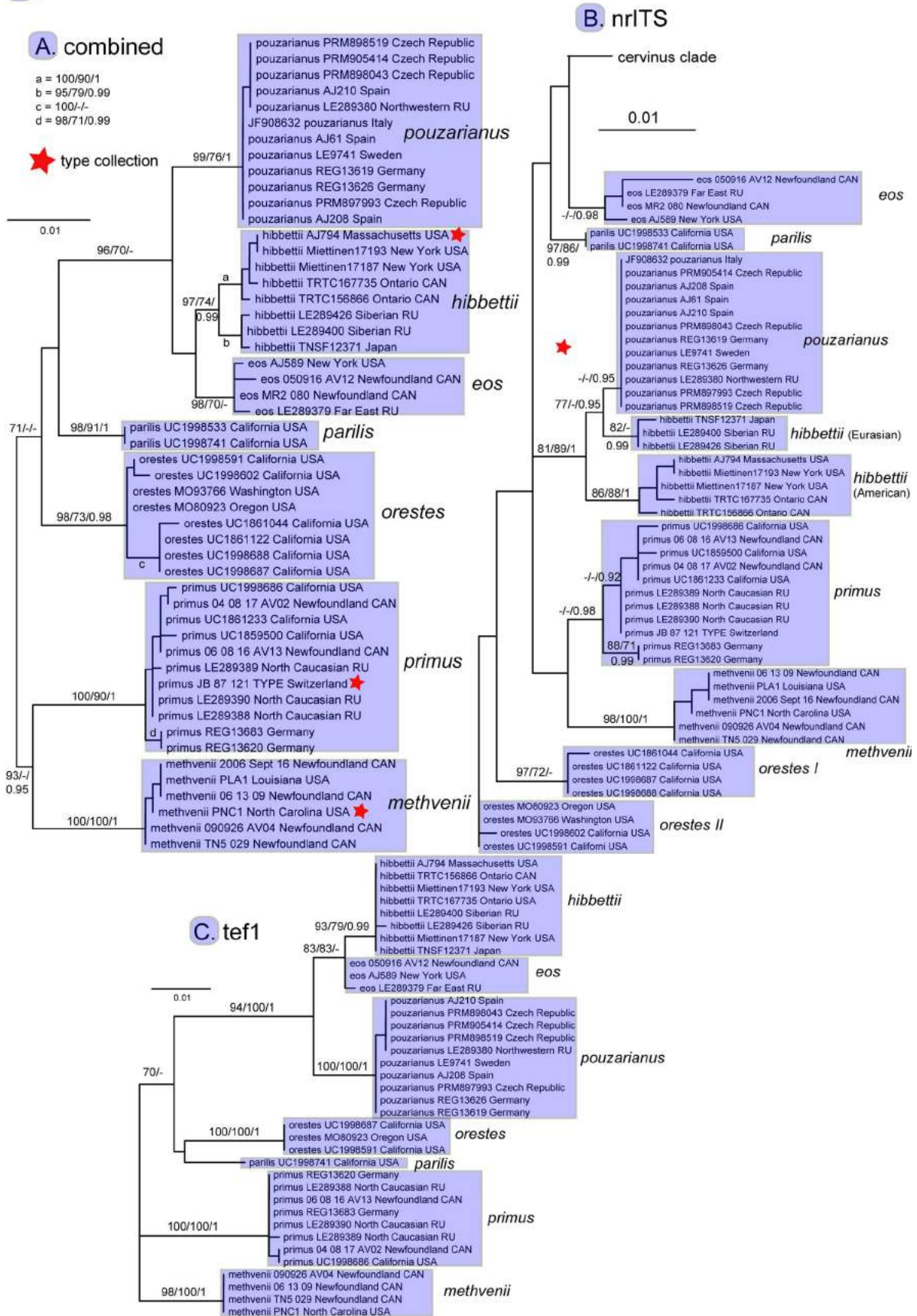


FIGURE 3. Detail of the best trees from the ML analyses of the combined (a), nrITS (b) and *tef1* datasets (c) focusing on the pouzarianus clade. Support Values (ML/MP/BY) are given on or below the branches. For each collection the collection number and country information are given. In the case of Canada (CAN), Russia (RU) and the United States of America (USA), the name of the province/federal district/state is also included.

III brunneidiscus clade

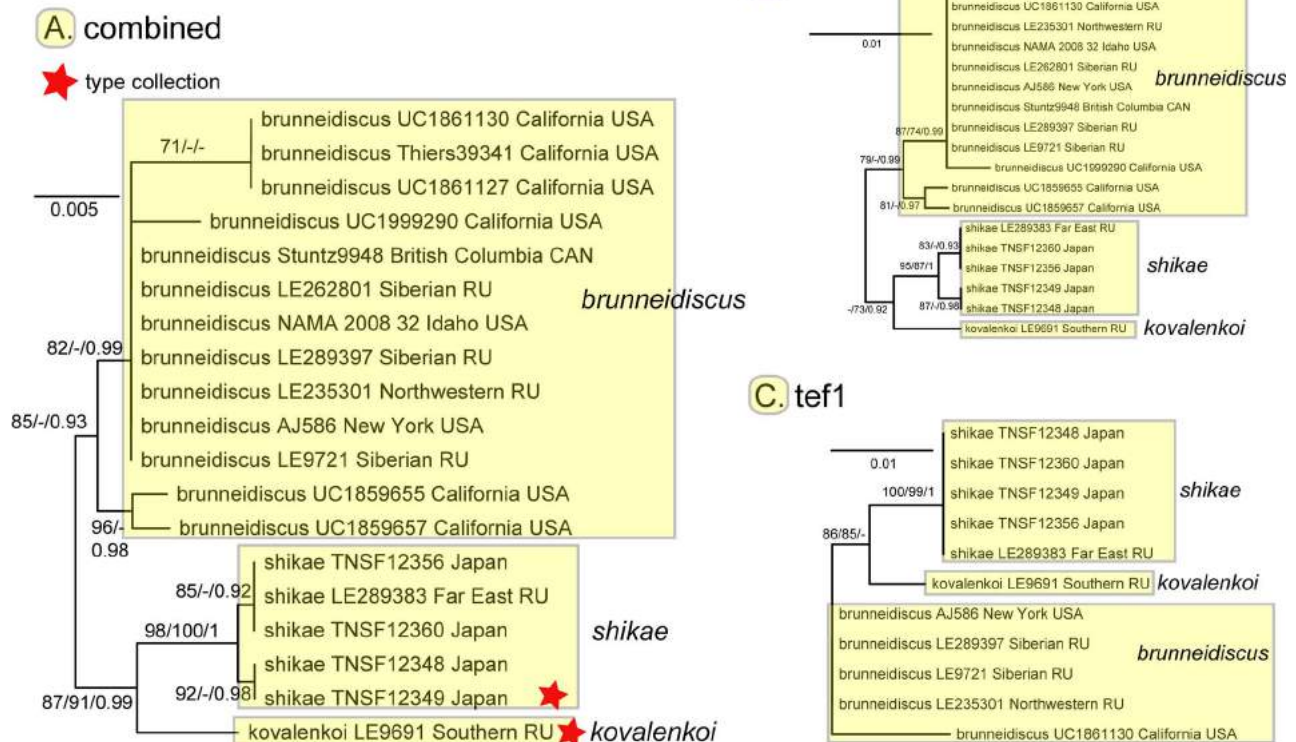


FIGURE 4. Detail of the best trees from the ML analyses of the combined (a), nrITS (b) and *tef1* datasets (c) focusing on the brunneidiscus clade. Support Values (ML/MP/BY) are given on or below the branches. For each collection the collection number and country information are given. In the case of Canada (CAN), Russia (RU) and the United States of America (USA), the name of the province/federal district/state is also included.

The salicinus clade (Fig. 6a) includes five species (*P. salicinus*, *P. americanus*, *P. sepiicolor*, *P. oreibatus* and *P. saupe*), all supported as monophyletic except *P. salicinus*. The isolates of *P. salicinus* do appear as a monophyletic group but that grouping only receives support in the ML analysis. The *P. americanus* isolate from the Russian Far East (LE 289369) appears as sister to all the American isolates. All sister-clade relationships are well supported except the grouping of *P. sepiicolor*, *P. americanus* and *P. salicinus*.

The atomarginatus clade (Fig. 7a) includes two species (*P. atomarginatus* and *P. atrofibrillosus*), both supported as monophyletic. The isolates of *P. atomarginatus* appear as two subclades according to their geographic origin (Eurasian vs. North American) but these clades receive no support.

nrITS dataset:—The dataset includes 374 isolates of *Pluteus* section *Pluteus*. The final dataset consists of 701 characters (gaps included): 410 constant, 55 parsimony uninformative and 236 parsimony informative. In the MP analyses 1308 most parsimonious trees were recovered (Length = 625; CI = 0.66, RI = 0.98). The overall topology of the MP, ML and BY trees is essentially the same.

The most notable differences with respect to the combined analyses regarding topology and statistical support include: (i) none of the backbone nodes of the phylogeny receives support (ii) the cervinus clade does not receive statistical support, although the cervinus clade minus *P. alniphilus* does (Fig. 2b) (iii) the species of the pouzarianus clade do not form a clade, instead they appear as a non-monophyletic assemblage between the brunneidiscus and cervinus clades (Fig. 3b) (iv) the isolates of the following species are not recovered as monophyletic: *P. rangifer* (Fig. 2b), *P. hibbettii* & *P. orestes* (Fig. 3b), *P. pellitus* (Fig. 5b), *P. salicinus* & *P. americanus* (Fig. 6b) and *P. atomarginatus* (Fig. 7b).

tef1 dataset:—The dataset includes 250 isolates of section *Pluteus*, and consists of 578 characters (gaps included): 352 constant, 14 parsimony uninformative and 212 parsimony informative. In the MP analyses 1198 most parsimonious trees were recovered (Length = 608; CI = 0.57, RI = 0.97). The overall topology of the MP, ML and BY trees is very similar, although they differ in the position of *Pluteus eos*. In the ML tree the isolates of *P. eos*

IV petasatus clade

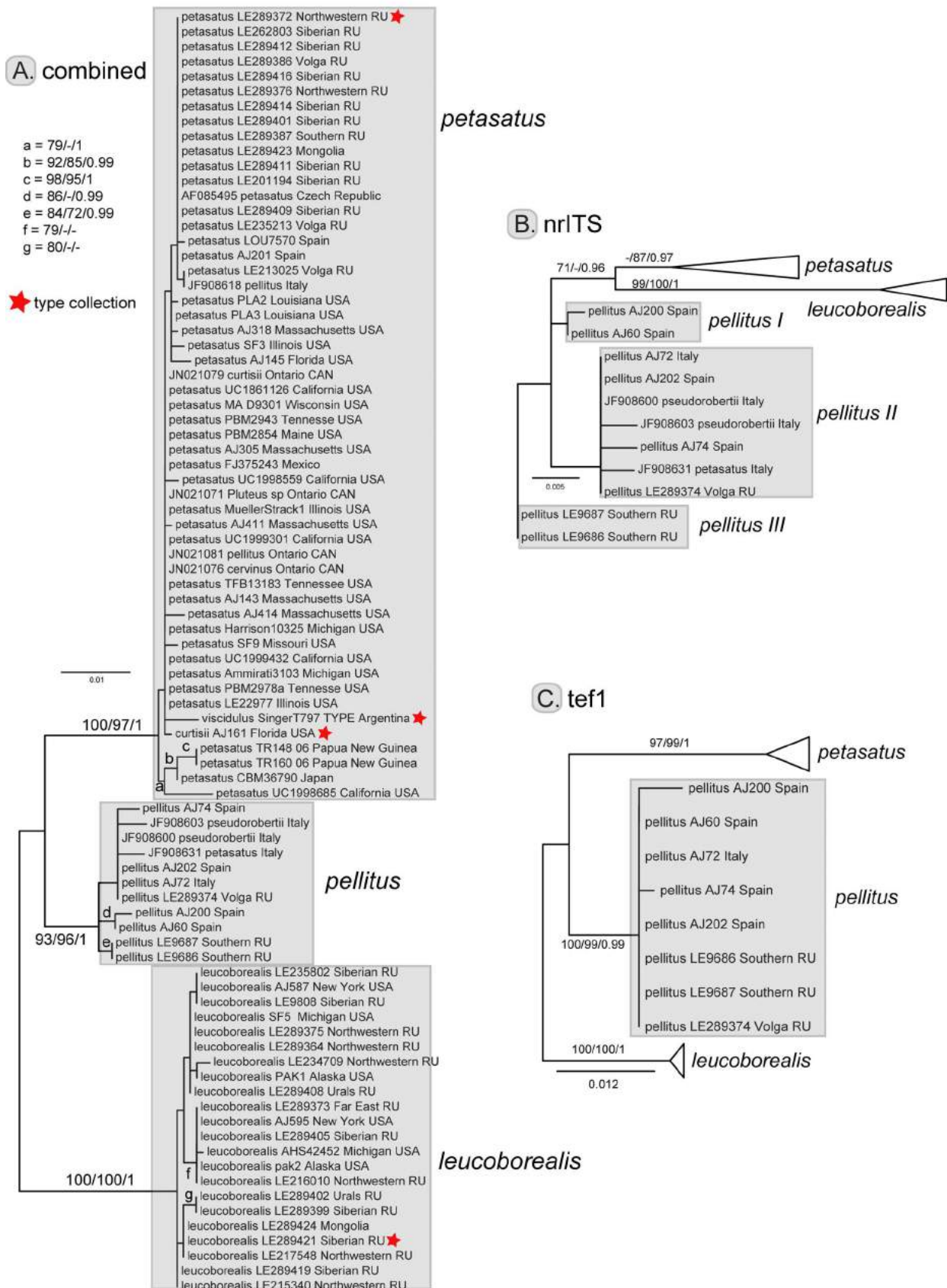


FIGURE 5. Detail of the best trees from the ML analyses of the combined (a), nrITS (b) and *tef1* datasets (c) focusing on the *petasatus* clade. Support Values (ML/MP/BY) are given on or below the branches. For each collection the collection number and country information are given. In the case of Canada (CAN), Russia (RU) and the United States of America (USA), the name of the province/federal district/state is also included.

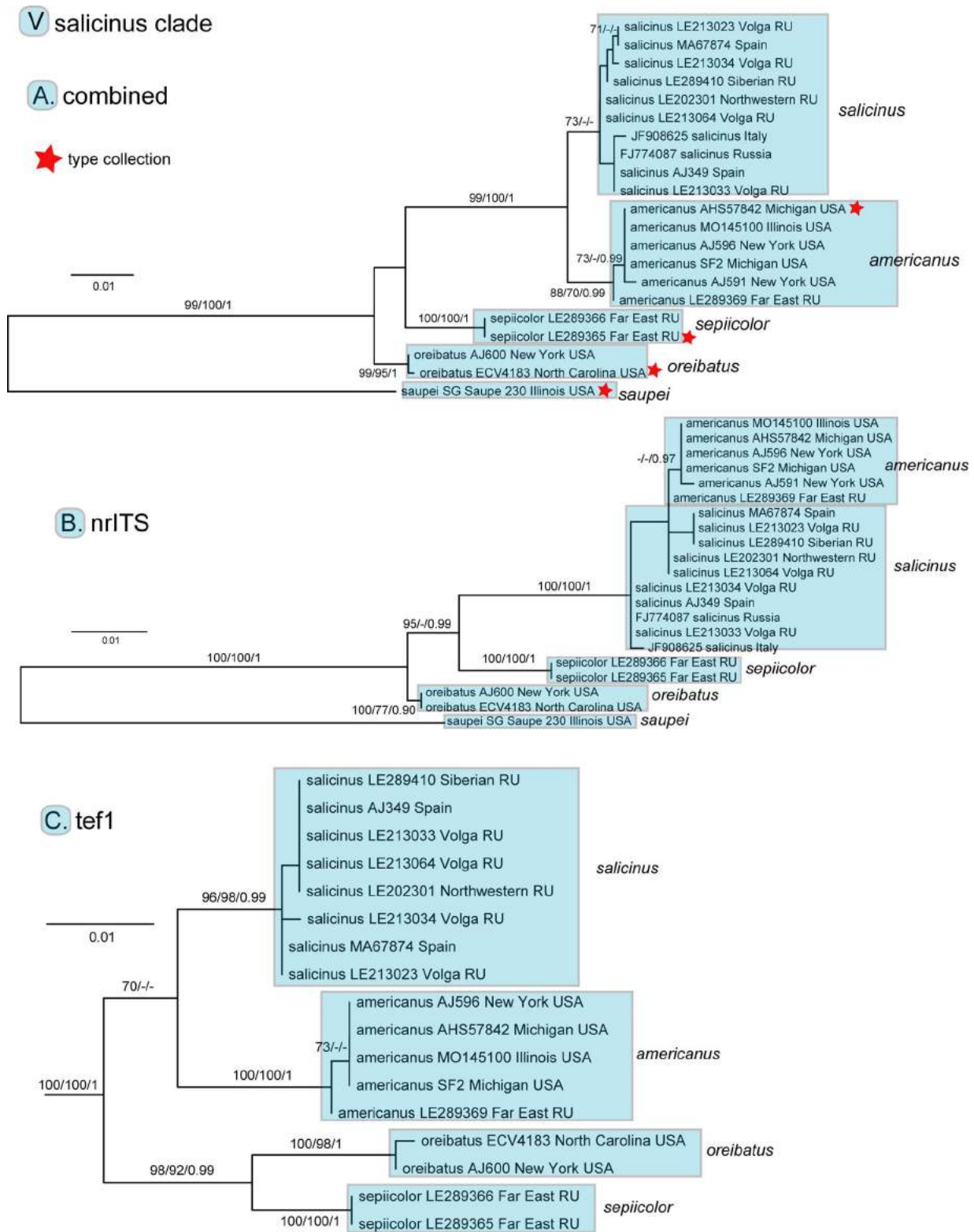


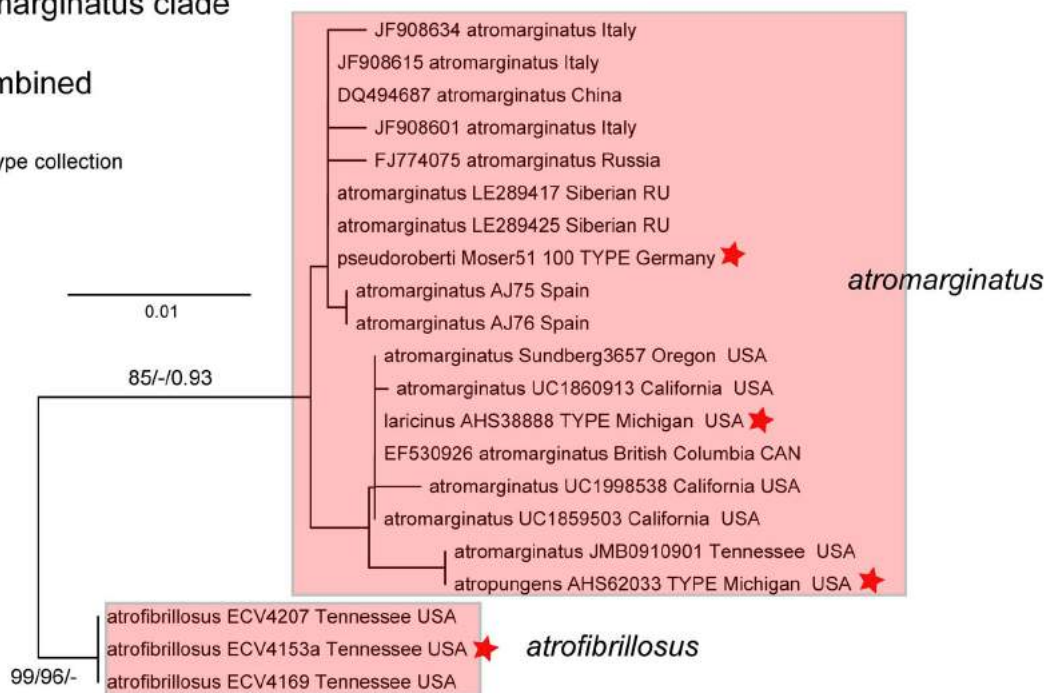
FIGURE 6. Detail of the best trees from the ML analyses of the combined (a), nrITS (b) and *tef1* datasets (c) focusing on the salicinus clade. Support Values (ML/MP/BY) are given on or below the branches. For each collection the collection number and country information are given. In the case of Canada (CAN), Russia (RU) and the United States of America (USA), the name of the province/federal district/state is also included.

appear as a non-monophyletic assemblage in the same clade as *P. hibbettii* (Fig. 3c); in the BY analysis they are recovered as a non-monophyletic assemblage in a more inclusive clade with *P. pouzarianus* (and separate from *P. hibbettii*); and in the MP analysis they appear alternatively as a non-monophyletic group together with *P. hibbettii* or as the monophyletic sister-species of *P. hibbettii*.

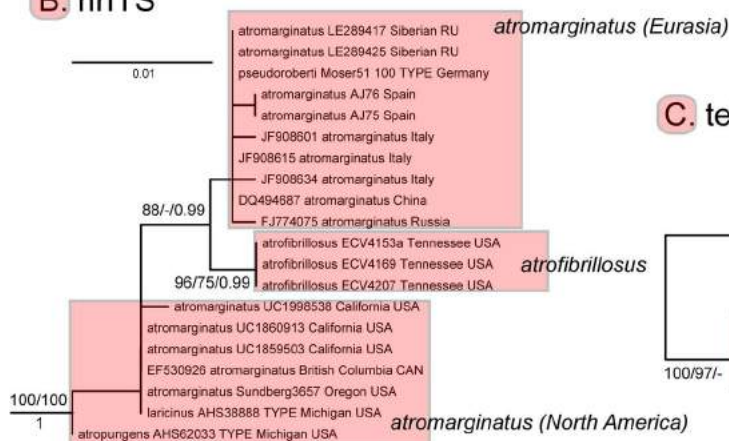
VI atromarginatus clade

A. combined

★ type collection



B. nrITS



C. tef1

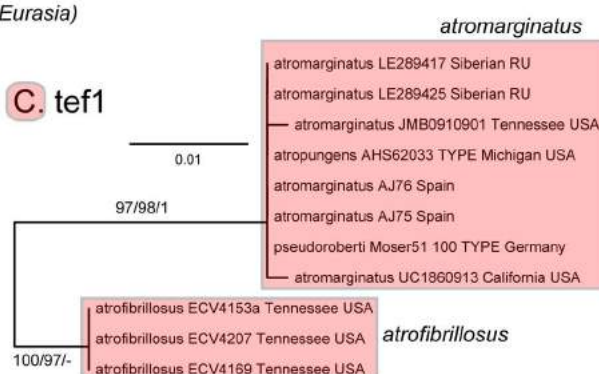


FIGURE 7. Detail of the best trees from the ML analyses of the combined (a), nrITS (b) and *tef1* datasets (c) focusing on the *atromarginatus* clade. Support Values (ML/MP/BY) are given on or below the branches. For each collection the collection number and country information are given. In the case of Canada (CAN), Russia (RU) and the United States of America (USA), the name of the province/federal district/state is also included.

The most notable differences with respect to the combined and nrITS analyses regarding topology and statistical support include: (i) all taxa recovered as non-monophyletic in the nrITS analyses (see above) are recovered as monophyletic in the *tef1* analyses. *Pluteus rangifer*, the only species recovered as non-monophyletic in the combined analyses, does appear as monophyletic in the *tef1* analyses (Fig. 2c) (ii) *Pluteus elaphinus* appears as sister to the clade including *P. cervinus*, *P. exilis* and *P. rangifer* (Fig. 2c), while in the nrITS and combined analyses *P. hongoi* appears in that position (iii) *Pluteus brunneidiscus* is not recovered as monophyletic (Fig. 4c) (iv) *Pluteus oreibatus* and *P. sepiicolor* appear as sister-taxa (Fig. 6c).

Conflicts between nrITS and *tef1* datasets:—The following differences between these datasets are statistically supported as conflicts: (i) the alternative placement of *P. elaphinus* (*tef1*) and *P. hongoi* (nrITS) as sister to the clade including *P. cervinus*, *P. exilis* and *P. rangifer* (Fig. 2). In the combined dataset these taxa appear in the same positions as in the nrITS dataset (ii) the monophyly (*tef1*) vs. non-monophyly (nrITS) of *P. hiebertii* (Fig. 3).

In the combined dataset *P. hibbettii* appears as monophyletic (iii) the sister-taxa (*tef1*) vs. non sister-taxa (nrITS) relationship of *P. oreibatus* and *P. sepiicolor* (Fig. 6). In the combined dataset they do not appear as sister-taxa; (iv.) the monophyly (*tef1*) vs. non-monophyly (nrITS) of *P. atomarginatus* (Fig. 7). In the combined dataset *P. atomarginatus* appears as monophyletic.

Species with structured nrITS variation:—In five of the 26 species studied here we observed the presence of different nrITS groups that were associated with a certain geographic origin and/or appear as well-supported clades in the nrITS phylogenies. (i) *P. hibbettii* (Fig. 3b). Eurasian and North American collections differ in seven SNPS (Table 1) (ii) *P. primus* (Fig. 3b). The collections from Germany have 2 SNP unique to them and the North American collections have one unique SNP (Table 2) (iii) *P. orestes* (Fig. 3b). The collections labelled as *orestes* I differ from the collections UC1998591 and UC1998602 in five SNPS , while the collections MO80923 and MO93766 are heterozygous at those positions (Table 3) (iv) *P. shikae* (Fig. 4b). Collections TNS-F 12360, TNS-F 12356 and LE89383 differ from the collections TNS-F 12349 and TNS-F 12348 in two SNPS (Table 4) (v) *P. atomarginatus* (Fig. 7b). Eurasian and North American collections differ in 4 SNPS and a five nucleotide indel (Table 5).

TABLE 1. SNPS that characterize the different nrITS types of *Pluteus hibbettii*. Nucleotide positions are given according to the alignment deposited in TreeBASE (S15767).

| | 6 | 27 | 29 | 120 | 164 | 477 | 579 |
|----------------------------|---|----|----|-----|-----|-----|-----|
| Eurasian collections | A | A | T | A | G | - | T |
| North American collections | G | T | C | G | A | A | G |

TABLE 2. SNPS that characterize the different nrITS types of *Pluteus primus*. Nucleotide positions are given according to the alignment deposited in TreeBASE (S15767).

| | 178 | 460 | 552 |
|----------------------------|-----|-----|-----|
| German Collections | C | A | A |
| Other Eurasian collections | T | A | T |
| North American collections | T | G | T |

TABLE 3. SNPS that characterize the different nrITS types of *Pluteus orestes*. Nucleotide positions are given according to the alignment deposited in TreeBASE (S15767).

| | 29 | 81 | 224 | 476 | 561 |
|---------------------------------------|----|----|-----|-----|-----|
| <i>orestes</i> I collections (Fig. 3) | T | T | T | C | G |
| UC1998591 and UC1998602 | C | C | A | T | T |
| MO80923 and MO93766 | Y | Y | W | Y | K |

TABLE 4. SNPS that characterize the different nrITS types of *Pluteus shikae*. Nucleotide positions are given according to the alignment deposited in TreeBASE (S15767).

| | 4 | 132 |
|---------------------------------------|---|-----|
| TNS-F 12360, TNS-F 12356 and LE 89383 | A | C |
| TNS-F 12349 and TNS-F 12348 | G | T |

TABLE 5. SNPS and indels that characterize the different nrITS types of *Pluteus atomarginatus*. Nucleotide positions are given according to the alingment deposited in TreeBASE (S15767).

| | 39 | 98 | 219 | 222-225 | 517 | 537 |
|----------------------------|----|----|-----|---------|-----|-----|
| Eurasian collections | C | G | C | AAAT | T | T |
| North American collections | T | A | – | – – – – | C | C |

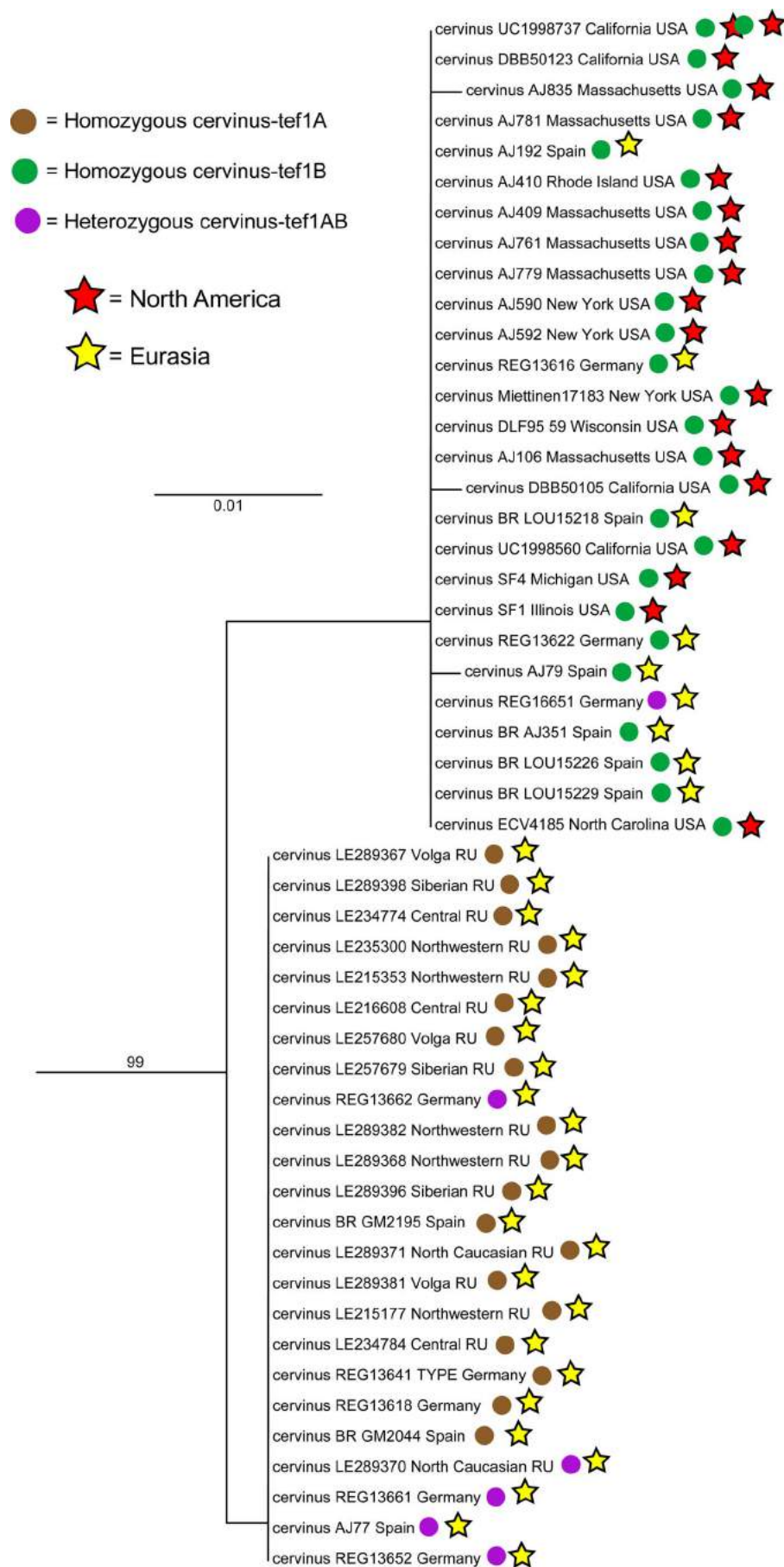


FIGURE 8. Detail of the Best tree from the ML analyses of the *tefl* dataset highlighting the distribution of *tefl* alleles in *P. cervinus*.

Species with structured *tefl* variation:—In *P. cervinus* we observed the presence of two different *tefl* variants. Given the single-copy nature of *tefl* these variants were inferred to represent two allelic variants, and collections with no double peaks in the *tefl* electropherograms were inferred to be homozygous for this locus. The distribution of these alleles, named for convenience *cervinus-teflA* and *cervinus-teflB*, is correlated with the geographic origin of the collections (Fig. 8). Nineteen collections were inferred to be homozygous *cervinus-teflA*, 26 are homozygous *cervinus-teflB* and 7 are heterozygous AB. Both alleles differ in 8 SNPS (Table 6). Four of these 8 polymorphic sites are situated on intron regions of *tefl* and the other four are situated on coding regions. The SNP at position 250 causes an amino acid change between aspartic acid (GAC) in *cervinus-teflA* and glutamic acid (GAA) in *cervinus-teflB*. The SNP at position 371 causes an amino acid change between proline (CCC) in *cervinus-teflA* and alanine (GCC) in *cervinus-teflB*.

TABLE 6. SNPS that characterize the different *tefl* alleles types of *Pluteus cervinus*. Nucleotide positions are given according to the alignment deposited in TreeBASE (S15767).

| | 244 | 250 | 371 | 382 | 385 | 409 | 426 | 473 |
|--|-----|-----|-----|-----|-----|-----|-----|-----|
| homozygous <i>cervinus-teflA</i> collections | T | C | C | C | T | G | T | C |
| homozygous <i>cervinus-teflB</i> collections | C | T | G | T | C | A | C | T |
| heterozygous AB collections | Y | Y | S | Y | Y | R | Y | Y |

Taxonomic Part

Here we present the descriptions of the 26 species currently known to occur in the Holarctic region. Generally speaking, morphological variation tends to be gradual and with some level of overlap between closely related species. There are very few clear-cut morphological or ecological differences, and in many cases identification of individual collections without molecular data will not be possible. Even with these caveats, we firmly believe that describing and naming these taxa is critical for a correct understanding of the natural history of section *Pluteus*. Regional endemics in this group are in need of further study to establish their conservation status.

We have kept the individual observations under each species as concise as possible, and avoided repetition whenever possible, e.g. if a pair of species is compared under the observations for one of them they will not be compared again in the observations for the other one. The reader is referred to the discussion section and to the synoptic key (Table 7) for further insights into the morphological variation in section *Pluteus* and an overview of the morphological differences between the species described here.

TABLE 7. Synoptic key based on the macromorphology, habitat, distribution across the Holarctic region and microscopic characters for the species described in this article. + = present; - = absent; (+) = rarely present

| | Brown lamellar edge | Blue-green tinges on pileus or stipe | On angiosperm wood | On conifer wood | On wood chips, sawdust, or terrestrial | In temperate forests | In boreal forests | In transitional or montane forests |
|---------------------|---------------------------|---|--------------------------|-----------------------|---|----------------------------|-------------------------|---|
| <i>P. cervinus</i> | - | - | + | (+) | (+) | + | - | + |
| <i>P. exilis</i> | - | - | + | + | - | + | - | - |
| <i>P. rangifer</i> | - | - | + | - | - | - | + | + |
| <i>P. hongoi</i> | - | - | + | - | + | + | - | (+) |
| <i>P. elaphinus</i> | - | - | + | - | - | - | - | + |

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TABLE 7 (continued)

| | Brown lamellar edge | Blue-green tinges on pileus or stipe | On angiosperm wood | On conifer wood | On wood chips, sawdust, or terrestrial | In temperate forests | In boreal forests | In transitional or montane forests |
|---------------------------|---------------------------|---|--------------------------|-----------------------|---|----------------------------|-------------------------|---|
| <i>P. alniphilus</i> | - | - | + | - | - | - | - | + |
| <i>P. pouzarianus</i> | - | - | - | + | (+) | + | + | + |
| <i>P. hibbettii</i> | - | - | - | + | - | - | + | + |
| <i>P. eos</i> | + / - | - | - | + | - | - | + | + |
| <i>P. orestes</i> | + / - | - | - | + | (+) | - | - | + |
| <i>P. primus</i> | - | - | - | + | + | + | + | + |
| <i>P. methvenii</i> | - | - | - | + | - | + | + | + |
| <i>P. brunneidiscus</i> | - | - | + | - | + | + | - | + |
| <i>P. shikae</i> | - | - | + | - | - | + | - | + |
| <i>P. kovalenkoi</i> | - | - | - | + | - | - | - | + |
| <i>P. petasatus</i> | - | - | + | - | + | + | - | - |
| <i>P. pellitus</i> | - | - | + | - | (+) | + | - | - |
| <i>P. leucoborealis</i> | - | - | + | - | - | - | + | + |
| <i>P. salicinus</i> | - | + | + | - | - | + | - | + |
| <i>P. americanus</i> | - | + | + | - | - | + | - | + |
| <i>P. sepiicolor</i> | - | - | - | + | - | - | - | + |
| <i>P. oreibatus</i> | - | - | - | + | - | - | - | + |
| <i>P. saupe</i> | - | + | ? | ? | ? | + | - | - |
| <i>P. atromarginatus</i> | + | - | - | + | (+) | + | - | + |
| <i>P. atrofibrillosus</i> | + | - | - | + | - | + | - | + |

TABLE 7 (continued)

| | Western Palearctic | Eastern Palearctic | Western Nearctic | Eastern Nearctic |
|-----------------------|--------------------|--------------------|------------------|------------------|
| <i>P. cervinus</i> | + | + | (+) | + |
| <i>P. exilis</i> | - | - | + | - |
| <i>P. rangifer</i> | + | + | - | + |
| <i>P. hongoi</i> | + | + | - | + |
| <i>P. elaphinus</i> | - | - | - | + |
| <i>P. alniphilus</i> | + | + | - | - |
| <i>P. pouzarianus</i> | + | - | - | - |

..... continued on the next page

TABLE 7 (continued)

| | Western Palearctic | Eastern Palearctic | Western Nearctic | Eastern Nearctic |
|---------------------------|--------------------|--------------------|------------------|------------------|
| <i>P. hibbettii</i> | - | + | - | + |
| <i>P. eos</i> | - | + | - | + |
| <i>P. orestes</i> | - | - | + | - |
| <i>P. primus</i> | + | - | + | + |
| <i>P. methvenii</i> | - | - | - | + |
| <i>P. brunneidiscus</i> | + | + | + | + |
| <i>P. shikae</i> | - | + | - | - |
| <i>P. kovalenkoi</i> | + | - | - | - |
| <i>P. petasatus</i> | + | + | + | + |
| <i>P. pellitus</i> | + | - | - | - |
| <i>P. leucoborealis</i> | + | + | + | + |
| <i>P. salicinus</i> | + | + | - | - |
| <i>P. americanus</i> | - | + | - | + |
| <i>P. sepüicolor</i> | - | + | - | - |
| <i>P. oreibatus</i> | - | - | - | + |
| <i>P. saupei</i> | - | - | - | + |
| <i>P. atromarginatus</i> | + | + | + | + |
| <i>P. atrofibrillosus</i> | - | - | - | + |

TABLE 7 (continued)

| | Basidiospores | | | Hooks on pleurocystidia (predominant type) | Intermediate Cystidia (predominant type) | Cheilocystidia (predominant type) | Clamp- connections on pileipellis |
|----------------------|---------------|---------|-----------|---|---|---|---|
| | avl | avw | avQ | | | | |
| <i>P. cervinus</i> | 7.0–8.1 | 5.0–5.7 | 1.35–1.50 | entire | no predominant type | clavate | no |
| <i>P. exilis</i> | 7.0–7.5 | 5.1–5.3 | 1.38–1.47 | entire | no predominant type | clavate | no |
| <i>P. rangifer</i> | 7.2–7.6 | 5.0–5.8 | 1.31–1.43 | entire | fusiform and without hooks | clavate | no |
| <i>P. hongoi</i> | 6.7–7.6 | 5.0–5.7 | 1.26–1.45 | bifid | no predominant type | clavate | no |
| <i>P. elaphinus</i> | 7.0–7.8 | 5.0–5.8 | 1.34–1.42 | bifid | no predominant type | clavate | no |
| <i>P. alniphilus</i> | 7.3–7.4 | 4.8–5.1 | 1.44–1.51 | entire | no predominant type | clavate to narrowly clavate | yes |

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TABLE 7 (continued)

| | Basidiospores | | | Hooks on pleurocystidia (predominant type) | Intermediate Cystidia (predominant type) | Cheilocystidia (predominant type) | Clamp- connections on pileipellis |
|---------------------------|---------------|---------|-----------|---|---|---|---|
| | avl | avw | avQ | | | | |
| <i>P. pouzarianus</i> | 6.8–7.5 | 4.8–5.2 | 1.35–1.52 | entire | no predominant type | clavate | yes |
| <i>P. hibbettii</i> | 7.3–7.6 | 4.5–4.7 | 1.50–1.65 | entire | no predominant type | clavate | yes |
| <i>P. eos</i> | 7.7–8.2 | 5.4–5.7 | 1.41–1.45 | bifid | no predominant type | narrowly clavate to cylindrical | yes |
| <i>P. orestes</i> | 9.0–9.9 | 6.0–7.3 | 1.35–1.51 | indistinct | no predominant type | narrowly clavate to cylindrical | yes |
| <i>P. primus</i> | 7.8–8.4 | 5.6–6.3 | 1.33–1.43 | entire | no predominant type | narrowly clavate to cylindrical | yes |
| <i>P. methvenii</i> | 7.1–8.9 | 5.3–5.9 | 1.33–1.50 | entire | no predominant type | clavate | yes |
| <i>P. brunneidiscus</i> | 7.1–8.1 | 5.1–6.2 | 1.30–1.45 | entire | no predominant type | clavate | yes |
| <i>P. shikae</i> | 6.5–7.1 | 4.4–5.0 | 1.42–1.56 | entire | no predominant type | clavate | yes |
| <i>P. kovalenkoi</i> | 7.8–8.2 | 5.2–5.5 | 1.49–1.60 | entire | no predominant type | clavate | yes |
| <i>P. petasatus</i> | 6.1–7.0 | 4.2–4.8 | 1.35–1.55 | entire | fusiform and without hooks | clavate | no |
| <i>P. pellitus</i> | 5.8–6.5 | 4.3–4.6 | 1.34–1.46 | entire | fusiform and without hooks | clavate or narrowly clavate | yes |
| <i>P. leucoborealis</i> | 6.8–7.4 | 5.3–5.5 | 1.26–1.36 | entire | fusiform and without hooks | clavate | no |
| <i>P. salicinus</i> | 8.3–9.5 | 6.2–6.8 | 1.32–1.48 | entire | no predominant type | clavate | yes |
| <i>P. americanus</i> | 7.9–8.5 | 5.6–6.1 | 1.35–1.44 | entire | no predominant type | clavate | yes |
| <i>P. sepiicolor</i> | 8.0–8.3 | 5.4–5.8 | 1.38–1.47 | bifid | no predominant type | clavate to narrowly clavate | yes |
| <i>P. oreibatus</i> | 7.9–8.3 | 5.5–5.9 | 1.42–1.45 | indistinct | no predominant type | narrowly clavate to cylindrical | yes |
| <i>P. saupii</i> | 7.7 | 5.8 | 1.33 | indistinct | no predominant type | lageniform | yes |
| <i>P. atromarginatus</i> | 6.8–7.5 | 4.8–5.2 | 1.32–1.52 | entire | no predominant type | clavate | yes |
| <i>P. atrofibrillosus</i> | 6.5–6.8 | 4.5–5.1 | 1.30–1.46 | entire | no predominant type | clavate | yes |

I. cervinus clade. Fig. 2

Species mostly growing on angiosperm wood or on the humus layer without apparent connection to wood; more rarely on conifer wood. Clamp-connections absent on pileipellis hyphae except in *P. alniphilus*.

***Pluteus cervinus* (Schaeffer) Kummer (1871: 138).** Fig. 9

Basionym: *Agaricus cervinus* Schaeffer (1774: 6). Lectotypus (designated by Justo *et al.* 2011a):—icon. in Schaeffer, *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur Icones* 1: Tab. X. 1774. Epitype (designated by Justo *et al.* 2011a):—1762.GERMANY. Bavaria: near Bodenwöhr, railroad embankment in direction Schwandorf, on wood chips, under *Frangula alnus*, 7 September 1995, *A. Bresinsky s.n. REG 13641*, nrITS HM562152, *tefl* KJ009860 (REG!).

Synonym: *Agaricus atricapillus* Batsch (1786: 77); *Pluteus atricapillus* (Batsch) Fayod (1849: 364). Lectotype of *Agaricus atricapillus* Batsch (designated here):—icon. in Batsch, *Elenchus fungorum. Continuatio prima*. Tab. XVI, illustration 76a. 1786. Epitype of *Agaricus atricapillus* Batsch (designated here):—GERMANY. Bavaria: Mittelsteighütte, Ludwigshain, on rotten wood, 15 October 1999, *B. Mende s.n. REG 13662*, nrITS HM562166, *tefl* KJ009858 (REG!).

Synonym: *Pluteus brunneoradiatus* Bonnard (1987: 141). Holotype:—SWITZERLAND. Jura, *J. Bonnard 86/128* (LAU!).

