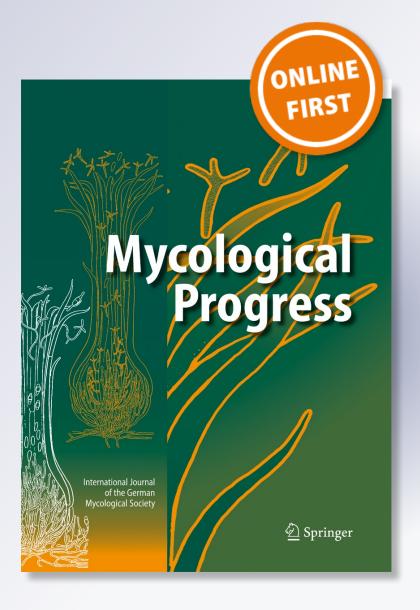
# Observations on Pluteus (Pluteaceae) diversity in South Siberia, Russia: morphological and molecular data

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#### **ORIGINAL ARTICLE**





### Observations on *Pluteus* (Pluteaceae) diversity in South Siberia, Russia: morphological and molecular data

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Abstract A study of *Pluteus* collections from the southern region of Siberia, Russia, revealed the occurrence of 20 species. One species (*Pluteus umbrosoides*) and one form (*P. tomentosulus* f. *brunneus*) are proposed as new. *Pluteus rugosidiscus* is a new record in Eurasia and *P. velutinus* is recorded for the first time in Russia. Most species in the studied territory occur in coniferous or mixed forests. Until now, there have been only sporadic finds of *Pluteus* in the sub-taiga zone and no finds in the steppe zone. Detailed morphological descriptions, illustrations and drawings of microstructures for new, rare and interesting taxa are provided. Phylogenetic analyses inferred from the internal transcribed spacer (nrITS) were conducted for species delimitation and for comparisons with closely related taxa.

**Keywords** Agaricales · Biodiversity · Taxonomy · Phylogeny · New species · New form

#### Introduction

The genus *Pluteus* Fr. is very species-rich and widespread from the arctic to tropical areas (Singer 1956, 1986; Vellinga 1990; Justo et al. 2011a, b, 2014). More than 300 species of the genus have been described worldwide (Kirk et al. 2008).

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However, the species diversity of this genus has not yet been comprehensively studied in Russia.

The mycobiota of South Siberia is poorly known due to the small number of mycological studies implemented in the region. Some areas have never been mycologically explored. Among them, is the territory of the Sayano-Shushensky State Biospheric Nature Reserve. Before our study, virtually nothing was known about *Pluteus* diversity in this area. The present study contributes to this knowledge.

We conducted a preliminary investigation of the taxonomy of *Pluteus* species. During the expedition to the Sayano-Shushensky State Biospheric Nature Reserve undertaken by the first two authors in 2015, more than 40 specimens of *Pluteus* were collected and preserved. Those specimens were found to belong to 19 known and 1 undescribed species from three sections of the genus (*Pluteus*, *Celluloderma* and *Hispidoderma*). The goal of the present study was to provide an annotated list of all species recorded, describe one new species and one new form, give detailed descriptions and illustrations of new and rare taxa, and to clarify the phylogenetic relationships of the revealed species and related taxa from the genus *Pluteus* based on sequence data of the internal transcribed spacer (nrITS).

#### Materials and methods

#### Studied area

The investigated area (Sayano-Shushensky State Biospheric Nature Reserve) covers approximately 390,000 ha and is located on the left bank of the Yenisey River, in the central part of Western Sayan and Altai-Sayan Mountain Land, 51°45′–52°38′N, 91°05′–92°27′E (Fig. 1). The plant cover is characterized by rich





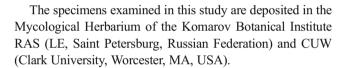
Fig. 1 The general study area and location of the Sayano-Shushensky State Biospheric Nature Reserve in South Siberia

communities of woody plants as well as clearly expressed altitudinal vegetation zones. The northern part of the reserve is occupied by mountain taiga dark coniferous, high-mountain open *Pinus sibirica* Du. Tour woodland, high-mountain tundra, meadows and shrub thicket sites. The southern part of the reserve consists of insufficiently moist areas of the Central Asian forest zone. The basis belt is formed by light coniferous herb forests (sub-taiga), forest-steppe and steppe.

As a result of our investigation, the overwhelming majority of *Pluteus* collections have been found mainly in coniferous or mixed forests of mountain taiga in the northern and central parts of the reserve.

#### Morphological analysis

Standard methods for describing the basidiocarps were applied, using the terminology of Vellinga (1988, 1990). Macroscopic descriptions are based on fresh basidiocarps from the original collections and photos taken at the site. Color terms in the macroscopical descriptions are from Kornerup and Wanscher (1978). The notation [60, 3, 2] indicates that measurements were made of 60 basidiospores from 3 basidiomata taken from 2 collections. We measured at least 20 basidiospores for each basidiocarp. All structures were examined in KOH (5 %) and Congo Red reagents. Basidiospore statistical dimensions include: Lm and Wm, the average of all lengths (widths) of spores measured; Q, the range of the length/width quotient for all the measured spores; and Qm, average of all calculated Q values.



#### Molecular techniques

The procedure of DNA extraction corresponded completely to the manufacturing protocol of the NucleoSpin® Plant II Kit (Macherey-Nagel, Germany). The primer pair ITS1F–ITS4B (Gardes and Bruns 1993) was used both for PCR and for sequencing of nrITS region, respectively. PCR products were purified applying the Fermentas Genomic DNA Purification Kit (Thermo Fisher Scientific, MA, USA). Sequencing was performed with an ABI model 3130 Genetic Analyzer (Applied Biosystems, CA, USA). Raw data were edited and assembled in MEGA 6 (Tamura et al. 2013).

#### Phylogenetic analysis

For this study, 51 new sequences of nrITS were generated. The additional 74 ITS sequences of *Pluteus* were retrieved from the GenBank database (Table 1) to estimate the general phylogenetic position of Siberian collections. The sequences were aligned using the Mafft v.7 web tool (http://mafft.cbrc.jp/alignment/server/) with the Q-INS-i option. The final alignment was manually corrected using MEGA 6. The alignment has been deposited in TreeBASE (S19275).

Phylogenetic reconstructions were performed for the ITS dataset with maximum likelihood (ML) and Bayesian (BA) analyses. ML analysis was run on ATGC servers (http://www.



Table 1	List of collections used
in the ph	vlogenetic analyses

Taxon name <sup>a</sup>	Collection (voucher or strain no.)	Country of origin	GenBank accession number (nrITS)	References (where sequence was published for the first time)
Pluteus chrysophaeus	LE 262704	Russia	KX216313	Present paper
P. chrysophaeus	LE 253890	Russia	KX216314	Present paper
P. chrysophaeus	LE 312949	Russia	KX216316	Present paper
P. chrysophlebius	LE 303694	Russia	KX216317	Present paper
P. chrysophlebius	LE 312854	Russia	KX216315	Present paper
P. chrysophlebius	LE 303664	Russia	KX216312	Present paper
P. chrysophlebius	LE 303663	Russia	KX216318	Present paper
P. chrysophlebius	LE 312733	Russia	KX216319	Present paper
P. chrysophlebius	AJ45 (MA)	Spain	HM562064	Justo et al. 2011a
P. chrysophlebius	TNSF12388	Japan	HM562088	Justo et al. 2011a
P. chrysophlebius	TNSF12383	Japan	HM562125	Justo et al. 2011a
P. chrysophlebius	SF11 (SIU)	USA	HM562181	Justo et al. 2011a
P. chrysophlebius	SF12 (BPI)	USA	HM562182	Justo et al. 2011a
P. cinereofuscus	AJ34 (MA)	Spain	HM562124	Justo et al. 2011a
P. cinereofuscus	AJ229 (LOU)	Portugal	HM562108	Justo et al. 2011a
P. aff. cinereofuscus	TNSF12400	Japan	HM562115	Justo et al. 2011a
P. aff. cinereofuscus	LE 303669	Russia	KX216325	Present paper
P. aff. cinereofuscus P. eludens	LE 303665	Russia USA	<b>KX216324</b> HM562185	Present paper Justo et al. 2011a
r. eudens P. eludens	SF15 (BPI) MA50497 (holotype)	Portugal	HM562118	Justo et al. 2011a
P. cf. eugraptus	TNSF12042	Japan	HM562116	Justo et al. 2011a
P. fenzlii	LE 303661	Russia	KX216339	Present paper
P. fenzlii	TNSF12376	Japan	HM562091	Justo et al. 2011a
P. fenzlii	LE 246083	Russia	FJ774082	Malysheva et al.
1. jenziii	EE 240003	Russia	13//4002	2009
P. galeroides	887	Italy	JF908610	Osmundson et al. 2013
P. galeroides	886	Italy	JF908609	Osmundson et al. 2013
P. granularis	Strack7 (SIU)	USA	HM562069	Justo et al. 2011a
P. granularis	SF20 (BPI)	USA	HM562189	Justo et al. 2011a
P. granulatus	AJ203 (LOU)	Spain	HM562048	Justo et al. 2011a
P. granulatus	LE 212990	Russia	FJ774086	Malysheva et al. 2009
P. hispidulus	A1882	Spain	KM983681	Menolli et al. 2015b
P. hispidulus var. cephalocystis	ARAN8200509	Spain	KM983695	Menolli et al. 2015b
P. hispidulus var. cephalocystis	LE 303683	Russia	KX216305	Present paper
P. hispidulus var. cephalocystis	LE 312864	Russia	KX216354	Present paper
P. leoninus	LE 303700	Russia	KX216310	Present paper
P. leoninus	LE 303695	Russia	KX216311	Present paper
P. leoninus	LE 303698	Russia	KX216309	Present paper
P. leoninus	601	Italy	JF908606	Osmundson et al. 2013
P. leoninus	AJ212 (LOU)	Spain	HM562045	Justo et al. 2011a
P. leoninus	Josserand s.n (MICH, as P. luteomarginatus)	France	HM562077	Justo et al. 2011a
P. leucoborealis	LE 303667	Russia	KX216342	Present paper
P. leucoborealis	LE 289421 (holotype)	Russia	KJ009746	Justo et al. 2014
P. leucoborealis	LE 289399	Russia	KJ009741	Justo et al. 2014
P. longistriatus	LE 312951	Russia	KX216355	Present paper
P. longistriatus	ASIS24529	South Korea	KM052568	_
P. longistriatus	Minnis309203 (SIU)	USA	HM562082	Justo et al. 2011a



