

БИОРАЗНООБРАЗИЕ,
СИСТЕМАТИКА, ЭКОЛОГИЯ

УДК 582.28 : 581.95

SUILLUS PALUSTER AND S. OCHRACEOROSEUS (BOLETALES) IN NORTH ASIA

© 2022 E. A. Zvyagina^{a,b,*}, N. A. Sazanova^{c,**}, and T. M. Bulyonkova^{d,***}

^aLomonosov Moscow State University, 119991 Moscow, Russia

^bYugra State University, 628012 Khanty-Mansiysk, Russia

^cInstitute of Biological Problems of the North of the Far East Branch of the Russian Academy of Sciences, 685000 Magadan, Russia

^dA.P. Ershov Institute of Informatics Systems, 630090 Novosibirsk, Russia

*e-mail: mycena@yandex.ru

**e-mail: nsazanova_mag@mail.ru

***e-mail: ressaure@gmail.com

Received March 25, 2022; revised April 25, 2022; accepted June 7, 2022

Specimens belonging to the *Suillus paluster* complex from North Asia and North America were analyzed. A molecular phylogeny of the ITS and *TEF1 α* sites indicates that two species from the *S. paluster* complex have a part of their range in North Asia. Most of the analyzed Asian specimens previously identified as *S. paluster* should be attributed to the Asian population of *S. ochraceoroseus*. The latter is distinguished by large fleshy fruiting bodies, bright pink, sometimes ochre scales and bitter taste. Based on the geography of collections and genetic sequences of ITS and *TEF1 α* , *S. ochraceoroseus* is distributed throughout the Asian part of Russia, as well as in Japan and China. Separate collections of this species were made in the European part of Russia in association with *Larix sibirica* plantings. According to the protologue, *Suillus paluster* has small fruiting bodies with large-pored, ribbed hymenophore and mild, slightly sour taste. In Eurasia, its presence was confirmed by molecular genetic methods in Eastern Siberia (Yakutia), the Far East (Magadan region) and in northern China. For the territory of Russia, *S. ochraceoroseus* is recorded for the first time. Descriptions of the morphology of collection specimens of *S. ochraceoroseus* and *S. paluster* from North Asia are provided. The Asian – Western North American disjunction of the range of *S. ochraceoroseus* and *S. paluster* is discussed.

Keywords: Beringia, biogeography, species range disjunction, *Larix*, mycorrhiza, phylogeny, *Suillaceae*, taxonomy

DOI: 10.31857/S0026364822050129

INTRODUCTION

Suillus paluster (Peck) Kuntze and *S. ochraceoroseus* (Snell) Singer are two phylogenetically close and morphologically similar species. Both species have a non-viscid pileus covered with fibrillose squamules, a decurrent radiating hymenophore, and a vanishing membranous ring. *S. ochraceoroseus* was described by Walter Henry Snell in 1941 from Idaho in the American Northwest as *Boletinus ochraceoroseus* Snell. The characteristic features of this species are large fleshy fruiting bodies of pink-ochre color and bitter taste, which is enhanced by heat treatment. The North American population of this species is possibly localized in the northwest of the continent (Washington, Montana, Idaho, Oregon in USA and Alberta, British Columbia, and Canadian Northwest Territories in Canada (Snell, 1941; Pomerleau, Smith, 1962; GBIF, 2022a; Mycoportal, 2022). Specimens collected in the northwest of North America are associated with tamarack (*Larix lyallii* Parl. and *Larix occidentalis* Nutt.). Collections outside this area are rare and were made in the artificial plantation of the western American larches (Nguyen et al., 2016; GenBank ID KX213794).

Suillus paluster was described as *Boletus paluster* Peck by Charles Horton Peck in 1870 (Peck, 1872) from State of New York in the northeastern United States. This species is characterized by slender and small fruitbodies with red scales, a strongly radiating hymenophore with pronounced radial ribs and very large angular pores, a rather thin stem and slightly sour taste. *Suillus paluster* occurs in northeastern North America and associated with *Larix laricina* (Du Roi) K. Koch. (Peck, 1872, Pomerleau, 1964; Mycoportal, 2022).

Suillus paluster occurrences were repeatedly published from the territory of Russia from the north of the European part to Siberia and the Far East (Bolshakov et al., 2021).

We analyzed herbarium specimens from North Asia stored at LE, YSU, and MAG herbaria as well as our own collections and images of observations and specimens presented at GBIF and Mycoportal. (GBIF, 2022b; Mycoportal, 2022). A preliminary visual revision of the collections and observations of *S. paluster* from northeastern Eurasia (European Russia, Siberia, Far East, northern China) showed the presence of two

morphological types among them: similar to the protologue of *S. paluster* and similar to the protologue of *S. ochraceoroseus*. We assumed that instead of one *S. paluster* species, two species, *S. paluster* and *S. ochraceoroseus*, may be present. In this case, we can observe two types of range disjunction in the species complex: the temperate Asian – East American disjunction in the range of *S. paluster* and the temperate Asian – West American disjunction in the range of *S. ochraceoroseus*.

The purpose of this work was a phylogenetic verification of the presence of two species – *S. paluster* and *S. ochraceoroseus* in North Asia, and the study of their phylogeographic relationships.

MATERIALS AND METHODS

The specimens collected by the authors in Subpolar Urals, Western Siberia and the Far East of Russia, as well as herbarium collections stored in the herbariums of Canadian National Mycological Herbarium – AAFC (DAOM), Institute of the Biological Problems of the North, Far-Eastern Branch of the Russian Academy of Sciences (MAG), Komarov Botanical Institute (LE), Royal Ontario Museum (TRTC), University of Michigan (MICH), Yugra State University (YSU) were analyzed.

Macroscopic descriptions were based on the study of both fresh and dried material as well as on photographs. Microstructures were observed at $\times 400$ and $\times 1000$ in squash preparations in 5% KOH, Congo Red, and Melzer's reagent. Up to 30 basidiospores, 10 cystidia, and 10 terminal elements of pileipellis per specimen were measured to obtain descriptive statistics. Measurements were made in ToupView V.3.7 (ToupTek Photonics) calibrated by an OMP object-micrometer (LOMO). Dimensions are given as (abs min) average min – average max (abs max), Q = average min – average max quotient (length/width ratio).

The color description is given in the RGB color model according to the cell fill mixer in MS Excel.

PCR ITS1–5.8S–ITS2 products were obtained without DNA extraction using the standard protocol of Thermo Scientific Phire Tissue Direct PCR Master Mix kit and amplification with ITS1-F and ITS4-B primers (Gardes, Bruns, 1993). For the PCR *TEF1 α* products primers EF1-983F and EF1-1567R (Rehner, Buckley, 2005) were used. Amplified products were sequenced using BigDyeH Terminator 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, California). The sequences were assembled in CodonCode Aligner V.9.0.1 (CodonCode Corporation) and manually interpreted to correct the ambiguous bases.

For phylogenetic inferences, 33 ITS sequences were used, of which 9 were obtained by the author in the course of this work, the rest were downloaded from the international NCBI GenBank database, as well as 22 *TEF1 α* sequences (19 downloaded from NCBI GenBank and 3 obtained by the authors). GenBank ID, Herbarium Numbers and Country of origin are

listed in Table 1. The datasets were aligned in MAFFT online v. 7 (<http://mafft.cbrc.jp/alignment/server>) (Kato et al., 2019). Phylogenetic differences were measured using Hamming dissimilarity in UGENE v.37 (Okonechnikov et al., 2012) in the ITS (33 sequences, 509 bp including alignment gaps) and *TEF1 α* (22 sequences, 506 bp including alignment gaps) datasets. ITS and *TEF1 α* Bayesian phylogenetic trees (Fig. 1a, 2) were generated in BEAST v1.10.4 (Suchard et al., 2018) using the GTR + I + G model, strict model of molecular clock without calibration, random starting tree and 10 million generations. Bayesian phylogeographic tree ITS (20 sequences, 501 bp including alignment gaps), was generated in BEAST v2.6.4 (Drummond, Bouckaert, 2014), using bModelTest (Bouckaert, Drummond, 2017), 10 M of generations.

RESULTS

Phylogenetic analyses of ITS and *TEF1 α* regions show a well-supported *S. ochraceoroseus/S. paluster* clade in both trees. Both species are also represented by well-supported subclades. The latter, in turn, diverge into groups corresponding to American and Asian populations. ITS and *TEF1 α* trees have the same topology (Figs 1, 2). The Hamming distance between species clades of *S. ochraceoroseus* and *S. paluster* are 1–2% according to ITS (4–9 bp from 506), according to *TEF1 α* 1% (4–6 bp from 509). However, the interspecific and intraspecific distance may overlap and depend on geography. *S. ochraceoroseus/S. paluster* clade is part of the boletinoide group, which also includes other species with similar morphology, *S. cavipes* (Klotzsch) A.H. sm. et Thiers and *Suillus asiaticus* (Singer) Kretzer et T.D. Bruns, formerly belonging to the section *Boletinus* (Smith and Thiers, 1964). *S. cavipes* is the closest sister species, Hamming distance from *S. ochraceoroseus/S. paluster* clade (ITS) is 4% (18–20 bp). The Hamming distance (ITS) to the most externally similar species, *S. asiaticus*, is 5% (23–28 bp).

Morphological features of the species *S. ochraceoroseus* and *S. paluster* are presented in Table 2. Images of fruiting bodies in situ are shown in Fig. 3. Microstructures demonstrating interspecies diagnostically important differences between *S. ochraceoroseus* and *S. paluster* are shown in Fig. 4.

