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The veiled stinkhorn *Dictyophora sibirica* in Russia – taxonomic position, epitypification and its conspecifity with *Phallus ultraduplicatus*

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Keywords: gasteromycetes, ITS nrDNA sequences, molecular phylogeny, mycobiota, mycological collections, stinkhorn.

Summary. The article presents the results of studying a lectotype specimen of *Dictyophora sibirica*. The abolition of the genus name *Dictyophora* justifies the transfer of this taxon to the genus *Phallus*, with a new combination being *Phallus sibiricus*. A recently collected specimen from the locus classicus corresponds to the original description and is designated as an epitype due to the impossibility of sequencing the DNA of the holotype. Synonymy between *Phallus sibiricus* and *P. ultraduplicatus* is proposed, based on morphology and comparison of ITS sequences.

Сетконоска *Dictyophora sibirica* в России – таксономическое положение, эпитипификация и синонимия с *Phallus ultraduplicatus*

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Ключевые слова: веселка, гастеромицеты, микобиота, микологические коллекции, молекулярная филогения, ITS-последовательность ярДНК.

Аннотация. В статье изложены результаты изучения типового образца *Dictyophora sibirica*. Упразднение родового названия *Dictyophora* оправдывает перенос этого таксона в род *Phallus* с новой комбинацией *Phallus sibiricus*. Недавно собранный образец из locus classicus соответствует первоначальному описанию и обозначен как эпитип из-за невозможности секвенирования ДНК голотипа. Предложена синонимия *Phallus sibiricus* и *P. ultraduplicatus*, основанная на морфологии и сравнении последовательностей ITS.

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Introduction

Phallus Junius ex L. is a widespread genus of basidiomycetes, with highest species diversity in tropical and subtropical regions. The genus *Dictyophora* Desv., which included species with indusium-bearing basidiomes, is united with *Phallus* according to morphological (Kreisel, 1996; Calonge, 2005) and phylogenetic (Li et al., 2016; Melanda et al., 2021) studies. New species are often described in different parts of the world in recent times (Cabral et al., 2019; Li et al., 2002, 2014; Moreno et al., 2009; Song et al., 2018; etc.). There are 43 species known by now (Li et al., 2021). As pointed by Cabral et al. (2019, p. 104), "*few morphological characters are available to delimit species in Phallus. In addition, most of the widely used diagnostic characters – such as colour and sizes – show high plasticity*…". The difficulty of reliable identification of *Phallus* specimens lies in the fact that mature basidiomes are very short-lived. After the spore-bearing part (gleba) exposed, it is partially consumed within a very short period (typically less than a day) by insects attracted to a specific smell, partially adheres to their bodies and spreads radially. The remaining basidiomes are quickly destroyed by invertebrates and microorganisms. The basidiomes strongly change its shape and color during herbarization, and, therefore, it is desirable to photograph them in natural conditions. Taking a sample for DNA analysis in matured basidiomes is difficult. Only gleba and mycelial strands are suitable for analysis, but in both cases the risk of contamination of foreign DNA is extremely high. For these purposes, it is more convenient to use enclosed basidiomes in "egg" stage, but during their herbarization we get practically no information about macromorphology. Therefore, to accurately ascertain the identity of *Phallus* specimens, the presence of several basidiomes at various stages of maturity and their photo are often required.

For a long time, the prevailing opinion was that specimens of stinkhorns with indusium found in Europe belongs to *Dictyophora duplicata* (Bosc) E. Fisch. (current name *Phallus indusiatus* Vent.) (Ulbrich, 1932; Flora ČSR, 1958). A detailed morphological study of European specimens revealed their obvious differences from *P. duplicatus* leading to the description of a new variation *P. impudicus* var. *pseudoduplicatus* O. Andersson (Andersson, 1989). According to Kreisel (Kreisel, Hausknecht, 2009), this variation is also common in Africa and presumably in Asia. However, this view requires clarification using molecular genetic methods. For example, recent studies by Cabral et al. (2019) suggest that the veiled stinkhorn *P. indusiatus* might conceal a significant number of undiscovered species.