ble 1 (continued)	Taxon name <sup>a</sup>	Collection (voucher or strain no.)	Country of origin	GenBank accession number (nrITS)	References (where sequence was published for the first time)
	P. longistriatus	SP393700	Brazil	HM562158	Justo et al. 2011a
	P. longistriatus	SP394386	Brazil	HM562172	Justo et al. 2011a
	P. pallescens	AJ214 (LOU)	Spain	HM562056	Justo et al. 2011a
	P. phlebophorus	LE 303673	Russia	KX216333	Present paper
	P. phlebophorus	LE 303674	Russia	KX216334	Present paper
	P. phlebophorus	LE 303684	Russia	KX216336	Present paper
	P. phlebophorus	LE 303679	Russia	KX216335	Present paper
	P. phlebophorus	LE 303681	Russia	KX216337	Present paper
	P. phlebophorus	LE 312918	Russia	KX216338	Present paper
	P. phlebophorus	TNSF12394	Japan	HM562117	Justo et al. 2011a
	P. phlebophorus	SF14 (SIU)	USA	HM562184	Justo et al. 2011a
	P. phlebophorus	AJ193 (LOU)	Spain	HM562144	Justo et al. 2011a
	P. phlebophorus	AJ194 (LOU)	Spain	HM562137	Justo et al. 2011a
	P. plautus	UBCF23774	Canada	KC581304	_
	P. plautus	AJ209 (LOU)	Spain	HM562055	Justo et al. 2011a
	P. plautus	LE 213024	Russia	FJ774076	Malysheva et al. 2009
	P. aff. plautus	Miettinen15459	Finland	KR022013	Menolli et al. 2015a
	P. aff. plautus	AJ621	USA	KR022010	Menolli et al. 2015a
	P. aff. plautus	AJ606	USA	KR022011	Menolli et al. 2015a
	P. aff. plautus	MO93671	USA	KR022009	Menolli et al. 2015a
	P. aff. plautus	AJ594	USA	KR022012	Menolli et al. 2015a
	P. aff. plautus	A5058325	Spain	KR022014	Menolli et al. 2015a
	P. aff. plautus	AJ227	Spain	KR022015	Menolli et al. 2015a
	P. aff. plautus	AJ597	USA	KR022016	Menolli et al. 2015a
	P. aff. plautus	AJ226	Spain	KR022025	Menolli et al. 2015a
	P. aff. plautus	A. Caballero 783	Spain	KR022026	Menolli et al. 2015a
	P. aff. plautus P. aff. plautus	LE 312950 LE 303680	Russia Russia	KX216350 KX216322	Present paper Present paper
	P. podospileus	LE 303682	Russia	KX216322 KX216331	Present paper
	P. podospileus	LE 303687	Russia	KX216332	Present paper
	P. podospileus	AJ204 (LOU)	Spain	HM562049	Justo et al. 2011a
	P. podospileus	TNSF12398	Japan	HM562122	Justo et al. 2011a
	P. podospileus	AJ782	USA	KM983687	Menolli et al. 2015b
	P. rangifer	LE 303690	Russia	KX216327	Present paper
	P. rangifer	LE 289384	Russia	KJ009654	Justo et al. 2014
	P. rangifer	LE 289406	Russia	KJ009653	Justo et al. 2014
	P. rangifer	LE 203210 (holotype)	Russia	KJ009650	Justo et al. 2014
	P. romellii	LE 303660	Russia	KX216326	Present paper
	P. romellii	AJ857	USA	KM983701	Menolli et al. 2015b
	P. romellii	TNSF12387	Japan	HM562123	Justo et al. 2011a
	P. romellii	AJ232 (LOU)	Spain	HM562062	Justo et al. 2011a
	P. romellii	LE 217944	Russia	FJ774073	Malysheva et al. 2009
	P. rugosidiscus	LE 303676	Russia	KX216323	Present paper
	P. rugosidiscus	Homola109 (MICH)	USA	HM562079	Justo et al. 2011a



<b>Table 1</b> (continued)	Table 1	(continued)	
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Taxon name <sup>a</sup>	Collection (voucher or strain no.)	Country of origin	GenBank accession number (nrITS)	References (where sequence was published for the first time)
P. salicinus	LE 303677	Russia	KX216330	Present paper
P. salicinus	LE 289410	Russia	KJ009758	Justo et al. 2014
P. salicinus	MA67874	Spain	HM562051	Justo et al. 2011a
P. salicinus	SF2 (BPI)	USA	HM562174	Justo et al. 2011a
P. semibulbosus	LOU18725	Spain	KR022022	Menolli et al. 2015a
P. semibulbosus	LE 227534	Russia	FJ774080	Malysheva et al. 2009
P. semibulbosus	LE 312914	Russia	KX216353	Present paper
P. aff. semibulbosus	TNSF12393	Japan	HM562090	Justo et al. 2011a
Pluteus sp.	AJ470	USA	KR022028	Menolli et al. 2015a
Pluteus sp.	UC 1861124	USA	KC147672	_
Pluteus sp.	UC 1861231	USA	KC147677	_
P. thomsonii	LE 303662	Russia	KX216329	Present paper
P. thomsonii	LE 303685	Russia	KX216328	Present paper
P. thomsonii	LE 234787	Russia	FJ774084	Malysheva et al. 2009
P. thomsonii	603	Italy	JF908607	Osmundson et al. 2013
P. tomentosulus	MO93719	USA	KM983672	Menolli et al. 2015b
P. tomentosulus	MO163564	USA	KM983673	Menolli et al. 2015b
P. tomentosulus f. brunneus	LE 312906	Russia	KX216306	Present paper
P. tomentosulus f. brunneus	LE 312907	Russia	KX216308	Present paper
P. tomentosulus f. brunneus	LE 312908 (holotype)	Russia	KX216307	Present paper
P. umbrosoides	LE 312735 (holotype)	Russia	KX216321	Present paper
P. umbrosoides	LE 312839	Russia	KX216348	Present paper
P. umbrosoides	LE 312920	Russia	KX216349	Present paper
P. umbrosus	LE 303696	Russia	KX216320	Present paper
P. umbrosus	LE 312837	Russia	KX216344	Present paper
P. umbrosus	LE 312842	Russia	KX216346	Present paper
P. umbrosus	LE 312843	Russia	KX216347	Present paper
P. umbrosus	LE 312840	Russia	KX216345	Present paper
P. umbrosus	LE 312838	Russia	KX216343	Present paper
P. velutinus	TNSF12365	Japan	HM562114	Justo et al. 2011a
P. velutinus	K12851 (TBGT) (holotype)	India	JN603205	Pradeep et al. 2012
P. velutinus	LE 303693	Russia	KX216340	Present paper
P. velutinus	LE 312913	Russia	KX216351	Present paper
P. velutinus	LE 312915	Russia	KX216352	Present paper
P. velutinus	LE 289495	Mongolia	KX216341	Present paper

GenBank accession numbers in bold indicate newly generated sequences for this study

atgc-montpellier.fr/phyml/), with the option of automatic model selection and with 100 rapid bootstrap replicates. Only support values ≥70 % were considered as significant. BA was performed with MrBayes 3.1 software (Ronquist and Huelsenbeck 2003), under a GTR model, with two parallel searches, four chains, 5 million generations with sampling

every 100 generations. A clade was considered strongly supported if it received posterior probability (PP) values ≥0.95. Pairwise distances between ITS sequences were calculated using MEGA 6, under the GTR model.

All newly generated sequences have been deposited in GenBank with corresponding accession numbers (Table 1).



<sup>&</sup>lt;sup>a</sup> Name given in accordance with the original collection identification and based on specimen labels

#### Results and discussion

#### **Phylogeny**

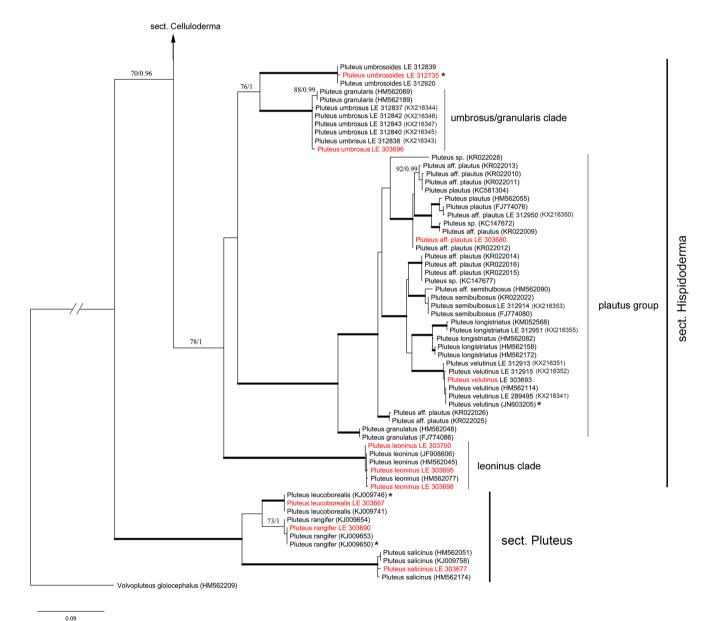
The dataset includes 125 nrITS sequences of *Pluteus* and q sequence of *Volvopluteus gloiocephalus* (HM562209) that was used as an outgroup. The final dataset consists of 664 characters including gaps.

In all analyses, the distribution of species by separate major clades corresponding to the sections is well supported and is in accordance with the infrageneric classification proposed by Justo et al. (2011a, b). The

morphological concepts of some species need further study in view of the molecular results presented here.