Synonym: *Pluteus exilis* var. *austriacus* Singer (1989: 94). Holotype:—AUSTRIA. Burgenland: Siegendorf, 19 September 1979, *R. Singer C9457*, nrITS KJ009643 (WU!).

Pileus 25–150 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, with or without a shallow depression at center; surface smooth, innately radially fibrillose or with very conspicuous radial fibrils, with or without well defined squamules at center; usually some shade of brown (7.5YR 3/3–3/4, 4/6, 5/6–5/8), more rarely with predominant gray-brown (7.5YR 5/1–5/2) or brown-orange (5YR 6/8, 7/8) hues, pure white variants also occur; dry or slightly viscid when moist; margin smooth or slightly translucently striate. Lamellae crowded, free, ventricose, up to 10 mm broad, white when young, later pink, with even, or white, flocculose edge. Stipe 40–100(–140) × 5–20 mm, cylindrical, with slightly broadened base (up to 20–25 mm); surface white, usually with longitudinal brown or gray-brown fibrils, sometimes grouped to form distinct squamules, very rarely completely glabrous. Context in stipe and pileus white. Smell raphanoid (radish-like), or reminiscent of raw potatoes, rarely indistinct. Taste similar to smell or earth-like. Spore print pinkish brown (2.5YR 7/6–7/8).

Basidiospores [390, 39, 34] 6.5–8.5(–9.0) × (4.5–)5.0–7.0 µm, $avl \times avw = 7.0\text{--}8.1 \times 5.0\text{--}5.7$ µm, $Q = (1.10\text{--})1.15\text{--}1.70$, $avQ = 1.35\text{--}1.50$, ellipsoid or broadly ellipsoid, more rarely oblong, very rarely subglobose, sometimes ovoid or slightly constricted in the middle. Basidia 15–35 × 5–10 µm, tetrasterigmate, rarely bisterigmate, clavate, some with median constriction. Pleurocystidia metuloid, (45–)55–110(–130) × 10–25 µm, fusiform, narrowly fusiform or narrowly utriform with 2–4(–6) apical hooks (usually entire), hyaline, thick-walled (–4 µm), frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia (10–)20–70 × 10–30 µm, (narrowly) clavate, spheropedunculate or narrowly utriform, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 50–150(–250) × (5–)9–25 µm; individual elements cylindrical, some strongly tapering towards apex, some (sub-) capitate, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–20 µm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections absent on pileipellis hyphae; in some collections present (but scarce) on the thin hyphae of the hymenophoral trama and at the base of some basidia and cheilocystidia.

Habit, habitat and phenology:—Solitary or gregarious, usually growing on well-decayed wood of angiosperms (e.g. *Acer*, *Betula*, *Eucalyptus*, *Fagus*, *Quercus*). More rarely on conifer wood (*Pinus*, *Picea*) or growing on the humus layer without apparent connection to wood. In temperate or transitional boreal/steppe forests, very rare in truly boreal forests (see *Pluteus rangifer*). Also in *Eucalyptus* plantations in California and Spain. Mostly June–November, but it can be found year round.

Distribution:—**Eurasia.** Widespread in Europe, but its distribution in northern areas (Fennoscandia) needs further study; eastwards into Siberia (Novosibirsk Region). **North America.** Widespread in eastern NA, from North Carolina to Massachusetts and westwards into Wisconsin. Also recorded in western NA (San Francisco Bay Area) but rare.

Observations:—*Pluteus cervinus* is a very variable species in terms of colors (brown, gray-brown, orange-brown, white), aspect of the pileus (with or without conspicuous squamules and radial fibrils), and size of the basidiocarps (pileus from 25 up to 150 mm in diameter) but molecular data support the recognition of all these morphological variants as one species.

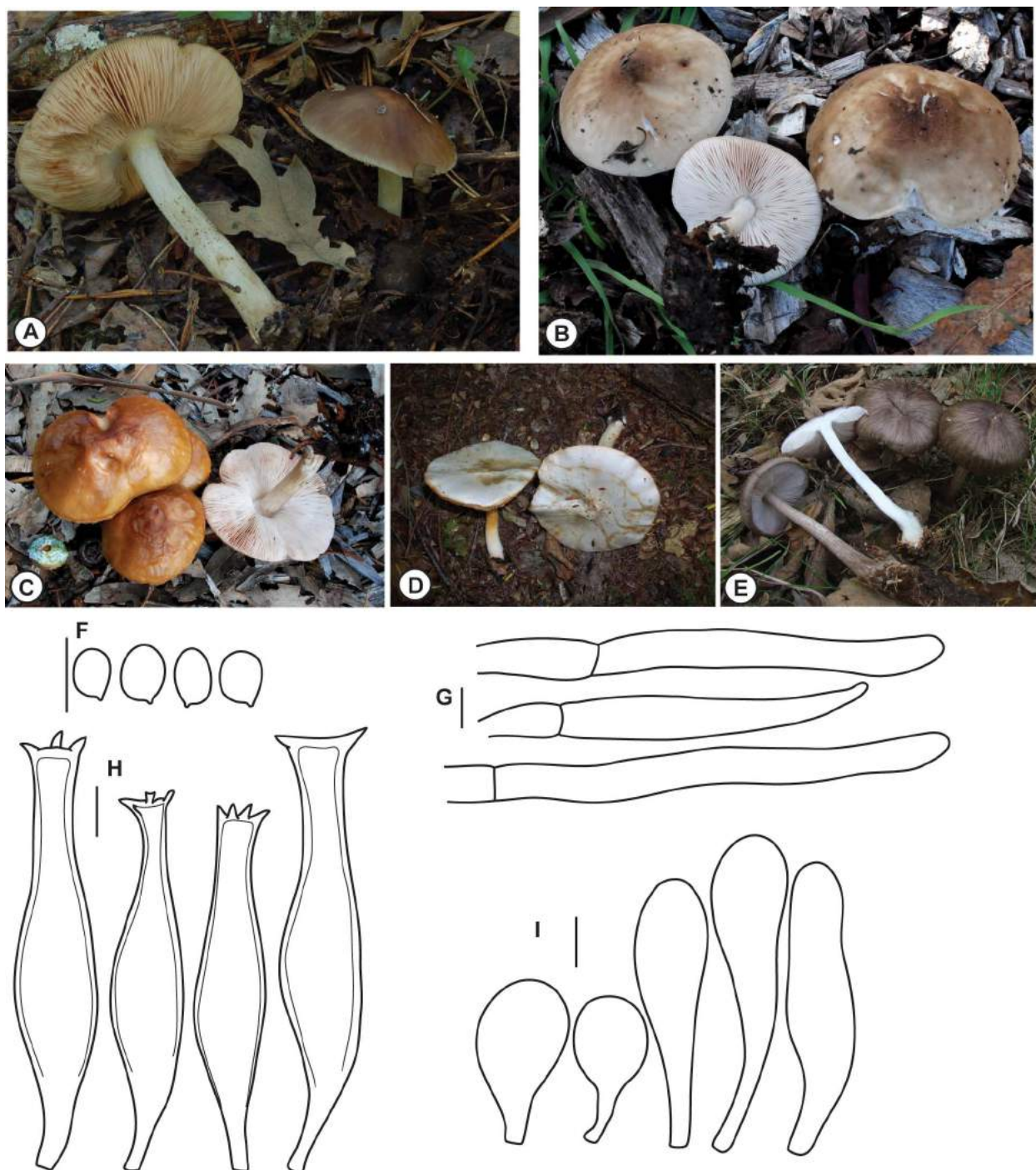


FIGURE 9. *Pluteus cervinus*. A. Collection GM 2044 (photo by G. Muñoz). B. Collection DBB 50105 (photo by D. Bojantchev). C. Collection DBB 50123 (photo by D. Bojantchev). D. Collection AJ 762 (white variant, photo by A. Justo). E. Collection AJ 351 (*brunneoradiatus*-like morphology; photo by L. A. Parra). F. Basidiospores. G. Pileipellis. H. Pleurocystidia. I. Cheilocystidia. F–I from collection REG 13641. All line drawings by A. Justo. Scale bars = 10 µm.

Pluteus atricapillus (Batsch.) Fayod is probably the most commonly encountered synonym of *P. cervinus*. The name is based on *Agaricus atricapillus* Batsch (1786) that was described from Schöndorf (Germany, Bavaria). The original description and illustration (Batsch 1786) could be applied to any of the European *cervinus*-like species described in the present paper. Singer (Singer & Cléménçon 1972) tried to typify *Pluteus atricapillus* but based his observations on *Agaricus atricapillus* Secretan, described in Secretan's *Mycographie Suisse* (1833), a suppressed work [Opera Utique Oppressa] according to the ICN (McNeill *et al.* 2012). He studied two collections from near Lausanne (Switzerland) and referred to them as “topotypes”, a term not recognized by the ICN. One of these Swiss collections is preserved at the Field Museum in Chicago (C5421, <http://plants.jstor.org/specimen/>

f0003928c?history=true) and listed as “topotype” though there is no official designation of any particular collection as a type in the publication. The collection at the Field Museum is not the type of *Pluteus atricapillus* and has no relevance in deciding on the application of the epithet *atricapillus*.

For the most part modern authors have considered the names *P. atricapillus* and *P. cervinus* as taxonomic (heterotypic) synonyms (Singer 1956; Vellinga 1990). One notable exception to this can be found in Banerjee & Sundberg (1995). These authors described *Pluteus atricapillus* with diagnostic characters as: “Pileus disc with brown squamules, pleurocystidia cervinus-type, pileipellis without clamp connections, basidiome with strong raphanoid odor”. All these characters are also present in their description of *Pluteus cervinus* making the morphological separation of both very unclear.

To finally settle the issue between both epithets we have designated here the original plate of *Agaricus atricapillus* as the lectotype and a modern collection from Bavaria as the supporting epitype (see nomenclature part above).

Pluteus brunneoradiatus Bonnard was described as a separate species based on the conspicuous radial fibrils on the pileus, the morphology of the intermediate cystidia and the presence of scarce clamp-connections on the thin hyphae of the hymenophoral trama (Bonnard 1987). No molecular data could be obtained from the type collection but all collections fitting the morphological concept of *P. brunneoradiatus* fall within the molecular variation of *P. cervinus* (Fig. 2a), therefore we consider both taxa synonymous.

Pluteus cervinus occurs mostly in temperate forests in Eurasia and eastern North America. The collections from Novosibirsk region (Siberia) mark the easternmost confirmed occurrence of *P. cervinus* in Eurasia. In this area *P. cervinus* occurs in the “sub-taiga belt” forest, a transitional forest between the taiga and the non-forested steppes. This type of forest is a mixture of *Betula pendula*, *Pinus sylvestris* and *Populus tremula* (co-dominant boreal species) yet without any typical temperate broadleaf species (*Tilia*, *Fagus*, *Quercus*) and also without key taiga species such as *Pinus sibirica*, *Picea obovata* and *Abies sibirica*. The closely related *P. rangifer* (mostly confined to the taiga) and *P. hongoi* (in various forest types) both occur in the Russian Far East and Japan. *Pluteus cervinus* is rare in California, where it grows on introduced (*Eucalyptus*) and possibly also native hardwood. Interestingly, it also is reported from *Eucalyptus* in Spain.

Additional collections examined:—GERMANY. **Bavaria:** Mittelsteighütte, Holle, on rotten wood, 26 October 1999, *B. Mende s.n. REG 13661*, nrITS HM562171, *tefl* KJ009862 (REG). Mittelsteighütte, Ludwigshain, temperate forest, on rotten wood, 29 June 1999, *M. Binder & M. Fischer s.n. REG 13652*, nrITS HM562165, *tefl* KJ009864 (REG). *ibid.*, 15 October 1999, *B. Mende s.n. REG 13662*, nrITS HM562166, *tefl* KJ009858 (REG). Mooshof, 06 September 1990, *REG 13618*, nrITS HM562153, *tefl* KJ009855 (REG). *ibid.*, 03 August 2005, *B. Breu & S. Holl s.n. REG 16651*, nrITS HM562150, *tefl* KJ009865 (REG). Pfatter, on rotten wood, 11 October 1999, *B. Mende s.n. REG 13616*, nrITS HM562155, *tefl* KJ009879 (REG). RUSSIA. **Central Federal District:** Moscow Region, Prioksko Terrasny Nature Biosphere Reserve, mixed forest, on decayed wood of *Betula*, 07 September 1992, *G.E. Levitskaya s.n. LE 216608*, nrITS KJ009629, *tefl* KJ009845 (LE). Tula Region, Efremovsky District, vicinities of Ishutino, oak forest on limestone slope, on buried wood, 27 August 2003, *T.Yu. Svetasheva s.n. LE 234784*, nrITS KJ009632, *tefl* KJ009859 (LE). Tula Region, The State Memorial and Natural Preserve Museum Estate of Leo Tolstoy “Yasnaya Polyana”, broadleaf forest, on *Betula* trunk, 31 August 2003, *T.Yu. Svetasheva s.n. LE 234774*, nrITS KJ009635, *tefl* KJ009850 (LE). **North Caucasian Federal District:** Teberdinsky Nature Reserve, vicinities of Teberda town, *Fagus* forest, on decayed wood of *Fagus*, 06 August 2009, *E.F. Malysheva s.n. LE289370*, nrITS KJ009638, *tefl* KJ009861 (LE). Teberdinsky Nature Reserve, floodplain of Baduk River, conifer forest with isolated *Fagus* trees, stump of *Picea*, 08 August 2009, *E.F. Malysheva s.n. LE289371*, nrITS KJ009639, *tefl* KJ009846 (LE). **Northwestern Federal District:** Leningrad Region, Kingiseppsky District, vicinities of Velkoto, *Quercus* forest, on fallen trunk of deciduous tree, 14 June 1996, *O.V. Morozova s.n. LE 215177*, nrITS KJ009625, *tefl* KJ009842 (LE); *ibid.*, *Quercus* forest, decayed wood of *Corylus*, 18 July 1995, *O.V. Morozova s.n. LE215353*, nrITS KJ009644, *tefl* KJ009843 (LE). Pskov Region, August 2005, *E.S. Popov s.n. LE 289368*, nrITS KJ009633, *tefl* KJ009847 (LE). St Petersburg, on stump of *Acer negundo*, 25 September 2009, *E.F. Malysheva s.n. LE 289382*, nrITS KJ009647, *tefl* KJ009857 (LE). Vologda Region, Kirillovsky District, National Park “Russian North”, vicinities of Rusanovo, bank of Itkla River, *Alnus spinney*, on decaying wood of *Alnus*, 27 August 2002, *E.S. Popov s.n. LE 235300*, nrITS KJ009634, *tefl* KJ009844 (LE). **Siberian Federal District:** Novosibirsk Region, Novosibirsk District, Akademgorodok, planted *Betula pendula* grove, on rotting trunk of *Betula*, 18 August 2011, *T.M. Bulyonkova s.n. LE 289396*, nrITS KJ009626, *tefl*

KJ009848 (LE); *ibid.*, shady patch of planted maple (*Acer negundo*) with indigenous trees nearby, on old stump of *Populus*, 13 September 2011, *T.M. Bulyonkova s.n. LE 289398*, nrITS KJ009630, *tefl* KJ009852 (LE). Ulyanovsk Region, Mainsky District, vicinities of Tagaj, mixed forest (*Betula*, *Pinus*), on buried wood, 05 August 2007, *E.V. Ilukhin s.n. LE 257679*, nrITS KJ009636, *tefl* KJ009856 (LE). **Volga Federal District:** Samara Region, vicinities of Pribrezhny, mixed forest, on stump of *Tilia cordata*, 12 June 2011, *E.F. Malysheva s.n. LE 289381*, nrITS KJ009631, *tefl* KJ009851 (LE). Samara Region, Zhigulevsky Nature Reserve, vicinities of Bakhilova Polyana, broadleaf forest, on fallen trunk of deciduous tree, 26 August 2000, *E.F. Malysheva s.n. LE 289367*, nrITS KJ009641, *tefl* KJ009849 (LE). Ulyanovsk Region, Zheleznodorozhny District, broadleaf forest, on decaying wood of deciduous tree, 08 August 2007, *E.V. Ilukhin s.n. LE 257680*, nrITS KJ009640, *tefl* KJ009841 (LE). **SPAIN. A Coruña:** Mañon, mixed broadleaf forest, on decayed fallen wood (hardwood), 21 July 2007, *J. Rodriguez & G.M.G s.n. AJ 79*, nrITS HM562135, *tefl* KJ009871 (LOU). **La Rioja:** Carbonera, mixed forest, apparently terrestrial, under *Fagus*, 30 July 2011, *G. Muñoz 2195*, nrITS KJ009642, *tefl* KJ009854 (CUW). Villoslada de Cameros, mixed *Pinus* and *Quercus* forest, apparently terrestrial, 28 October 2010, *G. Muñoz 2044*, nrITS KJ009687, *tefl* KJ009853 (CUW). **Ourense:** Verin, *Eucalyptus* plantation, on *Eucalyptus* stump, 28 March 1997, *M. Lago & E. Lago s.n. LOU 15229*, nrITS KJ009637, *tefl* KJ009867 (LOU). **Oviedo:** Endriga, mixed broadleaf forest, on *Fagus* wood, 05 October 2005, *L. Llorens s.n. AJ 192*, nrITS HM562134, *tefl* KJ009881 (LOU). Navia, *Eucalyptus* plantation, on decayed wood of *Eucalyptus*, 25 October 1998, *M. Lago & E. Luis s.n. LOU 15223*, nrITS HM562133, (LOU). **Palencia:** Cervera de Pisuerga, *Quercus pyrenaica* forest, on decayed wood of *Quercus pyrenaica*, 24 October 2010, *L.A. Parra s.n. AJ 351*, nrITS JN603200, *tefl* KJ009868 (CUW). **Pontevedra:** Mos, mixed forest, on hardwood stump, 25 November 2007, *A. Justo 82*, nrITS HM562035, (LOU). Pontearreas, mixed forest, on burnt terrain, 12 August 2006, *N. Alonso & GMG s.n. AJ 77*, nrITS HM562136, *tefl* KJ009863 (LOU). Pontevedra, *Eucalyptus* plantation, on decayed wood of *Eucalyptus*, 15 December 1998, *M. Lago s.n. LOU 15226*, nrITS KJ009645, *tefl* KJ009869 (LOU); *ibid.*, on *Eucalyptus* stump, 10 February 1998, *M. Lago s.n. LOU 15218*, nrITS KJ009646, *tefl* KJ009884 (LOU). **UNITED STATES OF AMERICA. California:** Alameda Co., Berkeley, Scenic Ave. at Cedar Ave, on decayed wood of *Acacia* sp. or *Pittosporum* sp., 29 February 2012, *E.C. Vellinga s.n. UC 1998737*, nrITS JX857458, *tefl* KJ460259 (UC). Contra Costa Co., Hercules, *Eucalyptus* grove, on wood chips, 26 March 2012, *D. B. Bojantchev 50105*, nrITS KJ009623, *tefl* KJ009883 (CUW); *ibid.*, 26 March 2012, *D. B. Bojantchev 50123*, nrITS KJ009615, *tefl* KJ009882 (CUW). Marin Co., Point Reyes National Seashore, Bear Valley 3/4 of the way to Arched Rock, 21 April 2012, *T.D. Bruns s.n. UC 1998560*, nrITS JX857462, *tefl* KJ460258 (UC). **Illinois:** Locality unknown, September 2009, *A.M. Minnis s.n. SF1-BPI 882764*, nrITS HM562200, *tefl* KJ009887 (BPI). **Massachusetts:** Berkshire Co., October Mt. State Forest, mixed forest, on decayed hardwood, 08 November 2011, *A. Justo 409*, nrITS KJ009621, *tefl* KJ009873 (CUW). Berkshire Co., Savoy Mountain State Forest, mixed forest, on decayed wood, 04 October 2012, *C. Webb s.n. AJ 779*, nrITS KJ009616, *tefl* KJ009872 (CUW); *ibid.*, *A. Justo 781*, nrITS KJ009619, *tefl* KJ009877 (CUW); *ibid.*, 16 June 2012, *A. Justo 835*, nrITS KJ009618, *tefl* KJ009889 (CUW). Worcester Co., Harvard Forest, on the ground among leaves, 23 June 2009, *A. Justo 106*, nrITS HM562043, *tefl* KJ009888 (MICH). Worcester Co., Ware River Watershed Trail, mixed forest, on decayed wood, 13 September 2012, *C. Webb s.n. AJ 761*, nrITS KJ009624, *tefl* KJ009875 (CUW). **Michigan:** Emmet Co., Hemlock Bog, on decorticated wood, 14 September 2007, *A.M. Minnis s.n. SF4-BPI 882767*, nrITS HM562176, *tefl* KJ009886 (BPI). **New York:** Essex Co., Adirondack Ecological Center, Huntington Wildlife Forest, mixed forest, on decayed wood, 14 August 2012, *A. Justo 590*, nrITS KJ009628, *tefl* KJ009878 (CUW); *ibid.*, 17 August 2012, *O. Miettinen s.n. AJ 592*, nrITS KJ009627, *tefl* KJ009874 (CUW). Essex Co., Wold Lake, Huntington Wildlife Forest, old growth mixed forest with *Fagus*, *Acer* and *Tsuga*, on decayed wood of *Acer saccharum*, standing dead tree, 21 September 2013, *O. Miettinen 17107*, nrITS KJ009788 (H). Essex Co., Newcomb, Harris Lake, mixed, middle-aged forest by the lake, on decayed wood of *Acer saccharum* or *Populus tremuloides*, fallen tree, 23 September 2013, *O. Miettinen 17183*, nrITS KJ009784, *tefl* KJ009880 (H). **North Carolina:** Haywood Co., White Oak, 09 October 2010, *E.C. Vellinga 4185*, nrITS KJ009617, *tefl* KJ009870 (TENN). **Rhode Island:** Providence Co., Lincoln Woods State Park, mixed forest, on decayed fallen wood, 28 June 2011, *A. Justo 410*, nrITS KJ009622, *tefl* KJ009885 (CUW). **Wisconsin:** Iron Co., Northern Highland State Forest, "plot 3", 12 July 1995, *D. Lindner DLF 95-59*, nrITS KJ009620, *tefl* KJ009876 (CFMR).

Pluteus exilis Singer (1989: 94). Fig. 10

Holotype:—UNITED STATES OF AMERICA. California: Marin Co., Muir Woods, on dead wood of *Notholithocarpus* (as “*Lithocarpus*” in the original description), 14 January 1983, *R. Singer N5105*, nrITS KJ009778 (F!).

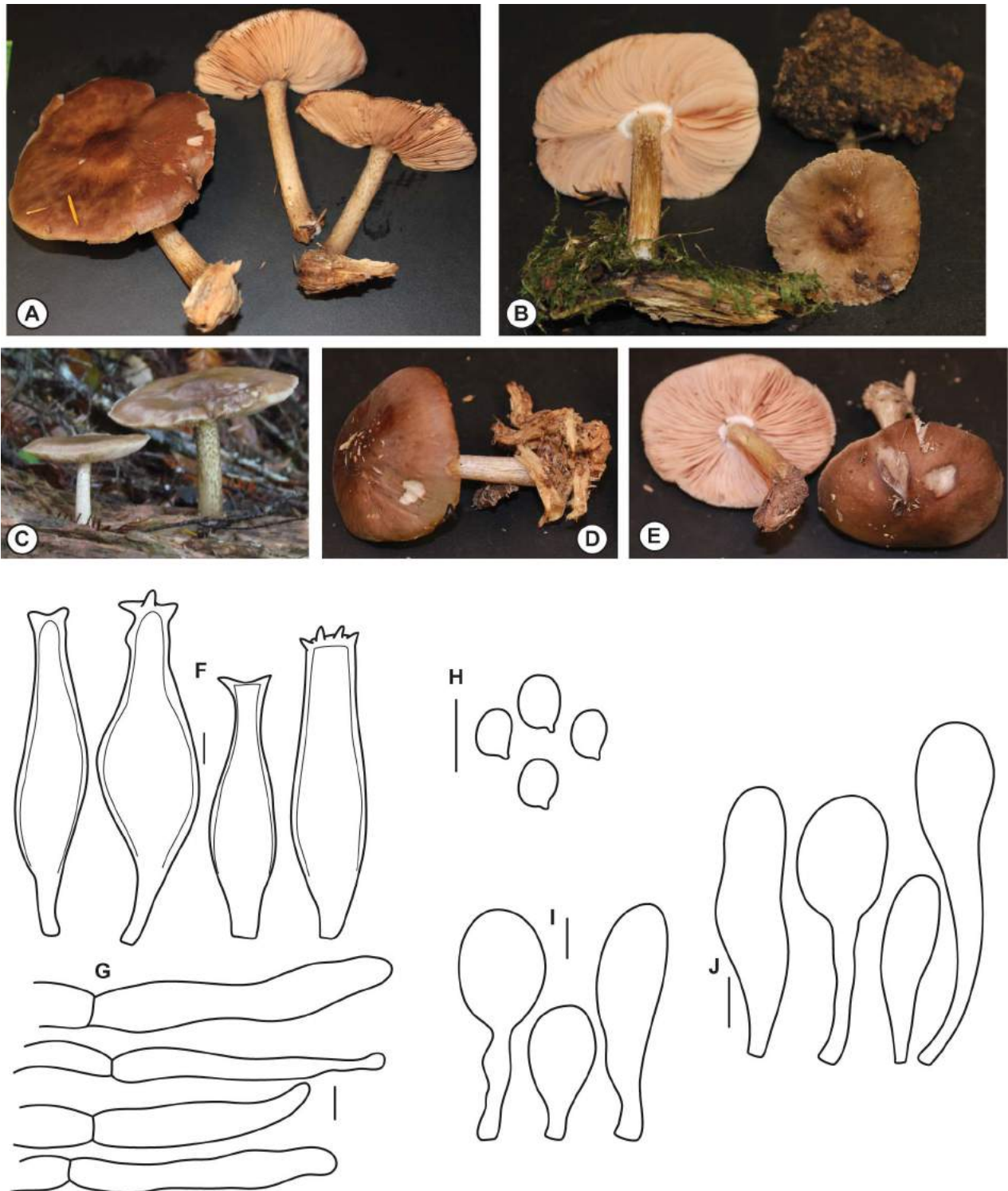


FIGURE 10. *Pluteus exilis*. A. Collection UC 1998537. B. Collection UC 1999431. C. Collection UC 1998537. D. Collection UC 1861131. E. Collection UC 1861133. All photographs by N. Nguyen. F. Pleurocystidia from *Singer N5105*. G. Pileipellis from *AJ 822*. H. Basidiospores from *Singer N5105*. I. Cheilocystidia from *Singer N5105*. J. Cheilocystidia from *AJ 822*. All line drawings by A. Justo. Scale bars = 10 µm.

Pileus 35–70 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex,

with or without a low, broad umbo, with or without a shallow depression at center; surface radially fibrillose, with or without well defined squamules at center; usually some shade of brown (7.5YR 3/2–3/4, 4/3–4/6); dry or slightly viscid when moist; margin smooth or slightly translucently striate. Lamellae crowded, free, ventricose, up to 7 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 40–100(–140) × 5–20 mm, cylindrical, with slightly broad base (–25 mm); surface white, usually with longitudinal brown or gray-brown fibrils, commonly grouped to form distinct squamules, rarely without fibrils. Context in stipe and pileus white. Smell indistinct or earth-like. Taste similar to smell. Spore print pinkish brown.

Basidiospores [40, 3, 3] 6.5–8.4(–9.0) × (4.5–)5.0–6.0 µm, $avl \times avw = 7.0\text{--}7.5 \times 5.1\text{--}5.3$ µm, $Q = 1.30\text{--}1.60(–1.70)$, $avQ = 1.38\text{--}1.47$, ellipsoid, rarely oblong, sometimes ovoid or slightly constricted in the middle. Basidia 20–35 × 7–12 µm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, (55) 60–100 (115) × 13–30 (35) µm, fusiform, narrowly fusiform or narrowly utriform, thick-walled (–3 µm) with 2–4(–6) apical hooks (usually entire), hyaline, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia (15–)20–75 × 10–25(–30) µm, (narrowly) clavate, spheropedunculate or narrowly utriform, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 60–120(–145) × 8–17(–30) µm; individual elements cylindrical, some strongly tapering towards apex, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–20 µm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections absent on pileipellis hyphae; not observed in any other part of the basidiocarp.

Habit, habitat and phenology:—Solitary or gregarious, growing on well-decayed wood of angiosperms (*Alnus*, *Notholithocarpus*) or conifers (*Picea*, *Pseudotsuga*). September–January.

Distribution:—**North America.** Western North America, known with certainty from Santa Cruz Co. (California, USA) north along the coastal forests up into British Columbia (Canada).

Observations:—Singer (1989) described this species based on a single collection from Muir Woods (Marin Co., California) and he considered the thin stipe (–5 mm wide; *exilis* means “the thin one”) and dimorphic cheilocystidia (short spheropedunculate up to 30 µm long and elongated ones up to 54 µm) to be diagnostic for *P. exilis*. However, later studies of both holotype and modern collections revealed that these characters have a wide and continuous variation similar to what is found in the other taxa of this species complex. The nrITS sequence obtained from the type collection is a perfect match to sequences obtained from modern collections and therefore the name *exilis* should be used for this taxon.

Pluteus exilis var. *austriacus*, described simultaneously by Singer (1989), represents *Pluteus cervinus* (Fig 2a). Rodríguez *et al.* (1997) reported this species from the city of Guadalajara (Mexico), however the collection described by those authors was found growing in an urban garden, had narrower basidiospores (“(3.2) 4–5.2 µm”), and many pleurocystidia lacked apical hooks. All these characters point to *Pluteus petasatus* rather than *P. exilis*.

Generally speaking *P. exilis* has a darker pileus and a more markedly squamose stipe than *P. cervinus*, but there is a significant level of overlap in these characters. Geographical distribution would serve as a differential character but *P. cervinus* has been recorded in the San Francisco Bay area (California, USA) although it is much rarer than *P. exilis*. It seems, however, that there is a pattern in the seasonality of *P. exilis* and *P. cervinus* in California. *P. exilis* starts fruiting in September–October in the northern part of its known range (British Columbia, Washington) and later, December–January in the southern part (California). All known collections of *P. cervinus* from California have been made outside of the main fruiting season in the San Francisco Bay area, from March (one collection “29 February 2012”) to April. More intense sampling is needed to establish if this seasonal pattern is a constant and reliable character to separate *P. exilis* and *P. cervinus* in this area.

Additional collections examined:—UNITED STATES OF AMERICA. **California:** Contra Costa Co., Tilden Regional Park, Nature Center, *Eucalyptus* grove, on decayed wood of hardwood, 24 December 2012, *E.C. Vellinga* s.n. UC 1999294, nrITS KF306008, (UC). Humboldt Co., Trinidad, on decayed wood of *Alnus*, 04 December 1956, *A.H. Smith* 56267, nrITS KJ009659 (MICH). Marin Co., Point Reyes National Seashore, 07 January 2012, UC 1861129, nrITS JX857444 (UC); *ibid.*, on decayed wood of *Alnus rubra*, 14 December 2011, *N.H. Nguyen* s.n. UC 1861131, nrITS JX857446, *tefl* KJ460252 (UC); *ibid.*, Horse Trail to Mt. Wittenberg, mature *Pseudotsuga menziesii* forest with mixed hardwoods, grasslands near the bay and *Quercus agrifolia*, on soil, 28 January 2006, *E.C. Vellinga* s.n. UC 1859495, nrITS KF306020 (UC); *ibid.*, on log of *Umbellularia californica*, 10 November 2012, *D. Klein* s.n. UC 1999289, nrITS KF306005 (UC); *ibid.*, Fire Trail area, 10 December 2011, *N.H. Nguyen* s.n. UC 1861133, nrITS JX857461 (UC); *ibid.*, Five Brooks area along Olema trail, on decayed wood of

Notholithocarpus densiflorus, 07 January 2011, *E.C. Vellinga s.n.* UC 1861125, nrITS JX857459 (UC); *ibid.*, Limantour Rd, Horse Trail, on decayed wood, 26 January 2013, *N.H. Nguyen s.n.* UC 1999431, nrITS KF306018, (UC); *ibid.*, Limantour Rd, Horse Trail, on decayed wood of *Notholithocarpus densiflorus*, 26 January 2013, *N.H. Nguyen s.n.* UC 1999430, nrITS KF306017 (UC); *ibid.*, forest, on wood near *Pseudotsuga menziesii*, 10 December 2005, *T.D. Bruns s.n.* UC 1859650, nrITS KF306022 (UC); *ibid.*, Sky Trail from trailhead to top of Wittenberg, mature *Pseudotsuga menziesii* forest with mixed hardwoods, scattered *Pinus* spp. and scrub, on wood/soil, 28 January 2006, *E.C. Vellinga s.n.* UC 1859498, nrITS KF306023 (UC); *ibid.*, Stewart Trail, south of Five Brooks trailhead, mature *Pseudotsuga menziesii* forest with mixed hardwoods, on wood near *Alnus* sp., 10 December 2005, *E.C. Vellinga s.n.* UC 1859653 nrITS KF306021 (UC). Mendocino Co., Caspar Cemetery, on decayed wood of *Picea sitchensis*, 28 January 2012, *L. Ovenden s.n.* UC 1998536, nrITS JX857449 (UC). Mendocino Co., Jackson State Forest, Camp One near Noyo River, on decayed wood of *Pseudotsuga menziesii*, 20 November 2011, *N.H. Nguyen s.n.* UC 1998537, nrITS JX857450 (UC); *ibid.*, *S. Branco s.n.* UC 1998736, nrITS JX857457 (UC). Santa Cruz Co., Henry Cowell State Park (NAMA Foray 2012), on dead log, with *Notholithocarpus densiflorus*, 14 December 2012, *J. Vinopa s.n.* UC 1999300 nrITS KF306013 (UC); *ibid.*, on decayed wood, 14 December 2012, *N. Burghardt s.n.* UC 1999299, nrITS KF306012 (UC); *ibid.*, woods with *Pinus attenuata*, *Pseudotsuga menziesii*, *Arbutus* sp., and *Quercus agrifolia*, on wood, 14 December 2012, *N.H. Nguyen s.n.* UC 1999297, nrITS KF306010 (UC); *ibid.*, 14 December 2012, *N.H. Nguyen s.n.* UC 1999298, nrITS KF306011 (UC). Santa Cruz Co., Scotts Valley, Mission Springs Center, mixed forest, on decayed wood, 13 December 2012, *E.C. Vellinga s.n.* AJ 822, nrITS KJ009658, *tefl* KJ009900 (CUW); *ibid.*, 13 December 2012, *E.C. Vellinga s.n.* AJ 828, nrITS KJ009657, *tefl* KJ009901 (CUW). **Washington:** King Co., Arboretum, 10 November 1982, *K. Cosley s.n.* Stuntz 21834, nrITS KJ009655, *tefl* KJ009899 (WTU). Locality unknown, *Stuntz* 277, nrITS KJ009656 (WTU). Pierce Co., Lower Tahoma Creek, Mt. Rainier National Park, on decayed wood of *Alnus*, 12 September 1952, *A.H. Smith* 39846, nrITS HM562075 (MICH).

Pluteus rangifer Justo, E.F. Malysheva & Bulyonkova, *sp. nov.* Fig. 11
 MycoBank 808724

Diagnosis:—Differs from *Pluteus cervinus* in the darker colors and the distribution in boreal areas.

Holotype:—RUSSIA. Republic of Karelia: Valaam, bank of Sisyyarvi Lake, *Picea* forest, on decayed wood, 29 July 1995, *O. Morozova s.n.* LE 203210, nrITS KJ009650, *tefl* KJ009898 (LE!).

Etymology:—*rangifer* comes from the scientific name of the reindeer/caribou (*Rangifer tarandus* L.), which has a similar distribution in the northern areas of Eurasia and North America.

Pileus 25–130 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, with or without a shallow depression at center; surface smooth to radially fibrillose, usually with a silky sheen, without well-defined squamules at center; brown (5YR 4/6, 5/6–5/8) to dark brown (5YR 4/2–4/4, 3/3–3/4) or gray-brown (7.5YR 4/1–4/2); dry or slightly viscid when moist; margin smooth or slightly translucently striate. Lamellae crowded, free, ventricose, up to 10 mm broad, white when young, later pink or pinkish brown, with even, or white, flocculose edges. Stipe 30–90(–135) × 5–12 mm, cylindrical with slightly broad base; surface white, with contrasting dark gray-brown fibrils and squamules all over, more rarely smooth. Context in stipe and pileus white. Smell raphanoid. Taste raphanoid or sweetish raphanoid. Spore print pinkish brown.

Basidiospores [40, 2, 2] 6.0–8.5(–9.0) × 4.5–6.5(–7.0) µm, $av_l \times av_w = 7.2\text{--}7.6 \times 5.0\text{--}5.8$ µm, $Q = 1.17\text{--}1.60$, $avQ = 1.31\text{--}1.43$, ellipsoid or broadly ellipsoid, rarely oblong, sometimes ovoid or slightly constricted in the middle. Basidia 15–29 × 7–13 µm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, (65–)70–100 × 14–25 µm, fusiform, narrowly fusiform or narrowly utriform, provided with 2–3(–4) apical hooks (usually entire, sometimes bifurcated), hyaline, with up to 3 µm thick wall, frequent all over lamellar faces. Intermediate cystidia predominantly fusiform and without hooks, 43–65 × 12–19 µm, some similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped. Lamellar edge sterile. Cheilocystidia (25–)35–65 × (10–)15–25 µm, narrowly to broadly clavate, spheropedunculate or narrowly utriform, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements (65–)80–130(–150) × 8–15(–27) µm; individual elements cylindrical, cylindrical or fusiform, some strongly tapering towards apex, mostly filled with brown intracellular pigment, sometimes slightly incrusting, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–20 µm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls.

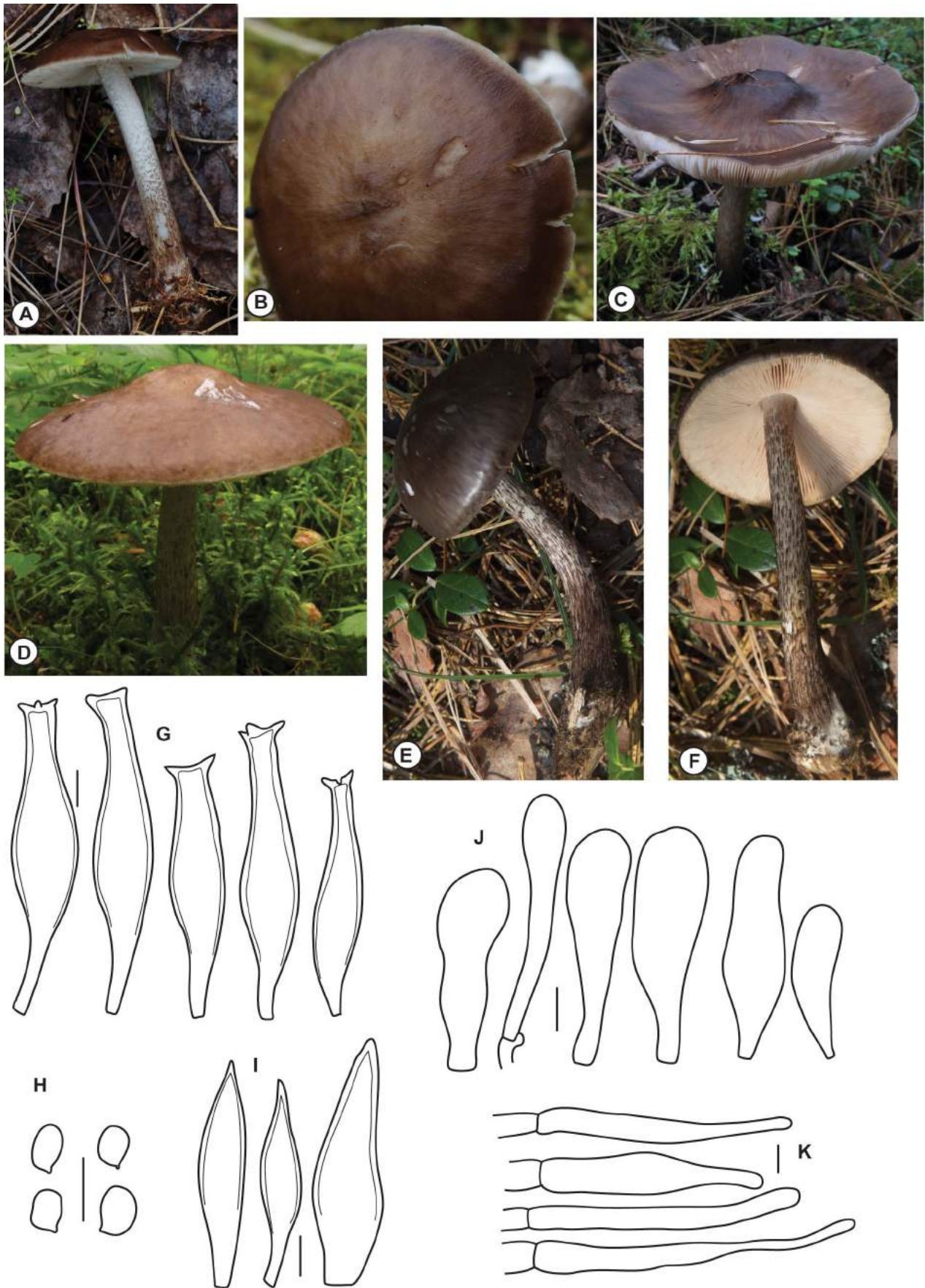


FIGURE 11. *Pluteus rangifer*. A–B. Collection LE 89406. C. Collection KH 1197. D. Collection LE 89407. E–F. Collection TB 2642. All photographs by T. Bulyonkova. G. Pleurocystidia. H. Basidiospores. I. Intermediates cystidia. J. Cheilocystidia. K. Pileipellis. G–K from collection TRTC 156990. All line drawings by A. Justo. Scale bars = 10 μ m.

Clamp-connections absent on pileipellis hyphae, in one collection (LE 289407) present but very scarce in the lower layer and pileitrama; in some collections present (but scarce) on the thin hyphae of the hymenophoral trama and at the base of some cheilocystidia.

Habit, habitat and phenology:—Solitary, growing on well-decayed wood of angiosperms (e.g. *Betula*, *Quercus*). In boreal or transitional boreal/temperate forests but not in truly temperate forests. July–September (Russia), June (Hokkaido) or October (Ontario).

Distribution:—**Eurasia.** Recorded from northwestern Russia to Hokkaido Island (Japan). **North America.** Only known from Algonquin Provincial Park (Ontario, Canada).

Observations:—*Pluteus rangifer* is essentially the boreal counterpart of *Pluteus cervinus*. These two species have a parapatric distribution in Eurasia, with *P. rangifer* being widely distributed in the northern forests, *P. cervinus* in the temperate forests and both species co-occurring in the transitional boreal/temperate areas. The easternmost confirmed occurrence of *P. cervinus* in Eurasia is in central Siberia (Novosibirsk district, Akademgorodok) while *P. rangifer* extends into the Russian Far East and northern Japan (Hokkaido). The environmental sample AM901879 from Finland (Fig. 2a) marks the westernmost occurrence of *P. rangifer*, although it is likely that the species occurs in boreal areas of northern Europe (e.g. Sweden, Norway). A similar pattern is expected in North America, since *P. rangifer* has not been recorded in the temperate areas, but more sampling is needed.

Generally speaking *P. rangifer*, just like *P. exilis*, has darker colors on the pileus and a more markedly squamose stipe than *P. cervinus*, but both characters are variable. Geographical distribution and ecological preferences are probably the best characters to separate these three species. In the nrITS phylogenies *P. exilis* and *P. rangifer* appear as separate from *P. cervinus*, but the separation of *P. exilis* and *P. rangifer* is unclear (Fig. 2), with a monophyletic *P. exilis* nested within a non-monophyletic *P. rangifer*. The *tefl* phylogenies (Fig. 2) do recover a neat and supported separation of *P. cervinus*, *P. exilis* and *P. rangifer*.

Pluteus brunneoolivaceus Horak (1964: 165) differs from *P. rangifer* in the markedly squamulose and smaller pileus (up to 25 mm), less ornamented stipe, and the cheilocystidia with brown intracellular pigment that are up to 80 µm long. This taxon is only known from the austral forests of the southernmost part of South America (Tierra del Fuego, Argentina). *Pluteus microspermus* Horak (2008: 15) and *Pluteus concentricus* Horak (2008: 18) may resemble *P. rangifer* in the coarsely ornamented stipe but both species have smaller basidiospores (less than 6.5 µm long) and pigmented lamellar edges. Both species are only known from New Zealand, where they grow in association with *Nothofagus* wood (Horak 2008).