Species from sister clades of *S. cavipes* and *S. asiaticus* differ from *S. ochraceoroseus* and *S. paluster* in having a hollow stipe. *S. phyloictus* Rui Zhang, X.F. Shi, P.G. Liu et G.M. Muell. and *S. spraguei* (Berk. et M.A. Curtis) Kuntze, also having a dry scaly brown-red surface of the cap and stem, are distinguished by a wooly fibrous partial veil, pubescent stipe, brown in KOH cystidia, collected in bundles and immersed in gelatinous exudate.

Analysis of Asian and American specimens showed that *S. paluster* differs from *S. ochraceoroseus* in slender fruiting bodies, prominent radial ribs of the hymenophore protruding over very large pores up to 5 mm,

Table 1. Molecular sequences used in this study

Taxonomic name**	Herbarium numbers*	ITS	TEF	Country (Province)
<i>Boletales</i> sp.	B3001	KY826105	–	Canada
<i>Boletinus asiaticus</i>	NSK1014446	MT302580	–	Russia (Altay)
<i>Rhizopogon luteorubescens</i>	MICH5462	NR119471	–	USA (Idaho)
<i>Rh. nigrescens</i>	MB06-070	–	GU187744	USA (Massachusetts)
<i>Suillus</i> ‘ <i>paluster</i> ’	YSU-F-11781	MK573966	–	Russia (KhMAO)
<i>S.</i> ‘ <i>paluster</i> ’	HKAS56229	KT964674	KU721583	China (Jiling)
<i>S.</i> ‘ <i>paluster</i> ’	HKAS63134	KT964671	KU721586	China (Heilongjiang)
<i>S.</i> ‘ <i>paluster</i> ’	HKAS63138	–	KU721579	China (Jiling)
<i>S.</i> ‘ <i>paluster</i> ’	HKAS63187	KU721252	KU721580	China (Heilongjiang)
<i>S.</i> ‘ <i>paluster</i> ’	KUN-HKAS63138	KT964672	–	China (Jiling)
<i>S.</i> ‘ <i>paluster</i> ’	LE262192	MK573968	–	Russia (Kamchatka)
<i>S.</i> ‘ <i>paluster</i> ’	SugaSp	AB284451	–	Japan (Nagano)
<i>S.</i> ‘ <i>paluster</i> ’	HKAS54411	KT964675	KU721581	China (Jiling)
<i>S.</i> ‘ <i>paluster</i> ’	LE216155	MK573971	–	Russia (Leningrad)
<i>S.</i> ‘ <i>paluster</i> ’	YSU-F-11775	MK573964	–	Russia (KhMAO)
<i>S. asiaticus</i>	F1128638	KU721247	KU721570	China (Jiling)
<i>S. asiaticus</i>	QXW2408	AF166504	–	China
<i>S. asiaticus</i>	HKAS63202	–	KY039441	China (Inner Mongolia)
<i>S. asiaticus</i>	LE-F-315925	KU059558	–	Russia (KhMAO)
<i>S. asiaticus</i>	LE-F-315926	KU059559	–	Russia (KhMAO)
<i>S. cavipes</i>	HKAS71862	–	KU721576	China (Sichuan)
<i>S. cavipes</i>	KUN-HKAS63148	–	KT964655	China (Heilongjiang)
<i>S. cavipes</i>	QXW2406, F1121457	AF166506	–	China (Jiling)
<i>S. cavipes</i>	TDB646	–	KU721572	USA (Michigan)
<i>S. cavipes</i>	SDR NAMA 2017-096	MK575433	–	USA (Wisconsin)
<i>S. luteus</i>	TENN060949	–	KU721608	New Zealand
<i>S. luteus</i>	TRH260	–	KU721609	Ecuador (Salinas)
<i>S. luteus</i>	UP531	DQ658862	–	Sweden
<i>S. ochraceoroseus</i>	F1186906	KU721258	KU721584	USA (Idaho)
<i>S. ochraceoroseus</i>	S191	KX213794	–	USA (Columbia DC)***
<i>S. ochraceoroseus</i>	MICH SAR84-137	L54093 (a)	KU721585 (b)	USA (Washington)
<i>S. paluster</i>	4438	KM248954	–	Canada (Quebec)
<i>S. paluster</i>	MN189	KX213717	–	USA (Minnesota)
<i>S. paluster</i>	HKAS63135	–	KU721582	China (Heilongjiang)
<i>S. paluster</i>	MAG4716	ON623672	ON637149	Russia (Magadan)

Table 1. (Contd.)

Taxonomic name**	Herbarium numbers*	ITS	TEF	Country (Province)
<i>S. paluster</i>	MAG4957	ON623673	ON637150	Russia (Magadan)
<i>S. paluster</i>	MAG5845	ON623674	ON637151	Russia (Magadan)
<i>S. paluster</i>	MQ18R122-QFB30638	MN992280	—	Canada (Quebec)
<i>S. paluster</i>	TRTC156531	JN021098	—	Canada (Quebec)
<i>S. spectabilis</i>	TDB641	—	KU721596	USA (Michigan)
<i>S. tridentinus</i>	HKAS72141	—	KU721663	Italy (Trentino)
<i>S. viscidus</i>	MW855905	MZ148547	—	China
<i>S. viscidus</i>	HKAS72139	—	KU721677	Italy (Lombardia)
Uncultured Suillus	—	HM044503	—	Italy
Uncultured Suillus	—	HM044472	—	Italy

Notes. Newly generated sequences are given in bold. *Herbaria and personal collections: Central Siberian Botanical Garden, Siberian Branch of Russian Academy of Sciences (NSK), Cryptogamic Herbarium of Kunming Institute of Botany (HKAS), Field Museum of Natural History (F), Institute of the Biological Problems of the North, Far-Eastern Branch of the Russian Academy of Sciences (MAG), Komarov Botanical Institute (LE), Laurentian Forestry Centre, Canadian Forest Service (QFB), Norwegian University of Science and Technology (TRH), Royal Ontario Museum (TRTC), T.D. Bruns (TDB), University of Michigan (MICH), University of Tennessee Herbarium (TENN), Yugra State University (YSU). **Taxonomic names are given as they are given in the names of sequences and herbarium specimens in GenBank. ***In a planted patch of Western American larch (*Larix lyallii*).

wider ellipsoid spores, and the structure of the pileipellis (Fig. 5). *S. paluster* has trichoderm from free septate hairs with elongated pointed ends, *S. ochraceoroseus* has plagiotrichoderm from glued septate hyphae, sometimes with pointed ends. The scales on the surface of the cap of *S. ochraceoroseus* are formed by raised patches of glued hyphae of the pileipellis. In addition, there are a number of less obvious differences. The color of the surface of the fruit bodies of *S. paluster* is more evenly red without changing from pink to ochre, the flesh is more yellow, the taste is mild without bitterness, the preferred habitats are wet, waterlogged with sphagnum.

S. ochraceoroseus is varying degrees of pink-buff with light yellow, sometimes bluish flesh, slightly bitter to acrid taste, and grows in a variety of environmental conditions.

We did not find significant intraspecific differences in morphological characters between populations from North Asia and North America.

Pronounced and stable morphological differences between species *S. paluster* and *S. ochraceoroseus* may indicate the genetic isolation. However, in this case, morphological differences are combined with a relatively small genetic distance between species with a comparable distance between populations of the same species. According to Genealogical concordance phylogenetic species recognition (GCPSR) (Taylor et al., 2000), the concordance of trees of different genes at the junction of species level branches arises as a result of the fixation of previously polymorphic loci due to genetic isolation and is a reliable criterion for species recognition.

Therefore, despite the fact that the nucleotide differences between the sequences of *S. ochraceoroseus* and *S. paluster* do not reach the psychological threshold of 3%, the concordance of the ITS and *TEF1 α* phylogenetic trees is at the level of the divergence of *S. ochraceoroseus* and *S. paluster*, good support for the branches of *S. ochraceoroseus* and *S. paluster* in both trees, significant differences in the morphology of the hymenophore, spores, and pileipellis make it possible to distinguish between these species.

DISCUSSION

According to the ITS phylogeographic tree (Fig. 5), the separation of *S. ochraceoroseus* and *S. paluster* may have originated in North America. The sequences of the Northwestern American clade of *S. ochraceoroseus* share substitutions with the Asian clade of the species and the Northeast American clade of *S. paluster* and a similar Hamming distance (3–5 and 4–5 differences per 501 bp).

The distribution of the species is shown in Fig. 6. The American part of the range of *S. ochraceoroseus* is confined to the distribution of the two Western American larches, *Larix lyallii* and *L. occidentalis* (Little, 1971). An illustration of the modern distribution of larches can be seen in the article by Semerikov and Lascoux (1999). The modern range of these larches does not contact with the range of *L. laricina*, the host of *Suillus paluster*. However, the extant American larch populations originate from glacial refugia that were located south of the ice sheet (Whitlock, 1995). More da-