The species diversity of the genus *Phallus* in Russia is estimated at 6 species (unpublished data). Previously, all specimens with indusium collected in Russia were identified as *Dictyophora duplicata* (Vasilkov, 1954; Sosin, 1973; Rtischeva, 1991; Perova, Gorbunova, 2001; Bulakh, 2015) or as *Phallus duplicatus* (Dudka et al., 2004). Based on these data, *P. duplicatus* was listed in the Red Data Book of the Russian Federation (Rebriev, 2008) as a rare but widely distributed species. Under the same name, the indusiate *Phallus* are included in many regional Red Data Books of the Russian Federation (Kolchanov, Maslova, 2004; Petrov, Matosova, 2010; Gorbunova, 2018; etc.). The name *P. impudicus* var. *pseudoduplicatus* is listed in Red Books of the Krasnodar Territory (Rebriev, 2017) and the Republic of North Ossetia – Alania (Rebriev, Nikolaev, 2022).

In 1936, *Dictyophora sibirica* Lavrov was described as new for science species (Lavrov, 1936). There are two syntypes were pointed: the first from vicinity of the rural locality Chemal (the Republic of Altai), and the second from vicinities of the Tomsk city (Tomsk Region). This name was previously classified as synonym of *Phallus duplicatus* (≡ *Dictyophora duplicata*) by B. P. Vasilkov (1954), but without any type specimens study. Later, this taxon was sometimes indicated in publications devoted to the biodiversity of the Tomsk Region (Milovidova et al., 1980; Rare and endangered…, 1984). In the article about the biodiversity of the gasteroid basidiomycetes of the Tomsk Region indusiate stinkhorns were named as *Phallus impudicus* var. *pseudoduplicatus* (Agaphonova et al., 2011).

The accumulation of new data on the taxonomic diversity of *Phallus* in the Russian Federation made facilitated clarification of the taxonomic status of some specimens with indusium collected in the Asian part. Molecular genetic methods were utilized to identify specimens from Novosibirsk Region (Rebriev et al., 2020), Tomsk Region (Kudashova et al., 2023) and Primorye Territory (Rebriev et al., 2022), and they were identified as *P. ultraduplicatus* X. D. Yu, W. Lv, S. X. Lv, Xu H. Chen et Qin Wang. This taxon was pointed for Krasnoyarsk Territory also but without molecular data (Kryuchkova, Goncharova, 2021).

Clarification of the true taxonomic position of *Dictyophora sibirica* Lavrov has been of significant interest. In the V. L. Komarov's Mycological Herbarium of the Botanical Institute of the Russian Aca-

demy of Sciences, a specimen LE 1582 was found and the information on its label is identical to one of the two specimens mentioned in the protologue. This specimen collected in the vicinity of Tomsk in 1933 was chosen by us as a lectotype. The objective of this study was to clarify the taxonomic status of the Russian indusiate stinkhorns specimens and current taxonomic position of *D. sibirica*.

Despite the well-preserved basidiome, all attempts to make a molecular genetic analysis of the type specimen of *D. sibirica* were unsuccessful. This is probably due to the long storage of the sample and/or its drying at high temperature. But the application of molecular data in phylogenetic analyses to delimit taxa has become a widespread, beneficial practice (Aime et al., 2021). Epitypification with sequencing of newly collected specimens is the most efficient way for unambiguous species delimitation (Buyck et al., 2019). Therefore, according to 9.9 of the "*International Code of Nomenclature…*" (Turland et al., 2018), an epitype was chosen. Based on morphological similarity, we designate as epitype the following specimen collected in locus classicus: LE F-348635.

Methods

Morphology

The specimens examined were obtained from the Mycological Herbarium of the Komarov Botanical Institute RAS (LE F) and from Yu. Rebriev's own collection. Basidiospores mounted in 5 % KOH solution were examined under the light microscope Mikmed-6 (LM). Light microscope photography has been implemented with the equipment of the Centre for cellular and molecular technology of studying plants and fungi at the Komarov Botanical Institute RAS (St. Petersburg).