Additional collections examined:—**CANADA. Ontario:** Nipissing, Algonquin Provincial Park, 03 October 2007, *M. Didukh & B. Dentinger s.n.* TRTC 156990, nrITS JN021074, *tefl* KJ009894 (TRTC). **JAPAN. Hokkaido:** Sapporo, mixed forest, on decayed wood buried in soil, 07 June 2003, *S. Takehashi s.n.* TNSF 12347, nrITS HM562104, *tefl* KJ009897 (TNS). **RUSSIA. Far East Federal District:** Primorsky Territory, Sikhote-Alinsky Nature Biosphere Reserve, vicinities of Kabany Reserve field station, mixed forest (*Abies*, *Pinus*, *Ulmus*), on decayed wood, 24 August 2011, *T.Yu. Svetasheva s.n.* LE 289385, nrITS KJ009651, *tefl* KJ009896 (LE); *ibid.*, vicinities Golubichny Reserve field station, *Quercus mongolica* forest, on decayed wood, 22 August 2011, *E.F. Malysheva s.n.* LE 289384, nrITS KJ009654, *tefl* KJ009892 (LE). **Northwestern Federal District:** Kola Peninsula, Khibiny Mountains, *Picea-Betula* forest, 18 August 1946, *B.P. Vassilkov s.n.* LE 9699, nrITS KJ009652, *tefl* KJ009895 (LE). Murmansk Region, Lapland Biosphere Reserve, *Betula* forest, on *Betula* stump, 10 September 1961, *N.V. Pushkina s.n.* LE 9702, nrITS KJ009648, *tefl* KJ009890 (LE). **Ural Federal District:** Khanty-Mansiyskiy District, Shapsha village, mixed dark conifer taiga (*Picea obovata*, *Abies sibirica*, *Pinus sibirica*, with scarce *Betula pendula*, *Populus tremula*, *Pinus sylvestris*), on decayed wood, 07 August 2008, *N.V. Filippova s.n.* LE 289407, nrITS KJ009649, *tefl* KJ009893 (LE). Yugra, Khanty-Mansiyskiy District, Mukhrino Field Station of the Ugra State University UNESCO chair, mixed dark conifer taiga (*Picea obovata*, *Abies sibirica*, *Pinus sibirica*, with scarce *Betula pendula*, *Populus tremula*, *Pinus sylvestris*), on decayed wood, 18 August 2010, *T.M. Bulyonkova s.n.* LE 289406, nrITS KJ009653, *tefl* KJ009891 (LE).

Pluteus hongoi Singer (1989: 95). Fig. 12

Holotype:—JAPAN. Honshu: Kyoto, Mt. Daimonji-yama, 14 September 1984, *R. Singer A4070*, nrITS KJ009564, *tefl* KJ009940 (F!).

Synonym: *Pluteus major* Singer (1989: 96). Holotype:—UNITED STATES OF AMERICA. Illinois: Cooke Co., Forest

Preserve east of Wheeling, 23 June 1985, *R. Singer* N5195, nrITS KJ009586, *tefl* KJ009920 (F!).

Synonym: *Pluteus albineus* Bonnard (2001: 131). Holotype:—SWITZERLAND. Canton Vaud: Apples, Les Bougeries, 19 August 1986, *J. Bonnard* 86/91, nrITS KJ009601 (LAU!).

Synonym: *Pluteus nothopellitus* Justo & Castro (2007b: 222). Holotype:—SPAIN. A Coruña: Cambre, Cecebre, on fallen branch of *Quercus robur*, 30 September 2004, *A. Justo* 58, nrITS HM562063, *tefl* KJ009912 (MA!).

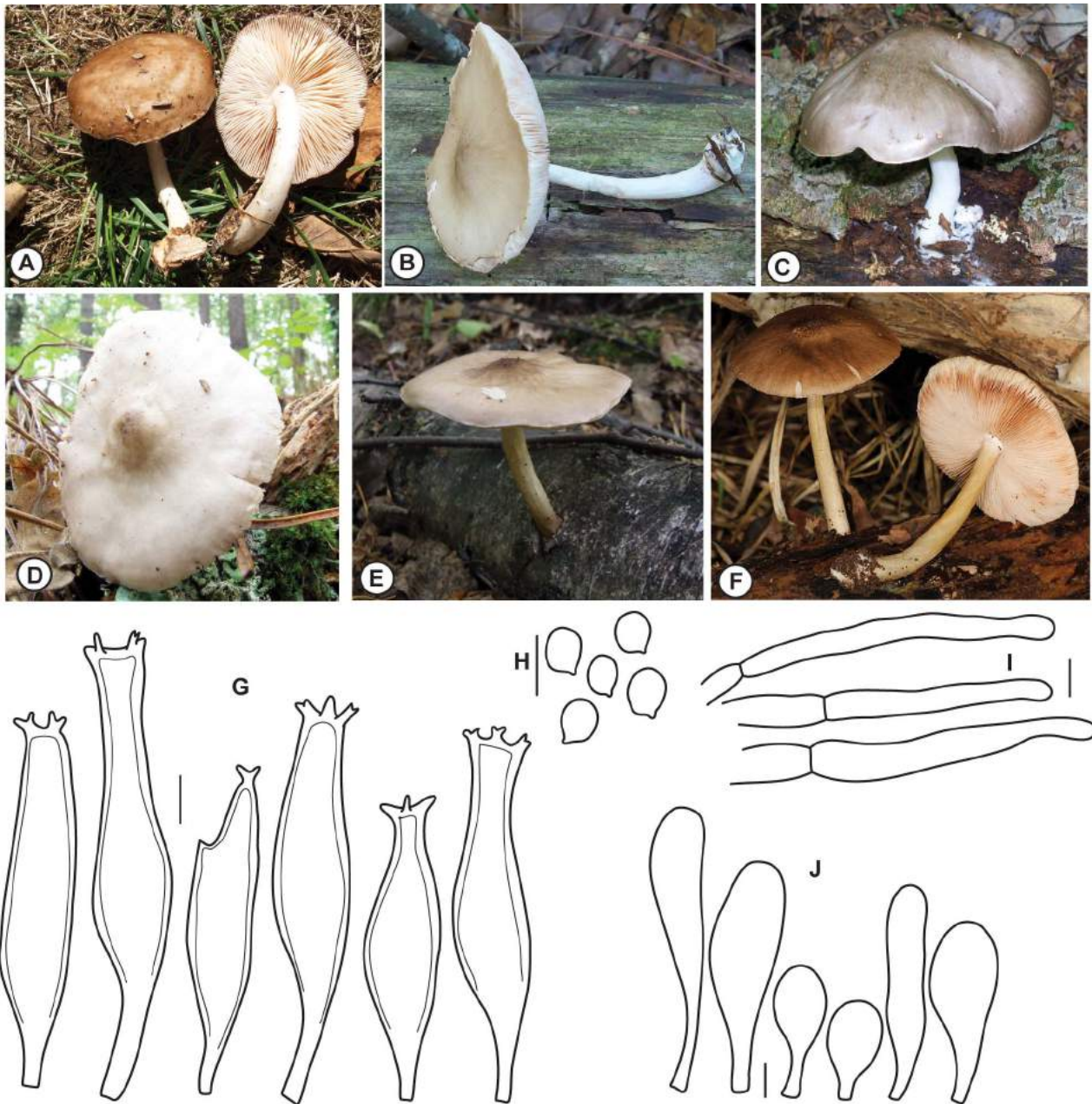


FIGURE 12. *Pluteus hongoi*. A. Collection AJ 339 (photo by A. Justo). B. Collection AJ 148 (photo by A. Justo). C. Collection AJ 836 (photo by A. Justo). D. Collection AJ 58 (photo by A. Justo). E. Collection LE 289420 (photo by E. Malysheva). F. Collection LE 289391 (photo by E. Malysheva). G. Pleurocystidia. H. Basidiospores. I. Pileipellis. J. Cheilocystidia. G–J from collection *Singer* N5195. All line drawings by A. Justo. Scale bars = 10 μ m.

Pileus 25–90(–100) mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, with or without a shallow depression at center; surface smooth to innately radially fibrillose, with or without well-defined squamules at center; usually some shade of brown (7.5YR 4/6, 5/6–5/8, 6/6–6/8, 7/6–7/8), or gray-brown (7.5YR 5/1–5/4, 6/3/6/4), occasionally pure white; dry or slightly viscid when moist; margin smooth or slightly translucently striate. Lamellae crowded, free, ventricose, up to 10 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 35–110 \times 3–15 mm, cylindrical, with slightly broad base; surface white, sometimes with yellowish tints near base, usually smooth or

whitely flocculose, rarely with longitudinal brown or gray-brown fibrils all over although these are more common at the base. Context in stipe and pileus white. Smell raphanoid (radish-like), or reminiscent of raw potatoes, rarely indistinct. Taste similar to smell or earth-like. Spore print pinkish brown (2.5YR 7/6–7/8).

Basidiospores [460, 43, 41] $5.5\text{--}9.0 \times 4.5\text{--}7.0 \mu\text{m}$, $avl \times avw = 6.7\text{--}7.6 \times 5.0\text{--}5.7 \mu\text{m}$, $Q = 1.15\text{--}1.60(1.70)$, $avQ = 1.26\text{--}1.45$, ellipsoid or broadly ellipsoid, rarely oblong, sometimes ovoid or slightly constricted in the middle. Basidia $12\text{--}33 \times 5\text{--}12 \mu\text{m}$, tetrasterigmate, rarely bisterigmate, clavate, some with median constriction. Pleurocystidia metuloid, $50\text{--}110 \times 15\text{--}30 \mu\text{m}$, fusiform, narrowly fusiform or narrowly utriform with 2–5 apical hooks (predominantly bifid, but entire hooks also present), rarely with some lateral hooks especially near the apex, hyaline, with up to $3 \mu\text{m}$ thick wall, frequent all over lamellar faces; sometimes both types on the same cystidium. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia $25\text{--}110(115) \times (10\text{--})15\text{--}30 \mu\text{m}$, clavate, narrowly clavate, spheropedunculate or narrowly utriform, hyaline, thin-walled; crowded and forming a well-developed strip or scarce and then present as scattered clusters on the lamellar edge. Pileipellis a cutis or ixocutis with terminal elements $50\text{--}135 \times 5\text{--}25 \mu\text{m}$; individual elements cylindrical, some strongly tapering towards apex, mostly filled with brown intracellular pigment, with thin, smooth walls. A gelatinous matrix is sometimes present, with embedded cylindrical hyphae $3\text{--}10 \mu\text{m}$ wide. Stipitipellis a cutis; hyphae $5\text{--}20 \mu\text{m}$ wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections absent on pileipellis hyphae; not observed in any other part of the basidiocarp.

Habit, habitat and phenology:—Solitary or gregarious, usually growing on well-decayed wood of angiosperms (e.g. *Acer*, *Betula*, *Fagus*, *Quercus*) or growing on the humus layer without apparent connection to wood. In temperate or transitional boreal/temperate forests. June–November, more rarely February–May.

Distribution:—**Eurasia.** Widespread, from Spain to the Russian Far East and Japan. **North America.** Widespread in eastern North America, from Florida to Massachusetts and westwards into Wisconsin. Not recorded from western North America.

Observations:—In its most typical form *Pluteus hongoi* can be separated from *P. cervinus*, with which it shares much of its distribution, by the following characters: pale pileus, stipe usually without distinct longitudinal fibrils or squamules, hooks on the pleurocystidia bifid, cheilocystidia not forming a well-developed and continuous strip along the lamellar edge. However, all these characters have been shown to be quite variable and do not necessarily occur simultaneously in all the collections, therefore specimens of *P. hongoi* morphologically indistinguishable from *P. cervinus* do occur. Molecular data (Fig. 2) support the separation of both taxa.

Of all the names available for this species *P. hongoi* and *P. major* were described by Singer (1989) in the same publication and therefore have equal nomenclatural priority until one is formally chosen and this choice effectively published (ICN Art. 11.5). Here we choose to use the epithet *hongoi* because the original description of this taxon is more complete than the one given for *P. major*. Molecular data from the type specimens of *P. major*, *P. albineus* (Bonnard 2001) and *P. nothopellitus* (Justo & Castro 2007b) indicate that all represent different morphological variants of *P. hongoi*.

Additional collections examined:—CHINA. Locality and date unknown, *TENN* 48297, nrITS KJ009613, *tefl* KJ009932 (TENN). GERMANY. **Bavaria:** On decayed *Betula* wood, 14 October 1999, *F. Bonke s.n.* *REG* 13658, nrITS HM562151, *tefl* KJ009919 (REG). Weltenburger, on *Fagus* stump, 29 June 1999, *B. Mende s.n.* *REG* 13664, nrITS HM562168, *tefl* KJ009911 (REG). JAPAN. No locality, 17 June 2007, *TNSF* 16091, nrITS HM562126, *tefl* KJ009933 (TNS). **Hokkaido:** Iwamizawa, Tonebetu, deciduous forest, on decayed wood, 25 June 2005, *S. Takehashi s.n.* *TNSF* 12370, nrITS HM562103, *tefl* KJ009938 (TNS); *ibid.*, mixed forest, 26 June 2003, *S. Takehashi s.n.* *TNSF* 12352, nrITS HM562102, *tefl* KJ009936 (TNS). Kuromatonai, deciduous forest, on decayed wood, 20 June 2005, *S. Takehashi s.n.* *TNSF* 12361, nrITS HM562100, *tefl* KJ009934, (TNS). Saporu, Mt. Teine, mixed forest, on decayed wood, 20 June 2004, *S. Takehashi s.n.* *TNSF* 12351, nrITS HM562101, *tefl* KJ009941 (TNS). **Honshu:** Tokyo, Fukiage Garden, 14 October 1998, *TNSF* 897, nrITS HM562128 (TNS). MONGOLIA. **North Mongolia:** Research Station “Khonin Nuga”, Mandal Sum, Selenge Aimak West-Khentee, montane *Betula-Larix* forest, on fallen *Betula* trunk, 10 August 2007, *A.V. Aleksandrova s.n.* *LE* 289422, nrITS KJ009567, *tefl* KJ009943 (LE). RUSSIA. **Central Federal District:** Moscow Region, Prioksko-Terrasny Nature Biosphere Reserve, *Picea* forest, on decayed wood of *Betula*, 27 June 1994, *G.E. Levitskaya s.n.* *LE* 216821, nrITS KJ009573, *tefl* KJ009944 (LE). Tula Region, Kurkinsky District, valley of Nizhny Dubik River, *Betula* forest with *Quercus*

and *Acer*, on decayed log, 26 July 2003, *T.Yu. Svetasheva s.n. LE 234781*, nrITS KJ009569, *tefl* KJ009930 (LE).

Far East Federal District: Primorsky Territory, Sikhote-Alinsky Nature Biosphere Reserve, vicinities of Blagodatnoye Reserve Field Station, *Quercus mongolica* forest with isolated *Betula platyphylla*, on stump of *Quercus*, 29 August 2011, *E.F. Malysheva s.n. LE 289392*, nrITS KJ009606, *tefl* KJ009942 (LE). Primorsky Territory, Ussuriisky Nature Reserve, vicinities of Peishula Reserve Field Station, near Koryavaya River, mixed forest (*Quercus mongolica*, *Acer mandshurica*, *Pinus koraiensis*), on decayed wood, 13 August 2011, *E.F. Malysheva s.n. LE 289378*, nrITS KJ009570, *tefl* KJ009935 (LE); *ibid.*, near Koryavaya River, mixed forest (*Quercus mongolica*, *Acer mandshurica*, *Pinus koraiensis*), on fallen tree trunk, 13 August 2011, *E.F. Malysheva s.n. LE 289391*, nrITS KJ009566, *tefl* KJ009937 (LE).

Northwestern Federal District: Novgorod Region, vicinities of Syuiska, mixed forest, on fallen trunk of *Betula*, 24 June 2011, *S. Arslanov s.n. LE 289377*, nrITS KJ009572, *tefl* KJ009908 (LE).

Siberian Federal District: Baikal region, vicinities of Listvenichnoye, mixed forest, on fallen *Betula* trunk, 16 July 1947, *LE 9710*, nrITS KJ009568, *tefl* KJ009931 (LE). Novosibirsk Region, Novosibirsk District, Akademgorodok, mixed forest (*Betula pendula* and *Pinus sylvestris*), on *Betula* rotten wood, 11 June 2008, *T.M. Bulyonkova s.n. LE 289420*, nrITS KJ009571, *tefl* KJ009945 (LE); *ibid.*, mixed, poorly lit eutrophic planted forest (*Pinus sylvestris*, *Betula pendula*, *Prunus padus*, *Acer negundo*) about 40 years old with a lot of dead trees, on decayed wood, 07 July 2011, *T.M. Bulyonkova s.n. LE 289404*, nrITS KJ009610, *tefl* KJ009947 (LE); *ibid.*, medium-aged *Betula pendula* forest with dense bush undergrowth, on decayed wood of *Betula*, 07 June 2011, *T.M. Bulyonkova s.n. LE 289413*, nrITS KJ009609, *tefl* KJ009939 (LE).

Southern Federal District: Krasnodarsky Territory, Stanitsa Kaluzhskaya, *Quercus* forest, on buried wood, 19 September 1979, *A.E. Kovalenko s.n. LE 9688*, nrITS KJ009611, *tefl* KJ009928 (LE).

Ural Federal District: Khanty-Mansiyskiy District, Mukhrino Field Station of the Ugra State University UNESCO chair, mixed dark conifer taiga (*Picea obovata*, *Abies sibirica*, *Pinus sibirica* and scarcer *Betula pendula*, *Populus tremula*, *Pinus sylvestris*), on decayed wood, 15 September 2010, *T.M. Bulyonkova s.n. LE 289403*, nrITS KJ009608, *tefl* KJ009946 (LE); *ibid.*, 17 September 2010, *T.M. Bulyonkova s.n. LE 289415*, nrITS KJ009607, *tefl* KJ009910 (LE). Sverdlovsk Region, Visimsky Nature Reserve, *Betula* forest, on fallen trunk, 07 July 1993, *L.V. Marina s.n. LE 258162*, nrITS KJ009612, *tefl* KJ009927 (LE). Yugra, Khanty-Mansiyskiy District, mixed dark conifer taiga, on decayed wood, 16 September 2010, *T.M. Bulyonkova s.n. LE 289418*, nrITS KJ009565 (LE).

Volga Federal District: Samara Region, Zhigulevsky Nature Reserve, vicinities of Bakhilova Polyana, broadleaf forest (*Tilia cordata*), on decayed wood, 27 July 2000, *E.F. Malysheva s.n. LE 289393*, nrITS KJ009614, *tefl* KJ009929 (LE).

SPAIN. Ourense: Nogueira de Ramuin, mixed forest, mostly *Quercus*, on decayed wood (probably *Quercus*), 15 October 2006, *P. Comesaña & GMG s.n. AJ 78*, nrITS HM562034, *tefl* KJ009909 (LOU).

UNITED STATES OF AMERICA. Connecticut: New Haven Co., West Rock Ridge State Park, mixed forest, 15 July 2012, *E.C. Vellinga s.n. AJ 837*, nrITS KJ009585 (CUW).

Florida: Leon Co., Tallahassee, Lake Overstreet, mixed forest, on decayed hardwood log, 24 August 2009, *A. Justo 148*, nrITS HM562085, *tefl* KJ009915 (MICH).

Illinois: Johnson Co., near Ozark, Camp Ondessonk, 25 September 2009, *A.M. Minnis PIL1*, nrITS KJ009605, *tefl* KJ009949 (BPI). Shelby Co., near Lake Shelbyville, 23 September 2006, *J. McFarland SF7-BPI 882769*, nrITS HM562178, *tefl* KJ009914 (BPI).

Louisiana: Baton Rouge, 23 February 1960, *B. Lowy s.n. LE 9746*, nrITS KJ009574, *tefl* KJ009904 (LE).

Massachusetts: Berkshire Co., Savoy Mountain State Forest, mixed forest, on decayed wood, 04 October 2012, *A. Justo 780*, nrITS KJ009591 (CUW); *ibid.*, 16 June 2012, *A. Justo 836*, nrITS KJ009590 (CUW). Middlesex Co., Mt. Misery Conservation Area, mixed forest, on decayed fallen wood, 21 June 2010, *A. Justo 324*, nrITS KJ009582, *tefl* KJ009924 (CUW). Worcester Co., Harvard Forest, mixed forest, on decayed fallen wood, 04 June 2010, *M. Nuhn s.n. AJ 319*, nrITS KJ009603, *tefl* KJ009926 (CUW); *ibid.*, on decayed hardwood log, 10 October 2009, *A. Justo s.n. AJ 181*, nrITS HM562098, *tefl* KJ009923 (MICH). Worcester Co., Holden Rail Trail, mixed forest, on decayed log, 02 September 2011, *A. Justo 415*, nrITS KJ009583, *tefl* KJ009921 (CUW). Worcester Co., Moore State Park, mixed forest, on decayed hardwood, 02 August 2012, *A. Justo 543*, nrITS KJ009578 (CUW). Worcester Co., Uxbridge, Cormier Woods, mixed forest, on decayed fallen wood, 09 October 2010, *A. Justo 339*, nrITS KJ009589, *tefl* KJ009913 (CUW); *ibid.*, *A. Justo 340*, nrITS KJ009600, *tefl* KJ009918 (CUW); *ibid.*, 28 May 2010, *A. Justo 306*, nrITS KJ009592, *tefl* KJ009922 (CUW); *ibid.*, on decayed hardwood branch, 21 June 2010, *A. Justo 323*, nrITS KJ009598, *tefl* KJ009906 (CUW). Worcester Co., Wachusett Mountain State Reservation, mixed forest, on decayed hardwood branch, 18 August 2011, *A. Justo 412*, nrITS KJ009584, *tefl* KJ009905 (CUW); *ibid.*, on decayed hardwood log, 29 September 2010, *A. Justo 329*, nrITS KJ009604 (CUW); *ibid.*, decayed hardwood, 08 November 2011, *D. Floudas s.n. AJ 413*, nrITS KJ009599, *tefl* KJ009916 (CUW).

Worcester Co., Ware River Watershed Trail, mixed forest, on wood, 13 September 2012, *A. Justo* 762, nrITS KJ009602 (CUW). **Michigan:** Emmet Co., Tahquamenon Falls State Park, 20 June 1953, *R. Singer* N81, nrITS KJ009594 (F). **New York:** Essex Co., Adirondack Ecological Center, Huntington Wildlife Forest, mixed forest, on decayed wood, 18 August 2012, *A. Justo* 593, nrITS KJ009580 (CUW); *ibid.*, *A. Justo* 605, nrITS KJ009595 (CUW); *ibid.*, 14 August 2012, *A. Justo* 607, nrITS KJ009593 (CUW); *ibid.*, 16 August 2012, *A. Justo* 610, nrITS KJ009575 (CUW); *ibid.*, on decayed wood of *Acer*, 18 August 2012, *A. Justo* AJ 599, nrITS KJ009576 (CUW). Essex Co., Huntington Wildlife Forest, Wold Lake, old-growth mixed forest with *Fagus*, *Acer* and *Tsuga*, on decayed wood of *Acer saccharum*, fallen tree, 21 September 2013, *O. Miettinen* 17105, nrITS KJ009787, *tefl* KJ009925, (H); *ibid.*, on *Fagus americanus*, fallen tree, 21 September 2013, *O. Miettinen* 17106, nrITS KJ009789 (H). Essex Co., Newcomb, Harris Lake, middle-aged, mixed forest with a lot of old storm damage, on hardwood, fallen tree, 23 September 2013, *O. Miettinen* 17148, *tefl* KJ009948 (H). **North Carolina:** Haywood Co., White Oak, 09 October 2010, *E.C. Vellinga* 4184, nrITS KJ009588 (TENN). Tennessee: Blount Co., 17 July 2006, *R.H. Petersen* 13290, nrITS KJ009597 (TENN). Cocke Co., Cosby, on decayed wood of deciduous tree, 05 August 2009, *E.C. Vellinga* 4055, nrITS KJ009579, *tefl* KJ009907 (TENN). Knox Co., Corryton House Mt. State Park, on rotten log, 23 April 2011, *B. Looney* 41, nrITS KJ009587 (TENN). Sevier Co., Gatlinburg, Cherokee Orchard, Rainbow Falls Trail, on decayed wood, 06 August 2009, *E.C. Vellinga* 4072, nrITS KJ009581, *tefl* KJ009917 (TENN). **Wisconsin:** Vilas Co., Northern Highland State Forest, “plot 8”, 20 July 1995, *D. Lindner* DLF-95-104, nrITS KJ009577 (CFMR).

Pluteus elaphinus Justo *sp. nov.* Fig. 13

MycoBank 808725

Diagnosis:—Distinct from *Pluteus cervinus* in the pleurocystidia with bifid hooks and from other species in this complex by the nrITS and *tefl* sequence data.

Holotype:—UNITED STATES OF AMERICA. Massachusetts: Berkshire Co., Savoy Mt. State Forest, on decayed wood, 4 October 2012, *A. Justo* 783, nrITS KJ009663, *tefl* KJ009902 (CUW!).

Etymology:—*elaphinus* comes from the Greek “ἐλάφος” meaning “deer” making reference to the relatedness and morphological similarity to *Pluteus cervinus*.

Pileus 25–65 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, with or without a shallow depression at center; surface innately radially fibrillose or with conspicuous radial fibrils, usually with well-defined squamules at center, sometimes cracking and showing the white context; brown (7.5YR 4/3–4/6, 5/4–5/8), sometimes very dark brown (7.5YR 3/3–3/4) especially at center; dry or slightly viscid when moist; margin smooth or slightly translucently striate. Lamellae crowded, free, ventricose, up to 7 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 35–80 × 4–10 mm, cylindrical, with slightly broad base; surface white, with conspicuous longitudinal brown or gray-brown fibrils, sometimes grouped to form distinct squamules. Context in stipe and pileus white. Smell reminiscent of raw potatoes, rarely indistinct. Taste similar to smell or earth-like. Spore print pinkish brown (2.5YR 7/6–7/8).

Basidiospores [140, 7, 7] 6.0–8.0(–9.0) × 4.5–6.5(–7.0) μm, avl × avw = 7.0–7.8 × 5.0–5.8 μm, Q = 1.25–1.55(–1.60), avQ = 1.34–1.42, ellipsoid or broadly ellipsoid, sometimes ovoid or slightly constricted in the middle. Basidia 12–30 × 5–10 μm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 55–90 × 10–20 μm, fusiform, narrowly fusiform or narrowly utriform, provided with 2–4 apical hooks (commonly bifid), hyaline, with up to 5 μm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia 25–65 × 14–25 μm, clavate, narrowly clavate, spheropedunculate or narrowly utriform, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 60–120 × 9–20 μm; individual elements cylindrical, some strongly tapering towards apex, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–20 μm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections absent on pileipellis hyphae; not observed in any other part of the basidiocarp.

Habit, habitat and phenology:—Solitary or gregarious, on well-decayed wood of angiosperms (e.g. *Acer*, *Betula*). In transitional boreal/temperate forests or temperate forest in mountainous areas.

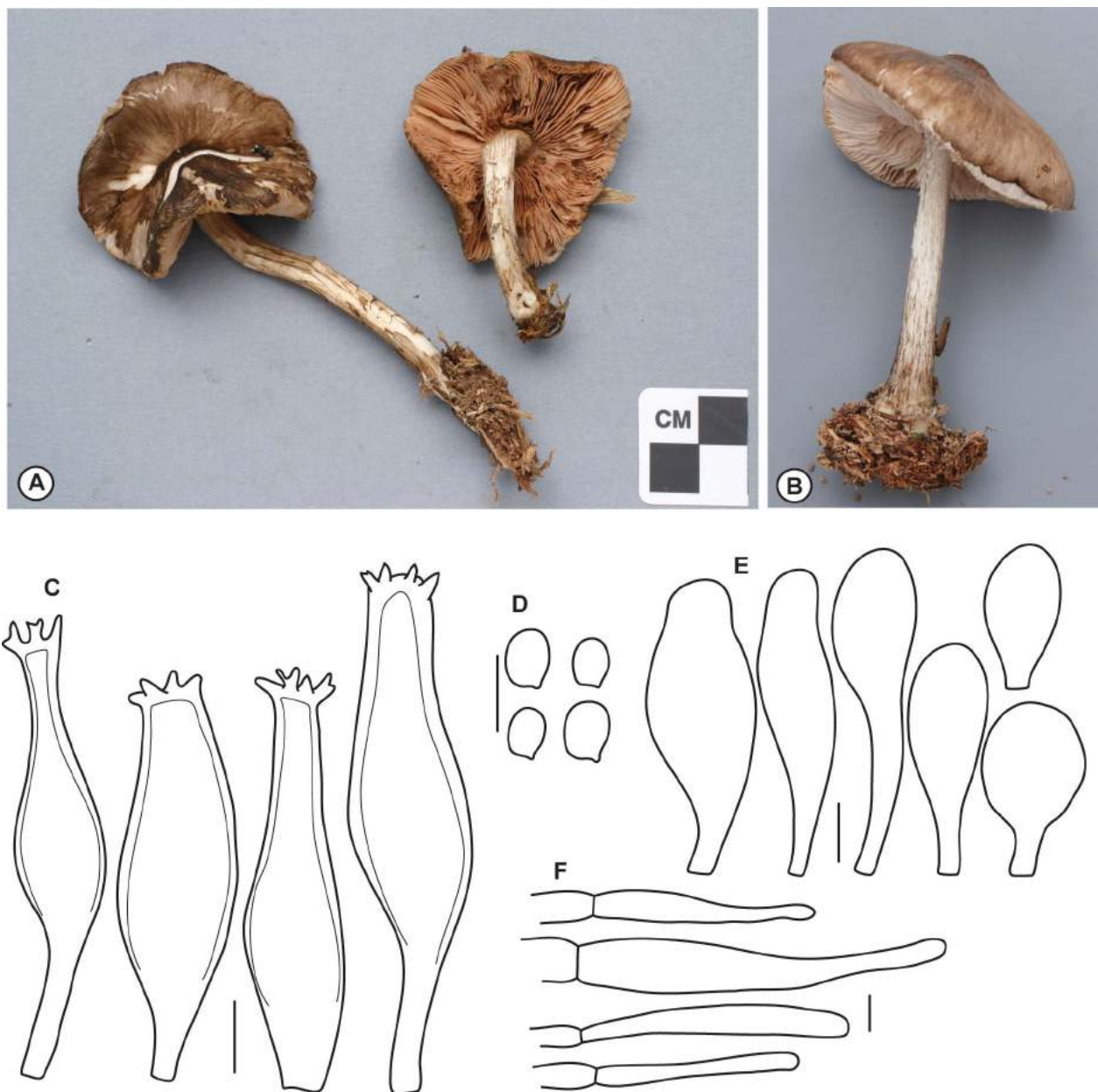


FIGURE 13. *Pluteus elaphinus*. A. Collection 2004-Sept-18 (photo by R. Smith). B. Collection MS9-018 (photo by R. Smith). C. Pleurocystidia. D. Basidiospores. E. Cheilocystidia. F. Pileipellis. C–F from collection AJ 783. All line drawings by A. Justo. Scale bars = 10 μ m.

Distribution:—**North America.** Ontario and Newfoundland Island (Canada); Adirondack Mountains (New York) and Berkshire Mountains (Massachusetts) in the USA.

Observations:—Morphologically, it is hard to tell *P. elaphinus* apart from other members of the *P. cervinus* clade, although molecularly it is a distinct species based on both nrITS and *tefl* data (Fig. 2). The pleurocystidia commonly provided with bifid hooks set it apart from *P. cervinus*; the strongly fibrillose pileus and stipe set it apart from *P. hongoi* but both characters are variable. Geographic distribution separates *P. elaphinus* and *P. exilis*. In morphological characters and ecological preferences *P. rangifer* comes very close to *P. elaphinus*, differing only in the predominantly entire hooks of the pleurocystidia and the fusiform and intermediate cystidia without hooks.

Pluteus elaphinus seems to be confined to the transitional boreal/temperate forests or mountainous forests of northeastern North America and it has not been recorded in geographically close but ecologically different areas, e.g., it occurs in the Berkshires of western Massachusetts but it is not present in the heavily sampled central and eastern parts of the state. This relatively restricted distribution overlaps with the distribution of other, widely distributed species in this group, and collections of *P. cervinus* (AJ781) and *P. hongoi* (AJ780) were made on the very same day and place (04 October 2012, Savoy Mt. State Forest) as the holotype of *P. elaphinus* (AJ783).

Pluteus brunneoolivaceus Horak is similar to *P. elaphinus* in the markedly squamulose/fibrillose pileus but in this species the cheilocystidia are filled with brown intracellular pigment and are up to 80 µm long (Horak 1964). This taxon is only known from the austral forests of the southernmost part of South America (Tierra del Fuego, Argentina).

Additional collections examined:—CANADA. **Newfoundland and Labrador:** Newfoundland Island, Bakers Brook Pond Trail, mixed woods, on decayed wood of *Betula*, 18 September 2004, *G. Rideout s.n.* 2004-September-18, nrITS KJ009779 (CUW). Newfoundland Island, Notre Dame Provincial Park, mixed woods, on decayed wood, 12 September 2009, *K. Liimatainen MS9-018*, nrITS KJ009782 (CUW). **Ontario:** Nipissing, Algonquin Provincial Park, on decayed log of *Acer saccharinum*, 02 October 2007, *M. Didukh & B. Dentinger s.n.* TRTC 156922, nrITS KJ009660, *tef1* KJ009903 (TRTC). West of Kirkland Lake, on well-decayed hardwood log, 03 September 1978, *VF Stanis s.n.* TRTC 154079, nrITS KJ009662 (TRTC). UNITED STATES OF AMERICA. **New York:** Essex Co., Adirondack Ecological Center, Huntington Wildlife Forest, mixed forest, on *Betula* wood, 16 August 2012, *A. Justo 612*, nrITS KJ009661 (CUW). Essex Co., Newcomb, Harris Lake, middle-aged, mixed forest with a lot of old storm damage, on decayed snag of *Populus tremuloides*, 23 September 2013, *O. Miettinen 17164*, nrITS KJ009786 (H).

Pluteus alniphilus Citérin & Deparis in Deparis (2003: 6). Fig. 14

Holotype:—FRANCE. Savoie, Val d'Isère, Le Fornet (1850 m elevation), on decayed wood of *Alnus alnobetula* (as "*Alnus viridis*" in the original publication), 25 July 2001, *L. Deparis s.n.* PC 0086107, nrITS KJ009678 (PC!).

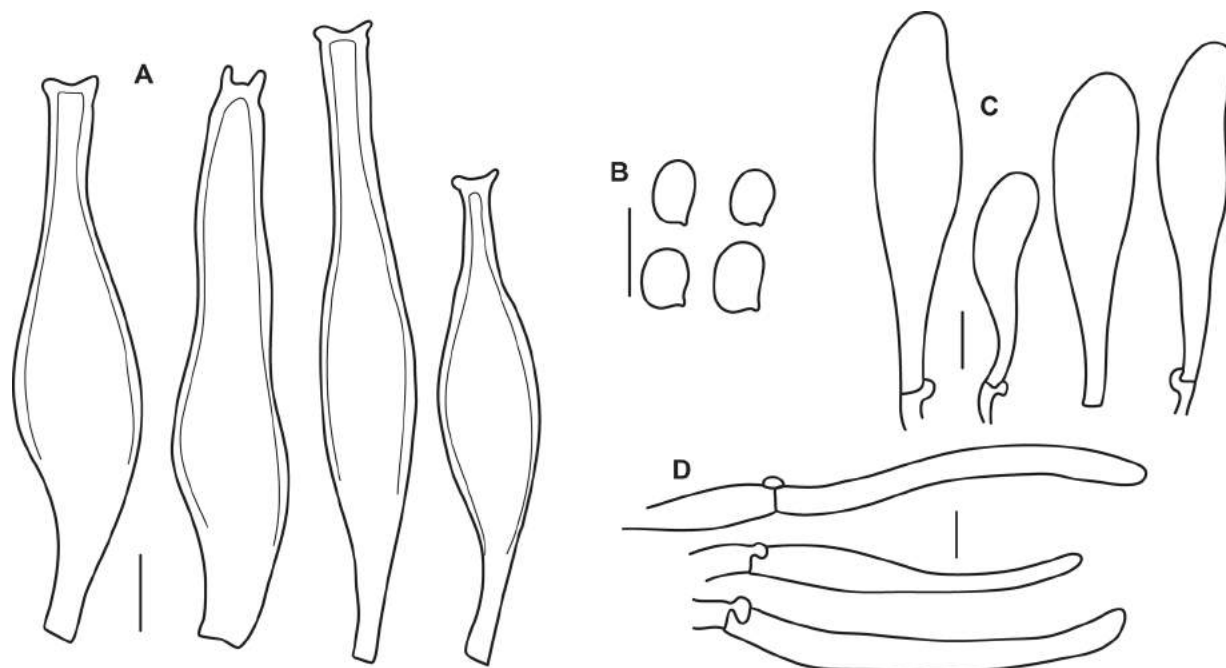


FIGURE 14. *Pluteus alniphilus*. A. Pleurocystidia. B. Basidiospores. C. Cheilocystidia. D. Pileipellis. All from collection PC 0086107. All line drawings by A. Justo. Scale bars = 10 µm.

Pileus 40–60 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with a low, broad umbo; surface strongly radially fibrillose and with well-defined squamules around center; gray-brown or brown (in the range of 7.5YR 4/3–4/6, 5/2–5/8); dry or slightly viscid when moist; margin smooth or slightly translucently striate. Lamellae crowded, free, ventricose, up to 7 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 45–85 × 5–10 mm, cylindrical, with slightly broad base; surface white, with conspicuous longitudinal brown or gray-brown fibrils, sometimes grouped to form distinct squamules. Context in stipe and pileus white. Smell raphanoid. Taste raphanoid. Spore print pinkish brown.

Basidiospores [40, 2, 2] 6–8.5(–9.2) × 4.5–6.0 µm, $av_l \times av_w = 7.3\text{--}7.4 \times 4.8\text{--}5.1$ µm, $Q = 1.23\text{--}1.73$, $avQ = 1.44\text{--}1.51$, broadly ellipsoid, ellipsoid or oblong, sometimes ovoid or slightly constricted in the middle. Basidia 20–35 × 5–10 µm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 50–95 × 10–30 µm, fusiform, narrowly fusiform or narrowly utriform with 2–4 apical hooks (usually entire and not very

prominent), hyaline, with up to 3 µm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia 30–80 × 8–22 µm, clavate, narrowly clavate, spheropedunculate or narrowly utriform, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 70–110 × 6–17 µm; individual elements cylindrical, some proportion inflated, some strongly tapering towards apex, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–20 µm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae but not at every septum; also observed in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary or gregarious, on decayed wood of *Alnus*, probably also on *Betula*. In alpine forests (France) or northern *Betula* forests (Russia).

Distribution:—**Eurasia.** Only known from the French Alps (Savoie) and Siberia (near Labytnangi).

Observations:—In the original description Deparis (2003) characterized *Pluteus alniphilus* by the combination of gray-brown pileus, presence of clamp-connections in the pileipellis and growth on alder wood in alpine forests (*alniphilus* means “alder-loving”). Other taxa in the cervinus clade that sometimes have predominant gray colors in the pileus include *P. cervinus* and *P. hongoi*, but both taxa lack clamp-connections on the pileipellis. The species in the complex around *P. pouzarianus* have clamp-connections on the pileipellis and can have predominantly gray hues in the pileus but these species have a strong preference for conifer wood.

Additional collections examined:—FRANCE. **Savoie:** Val d’Isère, Le Fornet (1850 m elevation), alpine forest, on decayed wood of *Alnus viridis*, 19 August 2002, *T. Deparis s.n. PC 0086106*, nrITS KJ009677 (PC). RUSSIA. **Siberian Federal District:** Tyumen Region, right bank of Ob River, vicinities of Labytnangi, *Betula* forest, on stump of deciduous tree, 19 August 1962, *B.P. Vassilkov s.n. LE 9713*, nrITS KJ009676, *tefl* KJ009840 (LE)

II. *pouzarianus* clade. Fig. 3

Species growing almost exclusively on conifer wood or on the humus layer under conifers; very rarely on angiosperm wood. Clamp-connections common and easy to spot on pileipellis hyphae.

Pluteus pouzarianus Singer (1984: 283). Fig. 15

Holotype:—CZECH REPUBLIC. Near Diana, on stump of *Picea abies*, 22 September 1967, *Z. Pouzar s.n. PRM 628956* (PRM!).

= *Pluteus pouzarianus* var. *albus* Bonnard (1993: 204). Holotype:—SWITZERLAND. Canton Vaud: Jorat, 24 October 1989, *J. Bonnard 89/61*, (LAU!).

Pileus 30–100(–150) mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, with or without a shallow depression at center; surface smooth or innately radially fibrillose, with or without well-defined squamules at center; brown (7.5YR 4/3–4/6, 5YR 4/2–4/6), gray-brown (10YR 4/1–4/4) or gray (10YR 5/1–5/2), pure white variants also occur; dry or slightly viscid when moist; margin smooth or slightly translucent-striate. Lamellae crowded, free, ventricose, up to 12 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 40–130(–160) × 4–20 mm, cylindrical, with slightly broad base; surface white, usually with longitudinal brown or gray-brown fibrils, sometimes grouped to form distinct squamules, very rarely completely glabrous. Context in stipe and pileus white. Smell raphanoid (radish-like), reminiscent of raw potatoes, or sweet, rarely indistinct. Taste similar to smell or earth-like. Spore print pinkish brown (2.5YR 7/6–7/8).

Basidiospores [250, 24, 20] 6.0–8.6(–9.5) × (4.0–)4.5–5.7(–6.2) µm, $av_l \times av_w = 6.8\text{--}7.5 \times 4.8\text{--}5.2$ µm, $Q = 1.25\text{--}1.65$, $avQ = 1.35\text{--}1.52$, ellipsoid, more rarely broadly ellipsoid or oblong, sometimes ovoid or slightly constricted in the middle. Basidia 17–35 × 5–12 µm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, (55–)65–100(–115) × 10–25(–30) µm, fusiform, narrowly fusiform or narrowly utriform with 2–4 apical hooks (usually entire), rarely with small lateral hooks, hyaline, with up to 4 µm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia 20–70 × 10–25(–30) µm, clavate, narrowly clavate or spheropedunculate, more rarely narrowly utriform, hyaline, thin-walled, crowded, forming a well-developed strip.

Pileipellis a cutis, with terminal elements $60\text{--}130(\text{--}150) \times 7\text{--}17(\text{--}25) \mu\text{m}$; individual elements cylindrical, some strongly tapering towards apex, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae $5\text{--}25 \mu\text{m}$ wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae but not at every septum; also observed in other parts of the basidiocarp.

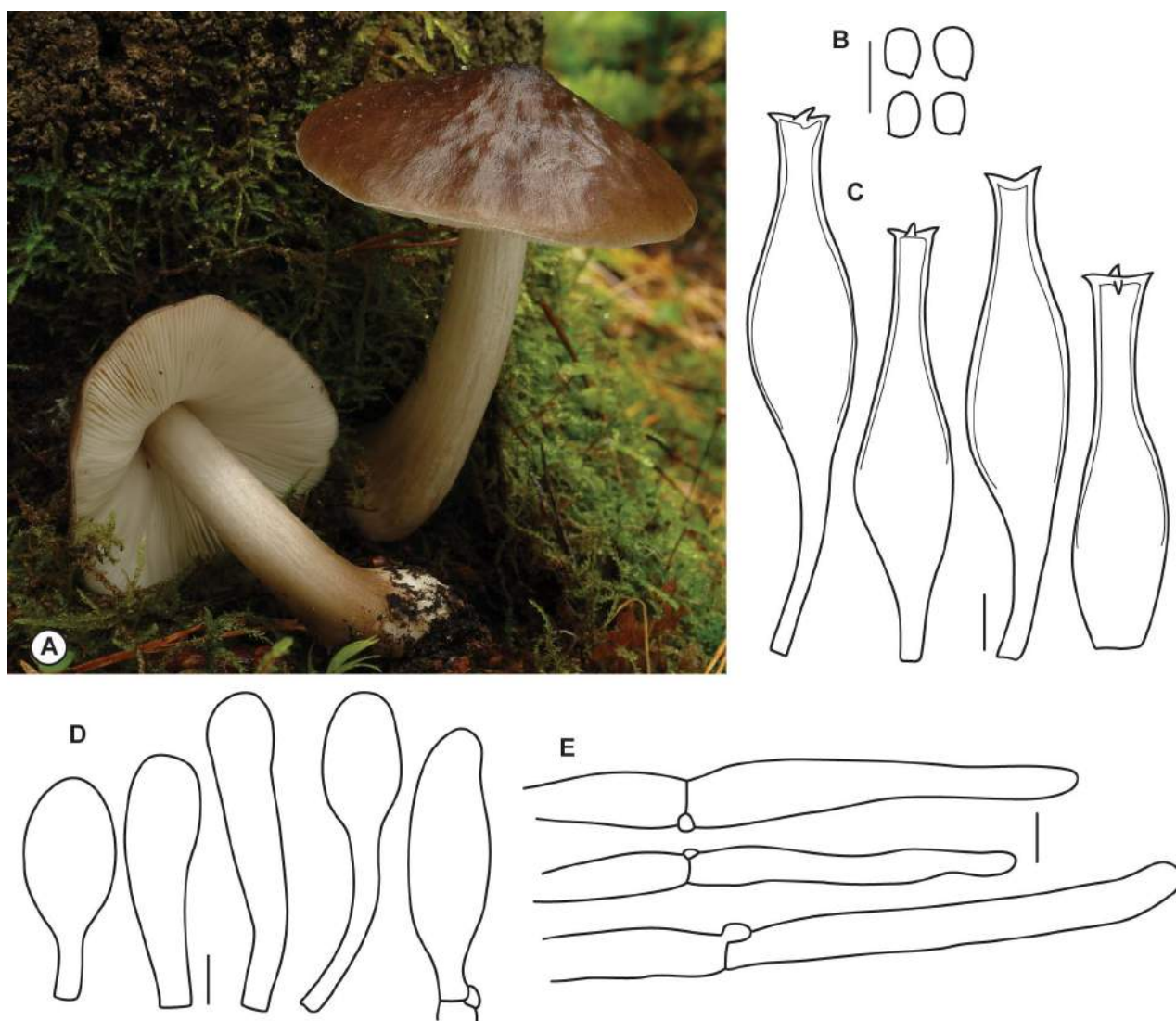


FIGURE 15. *Pluteus pouzarianus*. A. Collection LE 289380 (photo by O. Morozova). B. Basidiospores. C. Pleurocystidia. D. Cheilocystidia. E. Pileipellis. B–E from collection PRM 898519. All line drawings by A. Justo. Scale bars = $10 \mu\text{m}$.