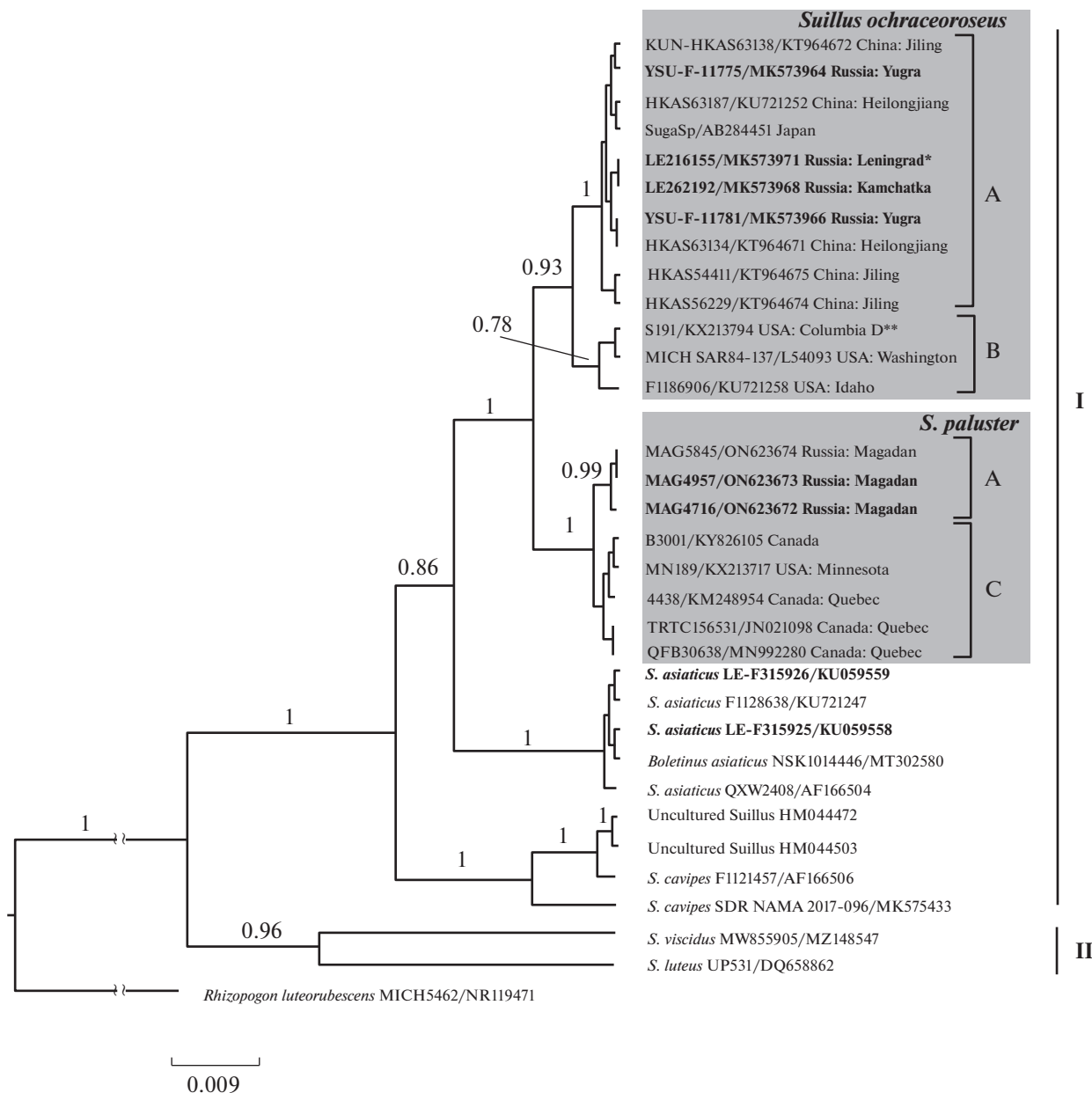


Fig. 1. Bayesian phylogenetic tree ITS, 10 M of generation, generated in BEAST v. 1.10.4, GTR + I + G model: I – *Boletinus* clade; II – *Suillus* clade. Specimens ecology and geography: A – North Asian larch range (*Larix sibirica*, *L. gmelinii*, *L. cajanderi*, + *L. kaempferi*), B – West American larch range (*L. occidentalis*, *L. lyallii*), C – East American larch range (*L. laricina*). Posterior probability above the branches (below 0.6 not shown). Specimens voucher ID/GenBank ID. Country and region of origin and/or taxonomic name in leaves. Newly generated sequences are given in bold. *In the plantings outside of natural range of North Asian larch *Larix sibirica*. **In the plantings outside of natural range of West American larch *L. lyallii*.

ta from both North America and Eurasia are needed to reconstruct the migration pattern and timing. However, there is evidence that both North Asian lineages of *S. ochraceoroseus* and *S. paluster*, which apparently formed independently of each other, are derivatives from the two North American species (Fig. 3).

In the case of *S. ochraceoroseus*, we can see a well-supported North Asian lineage and a somewhat weaker lineage from western North America. The North Asian lineage is represented by sequences of specimens col-

lected in the western (Western Siberia), eastern (Kamchatka), and southern parts of North Asia (Northern China and Japan). The northwestern North American lineage of *S. ochraceoroseus* contains sequences of specimens collected in Idaho and Washington (USA). Both groups contain sequences of the ‘alien’ specimens, originating from other geographical regions. Together with the North Asian sequences, the MK573971 sequence of LE216155 collected in the artificial plantation of Asian larches [*Larix gmelinii* (Rupr.) Kuzen., *L. sibirica* Ledeb.] Lindulovskaya Roshcha in the

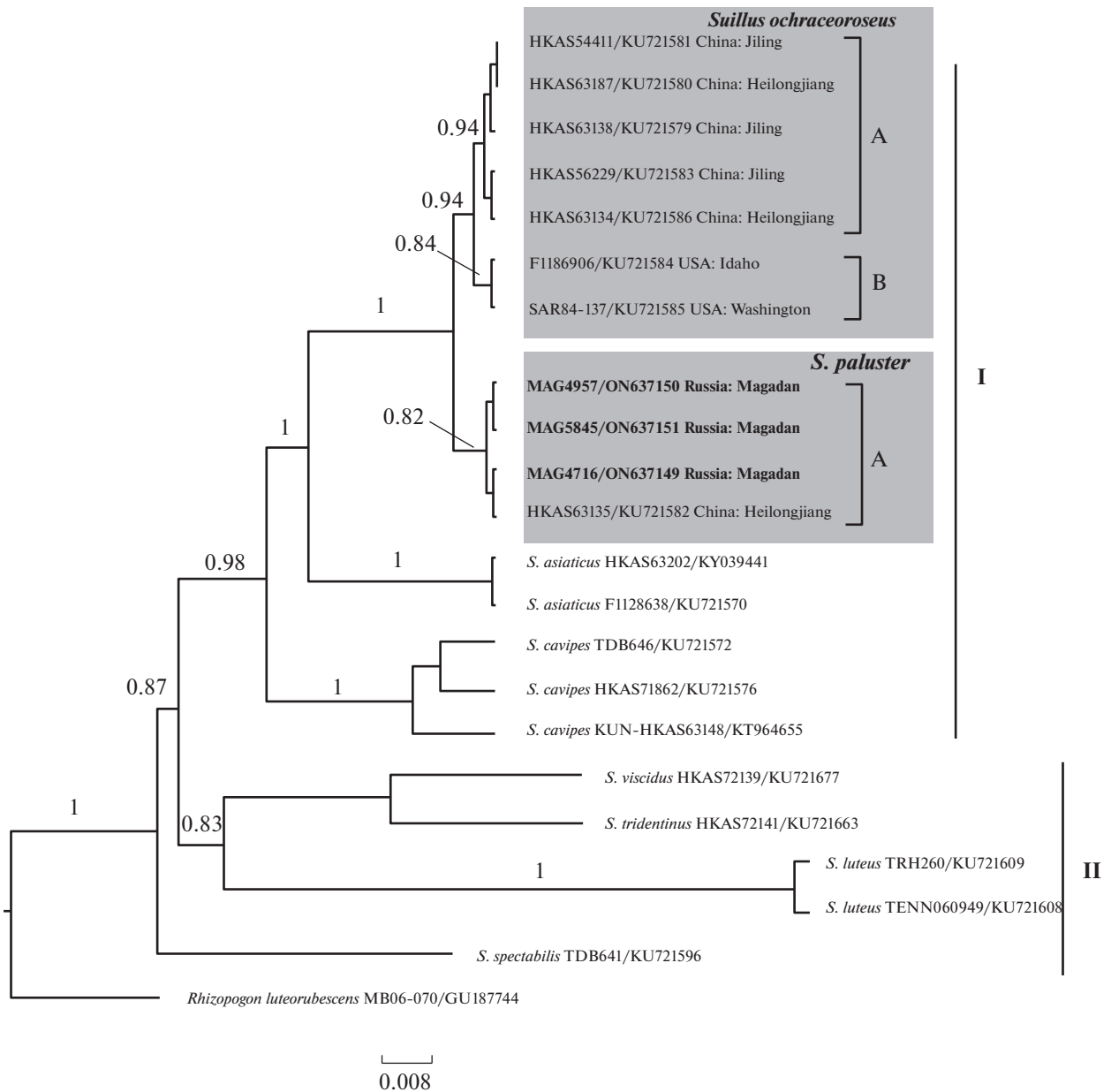


Fig. 2. Bayesian phylogenetic tree *TEF1α*, 10 M of generation, generated in BEAST v. 1.10.4, GTR+I+G model: I – *Boletinus* clade; II – *Suillus* clade. Specimens ecology and geography: A – North Asian larch range (*Larix sibirica*, *L. gmelinii*, *L. cajanderi*, + *L. kaempferi*); B – West American larch range (*L. occidentalis*, *L. lyallii*). Posterior probability above the branches (below 0.6 not shown). Specimens voucher ID/GenBank ID, Country and region of origin or taxonomic name in leaves. Newly generated sequences are given in bold.

Leningrad Region (Russia) is grouped. The Northwest American lineage contains the KX213794 sequence of specimen S191 from the Washington (DC, USA), collected according to the annotation in the park under *L. lyallii* (Nguen et al., 2016). In both cases, the host plant grew outside the boundaries of its natural range.

The *Suillus paluster* clade in the ITS tree consists of a well-supported North Asian lineage and a weakly supported clade of northeastern North American specimen sequences.

Therefore, in one complex of closely related species, we can observe two examples of Asian – North American disjunction: temperate Asian – East American disjunct species *S. paluster* and temperate Asian – West American disjunct species *S. ochraceoroseus*.

According to a recent checklist of agaricoid and boletoid species in Russia (Bolshakov et al., 2021), *S. ochraceoroseus* is mentioned now for the first time.