In sect. *Pluteus*, three well-supported clades correspond to known species (*P. rangifer*, *P. leucoborealis* and *P. salicinus*) (Fig. 2).

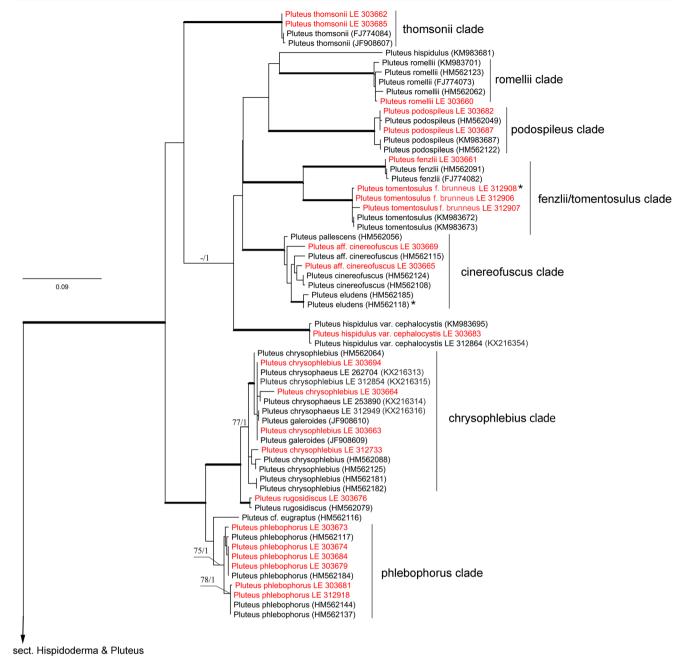
In the large clade including members of sect. *Celluloderma*, it is possible to recognize ten taxa including three species complexes that need further revision (*P. chrysophlebius*, *P. phlebophorus* and *P. cinereofuscus*) (Fig. 3). The species complexes of *P. chrysophlebius* and *P. phlebophorus* are organized into two distinct clades in the tree. The internal topology of both clades is poorly



**Fig. 2** Best tree from ML analyses for the ITS dataset of *Pluteus* sect. *Pluteus* and sect. *Hispidoderma*. Support values (BS  $\geq$  70 % / PP  $\geq$  0.95) are given above the branches. The branches are *bold* when BS  $\geq$  90 % and PP  $\geq$  0.95. Newly generated sequences from South Siberia are indicated

in *red*. The names are followed by the specimen voucher numbers and/or GenBank accession numbers in parentheses. \*Indicates a type collection. *Scale bar* indicates expected changes per site





**Fig. 3** Best tree from ML analyses for the ITS dataset of *Pluteus* sect. *Celluloderma*. Support values (BS  $\geq$  70 % / PP  $\geq$  0.95) are given above the branches. The branches are *bold* when BS  $\geq$  90 % and PP  $\geq$  0.95. Newly generated sequences from South Siberia are indicated in *red*.

The names are followed by the specimen voucher numbers and/or GenBank accession numbers in parentheses. \*Indicates a type collection. *Scale bar* indicates expected changes per site

resolved. Two sequences of *P. rugosidiscus* form a single clade sister to chrysophlebius group that confirms its status as an independent taxon. The cinereofuscus clade includes *P. pallescens*, *P. eludens* and *P.* aff. *cinereofuscus*. The sequences of *P. tomentosulus* are grouped into a highly supported clade sister to the fenzlii clade.

Section *Hispidoderma* in our analyses includes clades corresponding to known species, species complexes and undescribed taxa. As expected, the collections within and around the *P. plautus* species-complex are grouped into several

distant clades that have already been shown in previous studies (Justo et al. 2011a, b; Menolli et al. 2015a). In our phylogeny, they include *P. granulatus*, *P. velutinus*, *P. longistriatus*, *P. semibulbosus* and some potentially undescribed species (*Pluteus* aff. *plautus* represented by several clades and *Pluteus* sp.) (Fig. 2). Among them, one of our collections from South Siberia represents the same entity as the sequence from GenBank (KR022012), and they both are part of this "plautus" group with provisional designation here as *Pluteus* aff. *plautus*. The highly supported umbrosus/granularis clade includes one



Fig. 4 Basidiocarps. a Pluteus salicinus (LE 303677). b
P. pouzarianus (LE 303675). c
P. leucoborealis (LE 303668). d
P. rangifer (LE 312985). e
P. rangifer (LE 303671). f
P. rangifer (LE 303690). g
P. chrysophlebius (LE 303694). h
P. rugosidiscus (LE 303676).
Scale bars 1 cm



Siberian collection along with some European and Russian collections of *P. umbrosus* and two North American sequences of *P. granularis*. The question of the molecular delineation of *P. umbrosus* and *P. granularis* as well as their affiliation to different taxa requires further investigation. The newly described species *Pluteus umbrosoides* has a sister position in the tree to the umbrosus/granularis clade in all analyses. The sequences of *P. umbrosoides* are charasterised by 12.5–14 % of sequence divergence in comparison with the sequences of the umbrosus/granularis clade.

#### **Taxonomy**

#### Species of *Pluteus* recorded in South Siberia

The molecular data generally supported the infrageneric taxonomy of *Pluteus* proposed by Singer (1959, 1986)

with several modifications. In the recent papers devoted to molecular phylogeny and morphological subdivision of *Pluteus* (Justo et al. 2011a, b), it has been shown that all species with non-metuloid pleurocystidia and pileipellis as a cutis should be classified within sect. *Celluloderma* instead of sect. *Hispidoderma* sensu Singer or sect. *Villosi* sensu Vellinga and Schreurs (1985). The concept of sect. *Pluteus* has not been significantly changed. In this paper, all species are listed according to the updated infrageneric classification of *Pluteus*. For rare, interesting and new species detailed descriptions and illustrations are given.

#### Sect. Pluteus

*Pluteus atromarginatus* (Singer) Kühner, Bull. Mens. Soc. Linn. Lyon 4: 51, 1935.

**Collection examined** RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, vicinity of Talovka field station, 52°23′56.5″N, 92°18′56.1″E, slope, mixed forest (*Picea obovata, Pinus sibirica, Abies* 



sibirica, Betula pendula), on decayed wood of conifer, 19 Aug. 2015, E.F. Malysheva 303659 (LE).

*Pluteus salicinus* (Pers.) P. Kumm., Führ. Pilzk. (Zerbst): 99, 1871.

Fig. 4a

Collection examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, transect "Karakem", 52°23′13.1″N, 92°24′26.0″E, slope, mixed forest (*Larix sibirica*, *Abies sibirica*, *Populus tremula*, *Betula pendula*), on fallen branch of *Betula pendula*, 21 Aug. 2015, *E.F. Malysheva 303677* (LE).

*Pluteus pouzarianus* Singer, Sydowia 36: 283, 1984 [1983].

Fig. 4b

Collection examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, floodplain of Malaya Golaya River, mixed forest (*Abies sibirica*, *Pinus sibirica*, *Betula pendula*), on fallen trunk of *Abies sibirica*, 17 Aug. 2015, *E.F. Malysheva 303675* (LE).

*Pluteus leucoborealis* Justo, E.F. Malysheva, Bulyonk. & Minnis, Phytotaxa 180(1): 58, 2014.

Figs. 4c and 5

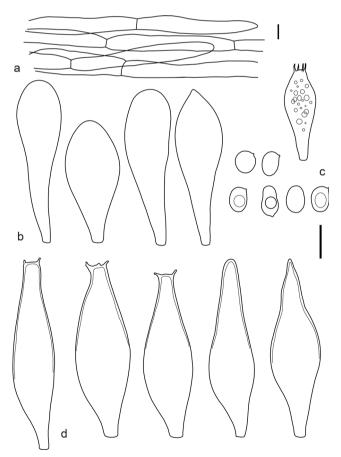


Fig. 5 Microscopic features of *Pluteus leucoborealis* (LE 303667). a Elements of pileipellis. b Cheilocystidia. c Basidium and basidiospores. d Pleurocystidia. *Scale bars*10 μm

*Pileus* 35–50 mm in diam., at first hemispherical, then convex, plano-convex to applanate with small low umbo; uniformly white or with beige or brownish beige tint (4C3, 6E3) at centre; surface smooth, minutely squamulose only at centre. *Lamellae* free, moderately crowded, ventricose, pink or brownish pink, with concolourous edges. *Stipe* 50–75 × 4–8 mm, cylindrical or uniformly thickened downwards, longitudinally fibrillose, white or yellowish, with white tomentum at base. Smell indistinct, taste indistinct.

Basidiospores [40/2/2] (5.4)6.0–8.0 × (4.8)5.0–6.2 μm (Lm = 6.9, Wm = 5.6, Q = 1.04–1.40; Qm = 1.24), broadly ellipsoid or ovoid, occasionally subglobose and globose, thickwalled. Basidia 18–25 × 7–9.5 μm, 4-spored, broadly clavate. Pleurocystidia metuloid,  $50-75 \times 10-20$  μm, abundant, broadly to narrowly fusiform or utriform, with 2–3(4) short and often poorly developed apical hooks, some without hooks, hyaline, walls up to 3 μm wide. Cheilocystidia  $30-75(85) \times 11-17$  μm, numerous, mostly broadly clavate or utriform, hyaline, thinwalled. Pileipellis a cutis, made up of slightly thick-walled cylindrical hyphae, up to 20 μm wide, hyaline or with yellowish intracellular pigment, with narrowly fusiform or cylindrical terminal elements, 100-150 μm long. Stipitipellis consists of cylindrical thin-walled hyaline hyphae 12-20 μm wide. Caulocystidia absent. Clamp connections absent.

Habitat solitary, on wood of Betula.

**Collections examined** RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, the mouth of the Uzun-Suk River, 52°03'42.2"N, 92°05'05.0"E, mixed forest (*Larix sibirica*, *Betula pendula*), on fallen trunk of *Betula*, 25 Aug. 2015, *E.F. Malysheva* 303667, 303668 (LE).