Phylogenetic analyses

DNA was extracted from the gleba of the dried immatured basidiomes (egg stage) using a standard CTAB-chloroform method (Doyle J. J., Doyle J. L., 1987). Subsequent amplification of internal transcribed rDNA spacers (ITS) was carried out using ITS1/ITS4 primer pair following the instructions provided by the authors (White et al., 1990). Amplification products were separated by electrophoresis in 1 % agarose gel stained with ethidium bromide. Fragments of the desired length were excised and purified using silica-based procedure (Malferrari et al., 2002). Sequencing PCR was performed using the Sanger method (Sanger et al., 1977) with the BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Thermo Fisher Scientific, Waltham, MA, USA), and nucleotide sequences were determined on an ABI PRISM 3500 genetic analyzer.

The nucleotide sequences were checked and manually edited using SeqScape V3.0 or Vector NTI Advance 11.5.1 software. Subsequently, they were compared with sequences deposited in GenBank using the BlastN search (Altschul et al., 1990). The newly obtained ITS sequences were deposited in GenBank under unique accession numbers which listed in the specimen's citation.

Five new ITS sequences of *Phallus* spp. were produced for our study (Table 1). Additionally, 26 sequences were retrieved from the GenBank. The specimens CCTR 6759 (GenBank sequence OP787980) was collected together with LE F-348635 and probably formed on a common mycelium. But the sequence of the second sample turned out to be longer and of better reading quality. *Itajahya galericulata* was chosen as the outgroup. The genus *Itajahya* was recognized as sister to *Phallus* (Melanda et al., 2021). Sequences were aligned in MAFFT (Katoh et al., 2019), then the alignment was manually optimized with MEGA 6 (Tamura et al., 2013).

The ITS rDNA phylogenetic tree (Fig. 1) was obtained using MrBayes v. 3.2.1 (Ronquist et al., 2012) using the GTR+I+G model with 5 M generations. The best tree was visualized in FigTree v. 1.2.3 and edited in Adobe Illustrator CS5 (Fig. 1).

Results

Molecular phylogeny

Our molecular data based on ITS sequences (Fig. 1) showed that all indusiate specimens from the Asian part of the Russian Federation are grouped with the *Phallus ultraduplicatus* sequences and formed own clade (PP = 1). These data are consistent with our previous phylogenetic data (Rebriev et al., 2020, 2022). The specimen YuR 3865 with indusium from European Russia is clustered with *P. impudicus*-clade.

Morphology

The indusiate specimens from the Asian part of the Russian Federation are fairly uniform in morphology. Minor variations in the size of the stipe, cup and indusium can be explained by the influence of environmental factors and growing conditions. All examined specimens correspond to the description of *P. ultraduplicatus* (Adamčík et al., 2015). It is very important to note that the basidiomes of stinkhorns significantly decrease in size when dried. This is evident when comparing the size of the specimen LE F-348635 in its fresh and dried states (table 2).

Table 1

Taxa, vouchers, locations, and GenBank accession numbers of DNA sequences used in the study