Below we provide descriptions of the morphology of the Asian specimens of *S. paluster* and *S. ochraceoroseus*.

Table 2. Morphological features of the species *Suillus ochraceoroseus* and *S. paluster*

Characters	<i>S. ochraceoroseus</i>					<i>S. paluster</i>		
	Protologue (Snell, 1941)	NW N America (Pomerleau, Smith, 1962)	NW N America	N Asia	Protologue (Peck, 1872)	NE N America (Pomerleau, 1964)	NE N America	N Asia
Spore size, μm	8–9.5 × 2.8–3.3	7.5–9.5 × 2.5–3.2	6.2–8.0 × 2.3–3.6	(6.8) 7.6–10.3 (11.2) × (2.5) 2.8–3.6 (3.9)	8.5	9–14 (16) × 2.5–4 **	(7.0) 7.2–9.9 (10.1) × (3.0) 3.1–4.1 (4.3)	(6.2) 6.7–9.4 (9.7) × (3.1) 3.2–4.2 (4.6)
Spores shape	narrowly elliptical	subcylindric	subcylindric	subcylindric	elliptical	elliptical	elliptical	elliptical
Q	—	—	2–3.3	(2.2) 2.5–3.2 (3.5)	—	(1.9) 2.0–2.7 (2.9)	(1.4) 1.9–2.7 (2.9)	
Cystidia, μm	30–35 × 5–6, 50–55 × 5–7	46–58 × 6–8	38–90 × 6.2–9.1	(26.9) 35.7–71.4 (82.1) × (7.2) 7.7–11.8 (13.8)	—	(41) 48.7–87.0 (97.6) × (7.0)	(41.6) 56.0–80.7 (89.5) × (6.7) 7.7–10.2 (12.1)	
Cystidia shape	clavate to irregularly lageniform or hyphoid, hyaline	subcylindric to subventricose, obtuse to abruptly acute, hyaline in KOH, thin-walled, often flexuous	cylindric, hyaline or light yellow in KOH	cylindric, hyaline or light yellow in KOH	—	hyaline, thin-walled, mostly single and occasionally in small clusters, rarely incrustated around the base	cylindric, subcylindric, subclavated, hyaline or light yellow in KOH	cylindric, subcylindric, subclavated, hyaline or light yellow in KOH
Basidia, μm	—	28–34 × 4.5–5.5	—	(16.8) 20.2–28.7 (29.9) × (3.2) 5.0–7.4 (8.3) (40) 51.1–92.2 (99.0) × (8.84) 9.8–18.2 (20.3)	—	15–25 × 5–7	(18.1) 20.2–27.0 (33.7) × (4.3) 5.3–6.4 (7.3)	
Pileipellis, μm	—	8–11	—	—	—	—	terminal cells: (30.1) 36.9–91.5 (106) × (7.1) 8.2–18.7 (20.8)	
Pileipellis morphology	—	cuticle of more compactly (then trama) interwoven hyphae, not otherwise differentiated except for red dissolved pigment which breaks down quickly in KOH	—	plagiotrichoderm, consisting of septate hyphae with pointed terminal hyphae, forming scales of tightly glued hyphae, other in KOH	—	trichoderm forming scales from bundles of individual long hairs swollen septate hyphae with elongated-pointed terminal cells, other in KOH	trichoderm forming scales from bundles of individual long hairs swollen septate hyphae with elongated-pointed terminal cells (30) 36.9–91.5 (106) × (7.1) 8.2–18.7 (20.8) μm , other in KOH	

Table 2. (Contd.)

Characters	<i>S. ochraceoroseus</i>				<i>S. paluster</i>			
	Protologue (Snell, 1941)	NW N America (Pomerleau, Smith, 1962)	NW N America	N Asia	Protologue (Peck, 1872)	NE N America (Pomerleau, 1964)	NE N America	N Asia
Clamp connection	—	absent	—	present	—	rarely found	present	present
Pileus diam, cm	6–14	8–15 (25)	****	6.5–11 (12)	1'–2' (2.5–5 icm)	2–5 (7)	****	1.5–4 (5)
Pileus surface	dry, fibrillose-squamulose	dry, fibrillose-squamulose	—	dry, fibrillose-squamulose	dry, floccose-tomentose	floccose-fibrillose to hairy squamulose, appearing somewhat viscid when fresh and during rainy periods, but soon dry	—	floccose-fibrillose to hairy squamulose
Pileus surface color	light rose with the fibrils or squamules buff	variable in color, often more or less bright lemon-yellow along the margin and pinkish beneath the fibrillose squamules on the disc, at times rose-pink to brick-red with little or no yellow visible or at times whitish from dense fibrillose covering	—	bright pink and ochre pink squamules on a light pink and yellow background	bright pinkish-red	bright red, carmine or scarlet and somewhat paler between squamules and fibrils	—	cherry scales on a light pink and bright yellow background
Pileus flesh	firm	thick, soft	—	thick, soft	thin	Context thickish at the disc, thin at the margin, rather soft	—	thin

Table 2. (Contd.)

Characters	<i>S. ochraceoroseus</i>				<i>S. paluster</i>			
	Protologue (Snell, 1941)	NW N America (Pomerleau, Smith, 1962)	NW N America	N Asia	Protologue (Peck, 1872)	NE N America (Pomerleau, 1964)	NE N America	N Asia
Pileus flesh color	light yellow, unchanging	pale bright yellow, often with a pinkish red zone under fibrils, unchanging when bruised or showing a very slight change to bluish or greenish blue	—	light yellow, pinkish yellow, sometimes turns bluish	—	whitish, reddish near the pellicle, unchanged when broken	—	yellow
Hymenophore	decurrent, short, compound, radially arranged with separating veins much like B. porosus but less prominently so, 1–5 mm	5 mm thick, adnate to decurrent, boletinoid, pores elongated to mostly angular (2–5 × 1–2 mm), radially arranged to sublimate, compound	—	boletinoid, decurrent	tubes large, angular, slightly decurrent, formed by wider radiating lamellae and more narrow transversely connecting and anastomosing dissepiments	decurrent, 2–4 mm long, somewhat separable, soft, strongly boletinoid and compound with radial lines. Pores, angular, up to 4 mm diam, arranged in radiating and lamellate rows and separated by narrow walls or veins between the rows, dotted with small dark points when old and dry.	—	boletinoid, decurrent, with pronounced radial ribs, protruding above the pores by 1–2 mm, pores angular, elongated, up to 4–5 mm, look like anastomoses between the ribs
Hymenophore color	deep dull yellow, becoming deep yellowish-brown, not changing to blue, drying ochraceous to ochraceous-brown.	bright straw yellow to dull olive-ocher, finally becoming dingy brown	—	dull yellowish ocher	yellow, becoming ochraceous	at first greenish yellow, then greenish ochraceous or greenish gray, darkening in age; pores concolorous	—	ocher-yellow, darkening

Table 2. (Contd.)

Characters	<i>S. ochraceoroseus</i>				<i>S. paluster</i>			
	Protologue (Snell, 1941)	NW N America (Pomerleau, Smith, 1962)	NW N America	N Asia	Protologue (Peck, 1872)	NE N America (Pomerleau, 1964)	NE N America	N Asia
Stipe size, cm	4-6 x 2-3	3-5 x 1-3 cm	-	5-8 x 1-1.5 cm	2"-3" thick	3-4 (5) x 0.4-0.7	-	0.3-0.7 x 1.5-3
Stipe shape	tapering upward, often bent	thick, solid, subequal, often with subulobous base frequently flared apex	-	short cylindrical with flared apex	slender, solid	often flexuous or oblique, rather tough, enlarged at the base and forming a white floccose mass with sphagnum moss or other debris	-	cylindrical
Stipe surface	more or less reticulate or venose-reticulate, usually to annulus, sometimes reticulate below	unpolished or fibrillose below the annulus	-	In the upper part covered with a net of decurrent hymenophore, under the ring glabrous, dry	nearly smooth	reticulate at the apex, fibrillose-squamulose below the annuliform zone	-	In the upper part covered with a net of descending hymenophore, under the ring it is bare, dry
Stipe surface color	mixed buff and rose	nearly concolorous with the tubes and usually reticulate above from the decurrent tubes, more sordid and often reddish at base or at times brownish	-	pinkish-buff above the annulus, patchy pink below	read, yellowish at the top and marked with the slightly decurrent walls of the tubes	greenish yellow or greenish ochraceous at the apex by decurrent lines, deep red or purplish red below the annuliform zone	-	in color of the pileus

Table 2. (Contd.)

Characters	<i>S. ochraceoroseus</i>				<i>S. paluster</i>			
	Protologue (Snell, 1941)	NW N America (Pomerleau, Smith, 1962)	NW N America	N Asia	Protologue (Peck, 1872)	NE N America (Pomerleau, 1964)	NE N America	N Asia
Stipe flesh	—	—	—	solid	—	solid	—	solid
Stipe flesh color	light yellow, unchanging	—	—	light yellow, sometimes turns bluish	—	yellowish	—	yellow
Partial veil	Veil delicately membranous, whitish-buffish, rupturing to form large portions on the margin of the pileus and a delicate annulus which is at first prominent, then becomes fibrillose fragments and finally almost disappears	thin, submembranous, pallid to yellowish, sometimes forming an evanescent annulus but usually adhering to the margin of the pileus	—	submembranous, covered on the outside with a bran-like bloom of a grayish-pink color, forming a thin vanishing ring	—	fugacious membranous	—	membranous, forming a thin membranous fugacious ring
Odor	—	acidulous	—	inconspicuous	—	not distinctive	—	not distinctive
Taste	—	very slightly acrid, bitterish in cooked specimens	—	the taste is more or less acrid, aggravated in cooked specimens, almost disappearing by drying	—	not distinctive	—	sourish

Table 2. (Contd.)