**Notes** The morphological features of the studied collections fit well to the original description of this species (Justo et al. 2014). The finding of new collections of *P. leucoborealis* in the territory of South Siberia is within the expected natural distribution of the species, extending in Russia from the Leningrad Region to the Republic of Buryatia.

In addition to the molecular delineation, *P. leucoborealis* differs morphologically from the similar species *P. petasatus* (Fr.) Gillet mainly by broader basidiospores (5.0–6.2  $\mu$ m vs. 3.5–5.5(6.0)  $\mu$ m in *P. petasatus*).

*Pluteus rangifer* Justo, E.F. Malysheva & Bulyonk., Phytotaxa 180(1): 25, 2014.

Figs. 4d–f and 6

Pileus 30–65 mm in diam., at first hemispherical or campanulate, then convex, plano-convex to applanate with broad low umbo or depression at centre; varying in colouration, from light brown, greyish brown (5D3-4) and yellowish brown (5D8, 5E8) to rust brown (6E8), dark brown (7F7) or blackish brown; surface smooth or radially fibrillose, sometimes with squamules at centre, margin even or slightly serrulate. Lamellae free, moderately crowded, ventricose, pink or brownish pink, with white flocculose edges. Stipe 40–95 × 4–10 mm, cylindrical or



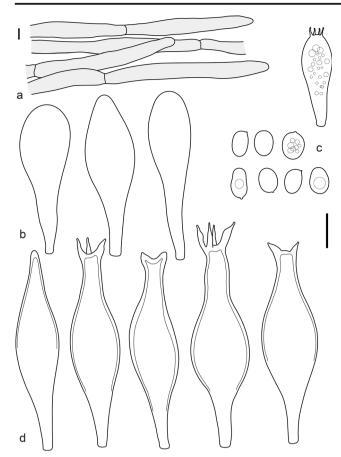
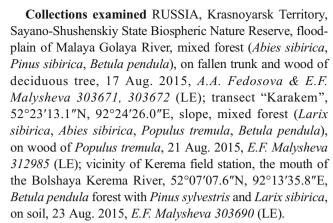


Fig. 6 Microscopic features of *Pluteus rangifer* (LE 303690). a Elements of pileipellis. b Cheilocystidia. c Basidium and basidiospores. d Pleurocystidia. *Scale bars* 10 μm

uniformly thickened downwards, longitudinally squamulose with dark brown squamules. Smell raphanoid, taste not recorded.

Basidiospores [80/4/4]  $6.5-9.0(9.7) \times 5.0-6.8$  µm (Lm = 7.7, Wm = 5.8, Q = 1.13 - 1.48; Qm = 1.33), mostlybroadly to narrowly ellipsoid or ovoid, in some specimens predominant shape is subglobose, in others, oblong or cylindrical, thick-walled. Basidia 18-27 × 7-10 µm, 4spored, broadly clavate. Pleurocystidia metuloid, 60- $90 \times (10)13-20$  µm, abundant, broadly to narrowly fusiform or utriform, with 2-3(4) short to very long (up to 7 μm) apical hooks (most entire, but bifurcated also present), some without hooks, hyaline, walls up to 3-5 µm wide. Cheilocystidia 40-85 × 13-30 μm, numerous, mostly broadly clavate, hyaline, thin- or slightly thick-walled. Pileipellis a cutis, made up of slightly thick-walled cylindrical hyphae, up to 18 µm wide, hyaline or with yellowish brown intracellular pigment, with narrowly fusiform or cylindrical terminal elements, 80-150 µm long. Stipitipellis consists of cylindrical thin-walled hyphae with yellow-brown intracellular pigment. Caulocystidia absent. Clamp connections absent.

**Habitat** solitary, on wood of deciduous trees, rarely on soil.



**Notes** The main distinctive characters of *P. rangifer* are the usually dark colouration of the pileus together with the presence of contrasting brown or black squamules on the stipe surface. It differs from the two close species, *P. cervinus* (Schaeff.) P. Kumm. and *P. exilis* Singer, by a darker colour of the basidiocarps, ecology and geographical distribution.

#### Sect. Celluloderma

*Pluteus chrysophlebius* (Berk. & Ravenel) Sacc., Syll. Fung. 5: 678, 1887.

Fig. 4g

Collections examined RUSSIA, Krasnovarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, transect "Karakem", 52°23′13.1″N, 92°24′26.0″E, slope, mixed forest (Larix sibirica, Abies sibirica, Populus tremula, Betula pendula), on wood of Populus tremula, 21 Aug. 2015, E.F. Malysheva 303664 (LE); vicinity of Kerema field station, the mouth of the Bolshaya Kerema River, 52°07'07.6"N, 92°13'35.8"E, Betula pendula forest with Pinus sylvestris and Larix sibirica, on decayed wood and large fallen trunk of Betula pendula, 23 Aug. 2015, E.F. Malysheva 303663, 303670, 303678 (LE); the same place, on wood of Betula pendula, 29 Aug. 2015, E.F. Malysheva 303694 (LE); the mouth of the Uzun-Suk River, 52°03'42.2" N, 92°05'05.0"E, mixed forest (Larix sibirica, Betula pendula), on fallen trunk of Betula, 25 Aug. 2015, N.V. Psurtseva 312733 (LE).

In determining the taxonomic affiliation of our collections, we followed the concept of Justo et al. (2011b), who proposed using the name *P. chrysophlebius* instead of *P. chrysophaeus* in the sense of Vellinga (1990).

As shown in previous studies (Justo et al. 2011b), the sequences of *P. chrysophlebius* are grouped in 3 distinct subclades according to the geographical origin (Europe, Japan and North America). It is interesting to note that four of the South Siberian collections studied here (LE303664, LE303694, LE312854, LE303663) group with the European sequences, while one collection (LE312733) groups with the Japanese sequences.

*Pluteus phlebophorus* (Ditmar) P. Kumm., Führ. Pilzk. (Zerbst): 98, 1871.



Figs. 7a-c and 8

Pileus 10-30 mm in diam., at first hemispherical or campanulate, then convex or plano-convex expanding to applanate, with broad low umbo or depression at centre; hygrophanous, translucently striate up to half of radius; varying in colouration, from light brown, greyish brown or clay (5D3-5) and brown (7D7-8, 6E86 7E8) to reddish brown (8E7-86 9E8, 9F8) or dark brown (7F6-8), often with light brown or yellow-brown margin (6D4-5); surface glabrous, weakly to strongly venous at centre. Lamellae free, moderately crowded, ventricose, pink or brownish pink, with brownish flocculose edges or with concolourous edges. Stipe 35-55 × 2-5 mm, cylindrical or uniformly thickened downwards, longitudinally fibrillose, whitish, pale yellow, greyish yellow (3B2-3) or greyish beige (4C2, 4D2), shiny. Smell indistinct, taste not recorded.

Basidiospores [140/7/6]  $(5.0)6.0-7.6(8.0) \times (4.9)5.5-$ 6.5(7.5) µm (Lm = 7.0, Wm = 5.7, Q = (1.02)1.08-1.37(1.43); Qm = 1.22), broadly ellipsoid to ellipsoid, some ovoid or subglobose, thick-walled. Basidia 20–28(35) × 6.5– 11 µm, 4-spored, broadly clavate. Pleurocystidia 30- $70(90) \times 9.5-30$  µm, abundant, broadly to narrowly lageniform, broadly utriform or broadly fusiform, rarely clavate, hyaline, thin-walled. Cheilocystidia (20)27–70 × 10– 40 μm, abundant, forming sterile edge of lamellae, broadly utriform, broadly clavate, a few lageniform with short neck, occasionally narrowly clavate or cylindrical, mostly with vellow-brown or brown intracellular pigment, occasionally hyaline, slightly thick-walled. Pileipellis an euhymeniderm, made up of uniform broadly clavate and spheropedunculate elements, 20-40 × 12-30 μm, with yellow-brown intracellular pigment, slightly thick-walled. Caulocystidia very rare in basal part of stipe, in clusters, cylindrical, utriform or narrowly

Fig. 7 Basidiocarps. a Pluteus phlebophorus (LE 303681). b P. phlebophorus (LE 303684). c P. phlebophorus (LE 312918). d P. thomsonii (LE 303685). e P. aff. cinereofuscus (LE 303665). f P. aff. cinereofuscus (LE 303669). g P. podospileus (LE 303682). h P. hispidulus var. cephalocystis (LE 303683). Scale bars 1 cm





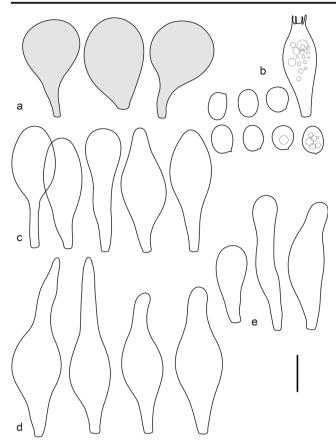


Fig. 8 Microscopic features of *Pluteus phlebophorus* (LE 303679, 303681, 312918). a Elements of pileipellis. b Basidium and basidiospores. c Cheilocystidia. d Pleurocystidia. e Caulocystidia. *Scale bar* 10 µm

clavate,  $25-60\times5.5-12~\mu m$ , yellowish brown or hyaline, thin-walled, or absent in some collections (LE 303679, LE 303684). Clamp connections absent in all tissues.

**Habitat** solitary or in small groups, on fallen branches or decayed wood of deciduous trees.

Collections examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, 2 km upstream of the Bolshaya Golaya River, slope, 52°33′50.0″N, 92°07'40.0"E, Betula pendula forest with solitary Populus tremula and Abies sibirica, on wood and fallen branch of Betula pendula, 16 Aug. 2015, E.F. Malysheva 303673, 303674 (LE); vicinity of Talovka field station, floodplain of Talovka River, mixed forest (Abies sibirica and Betula pendula with solitary Pinus sibirica,), on fallen trunk of Betula pendula, 20 Aug. 2015, E.F. Malysheva 303681(LE); transect "Karakem", 52°23′13.1″N, 92°24′26.0″E, slope, mixed forest (Larix sibirica, Abies sibirica, Populus tremula, Betula pendula), on decayed wood of Populus tremula, 21 Aug. 2015, E.F. Malysheva & A.E. Kovalenko 303684, 303679 (LE); vicinity of Kerema field station, the mouth of the Bolshaya Kerema River, 52°07′07.6″N, 92°13′35.8″E, Betula pendula forest with Pinus sylvestris and Larix sibirica,

on fallen trunk of *Betula pendula*, 23 Aug. 2015, *E.F. Malysheva 312918* (LE).