Habit, habitat and phenology:—Solitary or gregarious, growing on well-decayed wood of conifers (e.g. *Abies*, *Picea*, *Pinus*). More rarely on conifer sawdust or on the humus layer under conifers. One collection recorded as growing on a *Fagus* stump (AJ61). In natural conifer or mixed forests, also in conifer plantations. Recorded in temperate and boreal areas. Mostly recorded in the fall (September–December) but some collections made in February and June.

Distribution:—**Eurasia.** Widespread in Europe, including the Southern (Spain, Portugal, Italy), Central (Germany, Czech Republic, The Netherlands) and Northern areas (Sweden, European Russia).

Observations:—The collection LE289380, made near St. Petersburg (Russia), marks the easternmost confirmed occurrence of *P. pouzarianus* in Eurasia. All other collections in this species complex from the eastern parts of Eurasia and from North America have turned out to be different species.

Two other species with clamp-connections in the pileipellis and habitat on conifer wood occur in the same area. *P. primus* differs in the slightly larger basidiospores (on average $7.8\text{--}8.4 \times 5.6\text{--}6.3 \mu\text{m}$) and the longer cheilocystidia, up to $120(\text{--}200) \mu\text{m}$, with more common narrowly clavate and cylindrical ones. *P. atromarginatus* differs in the pigmented cheilocystidia.

Bonnard (1993) described pure white variants of this taxon as var. *albus*. White forms of normally pigmented taxa are common in other species of section *Pluteus* (e.g. *P. cervinus*, *P. hongoi*, *P. primus*).

Additional collections examined:—CZECH REPUBLIC. **South Bohemia:** Šumava Mountains, Čeňkova Pila, mixed forest with *Picea*, *Abies*, *Fagus*, on decayed wood of *Picea abies*, 11 October 1997, *J. Holec s.n.* PRM 898519, nrITS KJ009670, *tefl* KJ009800 (PRM). Šumava Mountains, Cettlový Hurky, mixed forest with *Alnus incana*, *Picea abies*, on decayed wood of *Picea abies*, 16 September 1999, *J. Holec s.n.* PRM 898043, nrITS KJ009664, *tefl* KJ009805 (PRM). Šumava Mountains, Zblesky, mixed forest with *Acer*, *Fagus*, *Sorbus*, *Abies*, *Fraxinus*, on decayed wood of *Abies alba*, 13 September 1999, *J. Holec s.n.* PRM 897993, nrITS KJ009666, *tefl* KJ009803 (PRM). Tabor, Svakov, on decayed wood of *Picea abies*, 01 October 2005, *F. Kotlaba s.n.* PRM 905414, nrITS KJ009669, *tefl* KJ009799 (PRM). GERMANY. **Bavaria:** Hohengebrachinger Forst, 30 September 1999, *B. Mende s.n.* REG 13626, nrITS HM562154, *tefl* KJ009806 (REG). Teublitz, on decayed wood, 04 October 1999, *B. Mende s.n.* REG 13619, nrITS HM562170, *tefl* KJ009802 (REG). RUSSIA. **Northwestern Federal District:** Leningrad Region, vicinity of Komarovo, “Komarovskiy bereg”, *Picea* forest, on decayed wood of *Picea*, 04 October 2009, *O.V. Morozova s.n.* LE 289380, nrITS KJ009668, *tefl* KJ009797 (LE). SPAIN. **A Coruña:** Sobrado dos Monxes, on unidentified conifer wood, 23 October 2004, *J.A. Díaz s.n.* LOU-Fungi 18717 (LOU). **Cantabria:** Lienares, on *Pinus* wood, 18 November 2004, *G. Carrascosa s.n.* LOU-Fungi 18715 (LOU). **Madrid:** Madrid, Casa de Campo, on unidentified conifer wood, 4 May 1980, *J. Laviada s.n.* MA-Fungi 4360 (MA). **Málaga:** Yunquera, Puerto de Saucillo, in forest of *Pinus halepensis*, *P. pinaster*, *Abies pinsapo*, on wood, 3 December 2003, *A. Gonzalez-Cruz & F. Prieto-García s.n.* JA-CUSSTA 2639 (JA). **Navarra:** Donamaria, on *Fagus sylvatica* wood, 11 July 1999, *J.M. Lekuona s.n.* AJ 61, nrITS HM562042 (MA). **Pontevedra:** Cangas, pine forest on coastal sand dunes, on decayed wood of *Pinus pinaster*, 14 February 2006, *J.C. Alonso s.n.* AJ 210, nrITS KJ009665, *tefl* KJ009800 (LOU). Redondela, on decayed wood of *Pinus pinaster*, 11 November 2001, *J. Rodriguez s.n.* AJ 208, nrITS HM562050, *tefl* KJ009804 (LOU). **Segovia:** Puerto de Los Leones, 23 October 1977, *F.D. Calonge s.n.* MA-Fungi 1685 (MA). **Soria:** Tardelcuende, on burned *Pinus pinaster* wood, 17 October 2002, *Ibon s.n.* VAL-Fungi 1997 (VAL). **Vizcaya:** Laga, on *Pinus* needles, 16 February 1975, *M.T. Tellería s.n.* MA-Fungi 5013 (MA). PORTUGAL. **Minho:** Mata do Camarido, on *Pinus* wood, 29 February 2004, *N. Alonso-Pereira & G.M.G. s.n.* LOU-Fungi 18842 (LOU). SWEDEN. Bondkyrka Uppland, Flogstad (near Upsala), farmyard, on sawdust heap, 14 October 1935, *H.G. Bruun s.n.* LE 9741, nrITS KJ009667, *tefl* KJ009798 (LE).

Pluteus hibbettii Justo, E.F. Malysheva & Bulyonkova, *sp. nov.* Fig. 16
MycoBank 808726

Diagnosis:—Distinguished from *P. pouzarianus* by the narrower basidiospores and geographical distribution, as it is known only from the eastern parts of Eurasia and North America.

Holotype:—UNITED STATES OF AMERICA. Massachusetts: Worcester Co., Harvard Forest, on decayed conifer wood (probably *Tsuga*), 12 October 2012, *M. Nuhn s.n.* AJ 794, nrITS KJ009685, *tefl* KJ009814 (CUW!).

Etymology:—*hibbettii* is dedicated to Dr. David Hibbett.

Pileus 20–55 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, with or without a shallow depression at center; surface smooth or innately radially fibrillose, with or without well-defined squamules at center; brown (7.5YR 4/3–4/6, 5/2–5/4), dark-brown (7.5YR 3/2–3/4) or gray-brown (7.5YR 4/3, 5/2); dry or slightly viscid when moist; margin smooth or slightly translucent-striate. Lamellae crowded, free, ventricose, up to 7 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 35–65 × 4–12 mm, cylindrical, with slightly broad base; surface white, smooth or with longitudinal brown or gray-brown fibrils especially near the base. Context in stipe and pileus white. Smell raphanoid or indistinct. Taste similar to smell. Spore print pinkish brown (2.5YR 7/6–7/8).

Basidiospores [100, 5, 5] (5.5–)6.5–8.5(–9.0) × 4.0–5.5 µm, $avl \times avw = 7.3\text{--}7.6 \times 4.5\text{--}4.7$ µm, $Q = 1.40\text{--}1.85(1.95)$, $avQ = 1.50\text{--}1.65$, ellipsoid to oblong, sometimes ovoid or slightly constricted in the middle. Basidia 14–35 × 5–15 µm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 55–80(–85) × (10–)14–24 µm, fusiform, narrowly fusiform or narrowly utriform with 2–4 apical hooks (usually entire, a few bifid), hyaline, with up to 3 µm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia 35–60(–70) × 12–25 µm, clavate, narrowly clavate or spheropedunculate, very rarely narrowly utriform or cylindrical, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis is a cutis, with

terminal elements $56\text{--}170 \times 8\text{--}17\ \mu\text{m}$, individual elements cylindrical, usually strongly tapering towards apex, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae $5\text{--}25\ \mu\text{m}$ wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae but not at every septum; also observed in other parts of the basidiocarp.

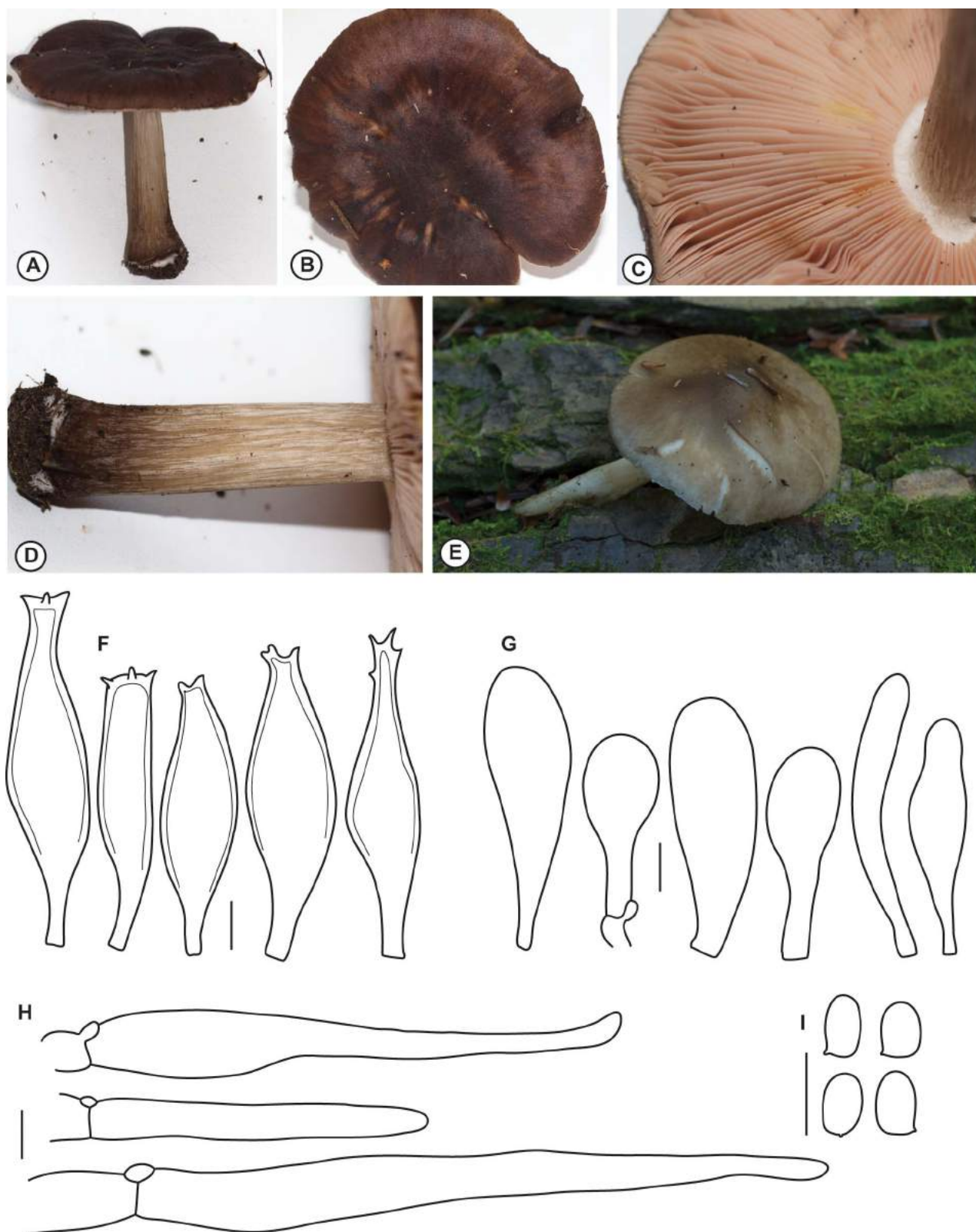


FIGURE 16. *Pluteus hibbettii*. A–D. Collection LE 289426 (photos by T. Bulyonkova). E. Collection Miettinen 17187 (photo by O. Miettinen). F. Pleurocystidia. G. Cheilocystidia. H. Pileipellis. I. Basidiospores. F–I from collection AJ 794. All line drawings by A. Justo. Scale bars = $10\ \mu\text{m}$.

Habit, habitat and phenology:—Solitary or gregarious, growing on well-decayed wood of conifers (e.g. *Pinus*, *Tsuga*). In natural conifer or mixed forests. Recorded in transitional boreal/temperate areas. Fruiting July–August (Siberia) or September–October (Japan and North America).

Distribution:—**Eurasia.** Known from central Siberia (Novosibirsk district) and Japan (Hokkaido). **North America.** Known from eastern North America (Ontario, New York, Massachusetts).

Observations:—The morphological differences between *Pluteus hibbettii* and *P. pouzarianus* are subtle and not always clear-cut. The basidiospores of *P. hibbettii* are slightly more elongated ($avQ = 1.50–1.65$) than in *P. pouzarianus* ($avQ = 1.35–1.52$); the pleurocystidia in *P. hibbettii* rarely exceed 80 μm in length while in *P. pouzarianus* they commonly reach up to 100 μm . In other morphological characters the two taxa are very similar. *P. hibbettii* occurs in the Eastern parts of Eurasia and North America, while *P. pouzarianus* seems to be confined to Western Eurasia.

Pluteus eos has a similar distribution and comes very close to *P. hibbettii* in the molecular analyses. It differs mainly by the comparatively broader basidiospores ($avQ = 1.41–1.45$), the pleurocystidia with compound ornamentation, narrowly clavate or cylindrical cheilocystidia, and in the partially pigmented lamellar edge.

Pluteus spegazzinianus Singer in Singer & Digilio (1952: 221) differs from *P. hibbettii* in the partially pigmented cheilocystidia and the habitat of *Nothofagus* wood. This species is only known from Argentina. *Pluteus similis* Horak (2008: 12) has smaller basidiospores, up to 6.5 μm long, that are less elongated than in *P. hibbettii*. This species is only known from New Zealand.

Additional collections examined:—CANADA. **Ontario:** Nipissing, Algonquin Provincial Park, 29 September 2009, *M. Didukh* & *B. Dentinger* s.n. TRTC 156866, nrITS KJ009684, *tefl* KJ009812 (TRTC). York Region, King Township, Jokers Hill, old-growth forest, on decayed log, 08 October 2007, *M. Didukh* s.n. TRTC 167735, nrITS KJ009686, *tefl* KJ009813 (TRTC). JAPAN. **Hokkaido:** Otaru, conifer forest, on decayed stump, 23 September 2005, *S. Takehashi* s.n. TNSF 12371, nrITS HM562096, *tefl* KJ009816 (TNS). RUSSIA. **Siberian Federal District:** Novosibirsk Region, Novosibirsk District, Akademgorodok, mixed forest (*Pinus sylvestris*, *Betula pendula*) with a lot of shrubs and fallen trees, on decayed wood of *Pinus*, rotten roots, 15 July 2011, *T.M. Bulyonkova* s.n. LE 289426, nrITS KJ009672, *tefl* KJ009811 (LE); *ibid.*, planted mixed forest (*Betula*, *Pinus sylvestris*, *Populus alba*) with lots of dead wood, on decayed wood of *Pinus*, rotten trunk, 23 August 2011, *T.M. Bulyonkova* s.n. LE 289400, nrITS KJ009671, *tefl* KJ009810 (LE). UNITED STATES OF AMERICA. **New York:** Warren Co., Warrensburg, Pack Demonstration Forest, old, dense hemlock forest, on *Tsuga canadensis*, fallen branch on the ground, 24 September 2013, *O. Miettinen* 17193, nrITS KJ009791, *tefl* KJ009815 (H); *ibid.*, on *Tsuga canadensis*, fallen tree crown, 24 September 2013, *O. Miettinen* 17187, nrITS KJ009790, *tefl* KJ009817 (H)

Pluteus eos Justo & E.F. Malysheva, *sp. nov.* Fig. 17
MycoBank 808727

Diagnosis:—Differs from *Pluteus hibbettii* in the pleurocystidia with bifid hooks, partially pigmented lamellar edge and broader basidiospores.

Holotype:—UNITED STATES OF AMERICA. New York: Essex Co., Adirondack Ecological Center, Huntington Wildlife Forest, well decayed conifer wood, 17 August 2012, *A. Justo* 589, nrITS KJ009683, *tefl* KJ009808 (CUW!).

Etymology:—*eos* is the transliteration of “Ἠώς” the name of the Greek goddess of dawn. It is given to this taxon for its distribution in the eastern parts of Eurasia and North America.

Pileus 20–50 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, with or without a shallow depression at center; surface smooth or innately radially fibrillose, with or without well defined squamules at center; dark brown (in the range of 5YR 3/2–3/4, 4/3–4/6) or gray-brown (5YR 4/1–4/2, 3/1); dry or slightly viscid when moist; margin smooth or slightly translucently striate. Lamellae crowded, free, ventricose, up to 8 mm broad, white when young, later pink, with pigmented edges but not uniformly so: dark brown in the 1/2 or 1/3 near the pileus margin and even, or white, flocculose in the part near the stipe. Stipe 30–65 \times 3–15 mm, cylindrical, with slightly broad base; surface white, smooth or with longitudinal brown or gray-brown fibrils, sometimes grouped forming small squamules especially near the base. Context in stipe and pileus white. Smell indistinct. Taste indistinct. Spore print not recorded.

Basidiospores [60, 3, 3] 6.5–9.0 \times 4.5–6.5 μm , $avl \times avw = 7.7–8.2 \times 5.4–5.7 \mu m$, $Q = 1.35–1.60$, $avQ = 1.41–1.45$, ellipsoid, sometimes ovoid or slightly constricted in the middle. Basidia 15–35 (40) \times 5–15 μm , tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 60–80(–100) \times 12–22(–30) μm ,

fusiform, narrowly fusiform or narrowly utriform with 2–4 apical hooks (commonly bifid, but entire hooks also present), rarely with small lateral hooks, hyaline, with up to 4 μm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia 40–70 \times 12–25 μm , narrowly clavate or cylindrical, more rarely clavate or narrowly utriform, hyaline or with evenly dissolved, intracellular, brown pigment, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 85–165 \times 7–17 μm , individual elements cylindrical, usually strongly tapering towards apex, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–25 μm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae but not at every septum; also observed in other parts of the basidiocarp.

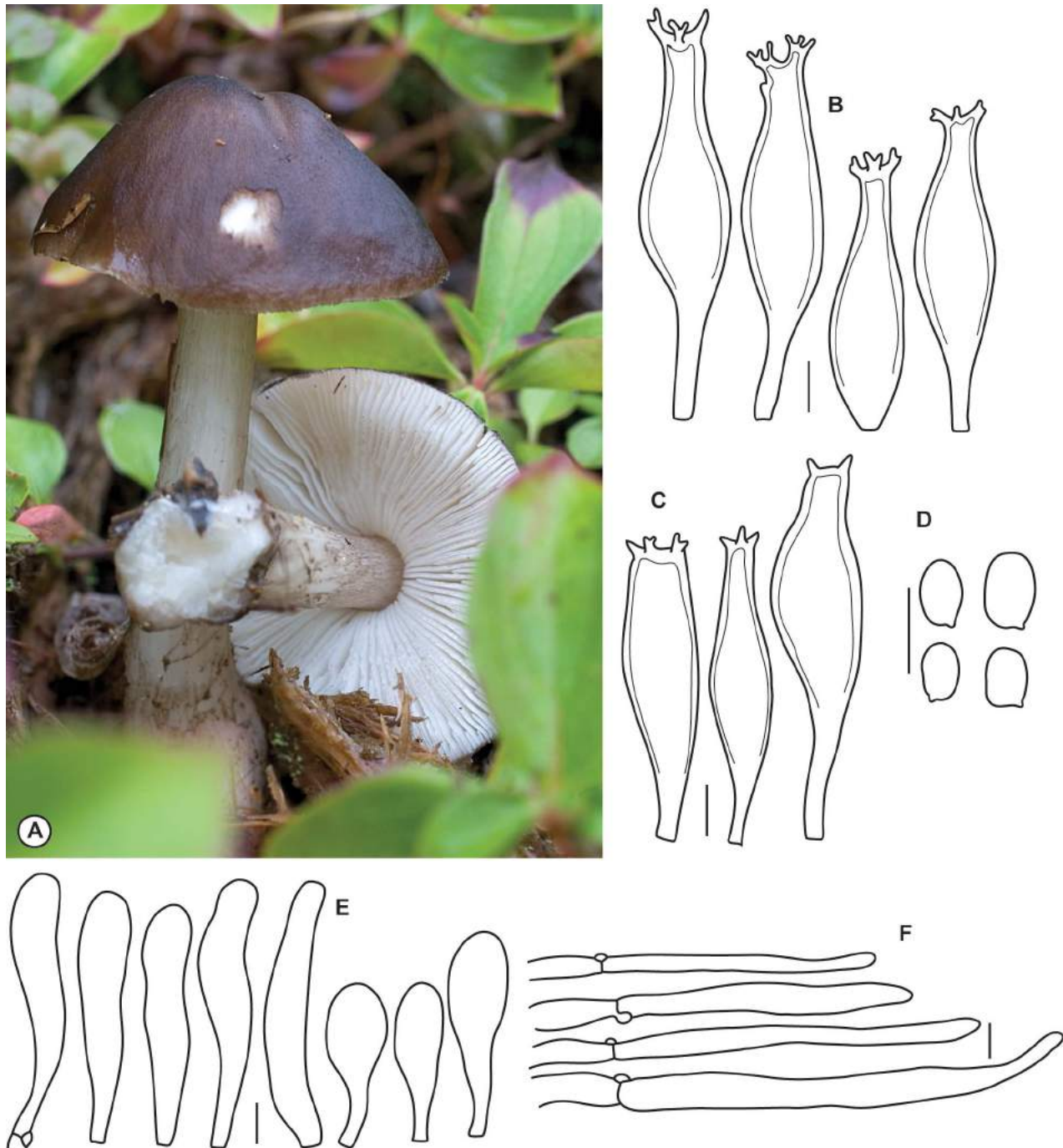


FIGURE 17. *Pluteus eos*. A. Collection 050916-AV12 (photo by Andrus Voitk). B. Pleurocystidia from 050916-AV12. C. Pleurocystidia from AJ 589. D. Basidiospores. E. Cheilocystidia. F. Pileipellis. D–F from collection AJ 589. All line drawings by A. Justo. Scale bars = 10 μm .

Habit, habitat and phenology:—Solitary or gregarious, growing on well-decayed conifer wood (e.g. *Tsuga*). In conifer or mixed forests. Recorded in transitional boreal/temperate or boreal areas. August–September.

Distribution:—**Eurasia.** Known from the Russian Far East (Primorsky Territory **North America.** Known from eastern North America (Newfoundland Island, New York).

Observations:—The combination of pigmented lamellar edges near pileus margin, pleurocystidia with bifid hooks and narrowly clavate to cylindrical cheilocystidia sets *Pluteus eos* apart from the other members of the pouzarianus clade. *Pluteus orestes* also has pigmented cheilocystidia but this species has differently shaped pleurocystidia and it is restricted to mountainous habitats in western North America.

Pluteus spegazzinianus resembles *P. eos* in the partially pigmented lamellar edges and the presence of clamp-connections but it can be separated from *P. eos* in the different ornamentation of the pleurocystidia and the predominantly clavate cheilocystidia (Singer & Digilio 1952). This species is only known from Argentina. *Pluteus microspermus* and *Pluteus concentricus* may resemble *P. eos* in the pigmented lamellar edges but both species have smaller basidiospores (less than 6.5 µm long) and lack clamp-connections (Horak 2008). Both species are only known from New Zealand, where they grow in association with *Nothofagus* wood (Horak 2008).

Additional collections examined:—**CANADA. Newfoundland and Labrador:** Newfoundland Island, Lower Main River, mixed woods, on mossy wood, 06 September 2011, *A. Voitk* MR2-080, nrITS KJ009796 (CUW). Pasadena Ski Trail, mixed woods, on decayed wood, 16 September 2005, *M. Voitk* 050916-AV12, nrITS KJ009795, *tefl* KJ009809 (CUW). **RUSSIA. Far East Federal District:** Primorsky Territory, Kedrovaya Pad Nature Reserve, Valley of Kedrovaya River, floodplain broadleaf forest, on decayed wood, 05 September 2011, *T.Yu. Svetasheva s.n.* LE 289379, nrITS KJ009675, *tefl* KJ009807 (LE).

Pluteus parilis nom. prov.

Etymology:—*parilis* means ‘similar’ because of the close resemblance to other species in this complex.
Description based on the collection UC1998533

Pileus 40–50 mm in diameter, applanate with low umbo, and deflexed margin; surface smooth to innately fibrillose, distinctly fibrillose at umbo, brown; margin slightly translucently striate, and irregular. Lamellae free, crowded, ventricose, pink with age, with white lamellar edge. Stipe 80–90 × 7–10 mm, distinctly widening downwards up to 12 mm, solid, white, with a few brown fibrils in lower half, but overall impression white. Smell slightly raphanoid. Basidiospores [20, 1, 1] 8.0–9.8 × 4.9–6.4 µm, avl × avw = 8.9 × 5.6 µm, Q = 1.4–1.9, avQ = 1.6, ellipsoid to oblong. Basidia 23–30 × 8.5–10 µm, tetrasterigmate, cylindrical, slightly constricted in the middle. Pleurocystidia abundant, 60–80 × 15–20 µm, fusiform, with thick walls in upper part, and 3 to 4 prominent to small hooks. Intermediate cystidia irregularly shaped, with 1, rarely 2 hooks, thinner walled than pleurocystidia. Lamellar edge sterile; cheilocystidia 36–75 × 13–20 µm, narrowly clavate, rarely narrowly utriform, thin-walled, hyaline. Pileipellis a cutis of cylindrical hyphae around 10 µm in diam.; terminal elements with rounded or slightly tapered at apex, with brown intracellular pigment. Clamp connections present in pileipellis, at most septa, also present in other parts of the basidiocarp.

Habit, habitat and phenology:—In small groups of 2 or 3 specimens, on wood in various mixed conifer or conifer-hardwood forests, up to an elevation of 1500 m. January on the coast, and June in the mountains.

Distribution. North America:—Known from two locations in California.

Observations:—The above description is based on one collection (UC1998533) from coastal northern California. The second collection (UC19987410, from Yosemite National Park) differs in the very pale gray colours of the basidiocarps, the pleurocystidia with small hooks in one basidiocarp, and well-developed hooks on the pleurocystidia of the second basidiocarp, and the smaller and broader basidiospores ([20, 1, 1] 7.3–8.8 × 5.4–6.9 µm, avl × avw = 8.0 × 6.0 µm, Q = 1.25–1.45, avQ = 1.34).

Because of these discrepancies in macroscopic and microscopic characters we refrain from formally describing *P. parilis* as a new taxon. We feel it is important to include this species here, even if only provisionally named, to facilitate future collections of this possibly endemic and rare taxon. More collections are needed to comprehensively circumscribe this species, and to distinguish it from other species with clamp-connections occurring in western North America.

Collections examined:—**UNITED STATES OF AMERICA. California:** Mendocino Co., Jackson State Demonstration Forest, 11 mi. east of Fort Bragg, 28 January 2012, *H. Smith s.n.* UC 1998533, nrITS JX857448 (UC). Tuolumne Co., Yosemite National Park, West Gate Parking along Hwy 120, 5 June 2010, *D. Smith s.n.* UC 19987410, nrITS JX857471 *tefl* KJ460257 (UC).

Diagnosis:—A rather pale brown to pale gray or white species, with clamp-connections in the pileipellis, relatively large basidiospores, and pleurocystidia with short and indistinct hooks. The relatively large basidiospores set it apart from similar taxa in the pouzarianus clade (*P. eos*, *P. hibbettii*).

Holotype:—UNITED STATES OF AMERICA. California: Tuolumne Co., Yosemite National Park, Carlon Meadow Road, 3 June 2010, *R. Pastorino s.n.* UC 1861122, nrITS JX857467 (UC!).

Etymology:—*orestes*, from the Greek “ορέστης” meaning “mountaineer, mountain hiker”. It is given to this species for its distribution in the mountain ranges of Western North America.

Pileus 45–90 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, with or without a shallow depression at center; surface smooth or innately radially fibrillose, usually with well-defined squamules at least around center; white or very pale grayish or grayish brown (10YR 7/1–7/3, 8/1–8/3), sometimes darker at center, more rarely brown all over (7.5YR 5/3–5/8, 6/3–6/8); dry or slightly viscid when moist; margin smooth or slightly translucent-striate. Lamellae crowded, free, ventricose, up to 12 mm broad, white when young, later pink; edges white and flocculose all over or pigmented dark brown near pileus margin. Stipe 60–110 × 8–20 mm, cylindrical, with equal or slightly narrowed base; surface white, sometimes with longitudinal brown or gray-brown fibrils, grouped forming small squamules. Context in stipe and pileus white. Smell indistinct or faintly raphanoid. Taste indistinct. Spore print pinkish brown (2.5YR 7/6–7/8).

Basidiospores [100, 5, 5] 8.0–10.5(–11.0) × 5.5–8.0 µm, $av_l \times av_w = 9.0\text{--}9.9 \times 6.0\text{--}7.3$ µm, $Q = 1.23\text{--}1.65$, $avQ = 1.35\text{--}1.51$, ellipsoid or broadly ellipsoid, more rarely oblong, some ovoid or slightly constricted in the middle. Basidia 15–35(–39) × 5–15 µm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 73–114(–123) × 17–30 µm, fusiform or narrowly fusiform with 2–3 short apical hooks (entire and not very prominent), or utriform to narrowly utriform with only one apical hook, hyaline, with up to 2 µm thick wall, frequent all over lamellar faces. Intermediate cystidia predominantly narrowly utriform and without apical hooks, a few similar to pleurocystidia. Lamellar edge sterile. Cheilocystidia 45–110(–145) × 14–24 µm, narrowly clavate or cylindrical, more rarely clavate or narrowly utriform, hyaline or with evenly dissolved, intracellular, brown pigment, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 93–205(–250) × 9–17 µm; individual elements cylindrical, usually strongly tapering towards apex, hyaline or filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–25 µm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae but not at every septum; also observed in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary or in pairs, growing on decayed conifer wood, more rarely on conifer litter. In conifer or mixed forests. Recorded only from mountain areas. May–October.

Distribution:—**North America.** Known only from western North America: Yosemite National Park (California), Mount Shasta area (California), Mount Ashland (Oregon) and Gifford Pinchot National Forest (Washington), at elevation of 1200–2400 m.

Observations:—*Pluteus orestes* is a white to pale gray or pale brown species growing on conifer wood in the mountains of western North America. It can be recognized by the presence of clamp-connections, the relatively large and broad basidiospores and the pleurocystidia with short hooks.

Pluteus velutinornatus Stevenson (1962: 69) may also present pleurocystidia with short and not very distinct hooks but it differs from *P. orestes* in the dark brown, fibrillose/squamulose pileus; the smaller basidiospores (up to 8 µm long) and the predominantly clavate and shorter (up to 70 µm long) cheilocystidia. This species is endemic to New Zealand (Horak 2008).

Additional collections examined:—UNITED STATES OF AMERICA. **California:** Siskiyou Co., c. 13 miles east of McCloud, near Algoma Campground, mixed conifer forest, on rotten wood, 26 May 2012, *T. Chesney s.n.* UC 1998688, nrITS JX857456 (UC); Siskoyou Co., Mount Shasta, Trout Creek Butte, in mixed conifer forest, 28 May 2012, *C.F. Schwarz s.n.* UC 1998687, nrITS JX857455 (UC); Tuolumne Co., Yosemite National Park, Crane Flat, mixed conifer forest, on wood, 30 September 2011, *D. Rust s.n.* UC 1998602, nrITS JX857469 (UC); *ibid.*, on conifer wood, 16 September 2011, *D. Rust s.n.* UC 1998591, nrITS JX857470, *tefl* KJ460256 (UC); Tuolumne Co., Yosemite National Park, Glacier Point Road, mixed conifer forest, on conifer wood, 29 October 2011, *E.C. Vellinga s.n.* UC 1861044, nrITS JX857466 (UC). **Oregon:** Jackson Co., Mt. Ashland, on conifer stump, 19

October 2011, *R. Pastorino* MO80923, nrITS KJ009673, *tef1* KJ009825 (CUW). **Washington:** Southeastern Gifford Pinchot National Forest, 19 June 2010, *S. Krstic* MO93766, nrITS KJ009674 (CUW).

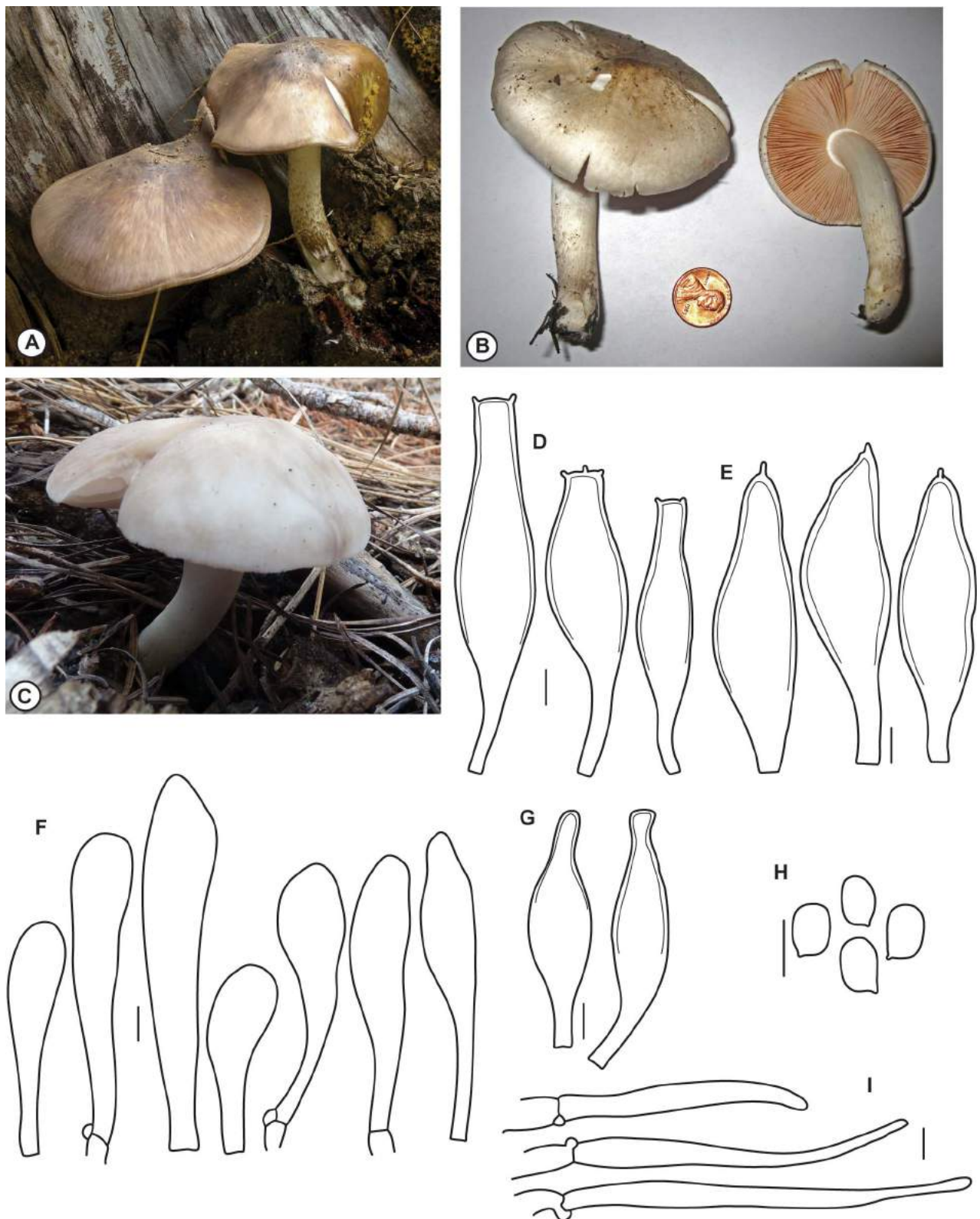


FIGURE 18. *Pluteus orestes*. A. Collection MO 80923 (photo by R. Pastorino). B. Collection MO 93766 (photo by S. Krstic). C. Collection UC 1998591 (photo by D. Rust). D. Pleurocystidia from MO 80923. E. Pleurocystidia from MO 93766. F. Cheilocystidia. G. Intermediate cystidia. H. Basidiospores. I. Pileipellis. F–I from collection MO 80923. All line drawings by A. Justo. Scale bars = 10 μ m.

Pluteus primus Bonnard (1991: 169). Fig. 19

Holotype:—SWITZERLAND. Canton Vaud, Jorat, on rotting conifer wood, JB 87/121, nrITS KJ009679 (LAU!).

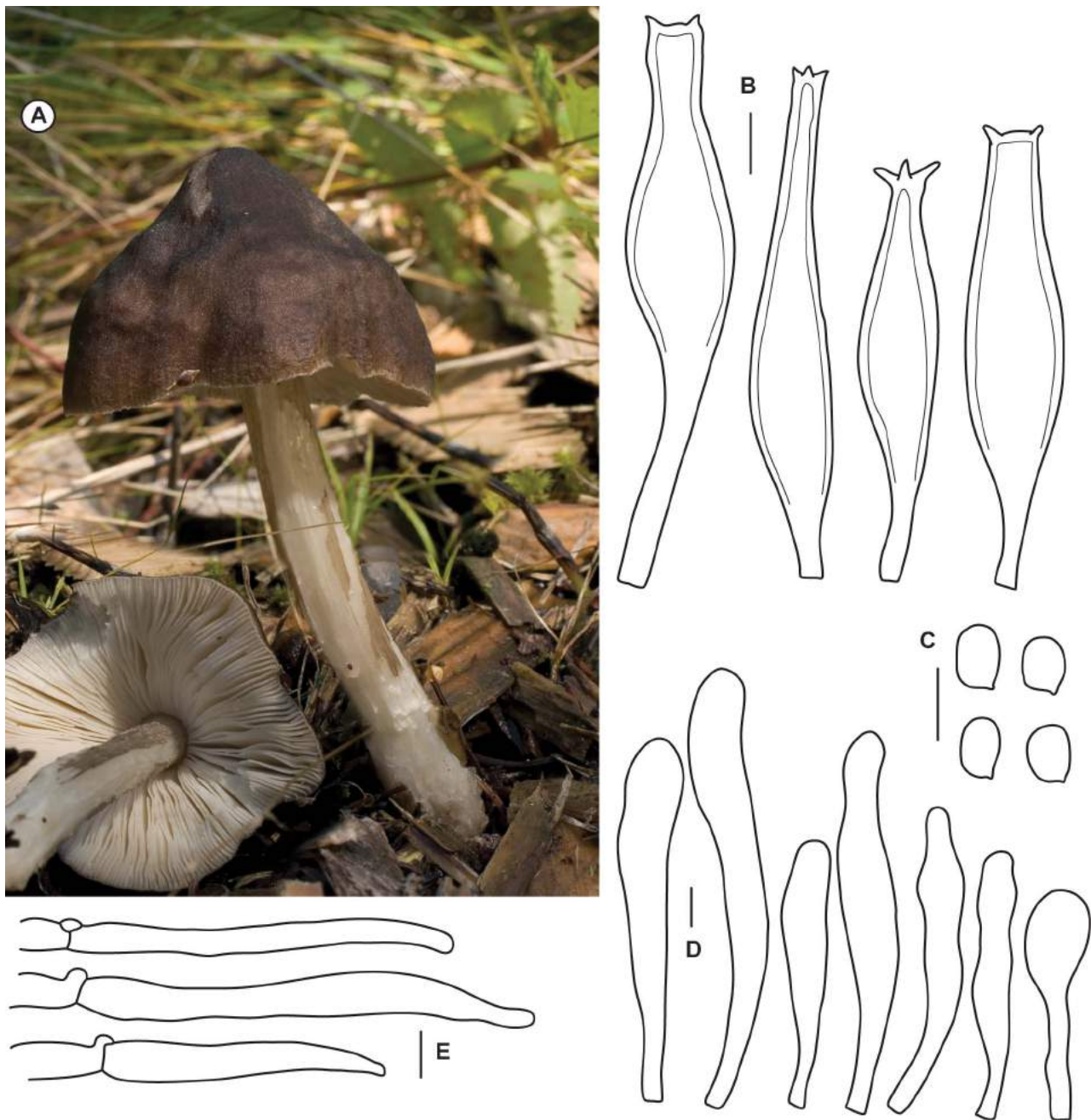


FIGURE 19. *Pluteus primus*. A. Collection 060816-AV13 (photo by Andrus Voitk). B. Pleurocystidia. C. Basidiospores. D. Cheilocystidia. E. Pileipellis. B–E from collection 060816-AV13. All line drawings by A. Justo. Scale bars = 10 μ m.

Pileus 35–100(–120) mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, with or without a shallow depression at center; surface smooth or innately radially fibrillose, with or without well-defined squamules at center; brown (7.5YR 4/2–4/6, 5/3–5/8) or gray-brown (7.5YR 4/1, 5/1–5/2), occasionally pure white; dry or slightly viscid when moist; margin smooth or slightly translucent-striate. Lamellae crowded, free, ventricose, up to 12(–15) mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 35–130(–170) \times 4–20 mm, cylindrical, with slightly broad base; surface white, smooth or with longitudinal brown or gray-brown fibrils. Context in stipe and pileus white. Smell raphanoid or rarely indistinct. Taste similar to smell. Spore print pinkish brown (2.5YR 7/6–7/8).

Basidiospores [100, 5, 5] 7.0–9.5(–10.0) \times (4.5–)5.0–7.0 μ m, avl \times avw = 7.8–8.4 \times 5.6–6.3 μ m, Q = 1.25–1.60,

avQ = 1.33–1.43, ellipsoid or broadly ellipsoid, sometimes ovoid or slightly constricted in the middle. Basidia 15–35 × 7–12 µm, tetrasterigmate, clavate, some with median constriction. According to Bonnard (1991) bisterigmate basidia also present. Pleurocystidia metuloid, 70–115(–130) × 15–25 µm, fusiform, narrowly fusiform or narrowly utriform with 2–4 apical hooks (usually entire, sometimes small and indistinct), hyaline, with up to 4 µm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices, without a predominant morphological type. Lamellar edge sterile. Cheilocystidia 55–120(–200) × 8–25(–30) µm, narrowly clavate or cylindrical, more rarely clavate or narrowly utriform, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 60–125 × 6–20 µm, individual elements cylindrical, some strongly tapering towards apex, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–25 µm wide, cylindrical, hyaline or with brown pigment, with thin, smooth walls. Clamp-connections observed at every septum on pileipellis hyphae and also present in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary or gregarious, growing on well-decayed wood of conifers (*Abies*, *Picea*, *Pseudotsuga*). Also recorded on conifer sawdust, woodchip piles or on the litter layer under conifers. One collection recorded as growing on a *Fagus* stump (REG 13620). In natural conifer or mixed forests, also in conifer plantations. Recorded in temperate and boreal areas. Found year round.

Distribution:—**Eurasia.** Widespread but rare in Europe (Switzerland, Germany, Caucasus). **North America.** Recorded from Newfoundland Island and California.