		<i>S. ochraceoroseus</i>				<i>S. paluster</i>		
Characters	Protologue (Snell, 1941)	NW N America (Pomerleau, Smith, 1962)	NW N America	N Asia	Protologue (Peck, 1872)	NE N America (Pomerleau, 1964)	NE N America	N Asia
Habitat	under conifers	under <i>Larix occidentalis</i>	—	larch and mixed forests	wet places and swamps among mosses	in conifer forest under <i>Larix</i>	larch swamps, mixed coniferous woods, sphagnum bogs	larch swamps, mixed coniferous woods, sphagnum bogs, sphagnum tundra. On sphagnum, soil and mossy rotten larch wood
Specimens	FH00543740*	MICH: Gruber 508, Smith A.H. 15814, 15665 , 15871, 44229, 44230, 44353, 44789, 44908, 44920, 44938, 58407, 23744, 28229	MICH 62024 (Smith 15665)	LE: 4402, 4502, 4503, 4504, 4505, 4510, 4511, 4511, 216155, 262192, 312269; MAG: 2001, 4290, 4805, 4965, 4975, YSU-F: 11775, 11776, 11777, 11778, 11779, 11780, 11781	—	***	LE: 4513 (Ex TRIC 44557), 4514 (Ex 93196) 4515 (Ex DAOM93197), 4516 (Ex MICH), 4517 (Ex DAOM 91054), 4518 (Ex DAOM 74138)	LE: 4506, 4507; MAG: 1350, 4957, 4769, 5845, 4935, 4716

Notes. Specimens analyzed by authors are given in bold. *E. Zvyagina was only able to examine a photograph of a herbarium specimen (<https://www.mycportal.org/portal/collections/individual/index.php?occid=9525865>). ** The boundaries of variability are shifted to the right relative to the size of the spores of the American specimens we analyzed. *** No numbers cited. **** Only dry specimens were analyzed.



Fig. 3. Basidiocarps of *Suillus ochraceoroseus* (a–c) and *S. paluster* (d–f) in situ: a – YSU-F-11775; b – observation (no specimens collected), Subpolar Urals, 28.07.2020 (photo by E. Zvyagina); c – observation, Magadan, 22.07.2011 (photo by N. Sazanova); d – observation, Magadan, 28.07.2011 (photo by N. Sazanova); e – MAG 5845; f – MAG 4957. Bars – 1 cm.

Suillus ochraceoroseus (Snell) Singer, Persoonia 7(2): 319, 1973. ≡ *Boletinus ochraceoroseus* Snell, Mycologia 33(1): 35, 1941. ≡ *Fuscoboletinus ochraceoroseus* (Snell) Pomerleau et Smith, Brittonia 14: 158, 1962.

Iconography: Pomerleau and Smith (1962: 159, pl. 1 as *F. ochraceoroseus*).

Basidiocarps boletoid. *Pileus* 6.5–11 (12) cm diam, convex at first, then flat or with raised edge. Surface dry and scaly, squamules fibrous, bright pink (R138G41B48) or ocher pink (R170G89B96) on a light pink and yellow background. Fragments of grayish-pink (R207G174B195) membranous partial veil re-

main along the edge of the cap, darkening with time. Hymenophore boletinoid, strongly decurrent with angular pores up to 2–3 mm wide, dirty buff (R219G213B147). Flesh thick, light yellow, pinkish-yellow, sometimes turning blue when cut. *Stipe* cylindrical, thick, central, 1–1.5 cm in diameter, 5–8 cm tall, covered with a network of decurrent hymenophore, pinkish-buff (R198G134B96) in the upper part, naked, dry, pink (R169G98B116) with light stains (R210G190B189) under the ring. Stipe flesh solid, yellow, in some cases bluing. *Partial veil* membranous, covered on the outside with a grayish-pink bran-like

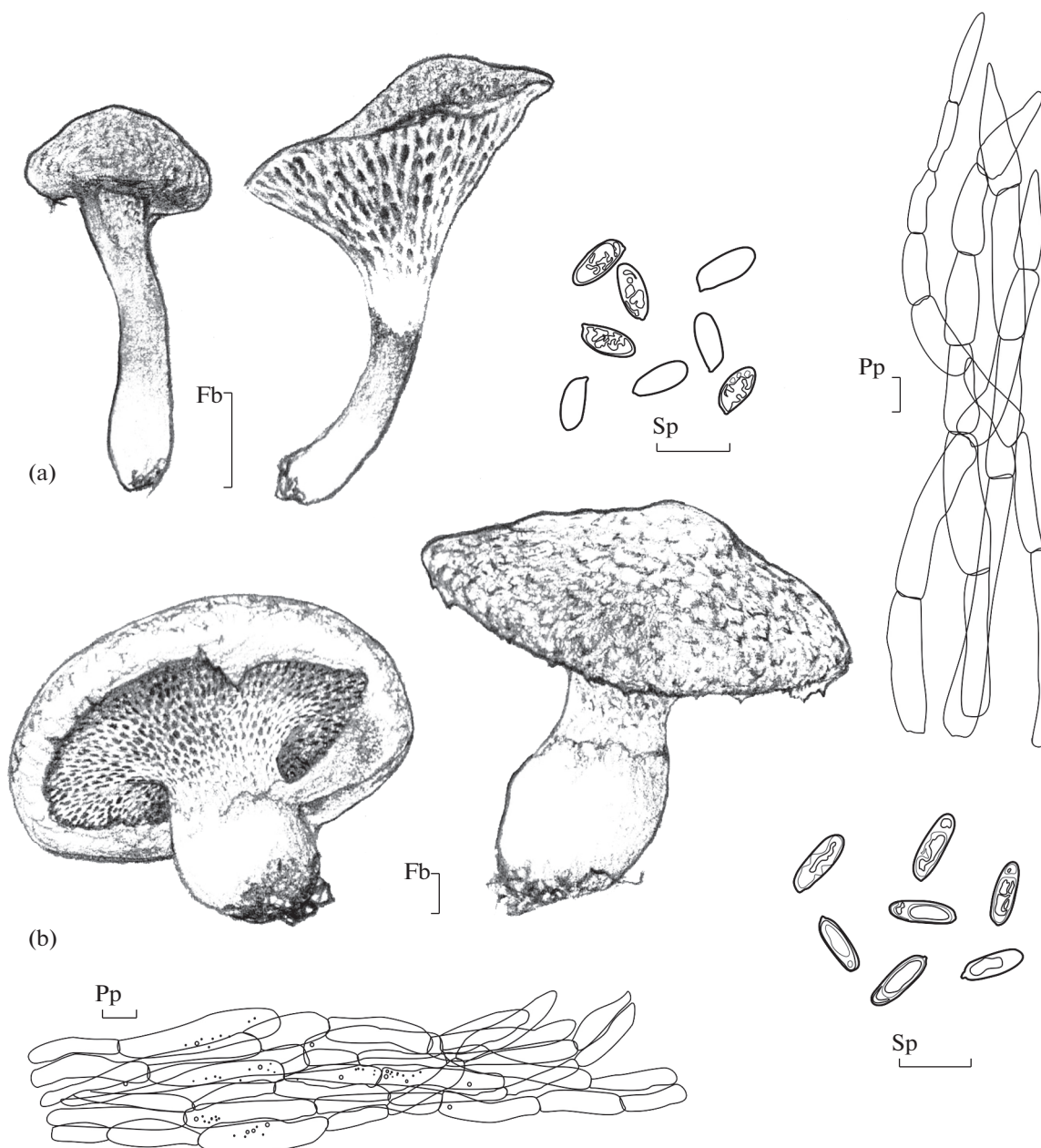


Fig. 4. Interspecies diagnostically important differences between *Suillus paluster* (a) and *S. ochraceoroseus* (b). Bars: Sp (spores) – 10 µm, Pp (pileipellis) – 20 µm, Fb (fruiting body) – 1 cm.

bloom, forming a thin membranous vanishing ring. *Smell* indistinct, taste bitter, intensifying with heat treatment, almost disappearing upon drying.

Basidiospores (6.8) 7.4–10.5 (11.2) × 2.8–3.6(3.7) µm, Q = 2.4–3.2, nearly cylindrical yellow in KOH. *Basidia* (16.8)20.0–29.2(29.9) × (3.2) 4.8–7.4(8.2) µm four-spored, club-shaped, hyaline or light yellow in KOH. *Cystidia* (26.9)37.8–74.5(82.1) × (7.2)7.7–12.2(13.8) µm, cylindrical, subfusiform, subclavated, sometimes with outgrowths or septa, hyaline or yellowish in KOH. *Pileipellis* – plagiotrichoderm, consisting of septate hyphae with pointed terminal hyphae (40.5)42.1–

92.8(99.0) × (8.8)9.6–17.2(19.3) µm, forming scales of tightly glued hyphae, ocher in KOH.

Habitat and distribution. In larch and mixed forests. Forms mycorrhiza with *Larix*. The Asian population enters Eastern Europe in the west along with plantings of *Larix sibirica*, occupies Siberia, the Far East and Japan in the north and east, and Northern China in the south. The American population is localized in the northwestern United States.