Notes The difficulties in taxonomic interpretation of the one large group of taxa around Pluteus phlebophorus including at least six or seven closely related species (viz. P. chrysophlebius, P. luctuosus Boud., P. cinereofuscus, P. pallescens P.D. Orton, P. rugosidiscus, P. cvanopus Quél. and P. nanus (Pers.) P. Kumm.) have been discussed by many mycologists since Singer (1956). The variability of many morphological features (colour of pileus, degree of rugosity of the pileus surface, shape and pigmentation of pleuro- and cheilocystidia) together with the absence of type specimens for most of these species greatly complicate matters. However, the recent study based on both morphological and molecular data (Justo et al. 2011b) showed the delimitation between the phlebophorus, chrysophlebius and rugosidiscus clades and their concordance with the most common taxonomic concepts of the corresponding species. It was also shown that P. luctuosus likely did not represent a distinct species but is rather a morphological variant of P. phlebophorus having brown lamellar edges and pigmented hymenial cystidia. According to the description of *P. luctuosus* presented by Vellinga (1990), the main distinctive characters of the species are the brown colour of the pileus, the greyish stipe without yellow hue, brown flocculose lamellar edges and pigmented hymenial cystidia. In our present study three collections with pigmented cheilocystidia and one collection with hyaline ones form a single subclade together with two GenBank sequences determined as P. phlebophorus (HM562184 from USA and HM562117 from Japan) within a larger phlebophorus clade. This clade includes also a second subclade with four sequences: two sequences originated from Spanish collections (HM562144, HM562137), and two of our collections characterized by concolourous lamellar edges and colourless cheilocystidia (LE 303681, 312918). The first subclade was non-supported but the support of the second subclade was rather high in both ML (BS = 78 %) and BA (PP = 1.00) analyses. However, the short branches and low percentage of sequence divergence between the two subclades (not exceeding 1.5 %) demonstrate the phylogenetic unity of the group of analyzed sequences within the phlebophorus clade. Therefore, all our studied collections are regarded here as representing P. phlebophorus in its morphological concept proposed by Vellinga (1990), also including Pluteus luctuosus.

Just like in the case of *P. chrysophlebius*, different nrITS types of *P. phlebophorus*, previously associated with different geographic origins, coexist in the same area of South Siberia.

*Pluteus rugosidiscus* Murrill, N. Amer. Fl. (New York) 10(2): 129, 1917.

Figs. 4h and 9

Pileus 10–15 mm in diam., convex becoming planoconvex to applanate, umbonate; hygrophanous, margin



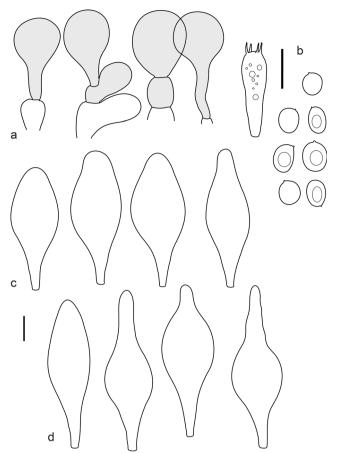
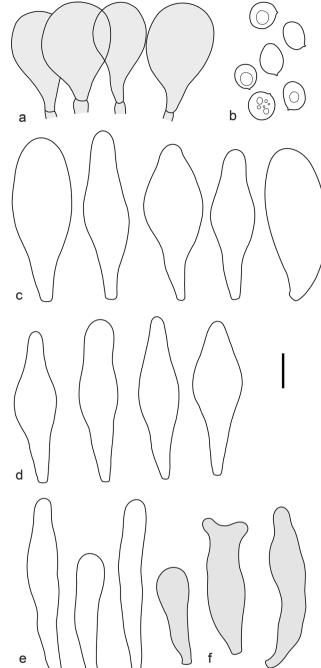


Fig. 9 Microscopic features of *Pluteus rugosidiscus* (LE 303676). a Elements of pileipellis. b Basidium and basidiospores. c Cheilocystidia. d Pleurocystidia. *Scale bars* 10  $\mu$ m

translucently striate or sulcate; yellow-brown or olive brown (4E4-8, 4F6), slightly darker at centre – mustard brown or tobacco brown (5E6, 5F6); surface glabrous, distinctly rugulose at centre. *Lamellae* free, subdistant, ventricose, pinkish, with concolourous and crenulate edges. *Stipe* 15–25 × 1–2 mm, cylindrical or tapering upwards, smooth, pale yellow at upper half (3A3) to straw yellow or cadmium yellow at base (3B4, 4A8). Smell indistinct, taste not recorded.

Basidiospores [40/2/1] (5.7)6.0–7.8(8.0) × 5.0–6.7(7.3) μm (Lm = 6.9, Wm = 5.7, Q = 1.10–1.35(1.42); Qm = 1.21), broadly ellipsoid, ovoid, subglobose to globose, thick-walled. Basidia  $20-30 \times 5.5-8.0$  μm, 4-spored, clavate. Pleurocystidia  $40-65 \times 11-15$  μm, scattered, rather numerous, broadly lageniform or fusoid-ventricose, hyaline, thin-walled. Cheilocystidia  $27-60 \times 10-22$  μm, abundant, forming sterile edge of lamellae, predominantly inflated lageniform with short neck or broadly utriform, occasionally clavate, hyaline, thin-walled. Pileipellis an euhymeniderm, made up of broadly clavate and spheropedunculate elements,  $20-45 \times 12-25$  μm, with yellow-brown intracellular pigment, slightly thick-walled. Caulocystidia absent. Clamp connections absent in all tissues.



**Fig. 10** Microscopic features of *Pluteus* aff. *cinereofuscus* (LE 303665, 303669). **a** Elements of pileipellis. **b** Basidiospores. **c** Cheilocystidia. **d** Pleurocystidia. **e** Caulocystidia at upper part of stipe. **f** Caulocystidia at base of stipe. *Scale bar* 10 μm

**Habitat** in small group, on decayed wood of *Populus*.

Collection examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, transect "Karakem", 52°23′13.1″N, 92°24′26.0″E, slope, mixed forest (*Larix sibirica*, *Abies sibirica*, *Populus tremula*, *Betula pendula*), on decayed wood of *Populus tremula*, 21 Aug. 2015, *E.F. Malysheva* 303676 (LE).



Fig. 11 Basidiocarps. a P. leoninus (LE 303691). b P. leoninus (LE 303695). c P. leoninus (LE 303700). d P. velutinus (LE 303693). e P. aff. plautus (LE 303680). f P. umbrosus (LE 303696). g P. umbrosoides (LE 312735, holotype). h P. umbrosoides (LE 312920). Scale bars 1 cm



**Notes** The olive or greenish tint in the pileus colour and the yellow stipe are notable macroscopic features of this species. Based on these macroscopic characters it differs from closely related species, *P. phlebophorus* and *P. chrysophlebius*, from which it is almost indistinguishable microscopically. In the field it also could be somewhat confused with *P. romellii* if the greenish tint is not so conspicuous, but it is easily distinguished from the latter under the microscope based on the shape of pleuro- and cheilocystidia.

This is the first record of the species in Russia. Until now, the species was known only from North America. Its actual distribution in Eurasia requires further investigation.

*Pluteus* aff. *cinereofuscus* J.E. Lange, Dansk bot. Ark. 2(7): 9, 1917.

Figs. 7e, f and 10

*Pileus* 10–15 mm in diam., plano-convex with broad low umbo, then expanding to applanate; hygrophanous,

translucently striate up to half of radius, sometimes sulcate at margin; leather brown, brown, camel or cinnamon at centre (6E6, 6D4-6, 7E6-8) with darker reddish-brown centre (8E7-8) and contrastingly paler on margin – pale orange grey to alabaster or white (5B2-3), light brown or terra cotta (7D6-7); opaque, glabrous, at centre slightly venose. *Lamellae* free, moderately crowded, ventricose, pink or brownish pink, with concolourous edges. *Stipe* 15–50 × 1–2.5 mm, cylindrical or uniformly thickened towards base, whitish or yellowish (4A2-3) or yellow-grey (3D2, 4B3) at upper part, with brownish grey base (5D3), longitudinally fibrillose, shiny. Smell indistinct, taste not recorded.

Basidiospores [80/4/2] (5.5)6.0–8.0(8.4)  $\times$  5.4–7.6(8.0)  $\mu$ m (Lm = 7.4, Wm = 6.3, Q = 1.00–1.33(1.43); Qm = 1.10), broadly ellipsoid to subglobose or globose, thick-walled. Basidia 20–30  $\times$  8–11  $\mu$ m, 4-spored, narrowly clavate. Pleurocystidia 40–70(80)  $\times$  10–20  $\mu$ m, scattered to abundant,



fusiform, lageniform or narrowly to broadly utriform, rarely clavate or broadly cylindrical, hyaline, thin-walled. *Cheilocystidia* 40–70(85) × 10–37  $\mu$ m, abundant, forming sterile edge of lamellae, varying in form, mostly fusiform, narrowly to broadly clavate, broadly utriform, rarely cylindrical, often with vacuolar content, hyaline, thin-walled. *Pileipellis* an euhymeniderm, made up of broadly clavate and spheropedunculate elements, 25–55 × 12–45  $\mu$ m, with yellow-brown or brown intracellular pigment, slightly thickwalled. *Caulocystidia* 25–55(70) × (5.5)7–13  $\mu$ m, in clusters or single, mostly cylindrical, fusiform or narrowly clavate, hyaline at upper part of stipe and pigmented at base, thinwalled. Clamp connections absent.