Observations:—*Pluteus primus* is mostly characterized by the narrowly clavate or cylindrical cheilocystidia up to 120 (–200) µm long and the pileipellis hyphae with clamp-connections at all septa.

Additional collections examined:—**CANADA. Newfoundland and Labrador:** Newfoundland Island, Gros Morne National Park, Western Brook Pond, mixed woods, on decayed wood, 17 August 2004, *A. Voitk 04-08-17-AV02*, nrITS KJ009780, *tefl* KJ009824 (CUW). Newfoundland Island, Pasadena Ski Trail, mixed woods, on wood chips, 16 August 2006, *A. Voitk 06-08-16-AV13*, nrITS KJ009781, *tefl* KJ009823 (CUW). **GERMANY. Bavaria:** Pienhofen, on *Fagus* stump, 18 October 1999, *B. Mende s.n. REG 13620*, nrITS HM562167, *tefl* KJ009821 (REG). Viergstetten, on bark mulch, *REG 13683*, nrITS HM562156, *tefl* KJ009822 (REG). **RUSSIA. North Caucasian Federal District:** Arkhyz Site of Teberdinsky Nature Reserve, near Kizgych river, mixed forest (*Abies*, *Fagus*), on decayed wood, 20 August 2009, *O.V. Morozova s.n. LE 289390*, nrITS KJ009680, *tefl* KJ009818 (LE); *ibid.*, mixed forest (*Picea*, *Abies*, *Fagus*), on decayed wood of deciduous tree, 18 August 2009, *E.F. Malysheva s.n. LE 289388*, nrITS KJ009682, *tefl* KJ009820 (LE). Teberdinsky Nature Reserve, Dzhemagat canyon, pine forest, on decayed wood of conifer tree, 15 August 2009, *A.E. Kovalenko s.n. LE 289389*, nrITS KJ009681, *tefl* KJ009819 (LE). **UNITED STATES OF AMERICA. California:** Alameda Co., Berkeley, Euclid Avenue near Oak Street, on wood chips, 11 March 2011, *E.C. Vellinga s.n. UC 1998686*, nrITS JX857454, *tefl* KJ460254 (UC). Marin Co., Point Reyes National Seashore, Estero Trail, *Pinus radiata* plantation, on soil, 28 January 2006, *E.C. Vellinga s.n. UC 1859500*, nrITS KF306026 (UC). Marin Co., Mt. Tamalpais, Bolinas-Fairfax Rd., near Alpine Lake along Kentlake pump road, mixed forest with *Pseudotsuga menziesii*, *Notholithocarpus densiflorus*, *Sequoia sempervirens*, *Arbutus* sp., 30 November 2011, *T.D. Bruns s.n. UC 1861233*, nrITS JX857447 (UC).

Pluteus methvenii Minnis & Justo, *sp. nov.* Fig. 20
Mycobank 808729

Diagnosis:—Differs from *Pluteus primus* in the shorter and predominantly clavate to narrowly clavate cheilocystidia.

Holotype:—UNITED STATES OF AMERICA. North Carolina: Yancey Co., Mount Mitchell (peak), spruce-fir forest, on log of red spruce (*Picea rubens*), 23 September 2011, *A.S. Methven PNC1*, nrITS KJ009689, *tefl* KJ009826 (BPI!).

Etymology:—*methvenii*, is dedicated to Dr. Andrew Scott Methven, collector of the holotype.

Pileus 28–60 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, with or without a shallow depression at center; surface smooth, innately radially fibrillose, or with conspicuous superficial radial fibrils, with or without well-defined squamules at center; brown (7.5YR 4/2–4/6, 5/3–5/8) or dark-brown (7.5YR 3/3, 3/4); dry or slightly viscid when moist; margin smooth or slightly translucently striate. Lamellae crowded, free, ventricose, up to 8 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 35–130(–170) × 3–20 mm, cylindrical, with slightly broad base; surface white, smooth or with longitudinal brown or gray-brown fibrils. Context in stipe and pileus white. Smell not recorded. Taste not recorded. Spore print not recorded.



FIGURE 20. *Pluteus methvenii*. A. Collection 090626-AV04 (photo by Andrus Voitk). B. Collection 060916 (photo by R. Smith). C. Collection TN5-029 (photo by R. Smith). D. Basidiospores. E. Pleurocystidia. F. Cheilocystidia. G. Pileipellis. D–G from collection 090626-AV04. All line drawings by A. Justo. Scale bars = 10 μ m.

Basidiospores [80, 4, 4] 7.0–9.5 \times 5.0–7.0 μ m, avl \times avw = 7.1–8.9 \times 5.3–5.9 μ m, Q = 1.20–1.60(–1.80), avQ = 1.33–1.50, ellipsoid or broadly ellipsoid, rarely oblong, sometimes ovoid or slightly constricted in the middle. Basidia 12–35 \times 7–15 μ m, tetrasporangiate, clavate, some with median constriction. Pleurocystidia metuloid, 60–100 \times 12–26 μ m, fusiform, narrowly fusiform or narrowly utriform, with 2–4 apical hooks (usually entire),

hyaline, with up to 3 µm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia 40–85 × 10–20 µm, clavate, narrowly clavate or cylindrical, more rarely narrowly utriform, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 70–195(–270) × 8–17 µm: individual elements cylindrical, some strongly tapering towards apex, some capitate or subcapitate, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–25 µm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae, but not at every septum; also present in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary or in pairs, growing on well-decayed wood of conifers (e.g. *Abies*, *Picea*). In conifer or mixed forests. Recorded from subtropical (Louisiana), temperate and boreal areas. September–November.

Distribution:—**North America.** Known only from eastern North America (Newfoundland Island, North Carolina, Louisiana).

Observations:—*Pluteus methvenii* comes very close to *Pluteus primus* and mainly differs in the shape of the cheilocystidia (clavate to narrowly clavate) and their length (up to 85 µm long). Similar species occurring in Eastern North America include *P. hibbettii*, with comparatively smaller and narrower basidiospores and *P. eos*, with compound ornamentation on the pleurocystidia and pigmented cheilocystidia close to the pileus edge.

Pluteus squamosopunctus Horak (1964: 169) differs from *P. methvenii* in the abundant pyramidal squamules on pileus, the pigmented lamellar edges, the smaller basidiospores (up to 7 µm long), and the smaller cheilocystidia (up to 52 µm long). *Pluteus raphanioidorus* Horak (1964: 173) differs in the pigmented lamellar edges, the smaller basidiospores (up to 5.6 µm long) and the growth on angiosperm (*Nothofagus*) wood. Both species are only known from Argentina (Horak 1964).

Additional collections examined:—CANADA. **Newfoundland and Labrador:** Newfoundland Island, Castle Hill National Historic Site, conifer forest, on decayed wood of *Abies balsamea*, 16 September 2006, *A. Voitek s.n.* 2006-Sept-16, nrITS KJ009794 (CUW). Newfoundland Island, Pasadena Ski Trails, mixed woods, on decayed wood, 26 September 2009, *A. Voitek* 090926-AV04, nrITS KJ009793, *tef1* KJ009829 (CUW). Newfoundland Island, Salmonier Nature Park, conifer forest, on decayed wood, 13 September 2006, *S. Knight* 06-13-09, nrITS KJ009783, *tef1* KJ009827 (CUW). Newfoundland Island, town of Terra Nova, mixed woods, on conifer wood, 10 September 2011, *G. Bishop* TN5-029, nrITS KJ009792, *tef1* KJ009828 (CUW). UNITED STATES OF AMERICA. **Louisiana:** Lafayette area, Moore foray location, Nov-2009, *NAMA Foray s.n.* PLA1, nrITS KJ009688 (BPI).

III. *brunneidiscus* clade. Fig. 4

Species growing mostly on angiosperm wood or on the humus layer without apparent connection to wood; more rarely on conifer wood. Clamp-connections common and easy to spot on pileipellis hyphae.

Pluteus brunneidiscus Murrill (1917: 131). Fig. 21

Holotype:—UNITED STATES OF AMERICA. Connecticut: Fairfield Co., Redding, on mossy log, 20 July 1902, *F.S. Earle* 524 (NY!).

Synonym: *Pluteus washingtonensis* Murrill (1917: 135). Holotype:—UNITED STATES OF AMERICA. Washington: King Co., Seattle, on decayed wood, 20 October–1 November 1911, *W.A. Murrill* 348 (NY!).

Pileus 30–60 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low broad umbo; surface smooth or innately radially fibrillose, with or without well-defined squamules at center; brown (7.5YR 5/2–5/8, 4/3–4/6) or gray-brown (7.5YR 5/1, 4/1–4/2), or pure white, dry or slightly viscid when moist; margin smooth or slightly translucent-striate. Lamellae crowded, free, ventricose, up to 7 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 30–70 × 3–6 mm, cylindrical, with slightly broad base; surface white, smooth or with longitudinal brown or gray-brown fibrils, especially near the base. Context in stipe and pileus white. Smell raphanoid. Taste similar to smell or indistinct. Spore print pink to pinkish brown.



FIGURE 21. *Pluteus brunneidiscus*. A. Collection BPI 884087 (photo by A. Minnis). B. Pleurocystidia. C. Basidiospores. D. Pileipellis. E. Cheilocystidia. B–E from collection AJ586. All line drawings by A. Justo. Scale bars = 10 µm.

Basidiospores [100, 4, 4] $6.5\text{--}9.6(-10.5) \times (4.5\text{--})5.0\text{--}7.1$ µm, $avl \times avw = 7.1\text{--}8.1 \times 5.1\text{--}6.2$ µm, $Q = 1.18\text{--}1.59$, $avQ = 1.30\text{--}1.45$, ellipsoid or broadly ellipsoid, sometimes ovoid or slightly constricted in the middle. Basidia $15\text{--}28 \times 6\text{--}12$ µm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, $50\text{--}100 \times 12\text{--}24(-30)$ µm, fusiform or narrowly fusiform or narrowly utriform with 2–4 apical hooks (usually entire, sometimes rounded and poorly developed), rarely with small lateral hooks, hyaline, with up to 3 µm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia $30\text{--}68 \times 12\text{--}22$ µm, clavate, narrowly clavate or spheropedunculate, more rarely narrowly utriform, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements $80\text{--}146 \times 8\text{--}15$ µm; individual elements cylindrical, some strongly tapering towards apex, a few with small lateral outgrowths, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae $5\text{--}25$ µm wide, cylindrical, hyaline or with brown

intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae but not at every septum; also observed in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary or gregarious, growing on decayed wood of hardwoods (*Betula*, *Umbellularia*, *Populus*) or on the humus layer under hardwoods or conifers. Mostly in temperate or transitional mixed forests. June–September, except in California (November–January).

Distribution:—**Eurasia.** Widespread but rare, known from the Russian Northwest and Siberia. **North America.** Widespread but rare, known from both the Western (California, Idaho, Washington, British Columbia) and Eastern parts (Connecticut, New York).

Observations:—Murrill (1917) described simultaneously *Pluteus brunneidiscus* from Eastern North America (Connecticut, USA) and *Pluteus washingtonensis* from the West Coast (Washington, USA). Examination of the type collections did not reveal significant differences between these taxa and therefore both were considered synonymous and the name *P. brunneidiscus* was chosen (Justo & Castro 2007a). The collections here studied fit the original descriptions of Murrill and the observations made on the types, and span the geographical range of both taxa, therefore we choose to use the name *Pluteus brunneidiscus* for this taxon, instead of describing it as a new species.

The name *Pluteus subcervinus* (Berkeley & Broome) Saccardo (1887: 666) was originally considered for some of these collections. This species was described from Sri Lanka (Berkeley & Broome 1871: 531), and the type collection is preserved at Kew; see Pegler (1986) and Justo & Castro (2007a) for type studies. The Indian collection of *Pluteus subcervinus* described in Pradeep *et al.* (2002) was sampled for molecular data (nrITS KJ009752; *tefl* KJ010010) and molecularly is quite different from all Holarctic species of section *Pluteus*. In a more inclusive analysis, with (sub)tropical and Southern Hemisphere representatives of section *Pluteus*, this species usually appears as sister to all taxa in the salicinus clade but with no strong statistical support (data not shown).

Additional collections examined:—CANADA. **British Columbia:** Hermit Bay, 26 June 1957, *D. Stuntz* 9948, nrITS KJ009690 (WTU). RUSSIA. **Northwestern Federal District:** Vologda Region, Kirillovsky District, National Park Russian North, vicinities of Sigovo, *Populus* forest, on buried wood, 21 June 2004, *O.S. Kirillova s.n.* LE 235301, nrITS KJ009691, *tefl* KJ009831 (LE). **Siberian Federal District:** Novosibirsk Region, Novosibirsk District, Akademgorodok, clearing in planted *Pinus sylvestris* and *Betula pendula* forest overgrown with weeds, on rotting trunk of *Betula*, 09 August 2011, *T.M. Bulyonkova s.n.* LE 289397, nrITS KJ009693, *tefl* KJ009832 (LE). Tomsk Akademgorodok, mixed forest (*Pinus*, *Populus*, *Betula*), on soil, 10 September 2010, *N.N. Agafonova s.n.* LE 262801, nrITS KJ009692 (LE). Vicinities of Krasnoyarsk, on decayed wood, 04 August 1961, *Peglyanova s.n.* LE 9721, nrITS KJ009695, *tefl* KJ009833 (LE). UNITED STATES OF AMERICA. **California:** Marin Co., Point Reyes National Seashore, 27 December 2011, *unknown collector* UC 1861130, nrITS JX857445, *tefl* KJ460253 (UC); *ibid.*, along the Old Pine Trail, mature *Pseudotsuga menziesii* forest with mixed hardwoods, on soil, 10 December 2005, *E.C. Vellinga s.n.* UC 1859657, nrITS KF306025 (UC); *ibid.*, Olema Trail, woods, on leaf litter under *Umbellularia californica*, 10 December 2005, *E.C. Vellinga s.n.* UC 1859655, nrITS KF306024 (UC); *ibid.*, on log of *Umbellularia californica*, 11 November 2012, *D. Klein s.n.* UC 1999290, nrITS KF306006 (UC); *ibid.*, Bear Valley Trail from the visitor's center to the start of the forest, open grassy meadow with *Quercus sp.* and *Pseudotsuga menziesii*, 07 January 2012, *D.B. Viess s.n.* UC 1861127, nrITS KF306002 (UC). San Mateo Co., San Francisco Watershed, on log, 21 January 1979, *San Francisco Mycological Society*, *H.D. Thiers* 39341, nrITS HM562068 (ILLS). **Idaho:** near McCall, on needle duff, 04 September 2008, *S. Campbell & A. Parker s.n.* BPI 884087, nrITS HM562217 (BPI). **New York:** Essex Co., Adirondack Ecological Center, Huntington Wildlife Forest, mixed forest, on decayed wood, 18 August 2012, *A. Justo* 586, nrITS KJ009694, *tefl* KJ009834 (CUW).

Pluteus shikae Justo & E.F. Malysheva, *sp. nov.* Fig. 22
Mycobank 808730

Diagnosis:—Distinct from *P. brunneidiscus* in the slightly shorter and narrower basidiospores.

Holotype:—JAPAN. Hokkaido: Sapporo, on decayed wood, 15 September 2003, *S. Takehashi s.n.* TNS-F 12349, nrITS HM562093, *tefl* KJ009837 (TNS!).

Etymology:—*shikae* comes from *shika* (鹿), the Japanese word for “deer”. It is given to this taxon for its morphological similarity with other “deer” mushrooms and the distribution in Japan.

Pileus 20–50 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo; surface smooth or innately radially fibrillose, with or without well defined

squamules at center; brown (7.5YR 4/2–4/6, 5/2–5/8); dry or slightly viscid when moist; margin smooth or slightly translucently striate. Lamellae crowded, free, ventricose, up to 6 mm broad, white when young, later pink, with even, or white, flocculose edges, very rarely with pale brown edges near pileus margin. Stipe 30–65(–70) × 3–6 mm, cylindrical, with slightly broad base; surface white, smooth or with longitudinal brown or gray-brown fibrils especially near the base. Context in stipe and pileus white. Smell not recorded. Taste not recorded. Spore print not recorded.

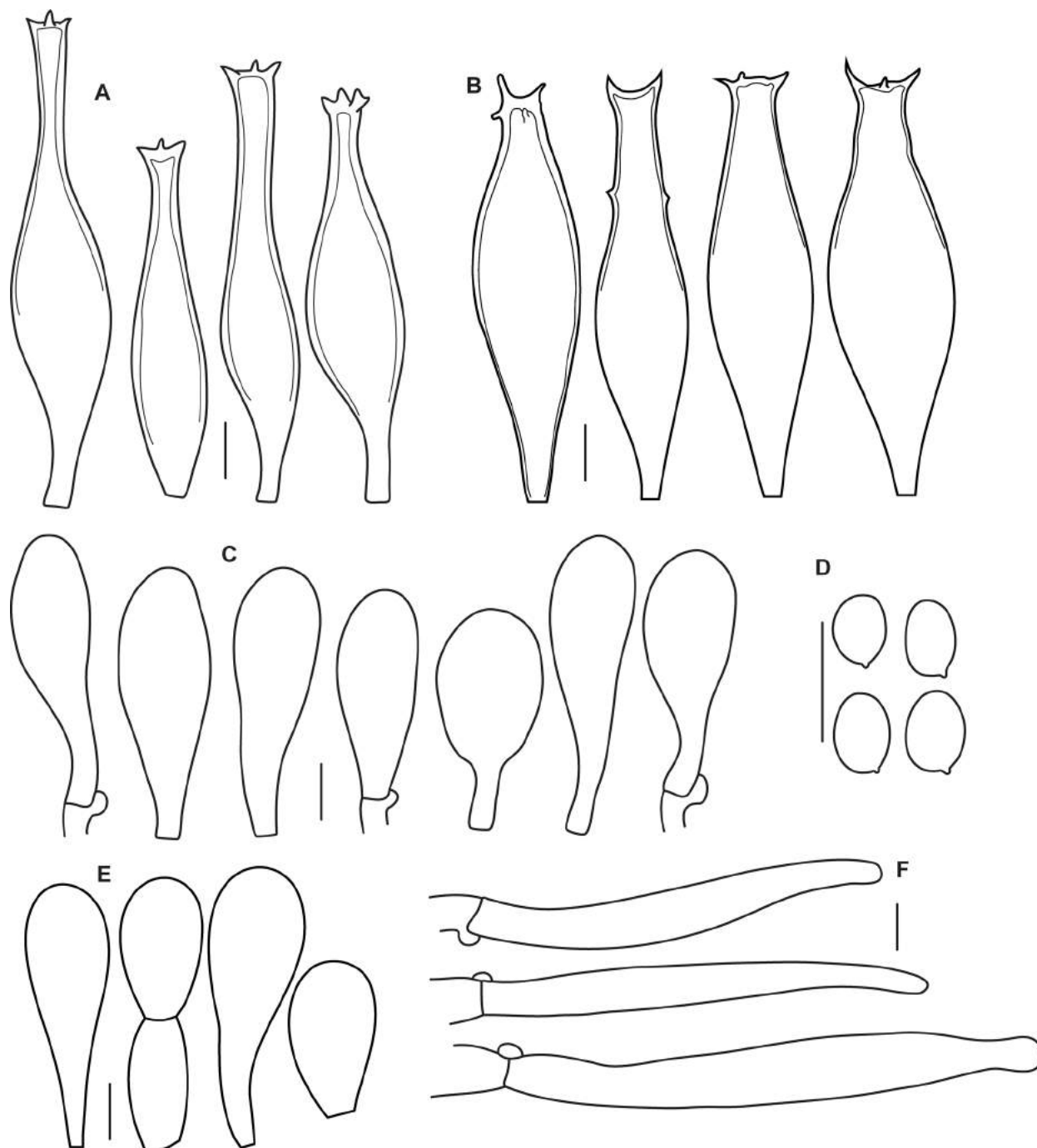


FIGURE 22. *Pluteus shikae*. A. Pleurocystidia from *TNS-F 12349*. B. Pleurocystidia from *LE 289383*. C. Cheilocystidia from *TNS-F 12349*. D. Basidiospores from *TNS-F 12349*. E. Cheilocystidia from *LE 289383*. F. Pileipellis from *TNS-F 12349*. All line drawings from *TNS-F 12349* by A. Justo. All line drawings from *LE 289383* by E. Malysheva. Scale bars = 10 µm.

Basidiospores [80, 4, 4] 5.5–8.0 × (3.5–)4.0–5.5(–6.0) µm, avl × avw = 6.5–7.1 × 4.4–5.0 µm, Q = 1.34–1.70, avQ = 1.42–1.56, ellipsoid to oblong, sometimes ovoid or slightly constricted in the middle. Basidia 18–27 × 6–10

µm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 60–97 × 12–22(–29) µm, fusiform, narrowly fusiform or narrowly utriform with 2–4 apical hooks (usually entire, a few bifid), sometimes with small lateral hooks, hyaline, with up to 3 µm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia (27–)34–55 (65) × 12–20(–29) µm, clavate or narrowly clavate, more rarely narrowly utriform or cylindrical, hyaline, very few with intracellular brown pigment and/or incrusting parietal pigment, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 90–150 × 7–17 µm, individual elements cylindrical, usually strongly tapering towards apex, a few subcapitate, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–20 µm wide, cylindrical, hyaline or with brown pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae but not at every septum; also observed in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary or subgregarious, growing on well-decayed wood of hardwoods (*Quercus*). In hardwood-dominated or mixed forests. June–September.

Distribution:—**Eurasia.** Known from northern Japan (Hokkaido) and the Russian Far East (Primorsky Territory).

Observations:—Based on molecular data *P. shikae* is a separate taxon from *P. brunneidiscus* but morphologically it is hard to distinguish them. *P. shikae* has slightly shorter and narrower basidiospores ($avl \times avw = 6.5\text{--}7.1 \times 4.4\text{--}5.0$ µm; $avQ = 1.42\text{--}1.56$) than *P. brunneidiscus* ($avl \times avw = 7.1\text{--}8.1 \times 5.1\text{--}6.2$ µm, $avQ = 1.30\text{--}1.45$). The ecological preferences and full geographical distribution of both taxa are still in need of further study to determine whether they are of any value in species delimitation.

Pluteus microspermus and *Pluteus concentricus* have only slightly shorter basidiospores than *P. shikae*, up to 6.0 and 6.5 µm respectively, but both taxa differ from *P. shikae* in the pigmented lamellar edges and the absence of clamp-connections (Horak 2008). Both species are only known from New Zealand (Horak 2008).

Additional collections examined:—**JAPAN. Hokkaido:** Ebetsu, Nopporo, mixed forest, on decayed wood, 01 June 2005, *S. Takehashi s.n. TNS-F 12356*, nrITS HM562097, *tef1* KJ009839 (TNS). Kuromatunai-cho, deciduous forest, on decayed wood, 20 June 2006, *S. Takehashi s.n. TNS-F 12360*, nrITS HM562095, *tef1* KJ009838 (TNS). Sapporo, mixed forest, on decayed wood, 15 September 2003, *S. Takehashi s.n. TNS-F 12348*, nrITS HM562094, *tef1* KJ009836 (TNS). **RUSSIA. Far East Federal District:** Primorsky Territory, Sikhote-Alinsky Nature Biosphere Reserve, vicinities of Blagodaty Reserve Field Station, *Quercus mongolica* forest with isolated *Betula platyphylla*, on decayed wood of *Quercus* (or *Betula*), 29 August 2011, *E.F. Malysheva s.n. LE 289383*, nrITS KJ009696, KJ009835 (LE).

Pluteus kovalenkoi E.F. Malysheva, *sp. nov.* Fig. 23
MycoBank 808731

Diagnosis:—Differs from *P. shikae* by the stipe surface features, basidiospore size and shape of pleurocystidial hooks.

Holotype:—**RUSSIA.** Southern Federal District (Caucasus): Krasnodar Territory, vicinities of Kamyshanova Polyana, on decayed wood, 5 October 1978, *A.E. Kovalenko s.n. LE 9691*, nrITS KJ009697, *tef1* KJ009830 (LE!).

Etymology:—*kovalenkoi* is dedicated to Dr. Alexander Kovalenko.

Pileus 37–49 mm in diameter, obtusely campanulate when young, expanding to convex or plano-convex, with a low, broad umbo; surface smooth, slightly glistening when moist, innately fibrillose, with well-defined squamules at center; brown or gray-brown (7.5YR 3/3–3/4, 4/6, 5/6–5/8, 5/1–5/2); margin slightly translucently striate. Lamellae crowded, free, slightly ventricose, up to 5 mm broad, white-cream when young, later pink, with concolorous edges. Stipe 70–80 × 5–6 mm, cylindrical, slightly broad towards base (up to 7–8 mm); surface white or white-cream in the upper part, yellowish brown or terracotta towards base, glabrous or slightly pruinose at apex, longitudinally fibrillose towards base, without distinct squamules in the lower part. Context in stipe and pileus white. Smell indistinct. Taste not recorded. Spore print not recorded.

Basidiospores [30/2/1] (7.3–)7.6–9.0(–9.5) × 4.6–5.8 µm, $avl \times avw = 7.8\text{--}8.2 \times 5.2\text{--}5.5$ µm, $Q = (1.38\text{--})1.44\text{--}1.70$, $avQ = 1.49\text{--}1.60$, broadly ellipsoid to oblong, a few ovoid, often slightly constricted in the middle. Basidia 18–30 × 5.5–8 µm, tetrasterigmate, narrowly to broadly clavate, some with distinct median constriction. Pleurocystidia metuloid, 70–90 × 10–25 µm, narrowly to broadly fusiform or broadly utriform,

provided with 2–3(–4) apical hooks (usually entire, sometimes obtuse and poorly developed), hyaline, with up to 2.7 μm thick-wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but often with thinner walls, predominantly inflated fusiform, with or without distinct apical hooks. Lamellar edges sterile. Cheilocystidia 30–55 \times 13–23 μm , clavate or broadly clavate, some spheropedunculate or utriform, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 70–110 \times 12–20 μm ; individual elements mostly cylindrical or slightly inflated, some tapering towards apex, hyaline or with pale yellow-brown intracellular pigment, thin-walled. Stipitipellis a cutis; hyphae 7–20 μm wide, cylindrical, hyaline or with yellow-brown intracellular pigment, with thin, smooth walls. Clamp-connections present on pileipellis hyphae, but not at every septum; also present in other parts of the basidiocarp.

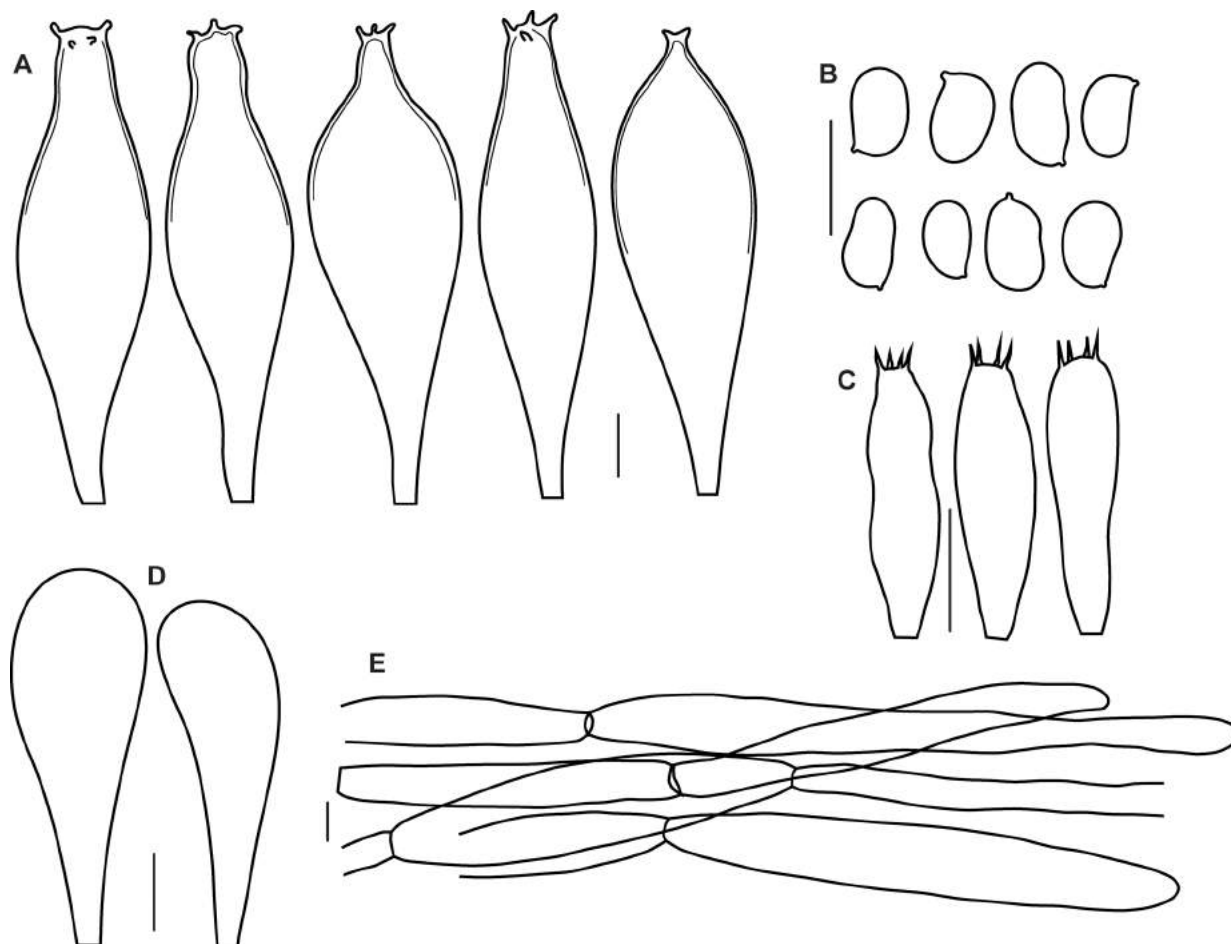


FIGURE 23. *Pluteus kovalenkoi*. A. Pleurocystidia. B. Basidiospores. C. Basidia. D. Cheilocystidia. E. Pileipellis. All from LE 9691. All line drawings by E. Malysheva. Scale bars = 10 μm .

Habit, habitat and phenology:—Subgregarious. In mixed forest. On well-decayed wood of conifers (October.

Distribution:—**Eurasia:** Only known from the type locality: Caucasus, Krasnodar Territory.

Observations:—Based on molecular data *P. kovalenkoi* is separated from *P. shikae* and *P. brunneidiscus* but morphologically it is very close to both of them. *P. shikae* differs in distinct gray-brown fibrils at lower part of stipe, smaller and more elongated basidiospores, pleurocystidia with developed apical hooks but all of these characters are rather variable; and only the shape of the pleurocystidia separates *P. kovalenkoi* from *P. brunneidiscus*. The ecological preferences could serve as an additional distinguishing character, but the strict conifer habitat of this new species requires further collections to be confirmed.

Pluteus microspermus and *Pluteus concentricus* have much shorter basidiospores than *P. kovalenkoi*, up to 6.0 and 6.5 μm respectively (Horak 2008). Additionally, both taxa differ from *P. kovalenkoi* in the pigmented lamellar edges and the absence of clamp-connections. Both species are only known from New Zealand (Horak 2008).

IV. *petasatus* clade. Fig. 5

Species growing mostly on angiosperm wood or on the humus layer without apparent connection to wood; one species (*P. petasatus*) relatively common in urban and ruderal areas. Clamp-connections absent on pileipellis hyphae (*P. petasatus*, *P. leucoborealis*) or present (*P. pellitus*).

Pluteus petasatus (Fr.) Gillet (1876: 395). Fig. 24

Basionym: *Agaricus petasatus* Fr. (1836: 142). Neotype (designated here):—RUSSIA. Northwestern Federal District: St Petersburg, Botanical Garden, stump of deciduous tree, 09 August 2011, *O. Morozova s.n. LE 289372*, nrITS KJ009705, *tefl* KJ009952 (LE!).

Synonym: *Agaricus curtisii* Berkeley (in Berkeley & Curtis 1849: 98); *Pluteus curtisii* (Berkeley) Saccardo (1887: 675).

Holotype:—UNITED STATES OF AMERICA. South Carolina: Beneath fallen trunks in woods. October, *Curtis 1523 s.n.* (K). Epitype (designated here):—UNITED STATES OF AMERICA. Florida: Leon Co., Tallahassee, Lake Overstreet, 24 August 2010, *A. Justo 161*, nrITS KJ009708, *tefl* KJ009977 (CUW!).

Synonym: *Agaricus patricius* Schulzer in Kalchbrenner (1874: 20); *Pluteus patricius* (Schulzer) Boudier (1905: 87). To the best of our knowledge, no holotype exists and no lectotype, neotype or epitype have been designated for this taxon.

Synonym: *Pluteus magnus* (1897: 383). Holotype:—UNITED STATES OF AMERICA. California: San Gabriel Canyon and near Los Angeles, *A.J. McClatchie NY 775453* (NY!).

Synonym: *Pluteus australis* Murrill (1945: 119). Holotype:—UNITED STATES OF AMERICA. Florida: Alachua Co., Gainesville, 24 October 1942, *FLAS 19140* (FLAS!).

Synonym: *Pluteus viscidulus* Singer in Singer and Digilio (1952: 255). Holotype:—ARGENTINA. Tucumán: near Tapia, 01 January 1949, *R. Singer T797* nrITS HM562110, *tefl* KJ009978 (holotype at LIL and isotype at MICH!).

Pileus 30–200 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo; surface completely smooth, squamose-fibrillose only around center or set with distinct brown squamules all over, with or without radial fibrils; pure white, pale gray-brown or brown (7.5YR 7/2–7/6, 6/2–6/7), more rarely with darker colors (7.5YR 4/4–4/6); dry or markedly viscid when moist, margin smooth or translucent-striate. Lamellae crowded, free, ventricose, up to 15(–20) mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 30–200 × 5–20 mm, cylindrical, with slightly broad base; surface white, smooth or with longitudinal brown or gray-brown fibrils, especially near the base. Context in stipe and pileus white. Smell strongly sweet and unpleasant, sweet-raphanoid or indistinct. Taste similar to smell or indistinct. Spore print pink to pinkish brown (2.5YR 8/4, 7/6–7/8; 5YR 7/6).

Basidiospores [840, 41, 37] 5.5–8.0(–9.5) × 3.5–5.5(–6.0) µm, avl × avw = 6.1–7.0 × 4.2–4.8 µm, Q = 1.20–1.70, avQ = 1.35–1.55, ellipsoid or broadly ellipsoid, more rarely oblong, sometimes ovoid or slightly constricted in the middle. Basidia 15–35 × 5–12 µm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 45–95 × 10–25(–30) µm, fusiform, narrowly fusiform or narrowly utriform with 2–3 apical hooks, some fusiform and without apical hooks (usually entire, sometimes poorly developed), sometimes this later type is predominant, some with small lateral hooks, hyaline, with up to 3 µm thick wall, frequent all over lamellar faces. Intermediate cystidia in most collections predominantly fusiform and without apical hooks, often with small lateral hooks, some similar to the pleurocystidia but smaller and/or with thinner walls. Lamellar edge sterile. Cheilocystidia 30–70 × 10–25 µm, clavate, narrowly clavate or spheropedunculate, hyaline, thin-walled, in most collections scarce and scattered, more rarely forming a well-developed strip. Pileipellis a cutis or ixocutis, with terminal elements 80–135 × 6–15 µm, individual elements cylindrical, some strongly tapering towards apex, hyaline or filled with brown intracellular pigment, with thin, smooth walls; in most collections a gelatinous matrix is present at least in the most external part, with embedded hyphae 2–5 µm wide, some with irregular outline. Stipitipellis a cutis; hyphae 5–20 µm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections absent on pileipellis hyphae; in some collections present on stipitipellis (but very scarce).

Habit, habitat and phenology:—Commonly gregarious to caespitose, more rarely solitary. Growing on decayed wood of hardwoods (*Acer*, *Betula*, *Quercus*, *Fagus*, *Populus*), also on wood chips, sawdust or on the humus layer. Common in urban parks, lawns, roadsides and other disturbed/ruderal areas but also occurring in natural, undisturbed forests. Recorded year round.

Distribution:—**Eurasia.** Widespread, recorded from Spain to Japan. **North America.** Widespread. In the East recorded from Florida and Louisiana northwards into Maine and Ontario, westwards into the Midwestern States (e.g. Missouri). Also known from the West Coast (California). Recorded from the Southern Hemisphere (Argentina, Papua-New Guinea).

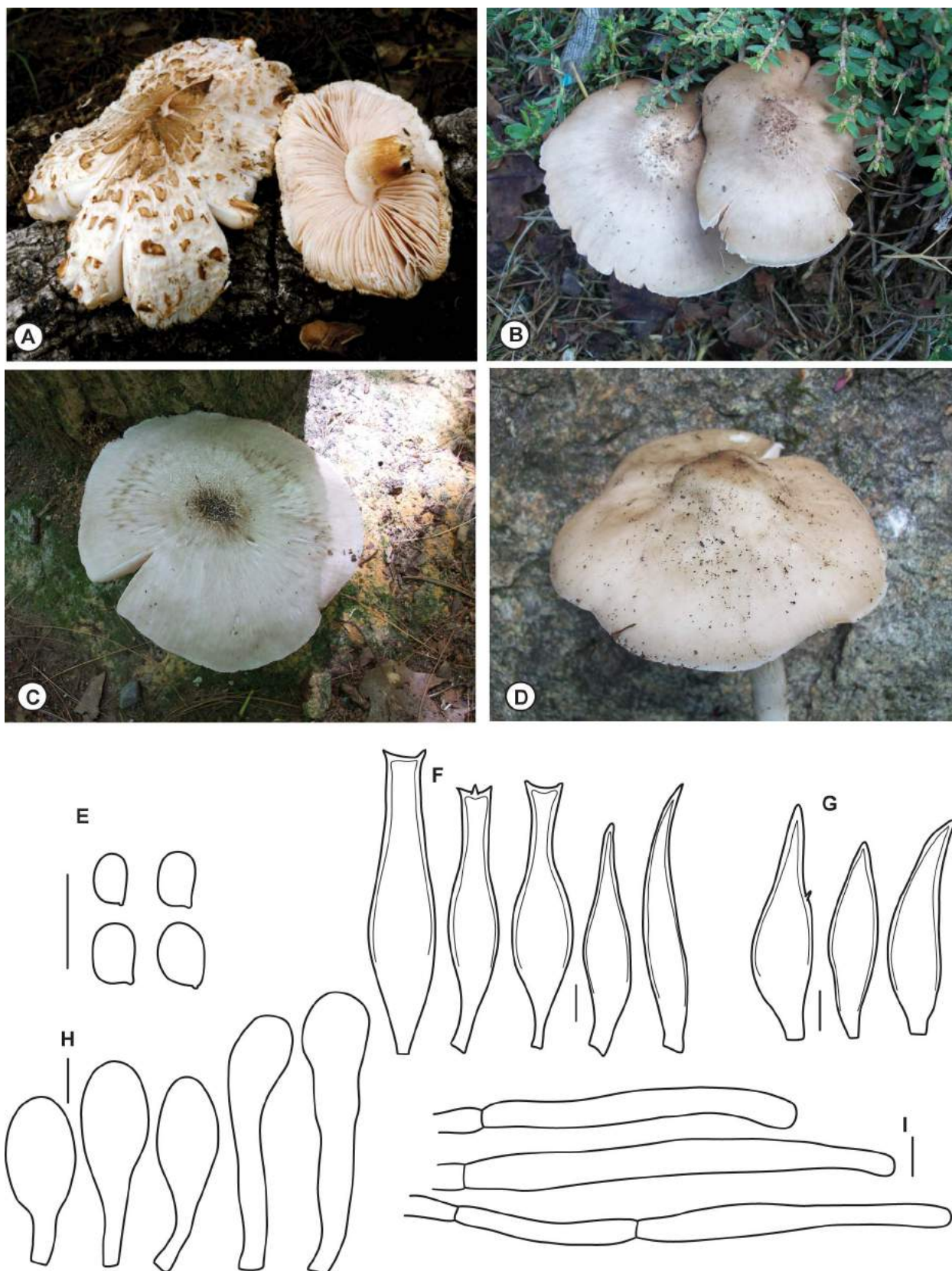


FIGURE 24. *Pluteus petasatus*. A. Collection A. Caballero 1945 (photo by A. Caballero). B. Collection AJ 143 (photo by A. Justo). C. Collection AJ 325 (photo by A. Justo). D. Collection AJ 541 (photo by A. Justo). E. Basidiospores. F. Pleurocystidia. G. Intermediate cystidia. H. Cheilocystidia. I. Pileipellis. E–I from AJ143. All line drawings by A. Justo. Scale bars = 10 μ m.

Observations:—Morphologically a highly variable fungus, *Pluteus petasatus* is the most widespread of all the species studied here. Its common occurrence in urban and man-made habitats may account for part of this extended geographical range, but it also occurs in natural, undisturbed forest areas throughout Eurasia, North America and extending even to the southern hemisphere.

At one extreme of the morphological variation of *Pluteus petasatus* are the collections with smooth and viscid pileus and at the other extreme are the collections with distinctly squamose and dry pileus. Between both extremes all kinds of intermediates regarding color (white, brown, brown-gray), presence of squamules and fibrils and viscosity of the pileus can be found. This great morphological variation accounts for the extensive synonymy of this species.

Agaricus petasatus was originally described from Uppsala (Sweden). To the best of our knowledge no original collections exist and no illustrations of *Agaricus petasatus* are cited in the protologue (Fries 1836). To stabilize the usage of this name a modern collection from northern Europe (LE289372, from the Russian Northwest) is designated here to serve as neotype.

Pluteus curtisii, a name that commonly appears in the taxonomic literature of the 20th century in connection with *P. petasatus* has a long and convoluted taxonomic history. *Agaricus curtisii* was originally described by Berkeley from South Carolina (USA) as a fungus with a “Pileus 2 inches or more broad, convex, dark liver-brown, smooth, not wrinkled, viscid when moist, with a satiny luster when dry” (Berkeley & Curtis 1849). Singer (1956) studied the type at Kew and other original collections at the Farlow herbarium and mentioned the existence of original colored paintings “which showed white pileus and stipe, and cinnamon-ochraceous squamulose centre, broad lamellae and the general habit of the fungus best known in Europe as *Pluteus cervinus* var. *patricius*”. Singer (1956) suggests that the original collections probably represent a mixture of species, and although his own interpretation of *Agaricus curtisii* corresponds to our concept of *Pluteus petasatus*, that does not settle the question of what the original description of *Agaricus curtisii* represents. Most authors (Murrill 1917; Orton 1960, 1986; Vellinga 1990; Banerjee & Sundberg 1995) have placed *Agaricus curtisii* in synonymy with *Pluteus cervinus* with some authors excluding Singer’s interpretation as representing *Pluteus petasatus* (Vellinga 1990) or *Pluteus patricius* (Orton 1986). From what we currently know about the diversity of *Pluteus* section *Pluteus* in the Southeastern USA, the name *Agaricus curtisii* could be applied to three species: *Pluteus cervinus*, *Pluteus hongoi* (in which case it would take precedence) or *Pluteus petasatus*. To settle the issue of the identity of *Agaricus curtisii* a modern collection made in the Southeastern USA (AJ 161, from near Tallahassee in Florida) that fits the original description by Berkeley (pileus brown [7.5 YR 6/4-6/8, 5/4-/58], smooth and viscid) has been selected here as the epitype of *Agaricus curtisii* (see nomenclature section above). This collection represents *P. petasatus* (based on microscopic and molecular data) and therefore *P. curtisii* is considered a synonym of *P. petasatus*.

Pluteus patricius is considered by some authors (Orton 1986; Banerjee & Sundberg 1995) as a species with a distinctly squamose and dry pileus in contrast with the smooth and viscid pileus they attribute to *P. petasatus*. Molecular data does not support the recognition of collections fitting the morphological concept of *P. patricius* (e.g. LOU 7570, AJ 201; Fig. 5a) as a separate species.

We have studied the type collections of *Pluteus magnus*, described from California and *Pluteus australis* described from Florida (see nomenclature section above). Although no molecular data could be obtained both taxa are considered to represent *P. petasatus* based on their morphological characteristics.

In contrast to the great variation in external appearance, the microscopic characters of *Pluteus petasatus* are rather constant and can be helpful for identification. *P. petasatus* can be separated from other taxa without clamp-connections in the pileipellis by the combination of: basidiospores relatively short and narrow (on average, 6.1–7.0 × 4.2–4.8 µm); intermediate cystidia predominantly fusiform and without apical hooks; cheilocystidia usually scattered and not forming a continuous strip; pileipellis with a gelatinous matrix at least in the most external part.