Specimens examined: Russia, Leningradskaya Oblast, Vyborgskiy rayon, Wildlife Sanctuary “Lindulovskaya Roshcha”, near the Roshchino station, route number 1, 60.236077°N, 29.544979°E, edge of bilberry Scots pine forest with spruce, roadside in artificial plantation of *Larix si-*

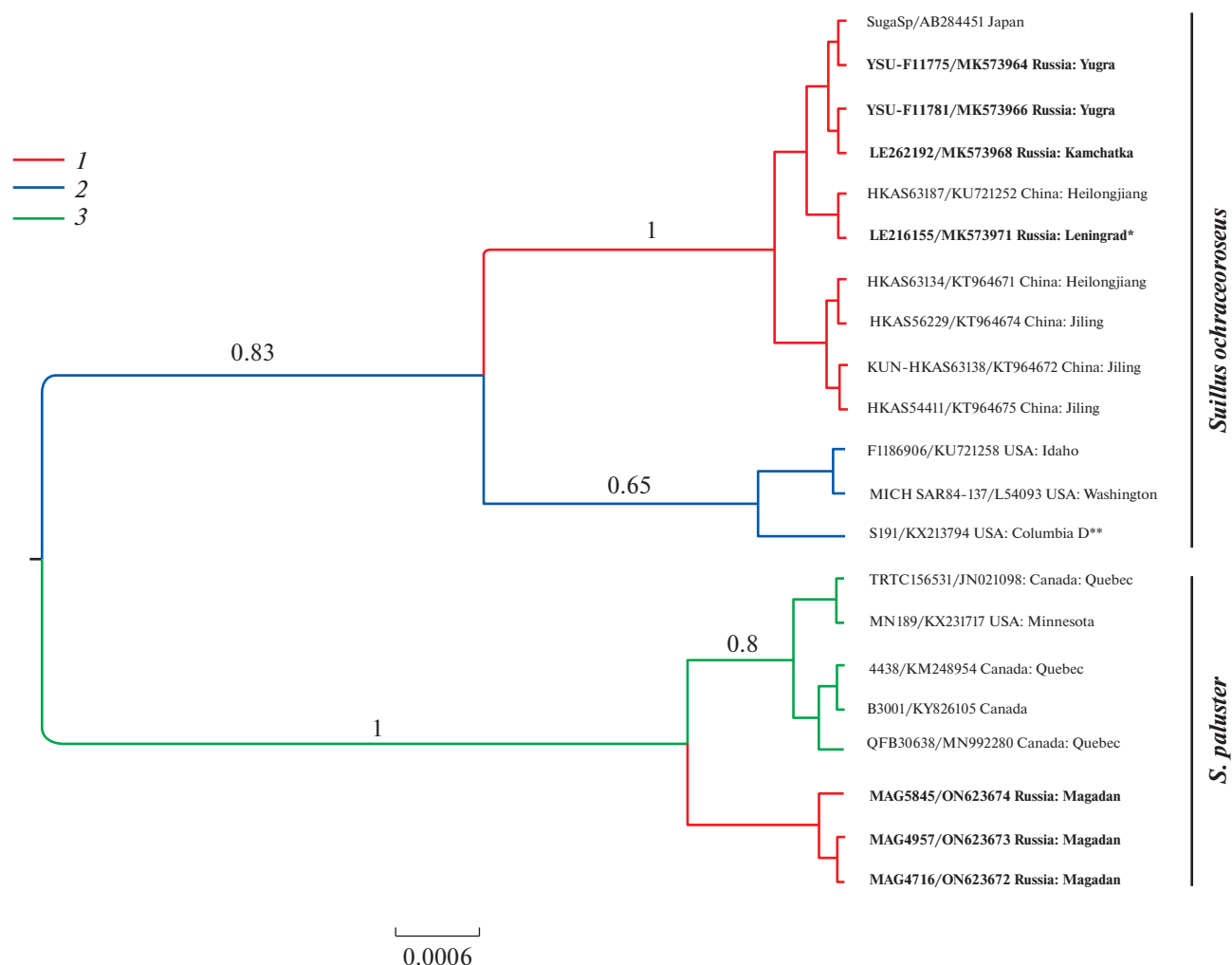


Fig. 5. Bayesian phylogenetic tree ITS + Location, 10 M of generation, generated in BEAST v. 2.6.4. Posterior probability above the branches (below 0.6 not shown). Specimens voucher ID/GenBank ID, Country and region of origin in leaves. Newly generated sequences are given in bold. Discrete geography of the specimen's origin locations in color: 1 – North Asia, 2 – Northwest North America, 3 – Northeast North America. *In the plantings outside of natural range of North Asien larch *Larix sibirica*. **In the plantings outside of natural range of Western American larch (*L. lyallii*).

birica, 19.08.1997, coll. O.V. Morozova (LE 216155, GenBank ITS MK573971); *ibid.*, 60.236077°N, 29.544979°E, under *Larix*, 03.08.1952, coll. E. Kosinskaya (LE 4503) (Vasilkov, 1952, as *Boletus paluster*); Yaroslavskaya Oblast, Breytovskiy Rayon, Zakharyino, Darwinovskiy zapovednik, 57.93832°N, 40.28116°E, 01.08.1951., coll. T. Kutova (LE 4511) (Vasilkov, 1952, as *Boletus paluster*); Yamalo-Nenetskiy Avtonomnyy Okrug, Labytnangi, 66.65553°N, 66.38592°E, 01.08.1962, coll. B. Vasilkov (LE 4504); *ibid.*, 66.65553°N, 66.385918°E, 07.08.1962, coll. E. Nezdoiminogo (LE 4505); Khanty-Mansiyskiy Avtonomnyy Okrug, Berezovskiy Rayon, Neroyka village vicinities, 64.54848°N, 59.6407°E, *Larix*-dominated forb sparse forest, 12.08.2020, coll. E. Zvyagina (YSU-F-11779); *ibid.*, Sovetskiy Rayon, Malaya Sos'va Nature Reserve, Khangokurt, 61.958009°N, 64.241868°E, *Pinus*-dominated forest with larch, 16.08.1990, coll. A. Vasina (LE 312269) (Zvyagina, Vasina, 2015, as *Suillus paluster*); *ibid.*, road Khanty-Mansiysk – Sovetskiy, 61.22826°N, 64.16629°E, pine and larch forest with dwarf shrubs and feather mosses in ground cover, 22.08.2010, coll. E. Zvyagina (YSU-F-11775, GenBank ITS MK573964); *ibid.*, Kondinskiye Oзера Nature Park, 60.92161°N, 63.68796°E, pine

and larch forest with dwarf shrubs and feather mosses in ground cover, 24.08.2010, coll. E. Zvyagina (YSU-F-11776); *ibid.*, Malaya Sosva Nature Reserve, Belaya Gora rangers station, 61.790608°N, 64.516273°E, pine and larch forest with dwarf shrubs and lichens in ground cover, 15.08.2013, coll. E. Zvyagina (YSU-F-11778) (Zvyagina, Vasina, 2015, as *Suillus paluster*); *ibid.*, Surgutskiy Rayon, Aitromyegan river, 61.690167°N, 74.353101°E, mixed taiga, 27.07.2010, coll. S. Babyuk (YSU-F-11781, GenBank ITS MK573966); *ibid.*, Ugut village, left bank of Ugutka river, 60.50823°N, 74.05491°E, pine and larch forest with dwarf shrubs and lichens in ground cover, 30.08.2011, coll. E. Zvyagina (YSU-F-11780); *ibid.* 60.48260°N, 74.06948°E, pine after fire forest, 05.09.2013, coll. E. Zvyagina (YSU-F-11777); Respublika Buryatiya, Barguzinskiy Rayon, Bukhta Sosnovka, North-East Baykal, 54.83253°N, 109.67543°E, *Larix sibirica*, *Pinus sibirica* Du Tour mixed forest, 15.08.1966, coll. E. Nezdoiminogo (LE 4510) (Nezdoiminogo, 1969 as *Boletinus paluster*); *ibid.*, Severo-Baykalskiy Rayon, Davsha, 54.35456°N, 109.50222°E, *Larix sibirica* crowberry-bearberry forest, 08.08.1969, coll. E. Nezdoiminogo (LE 4511); Magadanskaya Oblast, Khasynskiy Rayon, Myakit vicini-

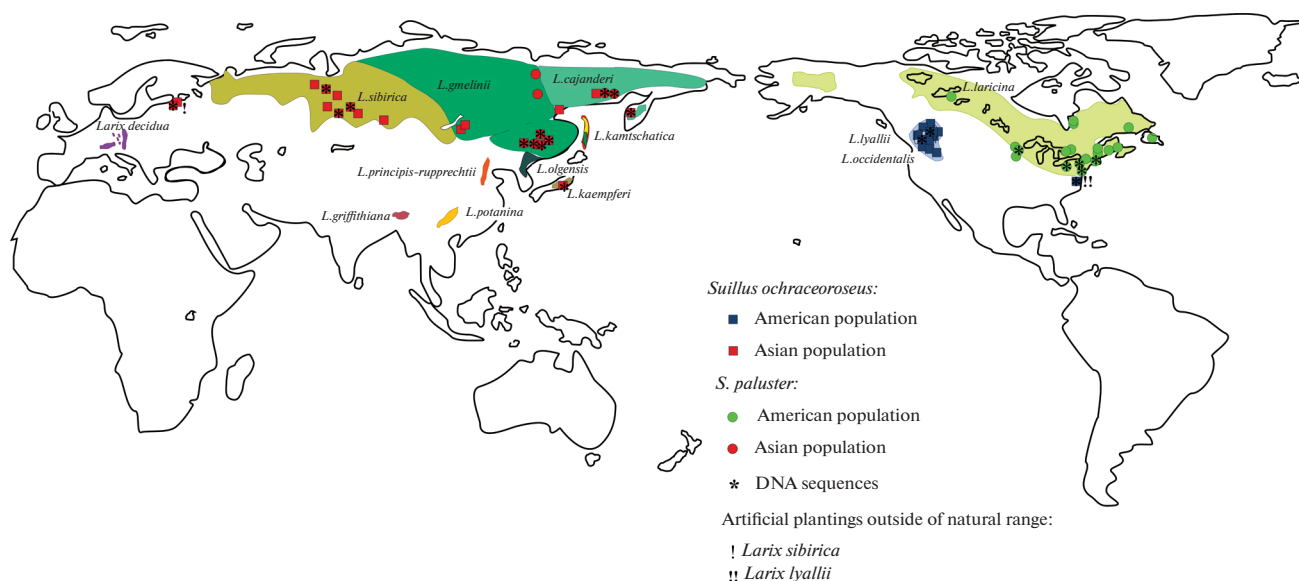


Fig. 6. *Suillus ochraceoroseus* and *S. paluster* distribution combined Peck (1873), Snell (1941), Slipp, Snell (1944), Pomerleau, Smith (1962), Pomerleau (1964), GBIF (2022 a, b), Mycoportal (2022), GenBank (Table 1), herbarium collections LE, MAG, YSU and Tatiana Bulyonkova personal collection. Distribution of *Larix* taxa adapted from Semericov and Lascoux (1999).