**Habitat** in small group or solitary, on decayed wood of *Betula*.

Collections examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, vicinity of Kerema field station, the mouth of the Bolshaya Kerema River, 52°07′07.6″N, 92°13′35.8″E, *Betula pendula* forest with *Pinus sylvestris* and *Larix sibirica*, on decayed wood of *Betula pendula*, 23 Aug. 2015, *E.F. Malysheva 303665*, 303669 (LE).

**Notes** Morphologically the studied collections are close to *Pluteus cinereofuscus*, *P. phlebophorus* and *P. nanus* (Pers.) P. Kumm., in the sense of Vellinga (1990). They are almost undistinguishable from *P. phlebophorus* based on macroand microscopic features besides fewer fusiform pleurocystidia. The latter species *P. nanus* differs by the predominantly darker colour of the pileus with the surface becoming opaque when gently rubbed and by the presence of narrowly clavate elements in the pileipellis.

The molecular data obtained in our study together with the recent phylogenetic investigation (Justo et al. 2011b) are not sufficient to completely solve the question about which clade actually represents *P. cinereofuscus*. The morphological boundaries of this species, as well as the other taxa within the cinereofuscus clade, remain uncertain. This problem needs further study. In the present paper we tentatively attribute our collections to *Pluteus* aff. *cinereofuscus*.

**Pluteus thomsonii** (Berk. & Broome) Dennis, Trans. Br. Mycol. Soc. 31(3–4): 206, 1948 [1947].

Fig. 7d

Collections examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, vicinity of Kerema field station, the mouth of the Bolshaya Kerema River, 52°07′07.6″N, 92°13′35.8″E, *Betula pendula* forest with *Pinus sylvestris* and *Larix sibirica*, on decayed wood of *Betula pendula*, 23 Aug. 2015, *E.F. Malysheva 303662* (LE); the same place, mixed forest, on decayed wood of *Betula pendula*, 29 Aug. 2015, *E.F. Malysheva 303685* (LE).

*Pluteus podospileus* Sacc. & Cub., Syll. Fung. (Abellini) 5: 672, 1887.

Fig. 7g

Collections examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, vicinity of Kerema field station, the mouth of the Bolshaya Kerema River, 52°07′07.6″N, 92°13′35.8″E, *Betula pendula* forest with *Pinus sylvestris* and *Larix sibirica*, on decayed wood and large fallen trunk of *Betula pendula*, 23 Aug. 2015, *E.F. Malysheva* 303682, 303687 (LE).

*Pluteus romellii* (Britzelm.) Lapl., Dictionnaire Iconographique des Champignons Supérieures, 533, 1894.

Collection examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, transect "Karakem", 52°23′13.1″N, 92°24′26.0″E, slope, mixed forest (*Larix sibirica*, *Abies sibirica*, *Populus tremula*, *Betula pendula*), on fallen trunk of *Betula pendula*, 21 Aug. 2015, *A.A. Kiyashko 303660* (LE).

*Pluteus fenzlii* (Schulzer) Corriol & P.-A. Moreau, Persoonia 19(2): 248, 2007.

Collections examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, 2 km upstream of the Bolshaya Golaya River, slope, 52°33′50.0″N, 92°07′40.0″E, *Betula pendula* forest with solitary *Populus tremula* and *Abies sibirica*, on fallen trunk of *Betula pendula*, 16 Aug. 2015, *E.F. Malysheva 303697* (LE); vicinity of Kerema field station, the mouth of the Bolshaya Kerema River, 52°07′07.6″N, 92°13′35.8″E, *Betula pendula* forest with *Pinus sylvestris* and *Larix sibirica*, on decayed wood of *Betula pendula*, 23 Aug. 2015, *A.A. Kiyashko 303661* (LE).

*Pluteus tomentosulus* Peck f. *brunneus* E.F. Malysheva & Justo, **f. nov.** 

Figs. 12a-c and 13

MycoBank No. MB 817079

It differs from type form of *P. tomentosulus* by coloured basidiocarps in brown tones as well as its geographical distribution.

Pileus 15-60 mm in diam., when closed almost ovoid or thimble-shaped, then broadly conical, campanulate or convex and plano-convex with broad umbo, with even or slightly incurved margin; not hygrophanous; uniformly coloured or slightly darker at centre, dark blonde, colour of coffee with milk, light brown or golden brown (5D4-6), in some basidiomata with cinnamon tint (6D6); surface densely flocculose-squamulose or velvety, often with overhanging floccules at margin, in dry conditions occasionally cracked demonstrating whitish flesh from below. Lamellae free, moderately crowded, ventricose, bright pink, with concolourous edges. Stipe  $40-70 \times 4-8$  mm, cylindrical or uniformly thickened towards subbulbous base, longitudinally squamulose with squamules more loosely located and concolourous with those on pileus. Smell indistinct, taste not recorded.

Basidiospores [60/3/3]  $6.0-8.0 \times (4.5)5.2-7.0 \mu m$  (Lm = 7.0, Wm = 5.8, Q = 1.02-1.38(1.43); Qm = 1.21), broadly ellipsoid, rarely subglobose, thick-walled. Basidia



Fig. 12 Basidiocarps of *Pluteus tomentosulus*. a f. brunneus (LE 312907). b f. brunneus (LE 312908, holotype). c f. brunneus (LE 312906). d *P. tomentosulus* (MO93719). e *P. tomentosulus* (MO163564). Scale bars 1 cm



 $18-27 \times 6.5-9.5$  µm, 4-spored, clavate. *Pleurocystidia* (25)40–95 × 15–30 µm, scarce or scattered, broadly utriform,

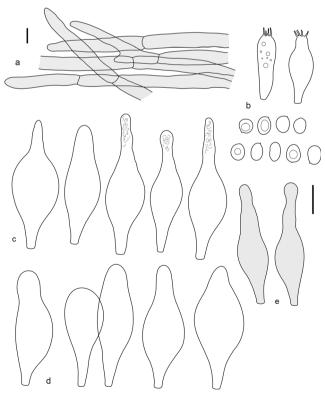
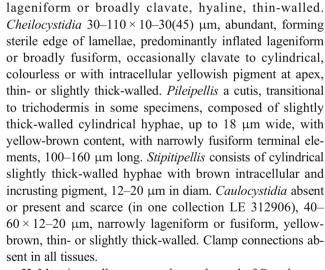


Fig. 13 Microscopic features of *Pluteus tomentosulus* f. *brunneus* (LE 312906, 312907, 312908). a Elements of pileipellis. b Basidia and basidiospores. c Cheilocystidia. d Pleurocystidia. e Caulocystidia. *Scale bars* 10 μm



Habitat in small group, on decayed wood of *Populus*.

Collections examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, Dzhoiskaya Sosnovka bay, *Populus tremula* forest, on decayed wood of *Populus tremula*, 14 Aug. 2015, *A.A. Kiyashko 312906* (LE); the same area, transect "Karakem", 52°23′13.1″N, 92°24′26.0″E, 210 m up the slope, mixed forest (*Larix sibirica, Abies sibirica, Populus tremula, Betula pendula*), on decayed wood of *Populus tremula*, 21 Aug. 2015, *V.F. Malysheva 312907* (LE), *312908* (LE, HOLOTYPE).

**Etymology** The epithet derived from Latin "brunneus" (brown) indicates a major difference from the type form in the colour of basidiocarps.



#### Description of North American collections of *P. tomentosulus* Peck f. *tomentosulus*

*Pluteus tomentosulus* Peck, Annual Report on the New York State Museum of Natural History 38: 136, 1885.

Fig. 12d, e

Pileus 30–60 mm in diam., ovoid or hemispherical when young, then broadly conical, campanulate or convex and plano-convex with or without broad umbo, with even or slightly curved margin; not hygrophanous; white all over; surface densely flocculose-squamulose or velvety. Lamellae free, moderately crowded, ventricose, bright pink, with concolourous edges. Stipe 40–90 × 4–8 mm, cylindrical, slightly broader at base; white all over; surface densely flocculose-squamulose or velvety. Smell and taste not recorded.

Basidiospores [60/2/2] 5.5-8.0 (9.5) × 5.0-6.5 (7.0) µm (Lm = 7.20, Wm = 5.70, Q = 1.17 - 1.39(1.45); Qm = 1.26),broadly ellipsoid or ellipsoid, thick-walled. Basidia 18-27 × 6.5–9.5 µm, 4-spored, clavate. Pleurocystidia 40– 95 × 19-30 μm, common, utriform or lageniform, some subcapitate or with long flexuose apex, hyaline, thin-walled. Cheilocystidia  $40-85 \times 15-40 \mu m$ , abundant but not crowded, lageniform or utriform, colourless, sometimes slightly thickwalled at apex. Pileipellis a very loosely arranged cutis, with groups of ascending elements, composed of slightly thickwalled cylindrical hyphae, up to 20 µm wide, hyaline, very frequently septated. Stipitipellis with two distinct layers, the external one a very loosely arranged cutis, similar to the pileipellis; the internal a cutis, made up of more tightly packed, narrower hyphae; hyaline. Caulocystidia absent. Clamp connections absent in all tissues.

Habitat solitary or in small groups, on decayed wood.

Collections examined USA, Oregon, Sauvie Island, on decayed wood, 29 April 2012, *Sava Krstic*, *MO93719* (CUW); Pennsylvania, Ricketts Glenn State Park, on decayed wood, 01 Aug. 2007, *Dave Wasilewski*, *MO163564* (CUW).

Notes Up to now, this species was unknown outside North America. In the original description of *P. tomentosulus* (Peck 1885) and Singer's description of an additional North American collection (Singer 1956) the colour of basidiocarps was always indicated as totally white or slightly pinkish. Two collections from Oregon and Pennsylvania examined by us matched the common macroscopic description of this species. The morphological examination of all Siberian collections revealed no other differences from P. tomentosulus except obvious brown colouration of their basidiocarps. Additional molecular studies performed in order to determine if North American and Siberian collections are separate taxa showed the identity of all collections studied based on ITS (the sequences similarity between two groups was 99 % or higher). Based on molecular data and similarity of most morphological features, it is our opinion that the Siberian populations represent the same species with North American collections. We prefer to consider these Siberian populations with brown colour of basidiocarps as a new form, *P. tomentosulus* f. *brunneus*, described here.