Taxon	ID (Specimen)	Country	GB no. ITS	Reference
Dictyophora indusiata (Vent.) Desv.	ASI 32011	? Republic of Korea	AF324160	Adamčík et al., 2015
" "	ASI 32001	? Republic of Korea	AF324172	Adamčík et al., 2015
D. rubrovolvata M. Zang, D. G. Ji et X. X. Liu	YZS047	China	KF939507	–
" "	YZS018	China	KF939513	–
D. phalloidea Desv.	–	? Republic of Korea	AF324162	Adamčík et al., 2015
Itajahya galericulata Möller	KSRF-0014	India	MF506819	Melanda et al., 2021
Phallus denigricans T. S. Cabral, B. D. B. Silva et Baseia*	INPA272383	Brazil	MG678486	Cabral et al., 2019
P. dongsun T. H. Li, T. Li, Chun Y. Deng, W. Q. Deng et Zhu L. Yang*	GDGM 75402	China	NR_171851	Li et al., 2020
P. fragrans M. Zang	HKAS126427	China	OQ025165	–
P. hadriani Vent.	SR1659	India	MT151615	–
" "	GDGM 83732	China	MW031862	–
" "	JLF7894	USA	MT101866	–
" "	YuR 180	Russia, Rostov Oblast	MG678525	Cabral et al., 2019
P. haitangensis H. Li Li, P. E. Mortimer, J. C. Xu et K. D. Hyde	HKAS 88199	China	KU705384	Li et al., 2016
P. impudicus L.	G.M. 2015-08-15.10	Luxembourg	OP603024	–
" "	**YuR 3865**	**Russia, Moscow Oblast**	**OR708694**	**–**
" "	–	Poland	MZ410690	
P. indusiatus Vent.*	INPA264931	Brazil	MG678502	Cabral et al., 2019
P. purpurascens T. S. Cabral, B. D. B. Silva et Baseia*	UFRN Fungos:2808	Brazil	NR_166233	Cabral et al., 2019
P. rigidiindusiatus T. Li, T. H. Li et W. Q. Deng*	GDGM 81196	China	NR_175754	Li et al., 2021
P. rugulosus (E. Fisch.) Lloyd	TNS-F-46049	Taiwan	MF372142	Pereira et al., 2017
P. serratus H. Li Li, L. Ye, P. E. Mortimer, J. C. Xu et K. D. Hyde	HKAS:78341	China	KF052623	Adamčík et al., 2015
P. ultraduplicatus X. D. Yu, W. Lv, S. X. Lv, Xu H. Chen et Qin Wang*	HMAS:253050	China	KJ591584	Adamčík et al., 2015
" "	HMAS:253051	China	KJ591585	Adamčík et al., 2015
" "	YuR 3374	Russia, Novosibirsk Oblast	MK965097	Rebriev et al., 2020
" "	LE-BIN 4670	Russia, Primorsky Territory	OL764905	Rebriev et al., 2022
" "	CCTR 6759	Russia, Tomsk Oblast	OP787980	Kudashova et al., 2023
" "	**LE F-348633**	**Russia, Krasnoyarsk Krai**	**OR708542**	**–**
" "	**LE 324109**	**Russia, Irkutsk Oblast**	**OR708543**	**–**
" "	**YuR 3715**	**Russia, Republic of Buryatia**	**OR708544**	**–**
" " *	**LE F-348635**	**Russia, Tomsk Oblast**	**OR712348**	**–**

Note. The new sequences are given in bold. Type specimens are marked with asterisk (*).

Table 2

Comparison of the sizes of basidiomes from types of *Dictyophora sibirica* and *Phallus ultraduplicatus* with some studied specimens

		P. ultraduplicatus (Adamčík et al., 2015)	*P. sibiricus* epitype LE F-348635	*D. sibirica* (Lavrov, 1936)	*P. sibiricus* YuR 3714
Fresh basidiomes	Immature basidiome	70–80 × 80–90 mm	45–47 × 52–70 mm	60–80 mm	
	Mature basidiome / Receptacle	190–250 mm tall	(130)140–160(200) mm	150–200 mm	
	Pileus	40–50 mm high	38–44–53 mm		
	Indusium	20–40 mm long	25–40(45) mm		
Dry basidiomes	Immature basidiome		43–48 mm	50–60 mm	32 × 48 mm
	Mature basidiome / Receptacle		100–130 mm	100–200 mm	95–150
	Pileus		27–45 mm	25 mm	30–40
	Indusium		32–35 mm	15–20 mm	30–43