ties., 61.37474°N, 152.01646°E, in artificial plantation of *Pinus sylvestris* L., mixed with *Larix cajanderi*, 13.08.2015, coll. N. Sazanova (MAG4290); *ibid.*, Olskiy Rayon, Raduzhniy, 59.70061°N, 150.153051°E, larch forest, 09.09.2002, coll. N. Sazanova (MAG2001); *ibid.*, zakaznik "Kavinskaya dolina", 59.68719°N, 147.49039°E, edge of larch forest, 19.08.2017, coll. N. Sazanova (MAG4965); *ibid.*, ruchej Omylen, 59.76876°N, 148.21369°E, mixed forest, 23.08.2017, coll. N. Sazanova (MAG4975); *ibid.*, Magadan vicinities, 59.55950°N, 150.812274°E, in *Larix cajanderi* Mayr forest with *Pinus pumila* (Pall.) Regel and *Betula middendorffii* Trautv., 01.09.1953, coll. B. Vasilkov (LE 4502); *ibid.*, 59.55950°N, 150.812274°E, 1953, coll. A. Vaskovskiy (LE 4402), Kamtchatskiy Kray, Bystrinskiy Rayon, Esso village vicinities, Bystrinskiy National Park, left bank of the Uboyny Stream, 55.99806°N, 158.72444°E, in *Larix cajanderi* forest, 06.08.2005, coll. A. Kovalenko, O. Morozova, N. Psurtseva (LE262192 Ex55 (Morozova, Popov, 2008 as *Boletinus paluster*), GenBank ITS MK573968); Khabarovskiy Kray, Okhotskiy Rayon, zakaznik "Kava", the valley of the river Kava near the creek Ikrimun (p. 88), 59.64011°N, 147.13524°E, in *Larix cajanderi* forest with *Pinus pumila* Regel and *Betula middendorffii* Trautv., 18.08.2017, coll. N. Sazanova, (MAG4805); United States of America, Idaho, E fork of Lake Fork Creek, Idaho National Forest, 44.9225°N, -115.9217°E, On humus under *Pinus* and *Larix*, 19.07.1941, coll. and det A. Smith (Smith 15665, MICH 62024).

Suillus paluster (Peck) Kuntze, Revis. gen. pl. (Leipzig) 3(3): 536, 1898. ≡ *Boletus paluster* Peck, Ann. Rep. Reg. N.Y. St. Mus. 23: 132. 1872. ≡ *Boletinus paluster* (Peck) Peck, Bull. N.Y. St. Mus. 2 (8): 78, 1889. ≡ *Boletinellus paluster* (Peck) Murrill, Mycologia 1 (1): 8, 1909. ≡ *Fuscoboletinus paluster* (Peck) Pomerl. et A.H. Sm., Mycologia 56 (5): 708, 1964. ≡ *Suillus paluster* (Peck) Kretzer et T.D. Bruns, Mycologia 88 (5): 784, 1996.

Iconography: Peck (1873: pl. 6, fig. 4–7 as *Boletus paluster*), Pomerleau (1964: 709, pl. 1 as *F. paluster*).

Basidiocarps boletoid. *Pileus* 1.5–4(5) cm diam, convex at first, then flat or with a raised edge. Surface dry scaly, scales fibrous, light cherry (R254G140B129) on a light pink and bright yellow background. Hymenophore boletinoid, decurrent, with pronounced radial ribs protruding 1–2 mm above pores. Pores angular, elongated 4–5 mm, look like anastomoses between the ribs, ochre yellow (R229G182B68), darkening. Flesh thin yellow. *Stipe* cylindrical, central, 0.3–0.7 cm diam, 1.5–3 cm long, covered with a net of descending hymenophore, bright yellow (R255G228B104) in the upper part, glabrous under the ring, dry, in the color of the cap. *Stipe* solid, flesh yellow. *Partial veil* membranous, forming a thin membranous evanescent ring. *Smell* indistinct, taste sourish.

Basidiospores (6.2)6.7–9.4(9.7) × (3.1)3.2–4.2(4.6) μm, Q = 1.9–2.7, ellipsoid, ochre yellow in KOH. **Basidia** (18.1)20.2–27.0(33.7) × (4.3)5.3–6.4(7.0) μm, four-spored, club-shaped, hyaline or light yellow in KOH. **Cystidia** (41.6)56.0–80.7(89.5) × (6.7)7.7–10.2(12.1) μm, cylindrical, subfusiform, subclavated, hyaline or light yellow in KOH. **Pileipellis** trichoderm, forming scales from bundles of individual long hairs swollen septate hyphae with elongated-pointed terminal cells (30)36.9–91.5(106) × (7.1)8.2–18.7 (20.8) μm, ochre in KOH.

Habitat and distribution. Mainly in swampy and waterlogged places. Sometimes in other habitats in communities with larch. Forms mycorrhiza with *Larix*. The Asian part of the range is poorly understood, known from Yakutia, Magadan region and Northern China. Common in northeastern America.

Specimens examined: Russia, Respublika Sakha (Yakutia), Yakutsk, 62.03087, 129.73602, 20.08.1967, coll.

- A. Vaskovskiy, det. B. Vasilkov (LE 4506); *ibid.*, Zhyganskiy Rayon, Ukhunku river, 66.75199°N, 123.39415°E, in larch-birch forest with *Pinus pumila*, 10.08.1967, coll. N. Medvedeva, det. B. Vasilkov (LE 4507); *ibid.*, Magadanskaya Oblast, Olskiy Rayon, Surroundings of Lake Chistoye, 59.54102°N, 151.81129°E, tussock-sphagnum tundra, 18.08.1990, coll. and det. N. Sazanova (MAG 1350, LE 208202); *ibid.*, Olskiy Rayon, zakaznik “Kavinskaya dolina”, 59.65777°N, 147.45388°E, in a solifluction crack-gap in a waterlogged larch forest, 19.08.2017, coll. and det. N. Sazanova (MAG 4769); *ibid.*, zakaznik “Kavinskaya dolina”, 59.68719°N, 147.49039°E, at the mouth of a stream, mixed forest descending from a high floodplain terrace, on mossy dead larches, N. Sazanova (MAG 4957, GenBank, TEF1 ON637150, LSU ON623713, ITS ON623674); *ibid.*, Khasynskiy Rayon, Elekchan lakes, 60.75754°N, 151.79047°E, pine plantations with larch, 12.08.2015, coll. and det. N. Sazanova (MAG 4314); *ibid.*, Tenkinskiy Rayon, Krutoy, Orotuk, 62.05591°N, 148.63593°E, sparse larch forest with *Pinus pumila*, 05.07.1995, coll. N. Sinelnikova, det. N. Sazanova (MAG 1354); *ibid.*, Mountain pass towards Orotuk, 62.05863°N, 148.62916°E, sparse larch forest with *Pinus pumila* and *Betula middendorffii*, 25.07.2011, coll. and det. N. Sazanova (MAG 4716, GenBank TEF1α ON637149, LSU ON623712, ITS ON623672); *ibid.*, Kontakt research station, 61.84598°N, 147.66127°E, sparse larch forest with *Pinus pumila* and *Betula middendorffii*, 02.09.2017, coll. V. Dokuchaeva, det. N. Sazanova (MAG 4935); *ibid.*, Kontakt research station, 61.85711°N, 147.65362°E, larch sparse forest along the Vstrecha stream, along the path, often, on sphagnum and on soil, 22.08.2018, coll. and det. N. Sazanova (MAG 5845, GenBank, TEF1 ON637151, ITS ON623673); Canada, Ontario, Muskoka District, University of Toronto Forest, 45.11099°N, -79.39875°E, 28.04.2022, coll. R. Cain (LE 4513, Ex TRTE 44557); *ibid.*, Dorset, 2 miles east of Forest Ranger School, 45.24424°N, -78.89427°E, In a pure Larch swamp, 08.09.1962, coll. M. Pantidou, C. Rogerson, det. M. Pantidou (LE 4517, Pantidou B-447-62, Ex DAOM 91054); *ibid.*, Quebec, La Verendrye Park, Near Lac Ronald, 48.03144°N, -89.92305°E, in a larch swamp, 13.09.1963, coll. and det. M. Pantidou (LE 4514, Ex DAOM 93196); *ibid.*, La Verendrye Park, Near Lac des Loups, 48.03144°N, -89.92305°E, 13.09.1963, coll. M. Elliott, M. Pantidou, det. M. Pantidou (LE 4515, Ex DAOM 93197); United States of America, Michigan, Marquette, 46.54862°N, -87.40375°E, on sphagnum in a bog, 09.04.1933, coll. A. Smith, E. Mainz, det. E. Mainz (LE 4516, Ex MICH); *ibid.*, New York, Quenell Farm, Paul Smith, 44.43826°N, -74.25259°E, in moss mixed coniferous woods, 28.04.2022, coll. and det. M. Pantidou (LE 4518, Ex DAOM 74138, Pantidou B-279-60).
- Suillus asiaticus* sequences (KU059558, KU059559) were generated in the laboratory of Dr. T. James at the University of Michigan, USA. The sequences of *S. paluster* and *S. ochraceoroseus* voucher specimens from Russia were obtained using the equipment of the Center for the collective use of scientific equipment “Cellular and molecular technologies for the study of plants and fungi” of the Komarov Botanical Institute RAS. The work of Elena Zvyagina was carried out with the support of the Russian Foundation for Basic Research (project No. 20-04-00349). The research of Nina A. Sazanova was carried out within the frame of government assignments for Institute of Biological Problems of the North FEB RAS (project AAAA-A17-117122590002-0 “Inventory and classification of taxonomic and spatial diversity of plants and plant communities of the Far East North of Russia”). The research of Tatiana M. Bulyonkova was carried out within the frame of government assignments for Yugra State University (project “Laboratory for the development of metagenomic analysis methods for express assessment of environmental impacts in conditions of intensive subsoil use”).