Additional collections examined:—JAPAN. **Honshu:** Chiba Prefecture, Chosei-gun, Nagara-machi, scattered on waste sawdust medium after cultivation of *Grifola frondosa*, 17 April 2007, A. Yashiro s.n. CBM 36790, nrITS HM562087, *tefl* KJ009972, (CBM). MONGOLIA. North Mongolia, Research Station “Khonin Nuga”, Mandal Sum, Selenge Aimak West-Khentee, mountain *Betula-Larix* forest, on fallen *Betula* trunk, 10 August 2007, A.V. Aleksandrova s.n. LE 289423, nrITS KJ009721, *tefl* KJ009953 (LE). PAPUA-NEW GUINEA. UOG campus, near Multi-P, EHP, 27 June 2006, K. Barakove TR 148-06 (M-0138487), nrITS KJ009730, *tefl* KJ009979 (M). UOG campus, EHP, 29 November 2006, Horosso TR 160-06 (M-0138488), nrITS KJ009731, *tefl* KJ009980 (M). RUSSIA. **Northwestern Federal District:** Novgorod Region, vicinities of Syuiska, on *Betula*

logs, 17 June 2010, *S. Arslanov s.n. LE 289376*, nrITS KJ009718, *tefl* KJ009968, (LE). **Siberian Federal District:** Buryatia, lower reaches of Selenga River, vicinities of Il'inka, on fallen trunk of *Betula*, 30 July 1997, *A.N. Petrov s.n. LE 201194*, nrITS KJ009724, *tefl* KJ009965 (LE). Novosibirsk Region, Kuybushev town vicinities, *Betula* forest, on rotting stump, 2005, *I.A. Gorbunova s.n. LE 289409*, nrITS KJ009720, *tefl* KJ009962 (LE). Novosibirsk Region, Novosibirsk District, Akademgorodok, planted *Betula pendula* grove ca. 40 years old with dense shrub undergrowth and relatively scarce grassy vegetation, on *Betula* trunk, 23 August 2011, *T.M. Bulyonkova s.n. LE 289416*, nrITS KJ009725, *tefl* KJ009967 (LE); *ibid.*, mixed forest (*Betula pendula*, *Pinus sylvestris*), on decayed wood, 2008, *I.A. Gorbunova LE 289411*, nrITS KJ009727, *tefl* KJ009957 (LE); *ibid.*, mixed forest (*Betula pendula*, *Pinus sylvestris*), on decayed wood, 08 July 2010, *T.M. Bulyonkova s.n. LE 289414*, nrITS KJ009722, *tefl* KJ009959 (LE); *ibid.*, lawn with planted trees (*Populus*, *Picea*), on rotten trunk of *Populus*, 08 August 2011, *T.M. Bulyonkova s.n. LE 289401*, nrITS KJ009723, *tefl* KJ009951 (LE); *ibid.*, mixed forest (*Betula pendula*, *Pinus sylvestris*), on decayed wood of *Betula*, 15 September 2010, *T.M. Bulyonkova s.n. LE 289412*, nrITS KJ009716, *tefl* KJ009958 (LE). Vicinities of Tomsk, on decayed wood, Aug-2007, *S.I. Gashkov s.n. LE 262803*, nrITS KJ009729, *tefl* KJ009981 (LE). **Southern Federal District:** Rostov Region, Sholokhovskiy District, vicinities of Veshenskaya, garden, at the base of the stump of *Prunus armeniaca*, 24 October 2011, *Yu.A. Rebriev, LE s.n. 289387* nrITS KJ009717, *tefl* KJ009960 (LE). **Volga Federal District:** Orenburg Region, Kuvandyksky District, Nature Reserve "Orenburgsky", on charred stump of *Populus nigra*, 25 July 2005, *O.A. Desyatova s.n. LE 235213*, nrITS KJ009726, *tefl* KJ009961 (LE). Samara Region, Zhigulevskiy Nature Reserve, broadleaf forest, on decayed wood of deciduous tree, 19 August 2007, *E.F. Malysheva s.n. LE 289386*, nrITS KJ009719, *tefl* KJ009954 (LE); *ibid.*, broadleaf forest (*Tilia cordata*, *Acer platanoides*), on fallen trunk of *Acer platanoides*, 28 July 2002, *E.F. Malysheva s.n. LE 213025*, nrITS KJ009728, *tefl* KJ009955 (LE). **SPAIN. A Coruña:** Brión, Adoufe, on unidentified stump, 17 September 1979, *L. Cabo s.n. LOU-Fungi 2714* (LOU). Santiago de Compostela, San Antolín de Toques, on unidentified wood, 7 October 1985, *F. Cabo s.n. LOU-Fungi 4123* (LOU); **Barcelona:** Argentona, on sawdust, 10 April 1988, *A. Rocabruna s.n. SCM474* (SCM); Cardedeu, Carretera de Cardedeu a St. Ignasi, on straw, 11 June 1987, *A. Rocabruna s.n. SCM 154* (SCM). **Cáceres:** Aldeanueva del Camino, on trunk of *Quercus suber*, 11 April 1996, *A. Caballero 1945* (LOU). Monfrague, Villareal de San Carlos, *Quercus suber* forest, on decayed wood of *Quercus suber*, 18 April 1994, *R. Gonzalez s.n. LOU 7570*, nrITS KJ009701, *tefl* KJ009964 (LOU). **Huelva:** La Rocina, Doñana, on *Quercus suber* wood, 24 March 1978, *J.M.Rey s.n. MA-Fungi 330* (MA). **La Rioja:** Villarroya, on *Quercus ilex* stump, 24 May 1988, *A. Caballero 1054* (LOU). Ortigosa de Cameros, terrestrial, 13 July 1988, *A. Caballero, 1125* (LOU). Villarroya, on *Quercus ilex* stump, 27 September 1999, *A. Caballero 2288* (LOU). **Madrid:** Valdetorras de Jarama, terrestrial, 25 June 1978, *J.L.Vicioso s.n. MA-Fungi 4716* (MA). **Segovia:** Riaza, on *Populus* wood, 17 June 1979, *C. Santonja s.n. MA-Fungi 2961*. **Sevilla:** locality unknown, March 2003, *A. Garcia s.n. AJ 201*, nrITS HM562038, *tefl* KJ009956, (LOU). Cazalla de la Sierra, Arroyo Hiel de la Vaca, on *Quercus suber* wood, 29 October 2002, *N. Rodríguez-Ramos & L. Cabrera-Muñoz s.n. COFC 3923* (COFC). Constantina, Navalvillar, on *Quercus ilex* subsp. *ballota* wood, 21 October 2003, *I. Olariaga s.n. COFC 2944* (COFC). El Pedroso, La Jarosa, habitat unknown, 30 April 2003, *N. Rodríguez-Ramos s.n. COFC 2961* (COFC). Las Navas de la Concepción, Embalse del Retortillo, habitat unknown, 29 November 2002, *COFC 2957* (COFC). **Valladolid:** Mucientes, on straw, 15 March 2003, *A. García-Blanco & al. s.n. MA-Fungi 55409* (MA); Villalba de los Alcores, on straw, 15 March 2003, *A. García-Blanco & al. s.n. MA-Fungi 55410* (MA). **UNITED STATES OF AMERICA. California:** Alameda Co., Berkeley, Scenic Ave, between Vine and Cedar streets, on rotten stump of ornamental tree, 28 January 2013, *E.C. Vellinga s.n. UC 1999432*, nrITS KF306019 (UC). Los Angeles Co., Burbank, 01 April 2007, *N. Wilson s.n. UC 1998685*, nrITS JX857453, *tefl* KJ460260 (UC). Marin Co., Point Reyes National Seashore, Fire Trail area, 10 December 2011, *N.H. Nguyen s.n. UC 1861126*, nrITS JX857460 (UC). San Mateo Co., San Francisco Watershed area, mixed forest with *Pinus radiata*, *Cupressus macrocarpa*, *Quercus agrifolia*, 02 December 2011, *E.P. Blanchard s.n. UC 1998559*, nrITS JX857452 (UC). Santa Cruz Co., Henry Cowell State Park (NAMA Foray 2012), on decayed wood, 15 December 2012, *R. Miller s.n. UC 1999301*, nrITS KF306014 (UC). **Florida:** Leon Co., Tallahassee, Lake Overstreet, mixed forest, apparently terrestrial, 24 August 2009, *A. Justo 145*, nrITS HM562109, *tefl* KJ009973 (MICH). **Illinois:** Locality and date unknown, *LE 22977*, nrITS KJ009713, *tefl* KJ009950, (LE). 25 September 2009, *Smith Foray participant, SF3-BPI 882766*, nrITS HM562175, *tefl* KJ009974 (BPI). Jackson Co., Carbondale, SIU Campus, on log, 08 June 1978, *Mueller-Strack1*, nrITS HM562070 (ILLS). **Louisiana:** Lafayette Parish, Lafayette, on decayed wood, 25 October 2009, *Bernadine PLA3*, nrITS KJ009709, *tefl* KJ009966 (BPI).

St. Martin Parish, St. Martinville, on leaf litter in live oak environs, 28 October 2009, *A. Bornstein* PLA2, nrITS KJ009703, *tefl* KJ009982 (BPI). **Maine:** Penobscot Co., Bradley, on decayed wood, 10 August 2007, *M. Ledeco* s.n. PBM 2854, nrITS KJ009711 (TENN). **Massachusetts:** Middlesex Co., Mt. Misery Trails, on the litter layer, 21 June 2010, *A. Justo* 325. Worcester Co., Harvard Forest, mixed forest, 29 July 2011, *M. Nuhn & A. Carlson* s.n. AJ 411, nrITS KJ009714, *tefl* KJ009969 (CUW). Worcester Co., Purgatory Chasm State Reservation, 06 May 2012, *A. Justo* 541 (CUW). Worcester Co., Worcester (Clark Univ. Campus), urban area, near planted trees, on dead wood, 11 June 2010, *M. Binder* s.n. AJ 318, nrITS KJ009715, *tefl* KJ009963 (CUW); *ibid.*, on decayed wood of hardwood, 27 May 2010, *A. Justo* 305, nrITS KJ009707, *tefl* KJ009975 (CUW); *ibid.*, on decayed wood of hardwood (at the base of tree), 17 August 2011, *A. Justo* 414, nrITS KJ009706, *tefl* KJ009970 (CUW); *ibid.*, apparently terrestrial, 02 July 2009, *A. Justo* 143, nrITS HM562065, *tefl* KJ009971 (MICH). **Michigan:** No locality data, *Harrison* 10325, nrITS HM562073 (MICH). Baraga Co., Erickson Sawmill, on sawdust, 16 July 1969, *J. Ammirati* 3103, nrITS HM562084 (MICH). **Missouri:** Mingo National Wildlife Refuge, 23 September 2005, *Mingo Foray participant*, SF9-BPI 882770, nrITS HM562179, *tefl* KJ009976 (BPI). **Tennessee:** Knox Co., Knoxville, 10 December 2007, *R.H. Petersen* TFB 13183, nrITS KJ009702 (TENN); *ibid.*, lawn, 31 July 2008, *P. B. Matheny* 2978a, nrITS KJ009704 (TENN); *ibid.*, lawn, on buried rotten wood, 15 June 2011, *P. B. Matheny* 2943, nrITS KJ009710 (TENN). **Wisconsin:** Dane Co., Madison, on wood mulch, 26 June 1977, *H. Burdsall* MAD 9301, nrITS KJ009712 (CFMR).

Pluteus pellitus (Persoon : Fries) Kummer (1871: 98). Fig. 25

Basionym: *Agaricus pellitus* Persoon (1801: 366); *Agaricus pellitus* Persoon : Fries (1821: 198). Neotype (Bonnard 1995):—FRANCE. Môle, 31 July 1960, *R. Kühner* SA-60-2 (G-K!).

Synonym: *Pluteus sandalioticus* Contu & Arras (2001: 137). Neotype (Justo *et al.* 2006):—SPAIN. Sevilla, Cazalla de la Sierra, La Atalaya, on decayed wood of *Quercus suber*, 21 March 2002, *N. Rodriguez-Ramos* s.n. COFC-F 2959 (COFC!).

Pileus 30–75(–130) mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo; surface smooth or innately radially fibrillose, usually with well-defined squamules at center; brown at center (7.5YR 4/4–4/6) and much paler towards margin (7.5YR 7/4–7/8) or white all over; dry or slightly viscid when moist; margin smooth or slightly translucent-striate. Lamellae crowded, free, ventricose, up to 7 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 35–70 × 5–15 mm, cylindrical, with slightly broad base; surface white, smooth or with longitudinal brown or gray-brown fibrils especially near the base. Context in stipe and pileus white. Smell indistinct. Taste indistinct. Spore print not recorded.

Basidiospores [140, 5, 5] 5.0–7.5(–8.0) × 3.5–5.0(–5.5) µm, avl × avw = 5.8–6.5 × 4.3–4.6 µm, Q = 1.24–1.71, avQ = 1.34–1.46, broadly ellipsoid, ellipsoid or oblong, sometimes ovoid or slightly constricted in the middle. Basidia 15–32 × 6–10 µm, tetrasperigmate, clavate, some with median constriction. Pleurocystidia metuloid, 50–95 × 12–25 µm, fusiform, narrowly fusiform or narrowly utriform, provided with 2–4 apical hooks, rarely fusiform and without hooks at apex, a few with lateral hooks (usually entire), hyaline, with up to 3 µm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; in some collections fusiform cystidia and cystidia with no hooks dominate, in others there is no predominant morphological type. Lamellar edge sterile. Cheilocystidia 34–100(–115) × 10–27 µm, clavate, narrowly clavate or cylindrical (either type predominant), a few spheropedunculate, hyaline, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 60–165 × 7–25 µm; individual elements cylindrical, usually strongly tapering towards apex, hyaline or filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–20 µm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae but not at every septum; also observed in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary or subgregarious, growing on well-decayed wood of hardwoods (e.g. *Quercus*, *Eucalyptus*) more rarely terrestrial. In temperate or Mediterranean forests, also in *Eucalyptus* plantations. May–November.

Distribution:—**Eurasia.** France, Italy, Spain, South-western Russia.

Observations:—The present concept of *P. pellitus* is in agreement with the neotypification made by Bonnard

(1995) that defines *P. pellitus* as a species with relatively small basidiospores, with clamp-connections in the pileipellis and growing on angiosperm wood or terrestrial. For a detailed discussion about this species and its different interpretations see Vellinga (1987), Bonnard (1995) and Justo & Castro (2007b). In the field it can be confused with white variants of other species, and the name has been variously misapplied. *Pluteus pellitus* is restricted to Europe.

Collections corresponding to the morphological concept of *P. sandalioticus* (Contu 2001; Justo *et al.* 2006), with pigmented pileus and longer cheilocystidia, fall within the molecular variation of *P. pellitus* (coll. AJ200, AJ60; Fig. 5a).

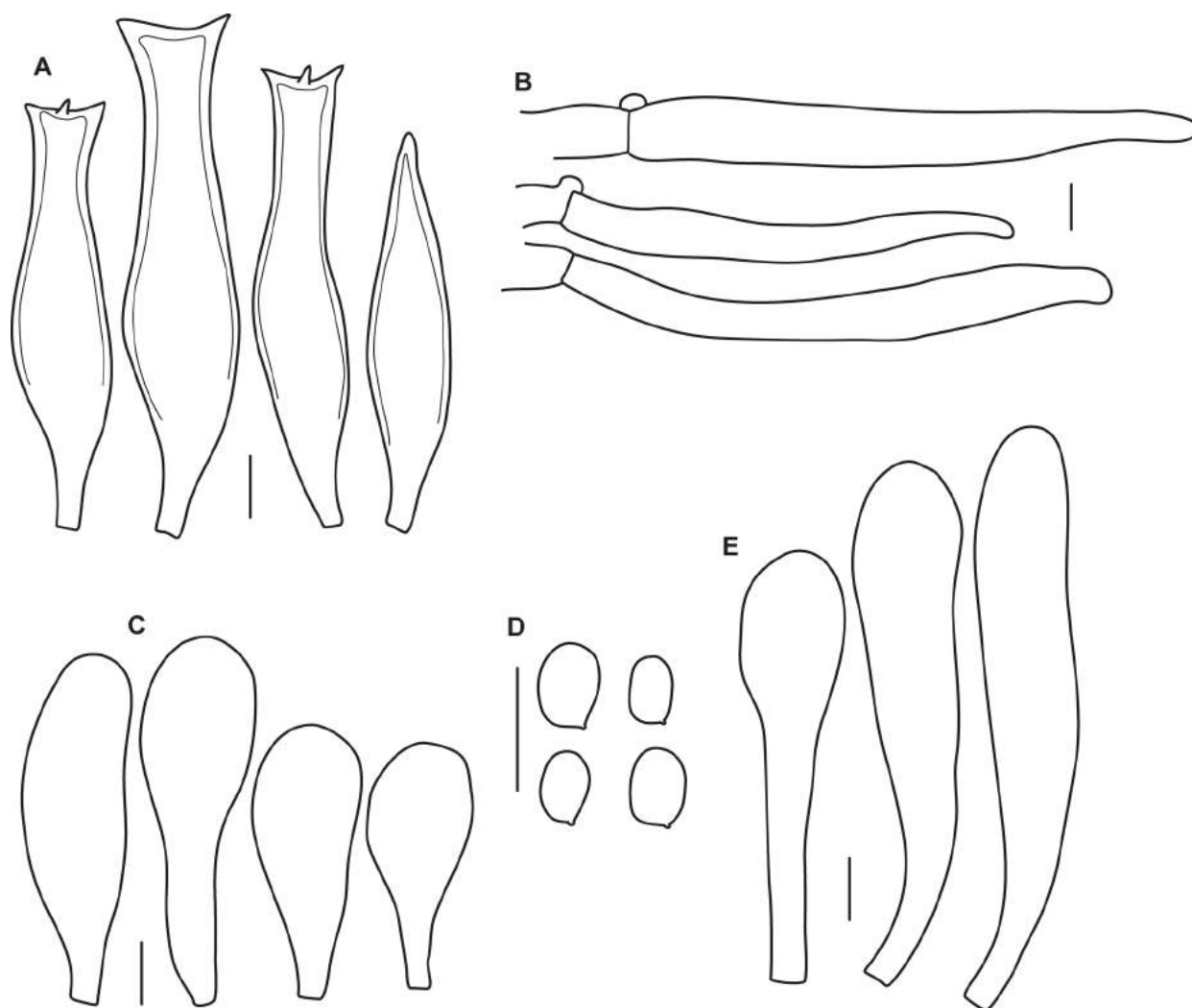


FIGURE 25. *Pluteus pellitus*. A. Pleurocystidia. B. Pileipellis. C. Cheilocystidia. D. Basidiospores. E. Cheilocystidia. All from AJ 74, except E from AJ 200. All line drawings by A. Justo. Scale bars = 10 µm.

Additional collections examined:—ITALY. **Sardinia:** Olbia-Citta, urban park, apparently terrestrial, 25 May 2008, *M. Contu s.n. AJ 72*, nrITS HM562036, *tef1* KJ009988 (LOU). RUSSIA. **Southern Federal District:** Krasnodarsky Territory, broadleaf forest (*Quercus*, *Carpinus*), 23 June 1974, *A.E. Kovalenko s.n. LE 9686*, nrITS KJ009700, *tef1* KJ009990 (LE); *ibid.*, Stanitsa Kaluzhskaya, *Quercus* forest, on stump, 19 September 1979, *A.E. Kovalenko s.n. LE 9687*, nrITS KJ009699, *tef1* KJ009983 (LE). **Volga Federal District:** Samara Region, Zhigulevsky Nature Reserve, vicinities of Bakhilova Polyana, broadleaf forest, on fallen trunk of deciduous tree, 08 August 2000, *E.F. Malysheva s.n. LE 289374*, nrITS KJ009698, *tef1* KJ009984 (LE). SPAIN. **Huelva:** Los Romeros, *Quercus* forest, on decayed wood of *Quercus*, 06 November 2003, *J. Siquier s.n. AJ 60*, nrITS HM562107, *tef1* KJ009986 (MA). **La Rioja:** Villaroya, *Quercus* forest, on decayed wood of *Quercus ilex*, 20 October 2011, *A. Caballero s.n. AJ 200*, nrITS HM562052, *tef1* KJ009989 (LOU). **Pontevedra:** Vigo, urban park, apparently terrestrial, October 2008, *A. Justo 74*, nrITS HM562047, *tef1* KJ009985 (LOU). **Sevilla:** mixed forest, on decayed wood of *Alnus glutinosa*, March 2003, *N. Rodriguez s.n. AJ 202*, nrITS HM562037, *tef1* KJ009987 (LOU).

Diagnosis:—Differs from *Pluteus petasatus* in the comparatively larger basidiospores and in the boreal distribution.

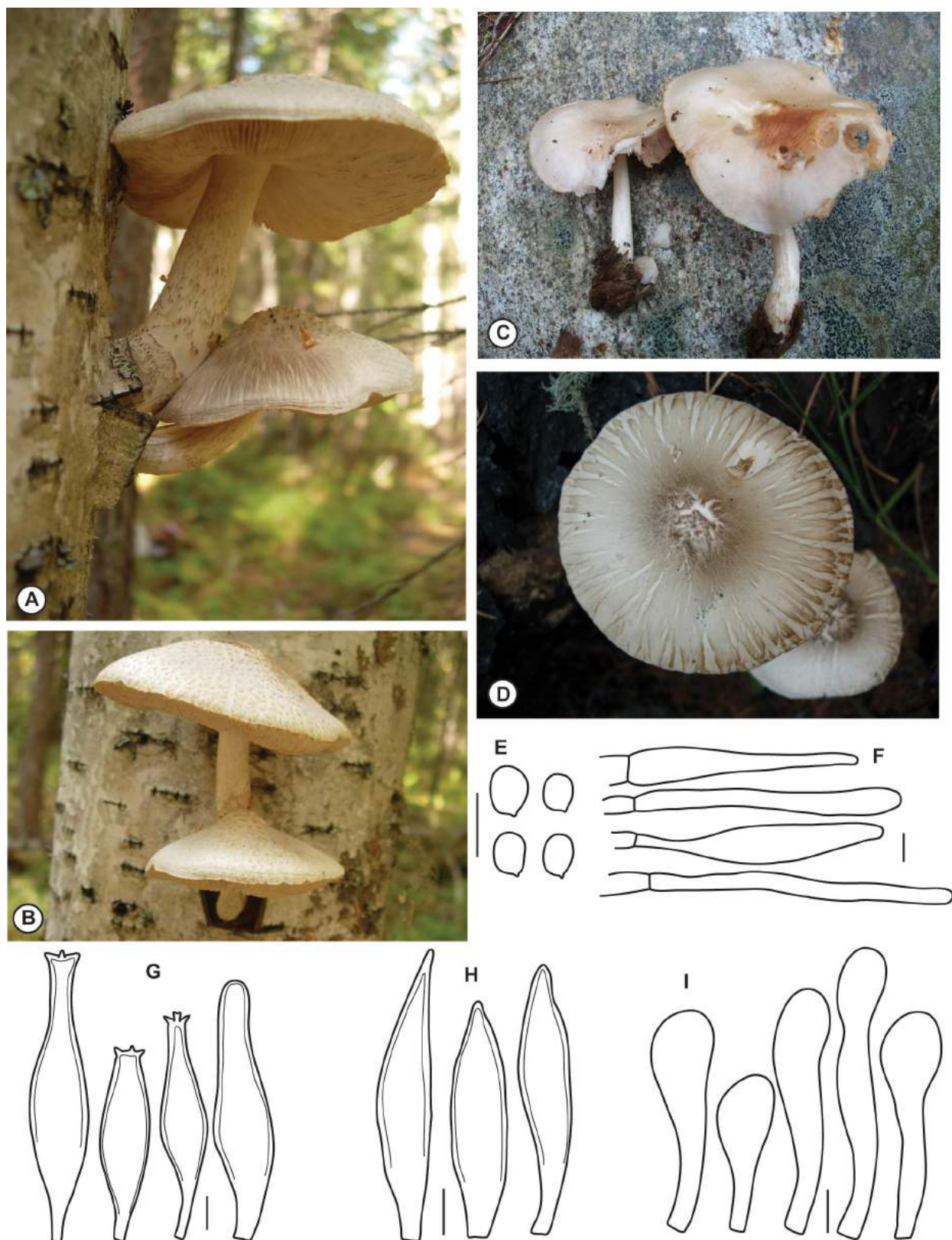


FIGURE 26. *Pluteus leucoborealis*. A–B. Collection LE 289421 (photo by A. Alexandrova). C. Collection AJ 587 (photo by A. Justo). D. Collection LE 289424 (photo by A. Alexandrova). E. Basidiospores. F. Pileipellis. G. Pleurocystidia. H. Intermediate cystidia. I. Cheilocystidia. E–I from AJ 587. All line drawings by A. Justo. Scale bars = 10 µm.

Holotype:—RUSSIA. Siberian Federal District: Krasnoyarsky Kray, Turukhansky District, right bank of Yenisei River, on decayed *Betula* trunk, 26 August 2009, *A.V. Aleksandrova s.n.* LE 289421, nrITS KJ009746, *tefl* KJ009994 (LE!).

Etymology:—*leucoborealis* is a combination of the Greek “λευκος” (white or pale) and the Latin *borealis* (derived from the Greek “βορειος” meaning northern), making reference to the external aspect and distribution of this species.

Pileus 20–60(–80) mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo; surface completely smooth, squamose-fibrillose only around center, with radial fibrils all over (sometimes forming a star-shaped pattern) or with distinct brown squamules all over; pure white but fibrils and squamules (when present) are brown or gray-brown (7.5YR 7/2–7/6, 6/2–6/8); slightly to distinctly viscid when moist; margin smooth or translucent-striate. Lamellae crowded, free, ventricose, up to 8 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 30–80 × 3–8 mm, cylindrical with slightly broad base; surface white, or yellowish near base, usually with distinct gray-brown squamules and fibrils near the base or all over, more rarely smooth. Context in stipe and pileus white. Smell indistinct. Taste indistinct. Spore print pink to pinkish brown.

Basidiospores [90, 3, 3] (5.5–)6.0–8.0(–8.5) × (4.5–)5.0–6.0 μm, $avl \times avw = 6.8\text{--}7.4 \times 5.3\text{--}5.5 \mu\text{m}$, $Q = 1.17\text{--}1.50$, $avQ = 1.26\text{--}1.36$, ellipsoid or broadly ellipsoid, sometimes ovoid or slightly constricted in the middle. Basidia 14–28 × 5–10 μm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 40–93 × 10–30 μm, fusiform, narrowly fusiform or narrowly utriform with 2–3(–4) apical hooks (usually entire, sometimes bifid or poorly developed), some fusiform and without apical hooks, sometimes this later type is predominant, some with small lateral hooks, hyaline, with up to 3 μm thick wall, frequent all over lamellar faces. Intermediate cystidia in most collections predominantly fusiform and without apical hooks, some similar to the pleurocystidia but smaller and/or with thinner walls. Lamellar edge sterile. Cheilocystidia 30–72(–85) × 10–23 μm, the majority narrowly clavate or clavate, a few cylindrical or narrowly utriform, hyaline, thin-walled, forming a well-developed strip, more rarely scarce and scattered. Pileipellis a cutis or ixocutis, with terminal elements 85–140(–170) × 7–17 μm; individual elements cylindrical, some strongly tapering towards apex, hyaline or filled with brown intracellular pigment, with thin, smooth walls; in some collections a gelatinous matrix is present in the most external part, with embedded hyphae 2–5 μm wide, some with irregular outline. Stipitipellis a cutis; hyphae 5–25 μm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections absent on pileipellis hyphae; in some collections present (but very scarce) in pileitrama, hymenophoral trama and/or stipitipellis.

Habit, habitat and phenology:—Commonly gregarious, more rarely solitary. Growing on decayed wood of *Betula*, more rarely *Alnus*. In boreal or transitional boreal/temperate forests. June–September.

Distribution:—**Eurasia.** Widespread from north-western Russia to Siberia. **North America:**—Widespread. In the East recorded from the northern parts of Michigan (Emmet Co., Tahquamenon Falls) and New York (Adirondacks). In western North America, only recorded from Alaska.

Observations:—*Pluteus leucoborealis* resembles externally *P. petasatus*, and has a similar degree of extensive morphological variation. Basidiospore size is the most reliable character to tell both species apart. *P. leucoborealis* has usually a well-developed strip of cheilocystidia but this character is less reliable than basidiospore size.

Pluteus leucoborealis is widespread geographically, from the St. Petersburg area in Russia to the Adirondacks in New York, but seems to be confined to boreal or transitional forests, and has not been recorded in geographically close but ecologically different areas like the temperate forests of western Europe or eastern North America. It has a strong preference for wood of *Betula* and *Alnus*.

Pluteus glaucus (Singer 1961a: 114) can also have very pale and squamulose pileus but it differs from *P. leucoborealis* in the presence of bluish green tinges on the pileus, the pigmented lamellar edges, the much smaller cheilocystidia (up to 27 μm long) and the abundant clamp-connections. This species is only known from Chile (Singer 1961a).

Additional collections examined:—MONGOLIA. North Mongolia, Research Station “Khonin Nuga”, Mandal Sum, Selenge Aimak West-Khentee, riparian *Betula-Picea* forest, on fallen *Betula* trunk at site of fire, 14 August 2007, *A.V. Aleksandrova s.n.* LE 289424, nrITS KJ009743, *tefl* KJ009999 (LE). RUSSIA. **Far East Federal District:** Primorsky Territory, Ussuriysky Nature Reserve, vicinities of Peishula Reserve Field Station, floodplain *Ulmus* forest, on decayed wood of *Alnus*, 13 August 2011, *E.F. Malysheva s.n.* LE 289373, nrITS KJ009734, *tefl* KJ009992 (LE). **Northwestern Federal District:** Leningrad Region, Luzhsky District, Shalovo-Perechinsky Reserve, *Picea* forest with isolated *Betula* and *Quercus*, on fallen trunk of *Betula*, 21 August 1997, *O.V. Morozova s.n.* LE 216010, nrITS KJ009744, *tefl* KJ009991 (LE). Leningrad Region, Vyborgsky District, vicinities of Lebedevka, *Betula* forest, on decayed wood of *Betula*, 24 July 1997, *O.V. Morozova s.n.* LE 215340,

nrITS KJ009742, *tefl* KJ010002 (LE); *ibid.*, vicinities of Roschino, “Lindulovskaya Roscha” Reserve, on fallen trunk of *Alnus*, 09 June 1995, *E.A. Fomina s.n. LE 289364*, nrITS KJ009748, *tefl* KJ010001 (LE). Novgorod Region, vicinities of Syuiska, mixed forest, on fallen trunk of *Betula*, 04 July 2011, *S. Arslanov s.n. LE 289375*, nrITS KJ009745, *tefl* KJ010000 (LE). Pskov Region, Sebezhsy District, National Park “Sebezhsy”, bank of Midino Lake, *Picea* forest, on fallen trunk of *Betula*, 23 July 2002, *O.V. Morozova s.n. LE 217548*, nrITS KJ009739 (LE). St Petersburg, Primorsky District, “Yuntolovsky” protected area, mixed forest (*Pinus*, *Betula*), on fallen trunk of *Betula*, 08 September 2004, *O.V. Morozova s.n. LE 234709*, nrITS KJ009751 (LE). **Siberian Federal District:** Baikal region, Barguzinsky Nature Reserve, conifer forest (*Pinus*, *Larix*), on fallen trunk, 10 August 1969, *E.L. Nezdoiminogo s.n. LE 9808*, nrITS KJ009749, *tefl* KJ010006 (LE). Novosibirsk Region, Novosibirsk District, Akademgorodok, planted *Betula pendula* grove with many fallen trees and dense shrub undergrowth, on *Betula*, rotten trunk, 19 July 2011, *T.M. Bulyonkova s.n. LE 289399*, nrITS KJ009741, *tefl* KJ010004 (LE). *ibid.*, mixed forest (*Betula pendula*, *Pinus sylvestris*), on *Betula*, rotten wood, 14 August 2007, *T.M. Bulyonkova s.n. LE 289419*, nrITS KJ009747, *tefl* KJ009995 (LE); *ibid.*, planted *Betula pendula* grove ca. 40 years old with dense shrub undergrowth and relatively scarce grassy vegetation, on rotten trunk, 05 July 2011, *T.M. Bulyonkova s.n. LE 289405*, nrITS KJ009735, *tefl* KJ009993 (LE). Tyumen Region, Berezovsky, Pripolarny Village, on fallen trunk of *Betula* at a burn site, 30 June 2010, *E. Zvyagina s.n. LE 235802*, nrITS KJ009736, *tefl* KJ010007 (LE). **Ural Federal District:** Yugra, Khanty-Mansiyskiy District, Shapsha Village, mixed dark conifer taiga (*Picea obovata*, *Abies sibirica*, *Pinus sibirica* with scarcer *Betula pendula*, *Populus tremula*, *Pinus sylvestris*), on decayed wood, 04 August 2007, *N.V. Filippova s.n. LE 289402*, nrITS KJ009740, *tefl* KJ010003 (LE). Yugra, Khanty-Mansiyskiy District, Mukhrino Field Station of the Ugra SU UNESCO chair, mixed dark conifer taiga (*Picea obovata*, *Abies sibirica*, *Pinus sibirica* with scarcer *Betula pendula*, *Populus tremula*, *Pinus sylvestris*), on rotten trunk of deciduous tree, 25 July 2009, *N.V. Filippova s.n. LE 289408*, nrITS KJ009737, *tefl* KJ009996 (LE). UNITED STATES OF AMERICA. **Alaska:** Fairbanks North Star Borough, Fairbanks, Large Animal Research Station, on decayed wood of *Betula*, 05 August 2011, *MSA Foray pak-2*, nrITS KJ009732 (BPI); *ibid.*, on decayed wood of *Betula*, 05 August 2011, *A.M. Minnis pak-1*, nrITS KJ009750, *tefl* KJ010009 (BPI). **Michigan:** Chippewa Co., Tahquamenon Falls State Park, on unidentified wood of broadleaf tree, 03 September 1953, *A.H. Smith 42452*, nrITS HM562060, *tefl* KJ009997 (MICH). Emmet Co., Hemlock Bog, on wood, 14 September 2007, *J. Steinke SF5-BPI 882768*, nrITS HM562177, *tefl* KJ010005 (BPI). **New York:** Essex Co., Adirondack Ecological Center, Huntington Wildlife Forest, mixed forest, on decayed wood, 17 August 2012, *O. Miettinen s.n. AJ 587*, nrITS KJ009738, *tefl* KJ010008 (CUW); *ibid.*, on decayed wood of hardwood, 16 August 2012, *O. Miettinen s.n. AJ 595*, nrITS KJ009733, *tefl* KJ009998 (CUW).

V. salicinus clade. Fig. 6

Species growing on angiosperm wood (*P. salicinus*, *P. americanus*, *P. saupe*) or on conifer wood (*P. sepiicolor*, *P. oreibatus*). Blue-green, or blue-gray tinges common on pileus, stipe and/or context. Clamp-connections common and easy to spot on pileipellis hyphae. For additional information on tropical and subtropical taxa belonging in the salicinus clade see Justo *et al.* (2011a, 2011b).

Pluteus salicinus (Pers.: Fr.) Kummer (1871: 99). Fig. 27

Basionym: *Agaricus salicinus* Persoon (1798: 9); *Agaricus salicinus* Persoon: Fries (1821: 202). To the best of our knowledge, no holotype exists and no lectotype, neotype or epitype have been designated for this taxon.

Pileus 25–60(–80) mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo; surface with distinct squamules at center, radially fibrillose or smooth towards margin; usually gray or gray-brown (7.5YR 4/1–4/2, 5/1–5/2; 10YR 5/1–5/4, 6/1–6/2), in some specimens with distinct blue-green tinges especially around center (Gley1 6/1, 7/1; Gley2 7/1, 8/1); dry or slightly viscid when moist; margin smooth or translucent-striate. Lamellae crowded, free, ventricose, up to 6 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 20–70 × 3–7 mm, cylindrical, with slightly broad base; surface white with distinct blue-green tinges (Gley1 6/1, 7/1; Gley2 7/1, 8/1) especially near the base, smooth or with longitudinal brown or gray-brown fibrils, especially near base. Context in stipe and pileus white or slightly grayish. Smell usually strong and like leaves of *Pelargonium*, more rarely slightly raphanoid or indistinct. Taste similar to smell or indistinct. Spore print pink to pinkish brown.



FIGURE 27. *Pluteus salicinus*. A. Collection AJ 349 (photo by L.A. Parra). B. Basidiospores. C. Pleurocystidia. D. Cheilocystidia. E. Pileipellis. All from AJ 349. All line drawings by A. Justo. Scale bars = 10 μ m.

Basidiospores [480, 20, 20] 7.0–10.0(–12.0) \times (4.5–)5.0–7.5(–8.0) μ m, avl \times avw = 8.3–9.5 \times 6.2–6.8 μ m, Q = 1.17–1.55(–1.70), avQ = 1.32–1.48, ellipsoid or broadly ellipsoid, more rarely oblong, sometimes ovoid or slightly constricted in the middle. Basidia 17–35(–47) \times 7–14 μ m, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 60–100(–110) \times 10–20(–25) μ m, fusiform, narrowly fusiform or narrowly utriform, provided with 2–4(–5) apical hooks (usually entire, rarely bifid, and well-developed), with up to 4 μ m thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia 25–70(–85) \times 10–25 μ m, predominantly clavate or narrowly clavate, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 80–200(–270) \times 6–18 μ m, individual elements cylindrical, some strongly tapering towards apex, hyaline or filled with brown intracellular pigment, sometimes grayish or bluish in fresh specimens, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–25 μ m wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae; also present and common in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary or subgregarious. Growing on decayed wood of hardwoods (e.g. *Alnus*, *Eucalyptus*, *Fagus*, *Populus*, *Quercus*,). In hardwood-dominated or mixed temperate forests, also in *Eucalyptus* plantations in Spain. May–November.

Distribution:—**Eurasia:** Widespread in western Europe and eastwards into Siberia.

Observations:—The collection LE289410 (Fig. 6a), made in the Novosibirsk Region (Russia), marks the easternmost confirmed occurrence of *P. salicinus* in Eurasia. All other collections in this species complex from the eastern parts of Eurasia and from North America have turned out to be different species.

Pluteus salicinus is relatively easy to recognize because of the combination of gray pileus with squamules at center; blue-green tinges in pileus and/or stipe; relatively large basidiospores; metuloids with well-developed hooks and presence of clamp-connections in pileipellis.

Additional collections examined:—RUSSIA. **Northwestern Federal District:** Leningrad Region, Kingiseppsky District, Kurgalsky Peninsula, *Alnus glutinosa* forest, on decayed wood of *Alnus*, 04 July 1997, O.V. Morozova s.n. LE 202301, nrITS KJ009755, *tefl* KJ010023 (LE). **Siberian Federal District:** Novosibirsk Region, Novosibirsk District, Akademgorodok, mixed forest (*Betula pendula*, *Pinus sylvestris*), on decayed wood, 2008, I.A. Gorbunova s.n. LE 289410, nrITS KJ009758, *tefl* KJ010025 (LE). **Volga Federal District:** Samara Region, Zhigulevsky Nature Reserve, *Betula* forest, on fallen trunk of deciduous tree, 11 June 2003, E.F. Malysheva s.n. LE 213033, nrITS KJ009753, *tefl* KJ010022 (LE); *ibid.*, broadleaf forest (*Tilia cordata*, *Acer platanoides*), on fallen trunk of deciduous tree, 25 July 2003, E.F. Malysheva s.n. LE 213034, nrITS KJ009756, *tefl* KJ010028 (LE); *ibid.*, broadleaf forest (*Tilia cordata*, *Acer platanoides*), on fallen trunk of deciduous tree, 26 July 2001, E.F. Malysheva s.n. LE 213064, nrITS KJ009754, *tefl* KJ010024 (LE); *ibid.*, broadleaf forest with *Tilia cordata*, on fallen trunk of deciduous tree, 25 July 2003, E.F. Malysheva s.n. LE 213023, nrITS KJ009757, *tefl* KJ010027 (LE). SPAIN. **Barcelona:** La Floresta, on unidentified wood, 5 October 2002, A.M. Tarín s.n. SCM 4598 (SCM). Rupit, Pruit, on *Fagus sylvatica* stump, 1 June 1999, M. Tabarés s.n. SCM 4599 (SCM). Sta. Fe del Montseny, on *Fagus sylvatica* stump, 24 June 1987, A. Rocabrúna s.n. SCM 120 (SCM); *ibid.*, 19 July 1987, A. Rocabrúna s.n. SCM 284 (SCM); *ibid.*, 01 June 1988, M. Tabarés & A. Rocabrúna s.n. SCM 1094 (SCM); *ibid.*, 17 June 1995, A. Rocabrúna s.n. SCM 2523 (SCM); *ibid.*, 15 August 1995, A. Rocabrúna s.n. SCM 2545 (SCM). **Cádiz:** Los Barrios, Arroyo del Tiradero, in forest of *Quercus canariensis*, *Q. suber*, *Alnus glutinosa*, on wood, 03 January 2004, A. González-Cruz & F. Prieto-García s.n. JA-CUSSTA 4098 (JA); Grazalema, Las Cumbres, on *Quercus suber* wood, 07 October 2001, A. Castro s.n. MA-Fungi 53681 (MA). **Girona:** Requesens, Castell, on *Populus* wood, 07 October 1995, A. Prunell s.n. LOU-Fungi 8264 (LOU). Riells, on wood of unidentified deciduous tree, 28 September 1996, A. Rocabrúna s.n. SCM 3140 (SCM). **Gipuzkoa:** Tolosa, on wood of unidentified deciduous tree (*Quercus rubra* or *Acer*), 23 June 2001, P. Pasabán ARAN s.n. (ARAN). **Granada:** Aldeire, Río Aldeire, in *Populus* forest, apparently terrestrial, 27 September 2003, A. Capilla s.n. JA-CUSSTA 4305 (JA). **Huelva:** Ribera del Múrtiga, La Nava, on *Populus nigra* wood, 18 October 1992, L. Romero de la Osa s.n. MA-Fungi 33470 (MA). **Navarra:** Bakaiku, *Fagus* forest, 07 November 2004, L. García Bona s.n. MA 67874, nrITS HM562051, *tefl* KJ010029 (MA). **Oviedo:** Lugones, mixed forest, on well-decayed hardwood log (probably *Quercus* or *Castanea*), 08 May 2005, L.A. Parra s.n. AJ 349, nrITS JN603199, *tefl* KJ010026 (CUW). Somiedo, Veigas, on unidentified wood, 22. August 1997, E. Rubio-Domínguez s.n. MA-Fungi 38383 (MA).

Pluteus americanus (P. Banerjee & Sundb.) Justo, E.F. Malysheva & Minnis, *comb. & stat. nov.* Fig. 28
MycoBank 808736

Basionym: *Pluteus salicinus* var. *americanus* Banerjee & Sundberg, Mycotaxon 47: 393. 1993. Holotype:—UNITED STATES OF AMERICA. Michigan: Emmet Co., Pellston Hills, west of Pellston, 03 September 1957, on wood of *Populus*, A.H. Smith 57842, nrITS KJ009762, *tefl* KJ010037 (MICH!).

Pileus 10–60 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, sometimes slightly depressed at center; surface usually with distinct squamules at center, radially fibrillose or smooth towards margin; usually with predominant brown or pale brown colors (10YR 7/3–7/8, 8/3–8/8), darker and more gray-brown at center (10YR 5/1–5/3, 4/1–4/3), in some collections with distinct blue-green tinges especially center (Gley1 6/1, 7/1; Gley2 7/1, 8/1); dry or slightly viscid when moist, strongly hygrophanous; margin smooth or translucent-striate. Lamellae crowded, free, ventricose, up to 6 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 15–65 × 3–6 mm, cylindrical, with slightly broad base; surface white, commonly with distinct blue-green tinges (Gley1 6/1, 7/1; Gley2 7/1, 8/1) especially near the base, sometimes all over the stipe, smooth or with longitudinal brown or gray-brown fibrils, especially near the base. Context in stipe and pileus white or slightly grayish. Smell usually strong and like leaves of *Pelargonium*, more rarely indistinct. Taste similar to smell or indistinct. Spore print pink to pinkish brown.