*Pluteus hispidulus* (Fr.) Gillet var. *cephalocystis* Schreurs, Persoonia 12(4): 348, 1985.

Figs. 7h and 14

*Pileus* 15 mm in diam., applanate with slight central depression, with broad low umbo; not hygrophanous, not striate at margin; brownish beige, greyish brown (6E3), at centre brown or agate (7E7-8); surface covered with scattered squamules, more densely located at centre and rare at margin showing whitish background surface. *Lamellae* free, moderately crowded, ventricose, pink, with concolourous edges. *Stipe* 45 × 1.5–2 mm, cylindrical, longitudinally fibrillose, greyish or silvery white (2B1-2), with darker base. Smell indistinct, taste not recorded.

Basidiospores [20/1/1] (5.0)5.4–6.5 × 4.6–5.5 μm (Lm = 5.8, Wm = 5.3, Q = 1.02–1.20; Qm = 1.10), broadly ellipsoid, ellipsoid or subglobose, thick-walled. Basidia 18–25 × 6–9 μm, 4-spored, clavate. Pleurocystidia absent. Cheilocystidia 32–80 × 10–20 μm, abundant, forming sterile edge of lamellae, inflated lageniform with short neck, broadly clavate, subcapitate, sometimes with points of apical encrustation, hyaline, thin-walled. Pileipellis a cutis, made up of slightly thick-walled cylindrical hyphae, up to 18 μm wide, with yellow-brown intracellular pigment, with narrowly fusiform or cylindrical terminal elements, 170–230 μm long. Caulocystidia absent. Clamp connections absent in all tissues.

**Habitat** solitary, on decayed wood of *Betula*.

**Collection examined** RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, vicinity of Kerema field station, the mouth of the Bolshaya Kerema River, 52°07′07.6″N, 92°13′35.8″E, *Betula pendula* forest

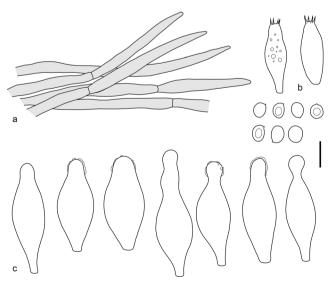


Fig. 14 Microscopic features of *Pluteus hispidulus* var. *cephalocystis* (LE 303683). a Elements of pileipellis. b Basidia and basidiospores. c Cheilocystidia. *Scale bar* 10 μm

with *Pinus sylvestris* and *Larix sibirica*, on decayed wood of *Betula pendula*, 23 Aug. 2015, *V.F. Malysheva 303683* (LE).

**Notes** The small size of basidiocarps, greyish brown squamulose pileus and subcapitate cheilocystidia are the distinctive characters of this variety of *P. hispidulus*. The type variety differs by the non-capitate cheilocystidia. The morphologically similar species *P. exiguus* (Pat.) Sacc. is distinguished by the pileipellis structure.

#### Sect. Hispidoderma

*Pluteus velutinus* C.K. Pradeep, Justo & K.B. Vrinda, Mycol. Progr. 11(4): 870, 2012.

Figs. 11d and 15

Pileus 20 mm in diam., plano-convex or obtusely conical without umbo; hygrophanous, striate at margin; fawn brown

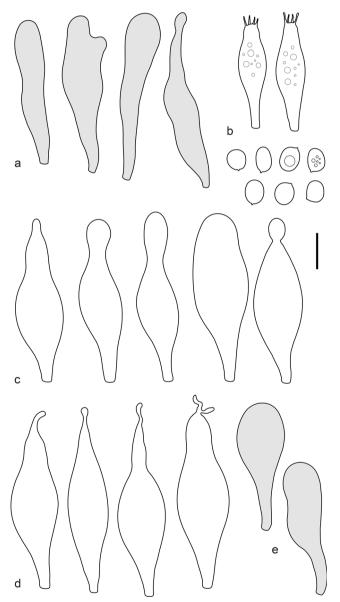


Fig. 15 Microscopic features of *Pluteus velutinus* (LE 303693). a Elements of pileipellis. b Basidia and basidiospores. c Cheilocystidia. d Pleurocystidia. c Caulocystidia. *Scale bar* 10 µm



to brown or agate (7E4-8), at centre dark brown (7F7-8); surface subgranulose, granulose or velutinous at centre, with barely visible pattern of veins radiating from centre towards margin. *Lamellae* free, moderately crowded, ventricose, pink, with concolourous edges. *Stipe* 40 × 2–2.5 mm, cylindrical, longitudinally striate, pruinose, brownish grey (7D2, 7E2), with darker base. Smell indistinct, taste not recorded.

Basidiospores [20/1/1]  $5.7-6.5(7.5) \times 5.4-6.0(6.3)$  µm (Lm = 6.2, Wm = 5.7, Q = 1.00 - 1.16(1.20); Qm = 1.08), predominantly globose and subglobose, occasionally broadly ellipsoid, thick-walled. Basidia 20–28 × 7–10 µm, 4-spored, broadly clavate. Pleurocystidia 30-70 × 10-25 μm, numerous, broadly lageniform or broadly fusiform, tapering into apex, often with irregularly shaped apical projections, hyaline or with pale brown content, thin-walled. Cheilocystidia 27- $60 \times 8-24$  µm, abundant, varying in shape, the most part broadly utriform, broadly lageniform with short neck and often with rounded apex, rarely with median constriction, hyaline, thin-walled. Pileipellis a trichohymeniderm, made up of cylindrical, narrowly clavate or irregularly shaped elements with undulating walls, 40-100 × 8-23 μm, with yellowbrown intracellular pigment, thin- or slightly thick-walled. Caulocystidia rather numerous, 27–60 × 12–25 µm, clavate, pyriform or spheropedunculate, with brownish content, thinor slightly thick-walled. Clamp connections absent in all tissues.

Habitat solitary, on litter.

**Collection examined** RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, the mouth of the Sarly River, 52°09′55.5″N, 92°18′43.9″E, floodplain forest (*Betula pendula*, *Populus tremula*, *Pinus sylvestris* and *Picea obovata*), on litter, 27 Aug. 2015, *A.G. Fedosova* 303693 (LE).

**Notes** *Pluteus velutinus* is a recently described species (Pradeep et al. 2012). The holotype collection was from India, and the additional collections mentioned in the original description were from Japan. It is noteworthy, that in a short period of time after the description there have been other records of this species from very distant geographical regions such as Brazil, Mongolia, European part of Russia, Russian Far East and now South Siberia. Based on all available materials the distribution area of *P. velutinus* may be assumed to be rather wide but at present it is difficult to find out the center of origin of the species as well as its distribution pattern in the past. Before our study data on the occurrence of this species in Russia were absent.

The most remarkable morphological character of the species that distinguishes it from the similar taxa *P. plautus* and *P. depauperatus* Romagn. is mainly the peculiar shape of pleurocystidia with apical projections.

We observed some morphological differences between our Siberian collection of *P. velutinus* and the original description: smaller basidiospores,  $5.7-6.5(7.5) \times 5.4-6.0(6.3) \mu m$  in our

collection, in comparison with  $5.5-9.5 \times 5-7.0 \,\mu m$  of the original description; basidiospores subglobose rather than ellipsoid; and pigmented pleurocystidia, which were also mentioned in the Brazilian record of this species (Menolli et al. 2015a). Molecularly, the ITS sequence of our specimen was almost identical (one nucleotide difference) to the sequence of the holotype (JN603205).

*Pluteus* aff. *plautus* (Weinm.) Gillet, Hyménomycètes: 394, 1876 [1878].

Figs. 11e and 16

Pileus 10–30 mm in diam., at first hemispherical, then convex to plano-convex without umbo; hygrophanous, translucently striate up to half of radius; brown (7E7-8), at centre dark brown with reddish tint (8 F4-8), at margin contrastingly paler – light brown (6D4) or brownish grey and brownish orange (5C3, 6C2-3); surface subgranulose, rather pruinose, covered with minute squamules. Lamellae free, moderately

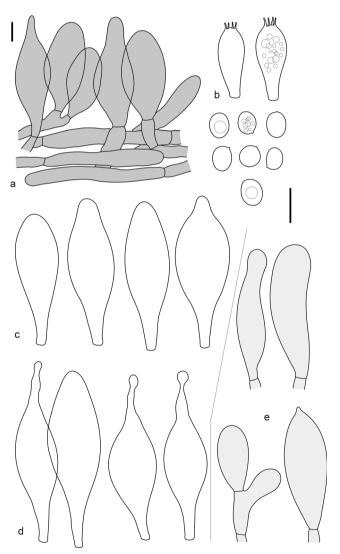


Fig. 16 Microscopic features of *Pluteus* aff. *plautus* (LE 303680). a Elements of pileipellis. b Basidia and basidiospores. c Cheilocystidia. d Pleurocystidia. e Caulocystidia. *Scale bars* 10 μm

crowded, ventricose, whitish then pink, with concolourous or whitish edges.  $Stipe\ 15-20\times2-4$  mm, cylindrical or thickened downwards, longitudinally striate, granulose-squamulose, camel or light brown (6D4-5), with greyish tomentum at base. Smell indistinct, taste not recorded.

Basidiospores [40/2/1]  $(6.2)6.6-8.0(8.6) \times (5.2)6.0 7.0(7.5) \mu m \text{ (Lm} = 7.4, Wm = 6.2, Q = 1.00 - 1.37(1.41);}$ Om = 1.20), predominantly broadly ellipsoid or ovoid, occasionally subglobose, thick-walled. Basidia 20–28 × 9–11 μm, 4-spored, broadly clavate. Pleurocystidia 40-70(80) × 12-27 µm, numerous, broadly to narrowly fusiform or broadly lageniform, with narrow neck tapering into apex which often subcapitate, hyaline or with very pale yellowish content, thinwalled. Cheilocystidia 27–65 × 10–30 μm, abundant, varying in shape, predominantly broadly lanceolate with obtuse apex, or broadly utriform, rarely lageniform with inflated body and short neck, hyaline, thin-walled. Pileipellis a hymeniderm, made up of narrowly to broadly clavate, broadly fusiform or utriform terminal elements, slightly thick-walled, 40-110(150) × 20–40 μm, with yellow-brown intracellular pigment, rising from underlying layer of cylindrical yellowbrown hyphae 10–14 µm wide. Stipitipellis a cutis of hyaline cylindrical hyphae up to 16 µm wide. Caulocystidia very numerous (especially at stipe base), 40–100 × 10–27 µm, narrowly clavate, inflated fusiform or lanceolate, with brownish content, thin- or slightly thick-walled. Clamp connections absent in all tissues.