REFERENCES

- Bolshakov S., Kalinina L., Palomozhnykh E. et al. Agaricoid and boletoid fungi of Russia: the modern country-scale checklist of scientific names based on literature data. *Biological Communications*. 2021. V. 66 (4). P. 316–325. <https://doi.org/10.21638/spbu03.2021.404>
- Bouckaert R.R., Drummond A.J. bModelTest: Bayesian phylogenetic site model averaging and model comparison. *BMC Evolutionary Biology*. 2017. V. 17 (1). 42. <https://doi.org/10.1186/s12862-017-0890-6>
- Drummond A.J., Bouckaert R.R. Bayesian evolutionary analysis with BEAST 2. Cambridge University Press, 2014.
- Gardes M., Bruns T.D. ITS primers with enhanced specificity for basidiomycetes: application to identification of mycorrhizae and rusts. *Mol. Ecol.* 1993. V. 2. P. 113–118.
- GBIF Occurrence Download. 2022a. <https://doi.org/>. Accessed 30.02.2022. <https://doi.org/10.15468/dl.pgk57b>
- GBIF Occurrence Download. 2022b. <https://doi.org/>. Accessed 30.02.2022. <https://doi.org/10.15468/dl.mevche>
- Katoh K., Rozewicki J., Yamada K.D. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics*. 2019. V. 20 (4). P. 1160–1166. <https://doi.org/10.1093/bib/bbx108>
- Kretzer A., Li Y., Szaro T.M. et al. Internal transcribed spacer sequences from 38 recognized species of *Suillus* sensu lato: Phylogenetic and taxonomic implications. *Mycologia*. 1996. V. 88 (5). P. 776–785.
- Kuntze O. *Revisio generum plantarum*. 1898. V 3(3). P. 1–576.
- Little E.L. *Atlas of United States trees*. Volume 1. Conifers and important hardwoods. Miscellaneous Publication 1146. Washington, Forest Service, 1971.
- Morozova O.V., Popov E.S. *Mycotheca Petropolitana ab Instituto Botanico nomine V.L. Komarovii Academiae Scientiarum Rossicae edita (series exsiccatorum)*. Fasc. III–V (nos. 41–100). St. Petersburg. 2008.
- Murrill W.A. *The Boletaceae of North America-1*. *Mycologia*. 1909. V.1 (1). P. 4–18.
- MyCoPortal. 2022. <https://www.mycportal.org/portal/index.php>. Accessed 30.02.2022.
- Nezdojminogo E.L. *Ad floram Agaricalium litoris lacus Balc septentrionali-orientalis*. *Novosti sistematiki nizshikh rastenii*. 1970. V. 6. P. 146–158 (in Russ.).
- Nguyen N.H., Vellinga E.C., Bruns T.D., et al. Phylogenetic assessment of global *Suillus* ITS sequences supports morphologically defined species and reveals synonymous and undescribed taxa. *Mycologia*. 2016. V. 108(6). P. 1216–1228. <https://doi.org/10.3852/16-106>
- Okonechnikov K., Golosova O., Fursov M. et al. Unipro UGENE: a unified bioinformatics toolkit. *Bioinformatics*

- ics. 2012. V. 28. P. 1166–1167.
<https://doi.org/10.1093/bioinformatics/bts091>
- Peck C.H. Boleti of the United States. Bulletin of the New York State Museum. 1889. V. 2 (8). P. 73–166.
- Peck C.H. Report of the Botanist (1869). Annual Report on the New York State Museum of Natural History. 1873. V. 23. P. 27–135.
- Peck C.H. Report of the Botanist (1870). Annual Report on the New York State Museum of Natural History. 1872. V. 24. P. 41–108.
- Pomerleau R. An addition to the genus *Fuscoboletinus*. Mycologia. 1964. V. 56 (5). P. 708–711.
- Pomerleau R., Smith A.H. *Fuscoboletinus*, a new genus of the *Boletales*. Brittonia. 1962. V. 14 (2). P. 156–172.
- Rehner S. A., Buckley E. A *Beauveria* phylogeny inferred from nuclear ITS and EF1- α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. Mycologia. 2005. V. 97. P. 84–89.
- Semerikov V.L., Lascoux M. Genetic relationship among Eurasian and American *Larix* species based on allozymes. Heredity. 1999. V. 83. P. 62–70.
<https://doi.org/10.1046/j.1365-2540.1999.00531.x>
- Singer R. Notes on bolete taxonomy. Persoonia. 1973. V. 7 (2). P. 313–320.
- Slipp A.W., Snell W.H. Taxonomic-ecologic studies of the *Boletaceae* in northern Idaho and adjacent Washington. Lloydia. 1944. V. 7. P. 1–66.
- Smith A.H., Thiers H.D. A contribution toward a monograph of North American species of *Suillus*. Privately published. Ann Arbor, MI, 1964.
- Snell W.H., Dick E.A. Notes on boletes. VI. Mycologia. 1941. V. 33. P. 23–37.
- Suchard M.A., Lemey P., Baele G. et al. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. Virus Evolution. 2018. V. 4.
<https://doi.org/10.1093/ve/vey016>
- Taylor J.W., Jacobson D.J., Kroken S. Phylogenetic species recognition and species concepts in fungi. Fungal Genet Biol. 2000. V. 31 (1). P. 21–32.
<https://doi.org/10.1006/fgbi.2000.1228>
- Vasilkov B.P. De speciebus nonnullis generis Boletini. Notulae systematicae e sectione cryptogamica Instituti Botanici nomine V. L. Komarovii Academiae Scientiarum URSS. 1952. V. 8. P. 113–117 (in Russ.).
- Whitlock C. The history of *Larix occidentalis* during the last 20 000 years of environmental changes. In: Ecology and Management of *Larix* Forests: A Look Ahead Proceedings of an international symposium, 5–9 October, 1992. Whitefish, MT, 1995, pp. 83–90.
- Zvyagina E.A., Vasina A.L. New data on macromycetes of the Malaya Sosva Nature Reserve (Khanty-Mansi Region). Mikologiya i fitopatologiya. 2015. V. 49 (6). P. 349–358 (in Russ.).
- Васильков Б.П. (Vasilkov) О некоторых видах рода *Boletus* // Ботанические материалы Отдела споровых растений БИН АН СССР. 1952. № 8. С. 113–117.
- Звягина Е.А., Васина А.Л. (Zvyagina, Vasina) Новые данные о макромицетах заповедника Малая Сосьва (Ханты-Мансийский автономный округ) // Микология и фитопатология. 2015. Т. 49. № 6. С. 349–358.
- Нездоймино Э.Л. (Nezdoyminogo) К флоре агариковых грибов северо-восточного побережья Байкала // Новости систематики низших растений. 1969. № 6. С. 146–158.

Suillus paluster и *S. ochraceoroseus* (*Boletales*) в Северной Азии

Е. А. Звягина^{1,2,#}, Н. А. Сазанова^{3,##}, Т. М. Бульонкова^{4,###}

¹Московский государственный университет имени М.В. Ломоносова, Москва, Россия

²Югорский государственный университет, Ханты-Мансийск, Россия

³Институт биологических проблем Севера ДВО РАН, Магадан, Россия

⁴Институт систем информатики им. А.П. Ершова Сибирского отделения Российской академии наук, Новосибирск, Россия

#e-mail: mycena@yandex.ru

##e-mail: nsazanova_mag@mail.ru

###e-mail: ressaure@gmail.com

В результате филогенетического и морфологического анализа образцов российских и зарубежных коллекций установлено, что на территории Северной Азии произрастают два вида из комплекса *Suillus paluster*. Большую часть азиатских образцов, идентифицированных ранее как *S. paluster*, можно отнести к азиатской популяции *S. ochraceoroseus*. Последний отличается крупными мясистыми плодовыми телами, ярко-розовым, местами охристым цветом чешуек и горьким вкусом. Исходя из географии сборов и генетических последовательностей ITS и *TEF1 α* , *S. ochraceoroseus* распространен как на северо-западе Сев. Америки, так и по всей Азиатской части России, а также в Японии и Китае. Отдельные сборы данного вида были сделаны в европейской части России в лиственных посадках. *S. paluster*, согласно протологу, имеет мелкие плодовые тела, с крупным ребристым гименофором и мягким вкусом и распространен в северо-восточной части Сев. Америки. В Евразии молекулярно-генетическими и молекулярно-генетическими методами его присутствие подтверждено в Восточной Сибири (Якутия), на Дальнем Востоке (Магаданская обл.) и в северной части Китая. Приводятся описания морфологии коллекционных образцов *S. ochraceoroseus* и *S. paluster* из Северной Азии. Для территории России *S. ochraceoroseus* упоминается впервые. Обсуждается Азиатско-Североамериканская дизъюнкция ареалов *S. ochraceoroseus* и *S. paluster*.

Ключевые слова: Берингия, биогеография, дизъюнкция ареалов, микориза, таксономия, филогения, *Larix*, *Suillaceae*