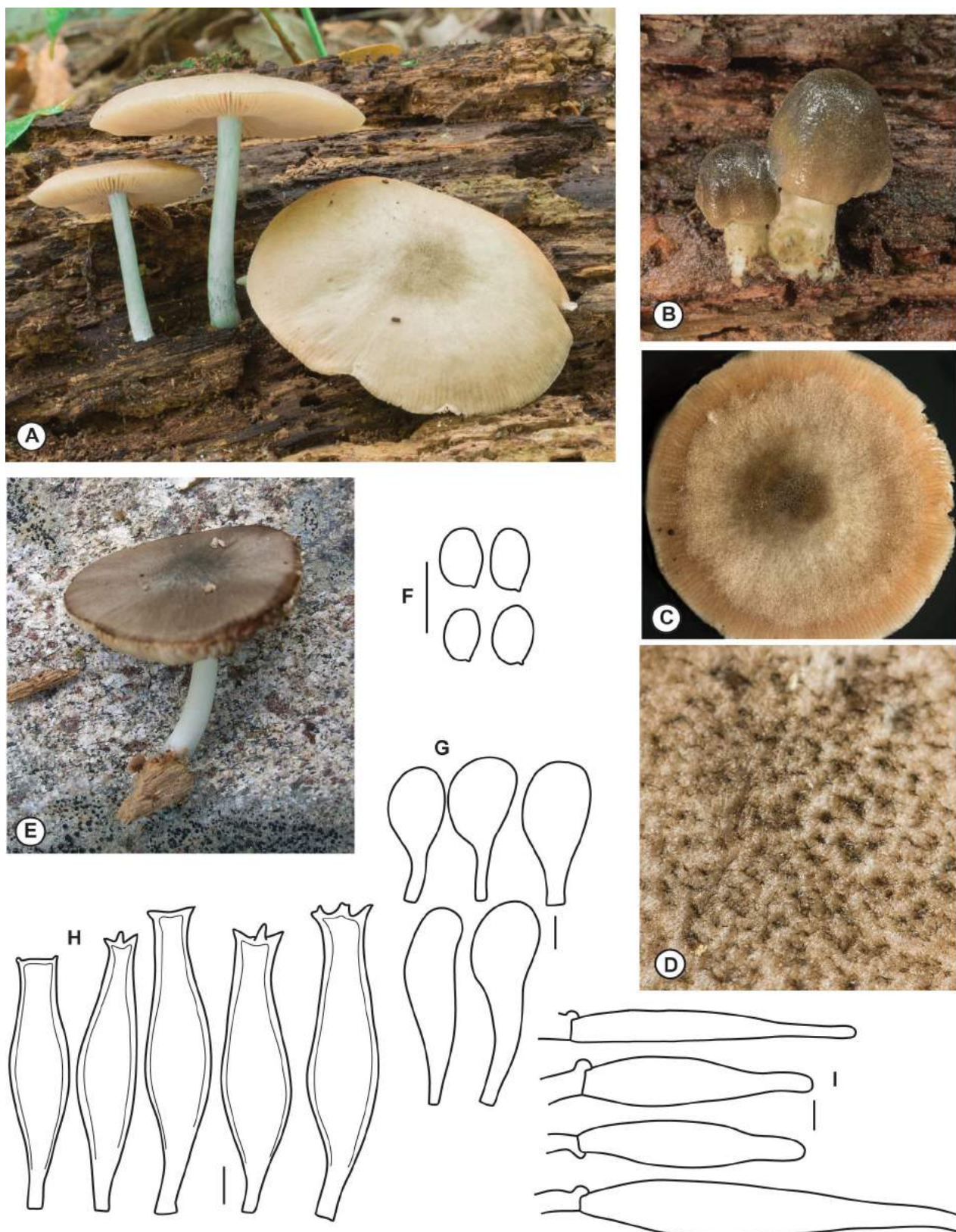


FIGURE 28. *Pluteus americanus*. A–D. Collection *MO 145100* (photos by A. Houghtby). A. Mature basidiocarps. B. Young basidiocarps. C. Detail of pileus showing the hygrophanous surface. D. Detail of pileus center. E. Collection *AJ 596*. F. Basidiospores. G. Cheilocystidia. H. Pleurocystidia. I. Pileipellis. F–I from *MO 145100*. All line drawings by A. Justo. Scale bars = 10 µm.

Basidiospores [110, 5, 4] 6.5–9.5(–11.0) × 4.5–7.0(–7.5) µm, avl × avw = 7.9–8.5 × 5.6–6.1 µm, Q = 1.29–1.59, avQ = 1.35–1.44, ellipsoid, more rarely broadly ellipsoid, sometimes ovoid or slightly constricted in the middle. Basidia 16–34 × 6–12 µm, tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 50–93 × 12–24(–28) µm, fusiform, narrowly fusiform or narrowly utriform with 2–4 apical hooks (usually entire and well-developed, sometimes bifid), with up to 4 µm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type. Lamellar edge sterile. Cheilocystidia 34–65(–70) × 12–22 µm, clavate, narrowly clavate or spheropedunculate, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 80–194 × 10–22 µm, individual elements cylindrical, some strongly tapering towards apex, hyaline or filled with brown intracellular pigment, sometimes grayish or bluish in fresh specimens, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–25 µm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae; also present and common in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary or gregarious. Growing on decayed hardwoods (*Fraxinus*, *Populus*). In hardwood-dominated or mixed, temperate or transitional forests. August–September.

Distribution:—**Eurasia.** Known only from the Russian Far East (Primorsky Territory). **North America.** Known with certainty from Illinois, Michigan and New York, probably more widespread in the Eastern parts. Not recorded from western North America.

Observations:—Banerjee & Sundberg (1993) described *Pluteus salicinus* var. *americanus* as different from the type variety based on the hygrophanous pileus, the translucent-striate pileus margin and pleurocystidia with “compound ornamentation” (i.e. with bifid hooks). Based on our observations, margin striation and the proportion of pleurocystidia with bifid hooks are not really different from what is found in *Pluteus salicinus*. *P. americanus* has a pileus with more predominantly brown tinges that is strongly hygrophanous while *P. salicinus* has a more grayish pileus that is less markedly hygrophanous but both characters intergrade to some extent. Geographical distribution is probably the best character to tell both species apart, with *Pluteus salicinus* confined to Eurasia and *Pluteus americanus* in North American and the Russian Far East. Many of the North American records of *Pluteus salicinus* probably correspond to *Pluteus americanus*, but some may correspond to other taxa in this group (e.g. *P. oreibatus*, *P. saupe*).

The separation of both taxa is not supported in the nrITS phylogenies, however they appear as separate species in the *tefl* and combined analyses, with statistical support in the former (Fig. 6).

Additional collections examined:—**RUSSIA. Far East Federal District:** Primorsky Territory, Ussuriysky Nature Reserve, Peishula Reserve Field Station, valley of Suvorovka River, floodplain forest (*Chosenia*, *Salix*, *Corylus*), on decayed wood of deciduous tree, 15 August 2011, *E.F. Malysheva s.n.* LE 289369, nrITS KJ009759, *tefl* KJ010034 (LE). **UNITED STATES OF AMERICA. Illinois:** Cook Co., Elk Grove Village, Busse Woods, mixed forest, on *Fraxinus* wood, 09 September 2013, *A. Houghtby MO145100*, nrITS KJ009785, *tefl* KJ010038 (CUW). **Michigan:** Emmet Co., French Farm, 25 September 2009, *M. Keirle SF2-BPI 882765*, nrITS HM562174, *tefl* KJ010035 (BPI). **New York:** Essex Co., Adirondack Ecological Center, Huntington Wildlife Forest, mixed forest, on decayed wood, 18 August 2012, *A. Justo 591*, nrITS KJ009760 (CUW); *ibid.*, *A. Justo 596*, nrITS KJ009761, *tefl* KJ010036 (CUW).

Pluteus sepiicolor E.F. Malysheva, *sp. nov.* Fig. 29
MycoBank 808733

Diagnosis:—Differs from other species in the *P. salicinus* complex (*P. salicinus*, *P. americanus*, *P. oreibatus*) by the combination of deep brown pileus, metuloid pleurocystidia with predominant bifid apical hooks, the presence of clamp-connections in pileipellis and growth on conifers.

Holotype:—**RUSSIA. Far East Federal District:** Primorsky Territory, Sikhote-Alinsky Nature Biosphere Reserve, vicinities of Kabany Reserve Field Station, *Picea-Abies* forest with isolated *Alnus* and *Betula*, on mossy wood, 24 August 2011, *A.E. Kovalenko s.n.* LE 289365, nrITS KJ009765, *tefl* KJ010030 (LE!).

Etymology:—*sepiicolor* refers to color of pileus (sepia, deep brown).

Pileus 40–60 mm in diameter, nearly hemispherical or obtusely campanulate when young, expanding to convex or plano-convex, with a low, broad umbo; surface smooth or innately radially fibrillose, at center squamulose with dark (almost black) slender squamules; deep brown or sepia (7.5YR 4/3–4/6, 3/3–3/4); dry or slightly viscid when moist, hygrophanous; translucent-striate at margin. Lamellae crowded, free, slightly ventricose, up to 5 mm broad,

white-cream when young, later pink, with concolorous edges. Stipe 50–70 × 4–6 mm, cylindrical, slightly broadened towards base (up to 7–8 mm); surface white or yellowish in the upper part, grayish brown in the lower part; longitudinally fibrillose, with blackish brown fibrils. Context in stipe and pileus white or slightly grayish yellow. Smell indistinct. Taste not recorded. Spore print not recorded.

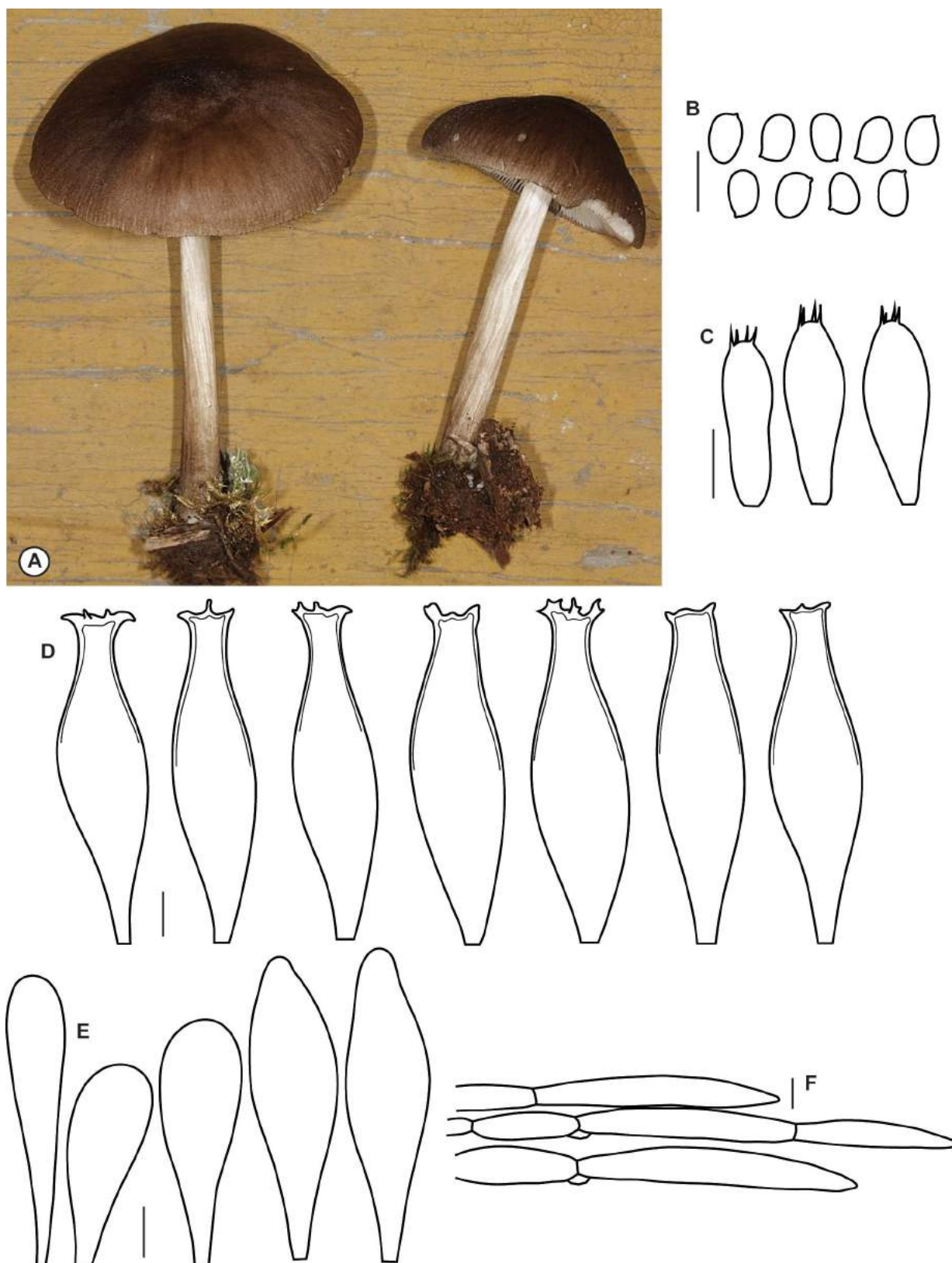


FIGURE 29. *Pluteus sepiicolor*. A. Collection LE 289365 (photo by E. Malysheva). B. Basidiospores. C. Basidia. D. Pleurocystidia. E. Cheilocystidia. F. Pileipellis. B–F from LE 289365. All line drawings by E. Malysheva. Scale bars = 10 µm.

Basidiospores [60/3/2] 7.8–8.6 (–9.0) \times 5.0–6.2 (6.5) μm , $\text{avl} \times \text{avw} = 8.0\text{--}8.3 \times 5.4\text{--}5.8 \mu\text{m}$, $Q = 1.29\text{--}1.60$, $\text{av}Q = 1.38\text{--}1.47$, ellipsoid to oblong, some ovoid, occasionally with medial constriction. Basidia 20–30 \times 5.5–10 μm , tetrasterigmate, narrowly to broadly clavate. Pleurocystidia metuloid, 40–90 \times 13–25 μm , fusiform, narrowly fusiform or narrowly utriform with 2–4(–5) apical hooks (commonly bifid, but entire hooks also present), hyaline, thick-walled (up to 2.7–3.0 μm). Intermediate cystidia similar to the pleurocystidia but slightly smaller and/or with thinner walls. Lamellar edge sterile. Cheilocystidia 40–70 \times 8–20 μm , clavate, narrowly clavate or narrowly utriform, some with slightly elongated apices, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with repent and slightly ascending hyphae; terminal elements 80–120 \times 10–25 μm , individual elements narrowly fusiform, filled with yellow-brown intracellular pigment, thin-walled. Stipitipellis a cutis; hyphae 7–20 μm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections present on pileipellis hyphae but not at every septum, also present and common in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary. Growing on decayed or mossy wood of conifers. In mixed or conifer forests in mountain area. August.

Distribution:—**Eurasia.** Known only from the Russian Far East (Primorsky Territory).

Observations:—*Pluteus sepiicolor* can be distinguished from *P. salicinus* and *P. americanus* by the growth on conifers and the dark brown colors of the pileus. *P. oreibatus* also grows on conifers but has differently shaped pleuro and cheilocystidia. Both nrITS and *tef1* phylogenies recover *P. sepiicolor* as a separate species in the *salicinus* clade.

Pluteus nigropallescens Singer (1961a: 116) can also have dark colors in the pileus but it differs from *P. sepiicolor* in the pleurocystidia with entire hooks and the terrestrial habitat. This species is only known from Venezuela (Singer 1961a). *Pluteus velutinornatus* can also present pleurocystidia with bifid hooks, but it has a more markedly fibrillose-squamulose pileus, usually wrinkled at center, and pigmented lamellar edges (Stevenson 1962; Horak 2008). This species is only known from New Zealand.

Additional collection examined:—**RUSSIA. Far East Federal District:** Primorsky Territory, Sikhote-Alinsky Nature Biosphere Reserve, vicinities of Kabany Reserve Field Station, conifer forest, on decayed wood, 24 August 2011, *N.V. Psurtseva s.n. LE 289366*, nrITS KJ009766, *tef1* KJ010031 (LE).

***Pluteus oreibatus* Justo, sp. nov.** Fig. 30

MycoBank 808734

Diagnosis:—Differs from other species in the *P. salicinus* complex (*P. salicinus*, *P. americanus*, *P. sepiicolor*) by the combination of pleurocystidia with poorly developed hooks, cheilocystidia cylindrical or lageniform, and the growth on conifer wood.

Holotype:—UNITED STATES OF AMERICA. North Carolina: Haywood Co., Great Smoky Mountains National Park, Cataloochee Valley, Rough Fork Trail, 09 October 2010, on fallen conifer wood, *E.C. Vellinga 4183*, nrITS KJ009763, *tef1* KJ010033 (TENN!).

Etymology:—*oreibatus* comes from the Greek term “ορειβατης” which roughly translates to “mountain ranging” or “to walk on mountains”. It is given to this species for its distribution in the Smoky Mountains and the Adirondacks.

Pileus 20–40 mm in diameter, convex or plano-convex, with a low, broad umbo; surface smooth or with some squamules and fibrils around center; dark brown or gray-brown (7.5YR 3/2–3/4, 4/1–4/6); dry or slightly viscid when moist; margin smooth or only slightly translucent-striate. Lamellae crowded, free, ventricose, up to 5 mm broad, white when young, later pink, with even, or white, flocculose edges. Stipe 20–50 \times 3–5 mm, cylindrical, with equal or slightly broadened base; surface white, smooth or with longitudinal brown or gray-brown fibrils, especially near the base. Context in stipe and pileus white. Smell sweetly raphanoid or indistinct. Taste not recorded. Spore print not recorded.

Basidiospores [40, 2, 2] (7.0–)7.5–9.0 \times 5.0–7.0 μm , $\text{avl} \times \text{avw} = 7.9\text{--}8.3 \times 5.5\text{--}5.9 \mu\text{m}$, $Q = 1.29\text{--}1.60$, $\text{av}Q = 1.42\text{--}1.45$, ellipsoid, more rarely broadly ellipsoid or oblong, sometimes ovoid or slightly constricted in the middle. Basidia 16–34 \times 6–12 μm , tetrasterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 55–75(–85) \times 12–20 μm , fusiform, narrowly fusiform or narrowly utriform with 2–3 apical hooks (not well-developed, usually rounded and not very prominent), some with truncate apex and/or without apical hooks, with up to 2 μm thick wall, frequent all over lamellar faces. Intermediate cystidia occurring in two morphological types (i) similar to the pleurocystidia with thinner walls; (ii) cylindrical or lageniform (similar to cheilocystidia) with slightly thickened walls and occurring in clusters; either type can be predominant. Lamellar edge sterile. Cheilocystidia 36–80 \times 9–15 μm , cylindrical, lageniform, narrowly utriform or narrowly clavate, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 80–132 \times 8–15 μm ,

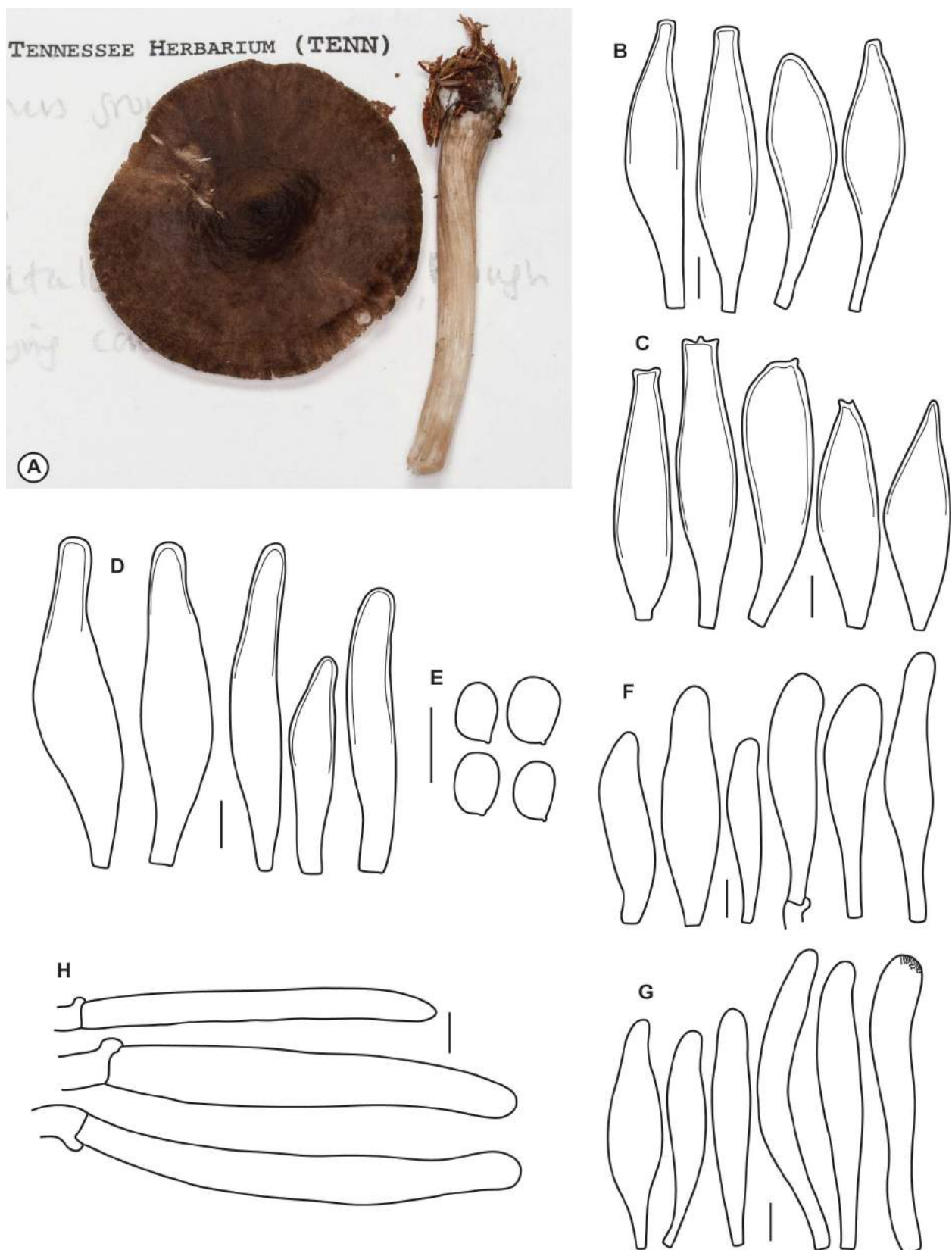


FIGURE 30. *Pluteus oreibatus*. A. Collection ECV 4183 (photo by M. Wood). B. Pleurocystidia from ECV 4183. C. Pleurocystidia from AJ 600. D. Intermediate cystidia from AJ 600. E. Basidiospores from ECV 4183. F. Cheilocystidia from AJ 600. G. Cheilocystidia from ECV 4183. H. Pileipellis from ECV 4183. All line drawings by A. Justo. Scale bars = 10 μ m.

individual elements cylindrical, some strongly tapering towards apex, hyaline or filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–22 μm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on the pileipellis hyphae at all septa or nearly so; also present and common in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary. Growing on decayed wood of conifers. In mixed forests in mountain areas. August–October.

Distribution:—**North America.** Known only from the Great Smoky Mountains National Park (North Carolina) and the Adirondack mountains (New York).

Observations:—*Pluteus oreibatus* can be separated from *P. americanus* by the growth on conifers and the shape of the cheilocystidia. *Pluteus saupe* also has lageniform cheilocystidia but it lacks the cylindrical or narrowly clavate ones that are present in *P. oreibatus*.

Pluteus amphyctistis (Singer 1958: 213) also has pleurocystidia without distinct apical hooks but it differs from *P. oreibatus* in the yellow coloration of the pileus, the smaller basidiospores (up to 6.3 μm long), the smaller cheilocystidia (up to 28 μm long) and the lack of clamp-connections. This taxon has been reported from Bolivia (Singer 1958), Martinique (Pegler 1983), India (Pradeep *et al.* 2002) and Mexico (Rodríguez 2014).

Additional collection examined:—UNITED STATES OF AMERICA. **New York:** Essex Co., Adirondack Ecological Center, Huntington Wildlife Forest, mixed forest, on decayed conifer wood, 17 August 2012, *D. Floudas s.n. AJ 600*, nrITS KJ009764, *tefl* KJ010032 (CUW).

Pluteus saupe Justo & Minnis in Justo *et al.* (2011a: 475). Fig. 31

Holotype:—UNITED STATES OF AMERICA. Illinois: Champaign Co., Urbana, Brownfield Woods, 05 August 1980, on decaying log, *S.G. Saupe 230*, nrITS HM562113 (ILLIS!).

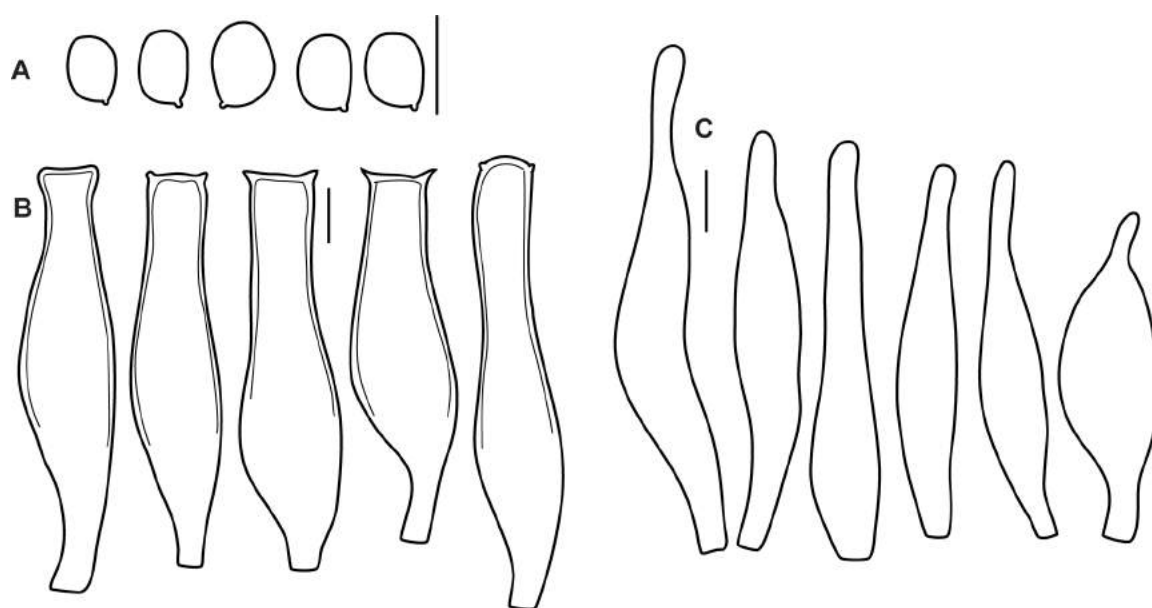


FIGURE 31. *Pluteus saupe*. A. Basidiospores. B. Pleurocystidia. C. Cheilocystidia. All from *SG Saupe 230*. All line drawings by A. Justo. Scale bars = 10 μm .

Pileus 10–35 mm in diameter, convex or plano-convex, with shallow depression at center; surface innately radially fibrillose, with blackish, spinulose squamules at center, gray to gray-brown, bruised regions become blue, with olive green tinges in older specimens; margin translucent-striate in older specimens. Lamellae crowded, free, ventricose, approx. 5 mm broad, pink, with slightly paler edges. Stipe 10–50 \times 3–5 mm, cylindrical, broadened towards base; surface white, with some longitudinal fibrils near the base, turning blue when bruised, with olive green tinges in older specimens. Context color not recorded, probably whitish. Smell and taste not recorded. Spore print pinkish brown.

Basidiospores [30, 1, 1] 6.5–9.0(–10.0) \times 5.0–6.5(–7.0) μm , $\text{avl} \times \text{avw} = 7.7 \times 5.8 \mu\text{m}$, $Q = 1.15\text{--}1.60(1.70)$, $\text{av}Q = 1.33$, (broadly) ellipsoid, rarely oblong. Basidia 17.5–26 \times 7.5–10 μm , tetrasterigmate, rarely bisterigmate,

clavate, oblong or ellipsoid, some with median constriction. Pleurocystidia metuloid, $70\text{--}85 \times 17\text{--}22\ \mu\text{m}$, fusiform or narrowly utriform, with 2–4 hooks at apices, but hooks usually poorly developed, hyaline, with up to $2\ \mu\text{m}$ thick walls, frequent all over lamellar faces. Lamellar edge sterile. Cheilocystidia $45\text{--}85 \times 9.5\text{--}19.5\ \mu\text{m}$, mostly lageniform with elongated apices, some fusiform or ovoid, hyaline, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements $80\text{--}135 \times 10\text{--}16\ \mu\text{m}$; individual elements cylindrical, some strongly tapering towards apex, mostly filled with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae $5\text{--}15\ \mu\text{m}$ wide, cylindrical, hyaline or with intracellular brown pigment, with thin, smooth walls. Clamp-connections present in all tissues, more abundant at the base of cheilocystidia and on pileipellis.

Habit, habitat and phenology:—Solitary. Growing on decayed wood. In mixed mesophytic upland forest. August

Distribution:—**North America:** Known only from central Illinois (USA).

Observations:—Nothing can be added to the original description (Justo *et al.* 2011) reproduced above. The predominantly lageniform cheilocystidia with elongated apices are the most distinctive morphological feature of *Pluteus saubei*.

VI. *atromarginatus* clade. Fig. 7

Species growing on conifer wood. Lamellar edges pigmented (brown, dark brown) over their entire length. Clamp-connections common and easy to spot on pileipellis hyphae.

Pluteus atromarginatus (Singer) Kühner (1935: 51). Fig. 32

Basionym: *Pluteus cervinus* var. *atromarginatus* Singer (1925: 40). The holotype collection has been destroyed (Singer 1956; Banerjee & Sundberg 1995) and no other kind of type has been designated.

Synonym: *Pluteus tricuspidatus* Velenovský (1939: 143). To the best of our knowledge, no holotype exists and no other material has been designated as any kind of type.

Synonym: *Pluteus cervinus* var. *nigrofloccosus* Schulz (1912: 102); *Pluteus nigrofloccosus* (Schulz) J. Favre (1948: 104). To the best of our knowledge, no holotype exists and no other material has been designated as any kind of type.

Synonym: *Pluteus pseudoroberti* Moser & Stangl (1963: 39), emend. Vellinga (in Vellinga & Schreurs 1985: 340). Holotype:—GERMANY. Baden-Württemberg: Aalen, Spitwald, 30 August 1951, rotting wood, *MM Moser 51/100*, nrITS KJ009769, *tefl* KJ010017 (M!).

Synonym: *Pluteus atropungens* Smith & Bartelli, (1965: 65). Holotype:—UNITED STATES OF AMERICA. Michigan: Marquette Co., Marquette, 20 October 1959, on sawdust, *I. Bartelli, A.H. Smith 62033*, nrITS HM562059, *tefl* KJ010013 (MICH!).

Synonym: *Pluteus laricinus* Banerjee & Sundberg (1993: 392). Holotype:—UNITED STATES OF AMERICA. Michigan: Oakland Co., Proud Lake Recreation Area, 30 October 1951, on rotten *Larix* log, *A.H. Smith 38888*, nrITS KJ009772 (MICH!).

Pileus 25–100(–120) mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo; strongly radially fibrillose all over or only around center, usually with distinct squamules around center; brown (7.5YR 5/4–5/8, 4/3–4/8, 3/3–3/4), or gray (Gley2 4/1, 5/1), usually darker at center; dry or slightly viscid when moist; margin smooth or translucent-striate. Lamellae crowded, free, ventricose, up to 10 mm broad, white when young, later pink, with distinct dark brown edges for the whole length of the lamella, very rarely only colored in the part near the margin of pileus. Stipe 40–120 \times 4–11 mm, cylindrical, with slightly broad base; surface white, or whitish gray, commonly covered with dense gray-brown fibrils all over, more rarely only near the base. Context in stipe and pileus white or slightly grayish. Smell sweet, fungoid or indistinct. Taste similar to smell. Spore print pink to pinkish brown.

Basidiospores [300, 15, 15] (5.5–)6.0–8.5(–9.0) \times 4.0–6.0(–7.0) μm , $avl \times avw = 6.8\text{--}7.5 \times 4.8\text{--}5.2(–5.9)\ \mu\text{m}$, $Q = (1.00\text{--})1.30\text{--}1.70$, $avQ = (1.24\text{--})1.32\text{--}1.52$, ellipsoid to oblong, more rarely broadly ellipsoid, very rarely globose or subglobose, sometimes ovoid or slightly constricted in the middle. Basidia 16–35 \times 6–12 μm , tetrasterigmate, rarely bisterigmate or monosterigmate, clavate, some with median constriction. Pleurocystidia metuloid, 60–110 \times 10–20(–25) μm , fusiform, narrowly fusiform or narrowly utriform, some with a bifurcated apex, provided with 2–5 apical hooks (usually entire and well-developed), rarely without apical hooks, with up to 5 μm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; without a predominant morphological type; some with intracellular brown pigment. Lamellar edge sterile. Cheilocystidia

25–110(–140) × 10–30 µm, mostly narrowly clavate or clavate, some narrowly utriform or spheropedunculate, the majority filled with intracellular brown pigment but hyaline ones also occur, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements (40–)70–190(–210) × 7–24(–30) µm; individual elements cylindrical, some strongly tapering towards apex, with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–20 µm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae; also present and common in other parts of the basidiocarp.

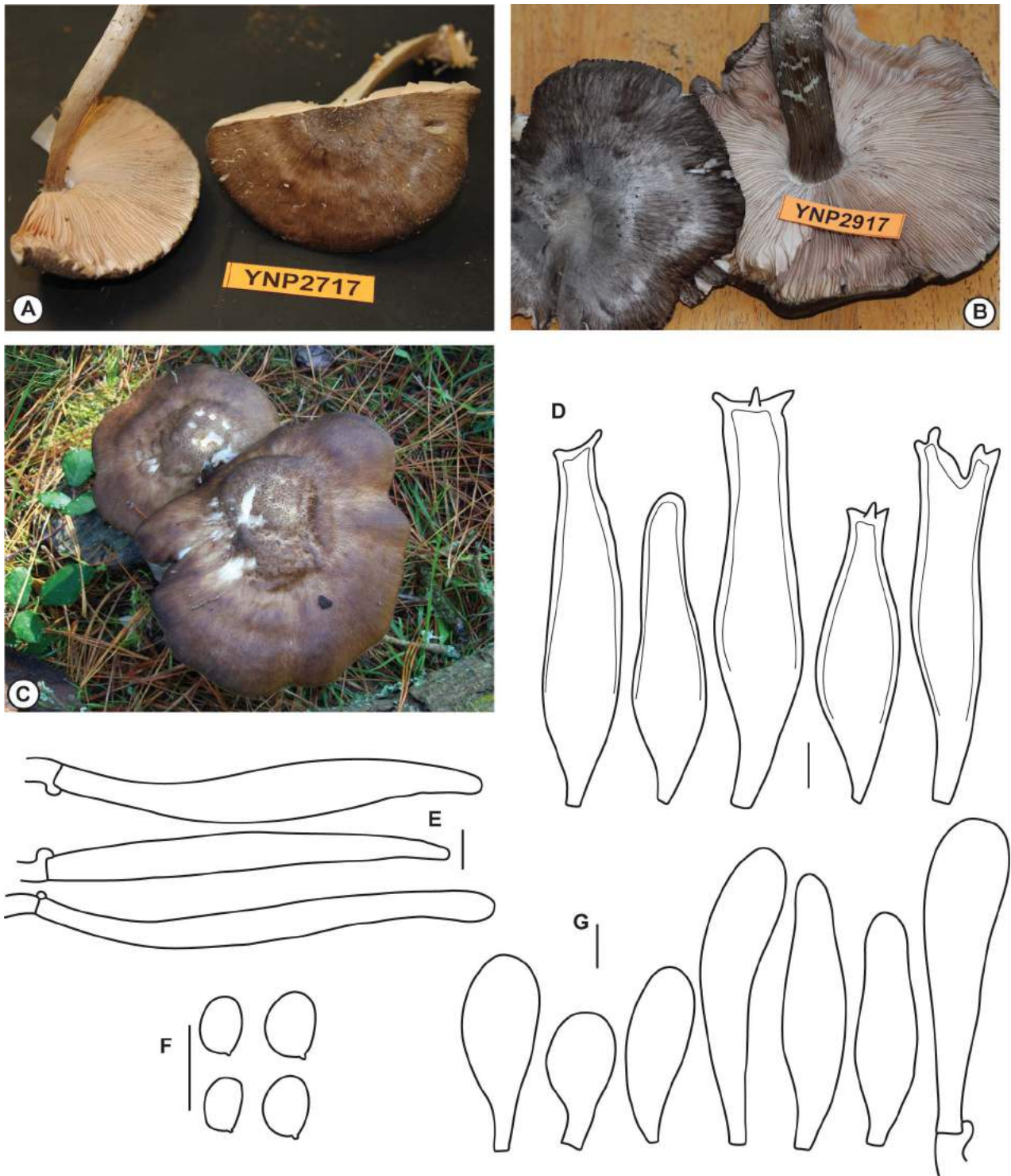


FIGURE 32. *Pluteus atromarginatus*. A. Collection UC 1860913 (photo by G. Cobian). B. Collection UC 1860914 (photo by G. Cobian). C. Collection AJ 75 (photo by A. Justo). D. Pleurocystidia. E. Pileipellis. F. Basidiospores. G. Cheilocystidia. D–G from AJ 75. All line drawings by A. Justo. Scale bars = 10 µm.

Habit, habitat and phenology:—Solitary or subgregarious. Growing on decayed wood of conifers (e.g. *Picea*, *Pinus*, *Larix*), very rarely on sawdust or angiosperm wood (e.g. *Populus*). In conifer-dominated or mixed forests and plantations, in temperate and mountainous areas. July–November (–February in Mediterranean areas).

Distribution:—**Eurasia.** Widespread in western Europe and eastwards into Siberia. **North America.** Widespread, known from the eastern and western parts.

Observations:—*Pluteus atromarginatus* is one of the most distinct taxa in the section, characterized by the relatively large basidiocarps, fibrillose-squamose pileus, dark brown lamellar edges, presence of clamp-connections, and very thick-walled pleurocystidia.

Molecular data from the type collections of *P. pseudoroberti*, *P. atropungens* and *P. laricinus* show that these species are synonyms of *P. atromarginatus*. All three represent unusual morphological variants of *P. atromarginatus*.

The presence of clamp-connections was not mentioned in the original description of *P. pseudoroberti* but the revision of the type by E.C. Vellinga did reveal numerous clamp-connections on the pileipellis, therefore the taxonomic concept of this species did radically change (Vellinga & Schreurs 1985). Most of the cheilocystidia in the collection are hyaline, and only a few have intracellular brown pigment (Bonnard 1995; pers. obs.) so a relation with *P. atromarginatus* was not suspected. The nrITS sequences in GenBank under the name *P. pseudoroberti* correspond to *P. hongoi* (JN021083) and *P. pellitus* (JF908600, JF908603).

Pluteus atropungens was described as a separate species (Smith & Bartelli 1965) because of the smooth metuloids without hooks. The type collection does have predominantly non-hooked metuloids, a phenomenon also observed in some collections from Spain (Justo & Castro 2007a). The type also has a wider than usual variation in size and shape of basidiospores; all exceptional values (in parentheses) for these two characters in the above description come from the type study of *P. atropungens*.

Pluteus laricinus was described by Banerjee & Sundberg (1993) based on a collection by Alexander Smith with grayish lamellar edges but only near the margin of the pileus. All other characters fit well our concept of *P. atromarginatus*.

Additional collections examined:—**RUSSIA. Siberian Federal District:** Novosibirsk Region, Novosibirsk District, Akademgorodok, mixed, poorly lit eutrophic planted forest (*Pinus sylvestris*, *Betula pendula*) ca. 40 years old with a lot of dead trees, on decayed wood of *Pinus*, rotten half-buried trunk, 07 July 2011, T.M. Bulyonkova s.n. LE 289425, nrITS KJ009770, *tefl* KJ010012 (LE); *ibid.*, relic Ob terrace *Pinus sylvestris* forest, on *Pinus* stump, 21 September 2011, Vlad Labetsky s.n. LE 289417, nrITS KJ009771, *tefl* KJ010011 (LE). **SPAIN. A Coruña:** Camariñas, *Pinus* forest, on decayed wood of *Pinus*, 19 October 2008, A. Justo & GMG AJ75, nrITS HM562061, *tefl* KJ010015 (LOU); *ibid.*, J. Rodríguez & GMG s.n. AJ76, nrITS HM562040, *tefl* KJ010016 (LOU). Corcubión, Finisterre, *Pinus* forest, 3 October 1983, L. Freire & M. Pérez-Froiz s.n. LOU-Fungi 6267 (LOU). Santiago de Compostela, on *Pinus pinaster* wood, 19 January 1986, L. Freire & M. Castro s.n. LOU-Fungi 2709 (LOU); *ibid.*, 26 October 1988, A. Zaera & L. Rodríguez s.n. LOU-Fungi 4437 (LOU). **Barcelona:** Dosrius, *Pinus pinaster* forest, 9 January 1993, M. Tabarés & al. s.n. SCM 2078 (SCM). **Castellón:** Fredes, Pinar Plá, on *Pinus sylvestris* wood, 17 October 2001, P. Daniels s.n. MA-Fungi 52174 (MA). Pina del Montalgrao, Umbría de Santa Bárbara, on *Pinus sylvestris* stump, 17 October 1996, F. Tejedor PT 108 (LOU). Vistabella del Maestrat, Sanahuja, on *Pinus sylvestris* stump, 26 October 1997, F. Tejedor PT 235 (LOU). **Gipuzkoa:** Ezkio Itsaso, on *Pinus radiata* wood, 30 August 1999, Z.E. Aranzadi s.n. ARAN 5037215. **Girona:** Nevà (Ripollès), on unidentified conifer wood, September 1996, M. Tabarés s.n. SCM 3128 (SCM). **Jaén:** Orcera, Los Negros, in *Pinus nigra* & *Pinus halepensis* forest, on wood, 25 October 2003, J. de Dios Reyes García s.n. JA-CUSSTA 4071 (JA). Navarra: Alsasua, on *Pinus sylvestris* stump, 23 September 1995, P. Pasabán s.n. ARAN s.n. (ARAN). **Pontevedra:** As Neves, on *Pinus pinaster* stump, 10 February 2002, J. Rodríguez-Vázquez s.n. LOU-Fungi 16667 (LOU). Cangas, Cabo Home, in *Pinus* forest in sand dunes, 18 October 1993, J. Rodríguez-Vázquez & L. Freire s.n. LOU-Fungi 7093 (LOU). Carretera de Porriño a Gondomar, 25 November 1982, F.D. Calonge s.n. MA-Fungi 4503 (MA). Sta. María de Oia, 15 December 2001, X. Varela s.n. LOU-Fungi 17382 (LOU). Vigo, Campus As Lagoas-Marcosende, on *Pinus* stump, 23 September 2002, A. Justo LOU-Fungi 18235 (LOU); Vigo, Parque Forestal de Beade, on *Pinus* stump, 20 October 2003, P. Lorenzo & A. Justo s.n. LOU-Fungi 18232 (LOU). Vigo, Saians, 6 December 2001, X. Varela s.n. LOU-Fungi 17309 (LOU). Vigo, Zamáns, on *Pinus pinaster* stump, 9 November 1980, C. Castro s.n. LOU-Fungi 2710 (LOU). **Soria:** Duruelo de la Sierra, in *Pinus sylvestris* forest, 15 September 1992, F. Martínez-Peña s.n. VALON 941 (VALON). Pinar Grande, on *Pinus pinaster* stump, 10 September 1992, F. Martínez s.n. VALON 959 (VALON). San Leonardo de Yagüe, on *Pinus sylvestris* stump, 5 June 1995, S.A. Romanillos s.n. VALON 1244 (VALON). Tardelcuende, on *Pinus pinaster* wood, 25 October 2001, Ibon s.n. VALON 1909 (VALON). UNITED

STATES OF AMERICA. **California:** Alameda Co., Berkeley, Santa Fe Ave., on decayed wood of *Pinus*, 22 November 2011, *N.H. Nguyen s.n. UC 1998538*, nrITS JX857451 (UC). Marin Co., Point Reyes National Seashore, at edge of recently burned coastal scrubland with scattered *Pinus*, on stump, 28 January 2006, *E.C. Vellinga s.n. UC 1859503*, nrITS KF306035 (UC). Tuolumne Co., Yosemite National Park, Along HWY 41, at Rail Creek, mixed conifer forest with *Pinus ponderosa*, *Pinus lambertiana*, *Calocedrus* sp., and *Quercus kelloggii*, on conifer wood, 29 October 2011, *N.H. Nguyen s.n. UC 1860913*, nrITS JX857464, *tefl* KJ460251 (UC); *ibid.*, pulloff on West Side of HWY 41, mixed conifer forest with *Pinus ponderosa*, *Pinus lambertiana*, *Calocedrus* sp., and *Quercus kelloggii*, 29 October 2011, *G. Cobian s.n. UC 1860914*, nrITS JX857465, (UC). **Oregon:** Jefferson Co., Suttle Lake area, near Sisters Deschutes National Forest, 07 October 1987, *W.J. Sundberg 3657*, nrITS HM562083 (ILLS). **Tennessee:** Knox Co., Knoxville, 21 September 2009, *J.M. Birkebak 09210901*, *tefl* KJ010014 (TENN).