Habitat subgregarious, on wood of deciduous tree.

**Collection examined** RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, vicinity of Talovka field station, meadow at the bank of Yenisei River, on large fallen trunk of deciduous, 19 Aug. 2015, *V.F. Malysheva* 303680 (LE).

Notes The studied collection is characterized by a convex, hygrophanous, dark brown, granulose-pruinose pileus, broadly ellipsoid basidiospores, subcapitate fusiform or lageniform pleurocystidia which are often pigmented, lanceolate cheilocystidia, hymenidermial pileipellis, and numerous clavate caulocystidia with brownish content. It is rather similar to P. plautus and differs from it by a darker colour of the pileus together with its pruinose surface, the shape of the pleurocystidia which never have a narrow neck in P. plautus, and the structure of the pileipellis. On the phylogenetic tree the sequence of the Siberian collection is grouped together with one sequence from GenBank named Pluteus aff. plautus (KR022012) from the USA but they do not form a monophyletic clade separate from other sequences of the P. plautus group. Therefore, based on our morphological and molecular studies, we prefer to consider the Siberian collection as Pluteus aff. plautus.

In general, the taxonomy and phylogeny of the taxa within the plautus group including apart from *P. plautus* s.l. also



P. granulatus Bres., P. longistriatus (Peck) Peck and P. semibulbosus (Lasch) Quél. is still unresolved (Vellinga 1990; Justo et al. 2011b; Pradeep et al. 2012; Menolli et al. 2015a). Besides these species, there are obviously several more members within the P. plautus species complex which are still unnamed and need to be studied and described (Justo et al. 2011b; Menolli et al. 2015a).

*Pluteus leoninus* (Schaeff.) P. Kumm., Führ. Pilzk. (Zerbst): 98, 1871.

Fig. 11a-c

Collections examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, 2 km upstream of the Bolshaya Golaya River, slope, 52°33′50.0″N, 92°07′40.0″E, Betula pendula forest with solitary Populus tremula and Abies sibirica, on wood and fallen branch of Betula pendula, 16 Aug. 2015, E.F. Malysheva 303691, 303698 (LE); vicinity of Talovka field station, floodplain of Talovka River, mixed forest (Abies sibirica and Betula pendula with solitary Pinus sibirica,), on fallen trunk and branches of Betula pendula or on litter, 20 Aug. 2015, E.F. Malysheva 303695, 303699, 303700 (LE).

*Pluteus umbrosus* (Pers.) P. Kumm., Führ. Pilzk. (Zerbst): 98, 1871.

Fig. 11f

Collections examined RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, vicinity of Kerema field station, the mouth of the Bolshaya Kerema River, 52°07′07.6″N, 92°13′35.8″E, *Betula pendula* forest with *Pinus sylvestris* and *Larix sibirica*, on decayed wood, 23 Aug. 2015, *A.E. Kovalenko 312734* (LE); the mouth of the Uzun-Suk River, 52°03′42.2″N, 92°05′05.0″E, mixed forest (*Larix sibirica*, *Betula pendula*), on decayed wood of *Betula pendula*, 25 Aug. 2015, *E.F. Malysheva 303696* (LE).

Pluteus umbrosoides E.F. Malysheva, sp. nov.

Figs. 11g, h and 17

MycoBank No. MB 817080

Distinguished from *P. umbrosus* by its lamellae without brown edges, absence of overhanging floccules on the pileus margin, smooth stipe without brown squamules, shape of pleurocystidia commonly wearing apical globular head, longer elements of pileipellis, narrowly fusiform caulocystidia  $(40-65\times13-28~\mu m)$ .

*Pileus* 40–50 mm in diam., hemispherical at first, then expanding to applanate with low umbo or depressed at centre; brown to dark brown (7E8, 7F7-8), pale towards margin; surface squamulose, sometimes looking velvety, with erect squamules densely located at centre and forming pattern of veins radiating from centre towards margin, and scarce at margin showing whitish background of surface. *Lamellae* free, moderately crowded, ventricose, pink, with concolourous edges. *Stipe* 40–55 × 4–6 mm, cylindrical or thickened downwards, longitudinally fibrillose, shiny,

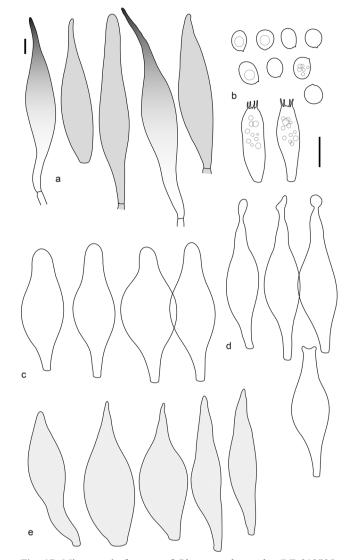


Fig. 17 Microscopic features of *Pluteus umbrosoides* (LE 312735, holotype). **a** Elements of pileipellis. **b** Basidia and basidiospores. **c** Cheilocystidia. **d** Pleurocystidia. **e** Caulocystidia. *Scale bars* 10 μm

yellowish or brownish grey (5C2-3), with darker base. Smell indistinct, taste not recorded.

Basidiospores [40/2/1] 5.3–6.3(7.0) × (4.3)4.7–5.5(5.8) μm (Lm = 6.0, Wm = 5.0, Q = (1.03)1.08–1.33(1.43); Qm = 1.19), predominantly ellipsoid and broadly ellipsoid, occasionally subglobose, thick-walled. Basidia 20–30 × 8–9.5 μm, 4-spored, clavate. Pleurocystidia 50–70(85) × 10–16(25) μm, numerous, broadly to narrowly lageniform or broadly fusiform, tapering into apex generally bearing a globular head, rarely apex with 1–2 irregularly shaped excrescences, hyaline, thin-walled. Cheilocystidia 55–67 × 19–27 μm, rather numerous, broadly utriform or broadly lageniform with short neck and obtuse apex, hyaline, thin-walled. Pileipellis a trichohymeniderm, consisting of narrowly to broadly fusiform terminal elements with tapering or obtuse apexes,  $100-360 \times 10-30$  μm, with yellow-brown



intracellular pigment, thin- or slightly thick-walled. *Stipitipellis* a cutis of hyaline cylindrical hyphae  $10-17~\mu m$  wide. *Caulocystidia* present only in the lower part of stipe, rather numerous, in clusters,  $40-65\times13-28~\mu m$ , fusiform, often with strongly inflated body and acute apex, with brownish intracellular pigment, slightly thick-walled. Clamp connections absent in all tissues.

Habitat in small groups, on wood of deciduous trees.

**Collection examined** RUSSIA, Krasnoyarsk Territory, Sayano-Shushenskiy State Biospheric Nature Reserve, the mouth of the Malye Ury River, 52°00′03.4″N, 91°57′56.6″E, mixed forest (*Larix sibirica*, *Picea obovata*, *Betula pendula*, *Salix* sp.), on fallen trunk of *Betula pendula*, 26 Aug. 2015, *E.F. Malysheva 312735* (LE, HOLOTYPE).

Additional collections examined from other parts of Russia RUSSIA, Samara Region, Zhiguli State Reserve, broadleaf forest (dominated by *Tilia cordata*), on decayed wood of deciduous tree, 20 Aug. 2001, *E.F. Malysheva 312839* (LE); Primorye Territory, "Land of Leopard" National Park, watershed of Gryaznaya River and Ananievka River, mixed forest (*Quercus, Carpinus, Ulmus, Alnus*), on mossy trunk of deciduous tree, 31 Aug. 2011, *E.F. Malysheva 312920* (LE).

**Etymology** The epithet derived from Latin "umbrosus" (shady, umbrageous) and Greek "-oides" (likeness) refers to the macromorphological similarity with *Pluteus umbrosus*.

**Notes** *P. umbrosoides* is characterized by the brown, densely squamulose pileus with squamules arranged in a vein pattern, pink lamellae with concolourous edges, smooth stipe, ellipsoid basidiospores, pleurocystidia predominantly capitate and pileipellis as trichohymeniderm.

The general morphological characters of this new species indicate its close similarity to the European *P. umbrosus* (Pers.) P. Kumm. and the North American *P. granularis* Peck. In the molecular analyses sequences of *P. umbrosoides* clustered in a different clade but sister to the umbrosus/granularis clade (Fig. 2). *Pluteus umbrosoides* differs from *P. umbrosus* in its lamellae never having brown edges, from both *P. umbrosus* and *P. granularis* in the absence of overhanging flocules on the pileus margin, smooth stipe without brown squamules, shape of pleurocystidia, longer elements of pileipellis, shape and size of caulocystidia, and nrITS sequences.

Based on some characters observed in the studied collections, this new species is somewhat similar to *P. punctipes* P.D. Orton of the *P. plautus* species complex having the most dark-coloured basidiocarps among all other species of this group. *Pluteus punctipes* originally described from England (Orton 1960) has some morphological features close to those typical for *P. umbrosoides* such as a brown or dark sepia pileus entirely covered with minute scales and wrinkled-sulcate at centre, similar shaped cheilocystidia, terminal elements of pileipellis of the same shape and length (110–300 μm), but

*P. punctipes* has a striated margin of the pileus, a squamose stipe, differently shaped pleurocystidia (fusiform or lageniform without any apical excrescences) with brown content, and clamp connections in pileipellis.

The additional collections from the European part of Russia and Far East examined by us were characterized by identical macro- and microscopic features and almost 100 % similarity of their sequences with Siberian specimens.

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