Pluteus atrofibrillosus Vellinga & Justo, *sp. nov.* Fig. 33
MycoBank 808735

Diagnosis:—Differs from *Pluteus atromarginatus* in the more loosely arranged fibrils and squamules on the pileus, the slightly smaller basidiospores and the pleurocystidia predominantly with 2 apical hooks.

Holotype:—UNITED STATES OF AMERICA. Tennessee: Sevier Co., Gatlinburg, near Little Creek, 07 October 2010, on conifer wood, *E.C. Vellinga 4153a*, nrITS KJ009774, *tefl* KJ010020 (TENN!).

Etymology: *atrofibrillosus* is from the Latin words “ater” (dark) and “fibrillosus” (with fibers) referring to the pileus covered with dark fibrils.

Pileus 25–55 mm in diameter, hemispherical or campanulate when young, expanding to convex or plano-convex, with or without a low, broad umbo, strongly radially fibrillose all over, fibrils usually group to form squamules around center, sometimes with small squamules all over; brown (7.5YR 6/6–6/8, 5/6–5/8), darker at center (7.5YR 3/3–3/4); dry or slightly viscid when moist; margin smooth or translucently striate. Lamellae crowded, free, ventricose, up to 5 mm broad, white when young, later pink, with distinct dark brown edges over the whole length of the lamella. Stipe 30–70 × 3–6 mm, cylindrical, with slightly broad base; surface white, or whitish gray, smooth or with longitudinal gray-brown fibrils, especially near the base. Context in stipe and pileus white. Smell not recorded. Taste not recorded. Spore print not recorded.

Basidiospores [90, 3, 3] 5.5–7.5 × 4.0–5.5(–6.0) μm, avl × avw = 6.5–6.8 × 4.5–5.1 μm, Q = 1.19–1.60, avQ = 1.30–1.46, ellipsoid or broadly ellipsoid, very rarely oblong, sometimes ovoid or slightly constricted in the middle. Basidia 16–29 × 6–9 μm, tetrasterigmate, some with median constriction. Pleurocystidia metuloid, 45–75 × 11–23 μm, fusiform, narrowly fusiform or narrowly utriform, some with a bifurcated apex, the majority provided with 2 apical hooks (usually entire and well-developed), more rarely with 3–4 or none, with up to 3 μm thick wall, frequent all over lamellar faces. Intermediate cystidia similar to the pleurocystidia but smaller and/or with thinner walls, a few irregularly shaped, without distinct apical hooks and/or with rounded apices; the non-hooked morphotype predominant, or without a predominant morphological type; some with intracellular brown pigment. Lamellar edge sterile. Cheilocystidia 41–65 × 9–22 μm, mostly narrowly clavate or narrowly utriform, the majority filled with intracellular brown pigment but hyaline ones also occur, thin-walled, crowded, forming a well-developed strip. Pileipellis a cutis, with terminal elements 68–143 × 9–16 μm; individual elements cylindrical, some strongly tapering towards apex, with brown intracellular pigment, with thin, smooth walls. Stipitipellis a cutis; hyphae 5–25 μm wide, cylindrical, hyaline or with brown intracellular pigment, with thin, smooth walls. Clamp-connections common and readily seen on pileipellis hyphae; also present and common in other parts of the basidiocarp.

Habit, habitat and phenology:—Solitary or subgregarious. Growing on decayed wood of conifers. In mixed temperate forests. October.

Distribution:—**North America.** Only known from three places in the Great Smoky Mountains National Park (Tennessee and North Carolina, USA)

Observations:—*Pluteus atrofibrillosus* is very similar to *Pluteus atromarginatus* but the fibrils and squamules on the pileus appear more loosely arranged. The slightly smaller basidiospores (on average 6.5–6.8 × 4.5–5.1 μm) and the pleurocystidia also smaller (45–75 × 11–23 μm) and mostly with only 2 hooks at apex may be helpful to separate both species on microscopical grounds, but this should be checked in future collections of *P. atrofibrillosus*.

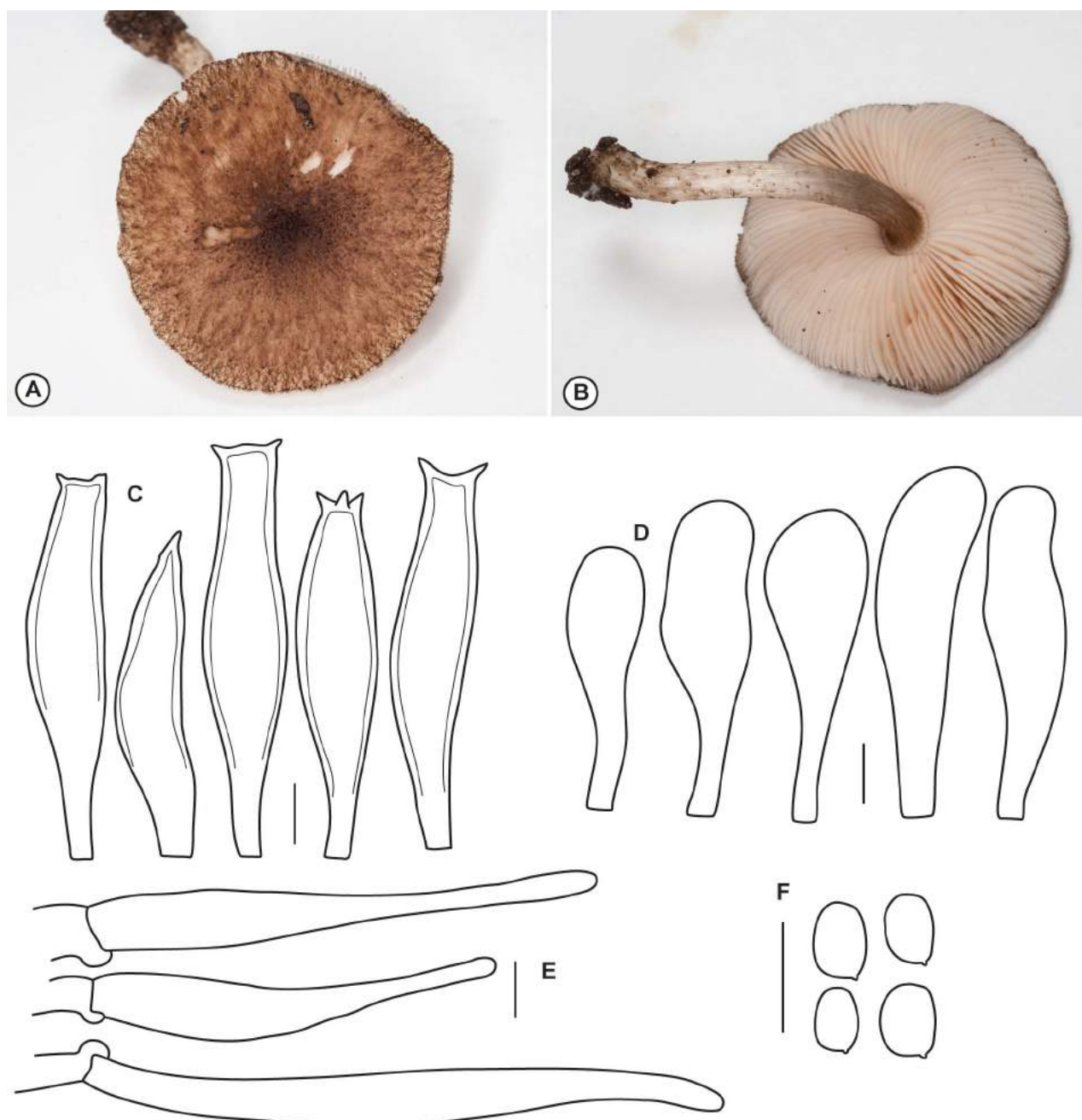


FIGURE 33. *Pluteus atrofibrillosus*. A–B. Collection ECV 4153a (photo by M. Wood). C. Pleurocystidia. D. Cheilocystidia. E. Pileipellis. F. Basidiospores. C–F from ECV 4153a. All line drawings by A. Justo. Scale bars = 10 μ m.

Pluteus similis has a darker pileus and pleurocystidia that are longer (up to 90 μ m long) and provided with 3–6 apical hooks (Horak 2008). *Pluteus microspermus* and *Pluteus concentricus* share with *P. atrofibrillosus* the pigmented lamellar edges but they lack clamp-connections (Horak 2008). All these species are endemic to New Zealand (Horak 2008). The South American species *Pluteus squamosopunctus* has darker colors in the pileus, which is covered with pyramidal squamules, and pleurocystidia provided with 4–6 apical hooks (Horak 1964).

Additional collections examined:—UNITED STATES OF AMERICA. **Tennessee:** Cocke Co., Cosby, near Low Gap Trail, on conifer wood, 10 October 2009, *E.C. Vellinga* 4207, nrITS KJ009773, *tef1* KJ010018 (TENN). Sevier Co., Gatlinburg, Cherokee Orchard Road, before Rainbow Falls Trailhead, on wood, 10 October 2009, *B. Looney* s.n. ECV 4169, nrITS KJ009775, *tef1* KJ010019 (TENN).

Insufficiently known and doubtful taxa

Pluteus cinerascens Banerjee & Sundberg (1993: 390).

Holotype:—UNITED STATES OF AMERICA. Michigan: Chippewa-Luce Co., Tahquamenon Falls State Park, near Paradise, 24 July 1957, on hardwood log, *A.H. Smith 57433* (MICH!).

This taxon was described as new in 1993 based on a collection made by Alexander Smith in 1957, and an additional collection from Illinois (Banerjee & Sundberg 1993). In the original description the locality of the type is given as “Proud Lake Recreation area, Oakland Co., Michigan” which is different from the data on the herbarium label kept with this collection at MICH (reproduced above). In the original notes by A.H. Smith the habitat is given as “hardwood log” but in Banerjee & Sundberg (1993) it appears as “solitary on a very rotten log” without mention of the type of wood.

The most distinctive character is that the injured or bruised places along the margin of the pileus become gray (Banerjee & Sundberg 1993). The presence of “magnus-type” (i.e. fusiform and without apical hooks) pleurocystidia near the lamellar edge was later emphasized by Banerjee & Sundberg (1995). However in the original description the same authors described these structures as “pleurocystidia near lamellar edge mostly of cervinus-type interspersed with a few magnus-type” (Banerjee & Sundberg 1993). Clamp-connections are reported as absent in the original description (Banerjee & Sundberg 1993).

We have not been able to obtain molecular data from the type collection. We examined it morphologically and found several discrepancies with respect to previous descriptions of *P. cinerascens*: (i) basidiospores are larger (7–9 (9.5) × 5–6 (6.5) µm) than reported by Banerjee & Sundberg [“6–7.4 × 4.4–5.6 µm”]; (ii) “magnus-type” cystidia are present near the amellar edge (Banerjee & Sundberg 1993) but not predominant (Banerjee & Sundberg 1995); (iii) clamp-connections are present on the pileipellis hyphae.

Pluteus cinerascens, as understood after our revision of the type collection, could correspond to what we describe here as *P. americanus* or maybe *P. brunneidiscus*. Given the lack of molecular data for the type and the discrepancies between our examination of the type and the original description we prefer to consider *P. cinerascens* a doubtful name and do not apply it to any of the species described here.

Pluteus heterocystis Banerjee & Sundberg (1993: 392).

Holotype:—UNITED STATES OF AMERICA. Washington: Clallam Co., Olympic National Park, 20 May 1939, on soil, *A.H. Smith 13616* (MICH!).

This taxon was described as new in 1993 based on a collection made by Alexander Smith in 1939 (Banerjee & Sundberg 1993). According to the original description the most distinctive characters are the dimorphic pleurocystidia “one form 50–80 × 10–25 µm clavate to broadly fusoid-ventricose, apices more or less truncate, many with several short horns at apex and others merely with aborted apical ornamentations; the second form with apex rounded and lacking horns, wall uniformly 1.2–1.8 µm thick, no lateral ornamentation seen” (Banerjee & Sundberg 1993). The authors also indicate “A.H. Smith (unpublished) found clamp connections in the pileipellis, but our repeated attempts failed to demonstrate them” (Banerjee & Sundberg 1993).

We have not been able to obtain molecular data from the type collection. We did study it morphologically and found clamp-connections to be present and fairly common on the pileipellis hyphae of the type collection. The variation in pleurocystidia shapes and ornamentation is similar to what is found in many other species described here. The “second” morphological type described by Banerjee & Sundberg (1993) probably corresponds to intermediate cystidia.

Given the lack of molecular data for the type and the discrepancies between our examination of the type and the original description we prefer to consider *P. heterocystis* a doubtful name and do not apply it to any of the species described here, although this collection very likely represents *Pluteus brunneidiscus* as described here.

Pluteus leaianus (Saccardo) Singer (1973: 63).

Basionym: *Pluteolus leaianus* Saccardo (1895: 60).

In the original description of *Agaricus (Mycena) leaianus* Berkeley gives the data on the type collection as follows “On dead trunk, Ohio, May, n 214. T.G. Lea, Esq” (Berkeley 1845). Saccardo (1891) explicitly mentions the publication by Berkeley and formally combined this taxon in the genus *Mycena* (as *Mycena “leajana”*).

Saccardo (1895) introduced the name *Pluteolus leaianus* for a species with viscid-mucidus pileus and basidiospores 10–12 × 6 µm. This is a different taxon from *Agaricus leaianus* Berk., as Saccardo explicitly cites

“Berk in herb, Cooke in litt,” as the previous mentions of this taxon. In the literature (Singer 1956) and online databases such as MycoBank and Index Fungorum it is possible to find the name *Pluteolus leaianus* Berk ex. Cooke, without any bibliographic reference, but as far as we know neither Berkeley nor Cooke ever validly published “*Pluteolus leaianus*” and the name must be attributed solely to Saccardo (1895) who only cites the following data “ad truncos, Ohio, Amer, bor. (I.G. Lea)”.

Singer (1956) discussed briefly *Pluteolus leaianus* (“Berk. ex Cooke in Sacc.”) claiming that “the type from Ohio, USA (K) is a species of the *Pluteus cervinus* type”. Later, Singer (1973) recombined *Pluteolus leaianus* in *Pluteus*, citing the basionym as “*Pluteolus leaianus* Berk. ex Cooke apud Sacc., Syll. 11: 60. 1895”. It is very unclear what *Pluteus leaianus*, in the sense Singer intended, actually represents. It is neither the same taxon that Saccardo described as *Pluteolus leaianus* (1895) nor what Berkeley described as *Agaricus leaianus* (1845). Based on the description by Singer (1956) it could be *P. cervinus* or *P. hongoi* as described here, but given the confusing history of the epithet *leaianus* we choose not to apply that name to any of the species described here.

***Pluteus lilacinus* (Montagne) Singer (1961b: 337).**

Holotype:—UNITED STATES OF AMERICA. Ohio: near Columbus, Sullivant no. 90, July (PC).

Basionym: *Agaricus lilacinus* Montagne (1856: 110), illegitimate, non *Agaricus lilacinus* Lasch (1828: 162), nec *Agaricus lilacinus* Schumacher (1803: 293); *Mycena lilacina* Saccardo (1887: 527), *nom. nov.* for *Agaricus lilacinus* Montagne under the rules of ICN.

The original description of *Agaricus lilacinus* (available at MycoBank # 482473) suggests a *Mycena* species similar to *Mycena pura*. Saccardo (1887) also considered this as a species of *Mycena*. Singer (1956, 1961b) studied the type collection of *Agaricus lilacinus* Montagne and concluded that it was a *Pluteus* in the *cervinus*-group. Based on the descriptions (Singer 1956, 1961b) *Pluteus lilacinus* sensu Singer probably represents *Pluteus petasatus*.

***Pluteus lipidocystis* Bonnard (1986: 36).**

Holotype:—SWITZERLAND, Canton Vaud, Apples, Les Bougeries, September 1986, JB 86/150 (LAU).

This was described as a separate species because of the abundant cells with lipid contents in the hymenium (Bonnard 1986). It is known only from the type collection.

We have not been able to obtain molecular data from the type. Besides the cells with lipid contents, the morphological characters, especially basidiospore sizes and the lack of a well-developed strip of cheilocystidia, fit well the concept of *P. petasatus* presented here.

Discussion

Morphological and ecological characters for species recognition:—Characters related to the external macromorphology commonly used in the taxonomy of section *Pluteus* include color of the pileus, presence and arrangement of fibrils and squamules on the pileus and stipe, presence of pigment on the lamellar edges, presence of blue or blue-green tinges in any part of the basidiocarp and the smell of the fresh basidiocarps. All these characters are, to a certain extent, useful in separating the taxa recognized here but in many instances there is some degree of overlap between closely related species, e.g. *P. cervinus* has usually conspicuous fibrils and/or squamules on the stipe while *P. hongoi* has a smooth stipe, but collections of *P. cervinus* without fibrils and of *P. hongoi* with some fibrils on the stipe do exist.

Identification of white basidiocarps in section *Pluteus* has always been challenging and species (e.g. *P. albineus*, *P. nothopellitus*) and varieties (e.g. *P. pouzarianus* var. *albus*) have been erected based on this character (Bonnard 1993, 2001; Justo & Castro 2007b). At least five taxa with normally brown pigmented pilei (*P. cervinus*, *P. hongoi*, *P. pouzarianus*, *P. primus* and *P. brunneidiscus*) can produce occasionally white variants. It is possible that this also occurs in other species for which white variants have not been recorded. Conversely, species that normally produce white or very pale basidiocarps can sometimes produce basidiocarps with brown or pale brown pilei (e.g. *P. petasatus*, *P. pellitus*, *P. orestes*). This extensive morphological plasticity makes identification based on macromorphology alone very challenging, unless one is presented with the most typical morphotype of a particular species.

Microscopic characters have played a central role in the species-rank taxonomy of this group, especially since the studies of Singer (1956) and Smith & Stuntz (1958). Important characters used for species delimitation include size and shape of basidiospores, pleuro- and cheilocystidia and presence of clamp-connections on the pileipellis hyphae.

Two morphological types of pleurocystidia occur. The first are the fusiform to utriform with 2–4(6) hooks at the apex (more common type). This is usually the predominant type and variations on this type include cystidia with bifid hooks (predominant type in *P. hongoi*, *P. elaphinus*, *P. eos* and *P. sepiicolor*) or with very indistinct hooks (predominant in *P. orestes*, *P. oreibatus* and *P. saupei*). A second morphological type is the fusiform cystidia without hooks at the apex. This type can be sometimes observed along the lamellar edges, and may even be predominant in some collections of *P. petasatus*, but it is usually found near the lamellar edges, in the transition area towards the cheilocystidia. We concur with Bonnard (1988) that the pleurocystidia near the lamellar edges should be studied and described separately from the rest and following her terminology we have named them in the descriptions above as “intermediate cystidia”. In most species the intermediate cystidia include a mixture of cystidia of the two morphological types just described and others that are thin-walled and/or non-hooked and/or have aberrant morphologies. In *P. rangifer*, *P. petasatus* and *P. leucoborealis* the intermediate cystidia are predominantly fusiform and non-hooked, and that can be used as an additional character for identification.

Most species have a well-developed and continuous strip of spheropedunculate to narrowly clavate, hyaline cheilocystidia that are, on average, less than 70 µm long. Any deviation from this pattern is usually of taxonomic significance; e.g. *P. hongoi* and *P. petasatus* do not have a well-developed strip of cheilocystidia; *P. atomarginatus* and *P. atrofibrillosus* have predominantly pigmented cheilocystidia.

The presence of clamp-connections on the pileipellis hyphae is an important discriminating character. When present, clamp-connections are common and readily seen in fresh specimens or herbarium collections where the tissue rehydrates well. For most species clamped and clampless septa are present on the same microscopical preparation but it should not take more than the observation of 10–15 individual septa to assess the presence of clamps. Bonnard (1993) proposed the use of the percentage of clamped septa as a character, but we have found this to be quite variable within the same species. *Pluteus primus* (and possibly *P. oreibatus*) has clamp-connections at every septum of the pileipellis hyphae. For all species with clamp-connections in the pileipellis they are also present in other parts of the basidiocarp (e.g. at the base of the cheilocystidia, in the stipitipellis, etc). There are seven species with no clamp-connections in the pileipellis hyphae (*P. cervinus*, *P. exilis*, *P. rangifer*, *P. hongoi*, *P. elaphinus*, *P. petasatus* and *P. leucoborealis*), which include the most common and widespread species in the section. In these species some collections are found with very rare clamp-connections in the hymenium or the stipitipellis but even in those collections clamps are absent on the pileipellis hyphae. The use of clamp-connections as a taxonomic character should be restricted to their presence or absence in the pileipellis hyphae, and in the species with exclusively clamped septa (*P. primus*, *P. oreibatus*) as an additional character to help identification.

The species described here appear on well-decayed wood (conifers or angiosperms) and more rarely on piles of woodchips, sawdust or humic-rich substrates without apparent connection to wood. All species in the pouzarianus clade, the atomarginatus clade, and *P. sepiicolor* and *P. oreibatus* are almost always found growing on conifer wood. *Pluteus leucoborealis* has only been found on *Betula* and *Alnus*; *P. alniphilus* probably has a similar ecology. *Pluteus cervinus*, *P. hongoi*, *P. elaphinus*, *P. petasatus*, *P. pellitus*, *P. salicinus* and *P. americanus* are almost always found growing on angiosperm wood or in the humus layer without apparent connection to wood (mostly *P. hongoi* and *P. petasatus*) or piles of woodchips (mostly *P. petasatus*). *Pluteus exilis* has been found on both angiosperm and conifer wood and more sampling is needed to determine if it has any preference. The ecology of the brunneidiscus clade requires further study.

Some species seem to be ecologically confined to specific types of forests, e.g. *Pluteus leucoborealis* and *P. rangifer* are found in the boreal or transitional boreal/temperate forests of Eurasia and North America but have not been recorded in the temperate forests present at both sides of their ranges.

Overview of species distributions:—For the purposes of the discussion we have considered four very general subdivisions of the Holarctic region (Kreft & Jetz 2010): Western Palearctic (Europe and European Russia up to the Urals); Eastern Palearctic (Temperate/Boreal areas of Asia); Western Nearctic (Temperate/Boreal North American West of the Rocky Mountains); Eastern Nearctic (Temperate/Boreal North American East of the Rocky Mountains). Considering this subdivision we can classify the species described here as:

- (i) Holarctic (present in at least 3 of the 4 Holarctic areas): Eight species fall within this category (*P.*

cervinus, *P. rangifer*, *P. hongoi*, *P. primus*, *P. brunneidiscus*, *P. petasatus*, *P. leucoborealis* and *P. atromarginatus*). Of these, only *P. leucoborealis* has been confirmed to have a continuous range across the four Holarctic areas, from Northwestern Russia to the Adirondacks in New York (USA).

- (ii) Palearctic (present in both Palearctic areas but not in the Nearctic): *P. alniphilus* and *P. salicinus* are the two species belonging to this category.
- (iii) Putatively disjunct (present in two, non-contiguous areas): It includes three species, *P. hibbettii*, *P. eos* and *P. americanus* which are present in the eastern Palearctic and the eastern Nearctic but absent in the western Nearctic. Our sampling of higher latitude western North America (e.g. Alaska) is quite limited at this point, so further collecting is necessary to assess the distribution of these taxa.
- (iv) Western Palearctic: *P. pouzarianus*, *P. kovalenkoi* and *P. pellitus*.
- (v) Eastern Palearctic: *P. shikae* and *P. sepiicolor*.
- (vi) Western Nearctic: *P. exilis*, *P. orestes* and *P. parilis*.
- (vii) Eastern Nearctic: *P. elaphinus*, *P. methvenii*, *P. oreibatus*, *P. saupe* and *P. atrofibrillosus*.

The eastern Nearctic has the highest number (5) of regional endemics, although all regions harbor their own endemics, and areas like western North America remain vastly undersampled. In terms of species number the eastern Nearctic is the richest, with 16 out of the 26 species in section *Pluteus* present there. While two species (*P. salicinus*, *P. alniphilus*) are exclusively Palearctic there is no exclusively Nearctic species, i.e. no species is present simultaneously in western and eastern North America while being absent from Eurasia.

Species with structured nrITS variation:—These include regional endemics (*P. shikae*, *P. orestes*), putative disjuncts (*P. hibbettii*) and taxa distributed across the Holarctic region (e.g. *P. primus*, *P. atromarginatus*). Comparison of the nrITS and *tef1* percent similarity between closely related species has consistently revealed a higher degree of molecular divergence in the *tef1* sequences than in nrITS, e.g. the nrITS sequences of *P. hongoi* are 97% identical with the nrITS sequences of *P. cervinus*, while the *P. hongoi tef1* sequences are only 92–93% identical with *P. cervinus tef1* sequences. These results are consistent to what has been found in a wide array of taxa (e.g. Gazis *et al.* 2011 on endophytic Ascomycota, Harder *et al.* 2013 on *Mycena*, Carlson *et al.* 2014 on *Trametes*) where *tef1* sequences of closely related taxa have a higher degree of molecular divergence than the respective nrITS sequences. In all these cases the *tef1* sequences from the different nrITS groups are identical or nearly so and do not reveal the same well-supported clades in the phylogenetic analyses. It is unlikely that the variation in nrITS sequences observed in these species is due to an elevated rate of evolution compared to *tef1*. Rather, we suggest that variation among nrITS copies reflects a complex history involving genetic bottlenecks followed by different retention of nrITS copies. Fixation of a certain nrITS variant following a genetic bottleneck has been shown to occur in cases of glacial survival and post-glacial recolonization and/or long distance dispersal events for both plants and fungi (Murat *et al.* 2004; Beatty & Provan 2012; Merényi *et al.* 2014). We suspect that a similar process has shaped, at least in part, the nrITS variation of the *Pluteus* species studied here, but the specific causes of the genetic bottlenecks and the post-bottleneck population dynamics requires further study.

The substrate preferences of the species seem to have played a role in their phylogeographic history. The conifer-associated species are rich in very closely related but different regional endemics (e.g. *P. pouzarianus* in Europe, *P. orestes* in western North America, *P. methvenii* in eastern North America) and the ones that are present in both Eurasia and North America usually have different nrITS types in each continent (*P. atromarginatus*, *P. hibbettii*, *P. primus*). All species that are distributed across the Holarctic, without showing a distinct phylogeographic structure for either nrITS or *tef1*, are associated with angiosperms. The only species with a confirmed continuous range from Europe to eastern North America (*P. leucoborealis*) seems to be exclusively associated with *Betula* and *Alnus*.

***tef1* variation in *Pluteus cervinus*:**—In Eurasia the collections of *P. cervinus* are homozygous for cervinus-*tef1A*, homozygous for cervinus *tef1B* or heterozygous (Fig. 8). All North American collections of *P. cervinus* are homozygous cervinus-*tef1B*. There are two alternative scenarios that might explain this distribution of alleles.

In the first scenario both allelic variants could have been maintained in Eurasia, where homozygous individuals for any of the alleles freely interbreed producing occasional heterozygous collections. The complete absence of cervinus-*tef1A* from North America could be explained because of a reduced genetic diversity following a genetic bottleneck (e.g. glacial survival, recent arrival from Eurasia followed by a founder effect). This scenario lacks a plausible explanation as to how *P. cervinus* has escaped the homogenization of *tef1* alleles observed in all other 25 species of section *Pluteus* studied here. A second, more plausible, scenario is that the

diversity of *tefl* alleles observed in Eurasia is the consequence of relatively recent secondary contact between two infraspecific lineages, each homozygous for a different *tefl* allele. The origin of each of the *tefl* lineages, and the mechanism by which they were isolated from each other and have become in contact again in Eurasia cannot be assessed with the current data and requires further study. The fact that *P. cervinus* does not occur in the boreal forest makes a natural migration between continents very unlikely.

More comprehensive historical phylogeographical analyses are currently underway to further investigate the biogeographical hypotheses presented here.

Identification keys

These keys represent our best attempt at separating the species described here using morphological characters but the reader should be aware that separation of certain species, or certain morphological variants (e.g. white basidiocarps), is not always possible without molecular data. In some cases nearly identical species are listed together at the end of an entry and the reader is referred to the full descriptions and observations in the main text. A complementary synoptic key is given in Table 7.

Species present in the Western Palearctic (Europe and European Russia)

1. Lamellar edge distinctly brown to dark brown over its whole length..... *Pluteus atromarginatus*
- Lamellar edge white or pink coloured 2
2. Clamp-connections present on pileipellis hyphae..... 3
- Clamp-connections absent on pileipellis hyphae 7
3. On conifer wood..... 4
- On angiosperm wood or terrestrial..... 5
4. Basidiospores $6.0\text{--}8.6\text{--}(9.5) \times (4.0\text{--})4.5\text{--}5.7\text{--}(6.2) \mu\text{m}$, $\text{avl} \times \text{avw} = 6.8\text{--}7.5 \times 4.8\text{--}5.2 \mu\text{m}$. Cheilocystidia $20\text{--}70 \times 10\text{--}25\text{--}(30) \mu\text{m}$, predominantly clavate, narrowly clavate or spheropedunculate. *Pluteus pouzarianus*
- Basidiospores $7.0\text{--}9.5 \times (4.5\text{--})5.0\text{--}7.0 \mu\text{m}$, $\text{avl} \times \text{avw} = 7.8\text{--}8.4 \times 5.6\text{--}6.3 \mu\text{m}$. Cheilocystidia $55\text{--}120\text{--}(200) \times 8\text{--}25\text{--}(30) \mu\text{m}$, predominantly narrowly clavate or cylindrical *Pluteus primus* (see also *Pluteus kovalenkoi*)
5. Pileus predominantly gray. Blue or blue-green tinges usually present on pileus and/or stipe. Basidiospores ($\text{avl} \times \text{avw}$) $8.3\text{--}9.5 \times 6.2\text{--}6.8 \mu\text{m}$ *Pluteus salicinus*
- Pileus predominantly white or brown. Without blue or blue-green tinges on the basidiocarp. Basidiospores ($\text{avl} \times \text{avw}$) $5.8\text{--}8.1 \times 4.3\text{--}6.2 \mu\text{m}$ 6
6. Pileus usually white, sometimes pale brown around center. Basidiospores $5.0\text{--}7.5\text{--}(8.0) \times 3.5\text{--}5.0\text{--}(5.5) \mu\text{m}$, $\text{avl} \times \text{avw} = 5.8\text{--}6.5 \times 4.3\text{--}4.6 \mu\text{m}$ *Pluteus pellitus*
- Pileus brown to dark brown all over. Basidiospores $6.0\text{--}9.6\text{--}(10.5) \times 4.5\text{--}7.1 \mu\text{m}$, $\text{avl} \times \text{avw} = 7.1\text{--}8.1 \times 4.8\text{--}6.2 \mu\text{m}$ *Pluteus alniphilus* and *Pluteus brunneidiscus* (check the respective descriptions; see also *Pluteus kovalenkoi*)
7. Intermediate cystidia predominantly fusiform and non-hooked 8
- Intermediate cystidia variable, without a predominant morphological type 10
8. Basidiospores $5.5\text{--}8.0 \times 3.5\text{--}5.5 \mu\text{m}$, $\text{avl} \times \text{avw} = 6.1\text{--}7.0 \times 4.2\text{--}4.8 \mu\text{m}$. Cheilocystidia usually not forming a well-developed and continuous strip. In parks, urban areas and temperate forests *Pluteus petasatus*
- Basidiospores $5.5\text{--}8.5 \times 4.5\text{--}6.5\text{--}(7.0) \mu\text{m}$, $\text{avl} \times \text{avw} = 6.8\text{--}7.6 \times 5.0\text{--}5.8 \mu\text{m}$. Cheilocystidia usually forming a well-developed and continuous strip. In boreal or transitional boreal/temperate forests 9
9. Pileus white, usually with well defined squamules or radial fibrils. Only recorded on *Betula* and *Alnus* *Pluteus leucoborealis*
- Pileus dark brown or gray-brown, innately radially fibrillose but without superficial squamules or fibrils. On various angiosperms (including *Betula*)..... *Pluteus rangifer*
10. Stipe usually with conspicuous longitudinal fibrils and/or squamules. Hooks on the pleurocystidia predominantly entire... *Pluteus cervinus* (if collected in boreal areas check also *Pluteus rangifer*)

- Stipe usually without conspicuous longitudinal fibrils and/or squamules. Hooks on the pleurocystidia predominantly bifid *Pluteus hongoi*

Species present in the Eastern Palearctic (Asian Russia, Japan)

1. Lamellar edge distinctly brown to dark brown over its whole length, or only in the half near the pileus margin 2
- Lamellar edge white or pink, without any parts brown or dark brown..... 3
2. Lamellar edge pigmented over its whole length. Pileus strongly radially fibrillose or fibrillose- squamulose. Basidiospores (avl × avw) 6.8–7.5 × 4.8–5.2(–5.9) µm. Pleurocystidia with predominantly entire hooks. Cheilocystidia predominantly clavate or narrowly clavate..... *Pluteus atromarginatus*
- Lamellar edge only pigmented in the half near the pileus margin. Pileus smooth or innately radially fibrillose. Basidiospores (avl × avw) 7.7–8.2 × 5.4–5.7 µm. Pleurocystidia with predominantly bifid hooks. Cheilocystidia predominantly narrowly clavate or cylindrical..... *Pluteus eos*
3. Clamp-connections present on pileipellis hyphae..... 4
- Clamp-connections absent on pileipellis hyphae 9
4. On conifer wood..... 5
- On angiosperm wood or terrestrial..... .6
5. Basidiospores (avl × avw) 7.3–7.6 × 4.5–4.7 µm; avQ = 1.50–1.65. Pleurocystidia with predominantly entire hooks *Pluteus hibbettii*
- Basidiospores (avl × avw) 8.0–8.3 × 5.4–4.8 µm; avQ = 1.38–1.45. Pleurocystidia with predominantly bifid hooks..... *Pluteus sepiicolor*
6. Pileus predominantly gray, if brown then strongly hygrophanous. Blue or blue-green tinges usually present on pileus and/or stipe 7
- Pileus predominantly brown but not hygrophanous. Without blue or blue-green tinges on the basidiocarp 8
7. Pileus predominantly gray, not or only slightly hygrophanous. Recorded from Central Siberia (Novosibirsk Region)..... *Pluteus salicinus*
- Pileus predominantly brown and strongly hygrophanous. Recorded from the Russian Far East (Primorsky Territory)..... *Pluteus americanus*
8. Basidiospores (avl × avw) 7.1–8.1 × 5.1–6.2 µm; avQ = 1.30–1.45. Recorded from the Russian Northwest and Siberia..... *Pluteus brunneidiscus* (see also *Pluteus alniphilus*)
- Basidiospores (avl × avw) 6.5–7.1 × 4.4–5.0 µm; avQ = 1.42–1.56. Recorded from the Russian Far East (Primorsky Territory) and Japan (Hokkaido)..... *Pluteus shikae*
9. Intermediate cystidia predominantly fusiform and not hooked 10
- Intermediate cystidia variable, without a predominant morphological type..... 12
10. Basidiospores 5.5–8.0 × 3.5–5.5 µm, avl × avw = 6.1–7.0 × 4.2–4.8 µm. Cheilocystidia usually not forming a well-developed and continuous strip. In parks, urban areas and temperate forests *Pluteus petasatus*
- Basidiospores 5.5–8.5 × 4.5–6.5(–7.0) µm, avl × avw = 6.8–7.6 × 5.0–5.8 µm. Cheilocystidia usually forming a well-developed and continuous strip. In boreal or transitional boreal/temperate forests 11
11. Pileus white, usually with well defined squamules or radial fibrils. Only recorded on *Betula* and *Alnus* *Pluteus leucoborealis*
- Pileus dark brown or gray-brown, innately radially fibrillose but without superficial squamules or fibrils. On various angiosperms (including *Betula*)..... *Pluteus rangifer*
12. Stipe usually with conspicuous longitudinal fibrils and/or squamules. Hooks on the pleurocystidia predominantly entire... *Pluteus cervinus* (if collected in boreal areas check also *Pluteus rangifer*)
- Stipe usually without conspicuous longitudinal fibrils and/or squamules. Hooks on the pleurocystidia predominantly bifid *Pluteus hongoi*

Species present in the Western Nearctic (USA and Canada west of the Rocky Mountains)

Sampling in the western states for this study was restricted to a small number of locations. There are undoubtedly more species than the 8 presented in this key.

1. Lamellar edge distinctly dark over its whole length *Pluteus atromarginatus*
- Lamellar edge light colored, occasionally brown near pileus edge, but not completely coloured 2
2. Pileus pale, off-white, pale grey 3
- Pileus brown or grey-brown 5
3. Pileus evenly coloured, pale grey, without darker squamules at centre. Clamp-connections abundant and easy to spot in pileipellis. Known from the western mountain ranges (Sierra Nevada, Cascade Range) *Pluteus orestes*
- Pileus predominantly white, with or without brown squamules or fibrils at centre. Clamp-connections absent from pileipellis (if present but other characters not completely as the option above compare to *P. primus*). Widespread or in boreal areas, not recorded from the western mountain ranges 4
4. Basidiospores $5.5\text{--}8.0\text{--}(9.5) \times 3.5\text{--}5.5\text{--}(6.0) \mu\text{m}$, $\text{avl} \times \text{avw} = 6.1\text{--}7.0 \times 4.2\text{--}4.8 \mu\text{m}$. Smell often sweet. On various substrates, including wood chips. Widespread, but not known from boreal areas *Pluteus petasatus*
- Basidiospores $(5.5\text{--})6.0\text{--}8.0\text{--}(8.5) \times (4.5\text{--})5.0\text{--}6.0 \mu\text{m}$, $\text{avl} \times \text{avw} = 6.8\text{--}7.4 \times 5.3\text{--}5.5 \mu\text{m}$; smell indistinct. On *Betula* and *Alnus* wood in boreal forests. Known from central Alaska *Pluteus leucoborealis*
5. Clamp-connections absent from pileipellis *Pluteus exilis* (and *Pluteus cervinus*, see observations under *P. exilis*)
- Clamp-connections present and easy to spot in pileipellis 6
6. Pileus usually pale colored, rarely brown. Pleurocystidia predominantly with small inconspicuous hooks. Known from the western mountain ranges (Sierra Nevada, Cascade Range) *Pluteus orestes*
- Pileus brown, brown-grey, grey-brown. Pleurocystidia with well-developed hooks. Not known (yet) from the mountains ..
..... 7
7. Cheilocystidia $55\text{--}120\text{--}(200) \times 8\text{--}25\text{--}(30) \mu\text{m}$, predominantly narrowly clavate or cylindrical *Pluteus primus*
- Cheilocystidia $30\text{--}68 \times 12\text{--}22 \mu\text{m}$, predominantly clavate, narrowly clavate or spheropedunculate .. *Pluteus brunneidiscus*

Species present in the Eastern Nearctic (USA and Canada East of the Rocky Mountains)

1. Lamellar edge distinctly brown to dark brown over its whole length or only in the half near the pileus margin 2
- Lamellar edge white or pink, without any parts brown or dark brown 4
2. Lamellar edge only pigmented in the half near the pileus margin. Pileus smooth or innately radially fibrillose. Basidiospores ($\text{avl} \times \text{avw}$) $7.7\text{--}8.2 \times 5.4\text{--}5.7 \mu\text{m}$. Pleurocystidia with predominantly bifid hooks. Cheilocystidia predominantly narrowly clavate or cylindrical *Pluteus eos*
- Lamellar edge pigmented over its whole length. Pileus strongly radially fibrillose or fibrillose squamulose. Basidiospores ($\text{avl} \times \text{avw}$) $6.5\text{--}7.5 \times 4.5\text{--}5.2 \mu\text{m}$. Pleurocystidia with predominantly entire hooks. Cheilocystidia predominantly clavate or narrowly clavate 3
3. Fibrils and squamules on the pileus rather loosely arranged. Basidiospores ($\text{avl} \times \text{avw}$) $6.5\text{--}6.8 \times 4.5\text{--}5.1 \mu\text{m}$. Pleurocystidia $45\text{--}75 \times 11\text{--}23 \mu\text{m}$, predominantly with 2 hooks. Known only from the Great Smoky Mountains National Park (Tennessee and North Carolina) *Pluteus atrofibrillosus*
- Fibrils and squamules tightly arranged. Basidiospores ($\text{avl} \times \text{avw}$) $6.8\text{--}7.5 \times 4.8\text{--}5.2 \mu\text{m}$. Pleurocystidia $60\text{--}110 \times 10\text{--}20 \mu\text{m}$, with 2–5 hooks. Widespread in Eastern North America *Pluteus atromarginatus*
4. Clamp-connections present on pileipellis hyphae 5
- Clamp-connections absent on pileipellis hyphae 12
5. On conifer wood 6
- On angiosperm wood or terrestrial 10
6. Pleurocystidia with indistinct, rounded hooks at apex or without hooks; walls less than $2 \mu\text{m}$ thick 7
- Pleurocystidia with distinct, prominent hooks at apex; walls commonly more than $2 \mu\text{m}$ thick 8

7. Cheilocystidia predominantly cylindrical, lageniform and narrowly clavate. Known from the Adirondacks (New York) and the Smoky Mountains (North Carolina)..... *Pluteus oreibatus*
- Cheilocystidia predominantly lageniform with elongate apices, without cylindrical or narrowly clavate ones. Known from central Illinois..... *Pluteus sauvei*
8. Cheilocystidia $55\text{--}120\text{--}(200) \times 8\text{--}25\text{--}(30) \mu\text{m}$, predominantly narrowly clavate or cylindrical *Pluteus primus*
- Cheilocystidia $30\text{--}70 \times 12\text{--}25 \mu\text{m}$, predominantly clavate, narrowly clavate or spheropedunculate 9
9. Basidiospores ($\text{avl} \times \text{avw}$) $7.3\text{--}7.6 \times 4.5\text{--}4.7 \mu\text{m}$; $\text{avQ} = 1.50\text{--}1.65$ *Pluteus hibbettii*
- Basidiospores ($\text{avl} \times \text{avw}$) $7.1\text{--}8.9 \times 5.3\text{--}4.9 \mu\text{m}$; $\text{avQ} = 1.33\text{--}1.50$ *Pluteus methvenii*
10. Pleurocystidia with indistinct, rounded hooks at apex or without hooks; walls less than $2 \mu\text{m}$ thick. Cheilocystidia predominantly lageniform with elongate apices..... *Pluteus sauvei*
- Pleurocystidia with distinct, prominent hooks at apex; walls commonly more than $2 \mu\text{m}$ thick. Cheilocystidia predominantly clavate, narrowly clavate or spheropedunculate..... 11
11. Pileus strongly hygrophanous. Blue or blue-green tinges usually present on pileus and/or stipe. Smell like leaves of *Pelargonium*..... *Pluteus americanus*
- Pileus not hygrophanous. Without blue or blue-green tinges on pileus and/or stipe. Smell raphanoid..... *Pluteus brunneidiscus*
12. Intermediate cystidia predominantly fusiform and not hooked 13
- Intermediate cystidia variable, without a predominant morphological type..... 15
13. Basidiospores $5.5\text{--}8.0 \times 3.5\text{--}5.5 \mu\text{m}$, $\text{avl} \times \text{avw} = 6.1\text{--}7.0 \times 4.2\text{--}4.8 \mu\text{m}$. Cheilocystidia usually not forming a well-developed and continuous strip. In parks, urban areas and temperate forests *Pluteus petasatus*
- Basidiospores $5.5\text{--}8.5 \times 4.5\text{--}6.5\text{--}(7.0) \mu\text{m}$, $\text{avl} \times \text{avw} = 6.8\text{--}7.6 \times 5.0\text{--}5.8 \mu\text{m}$. Cheilocystidia usually forming a well-developed and continuous strip. In boreal or transitional boreal/temperate forests 14
14. Pileus white, usually with well defined squamules or radial fibrils. Only recorded on *Betula* and *Alnus* *Pluteus leucoborealis*
- Pileus dark brown or gray-brown, innately radially fibrillose but without superficial squamules or fibrils. On various angiosperms (including *Betula*)..... *Pluteus rangifer*
15. Hooks on the pleurocystidia predominantly entire *Pluteus cervinus* (if collected in boreal areas check also *Pluteus rangifer*)
- Hooks on the pleurocystidia predominantly bifid..... 16
16. Stipe with conspicuous longitudinal brown or gray-brown fibrils all over, sometimes grouped to form distinct squamules. Only in transitional boreal/temperate or mountainous areas e.g. Berkshires (Massachusetts); Adirondack Mountains (New York); Newfoundland (Canada) *Pluteus elaphinus*
- Stipe smooth, sometimes with a few fibrils near the base. Common and widespread in the temperate forests of Eastern North America (from Florida to New England, and westwards into the Great Lakes region) *Pluteus hongoi*

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