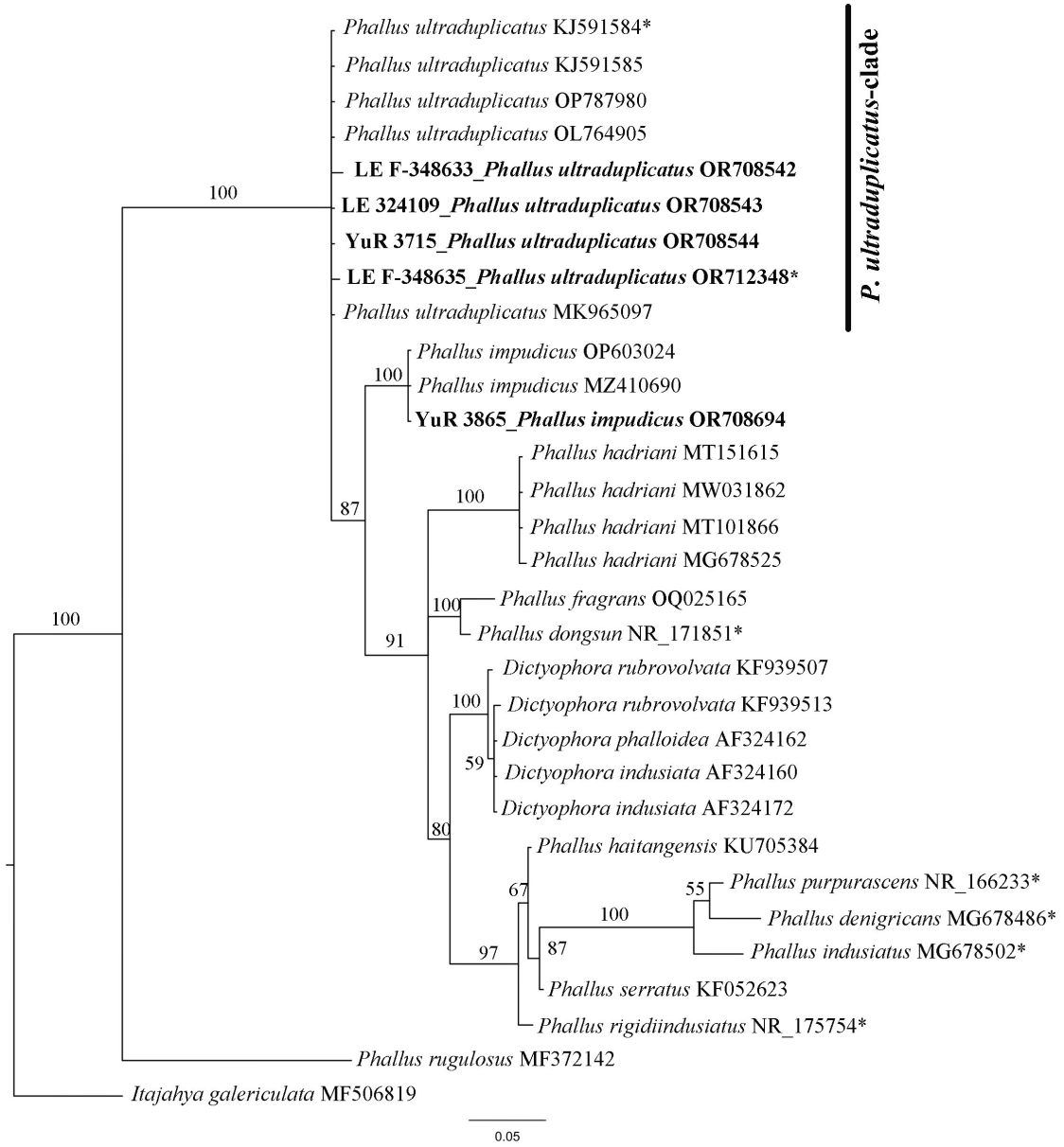

Fig. 1. ITS phylogenetic tree generated using MrBayes v. 3.2.1 under GTR + I + G model for 5 M generations. The GenBank accession numbers are indicated after each species name. Support values are indicated on the branches (posterior probabilities). The novel species is shown in bold text. Type specimens are pointed with asterisk.

The dimensions of the fresh basidiomes LE F-348635 are in good agreement with the description of *P. ultraduplicatus*, while the measurements of the same basidiomes in the dried state are closer to the description of *Dictyophora sibirica* (Lavrov, 1936). Our measurements of the type specimen of *D. sibirica* correspond to the description of this species. This confirms that already dried material was used in the Latin language description (along with additional measurements of immature basidiomes and receptacle in Russian language description). Based on these data, we conclude that morphological descriptions of *D. sibirica* and *P. ultraduplicatus* exhibit notable similarities.

Dictyophora sibirica type LE 1582 study (Fig. 2).

The lectotype is one basidiome 8.8 cm high, without volva and with a pileus and upper part of receptacle covered by peridium. The pileus slightly asymmetric, up to 2.5 cm high. The receptacle is broken, the widest in the central part and tapering to both ends, 1.5 cm thick in widest upper part and 1.1 cm at the bottom. The indusium is partially visible from under the peridium, up to 2.5 cm.

Basidiospores 4.0–4.5 × 1.8–2.2 μm, oblong, smooth, thin-walled, hyaline.

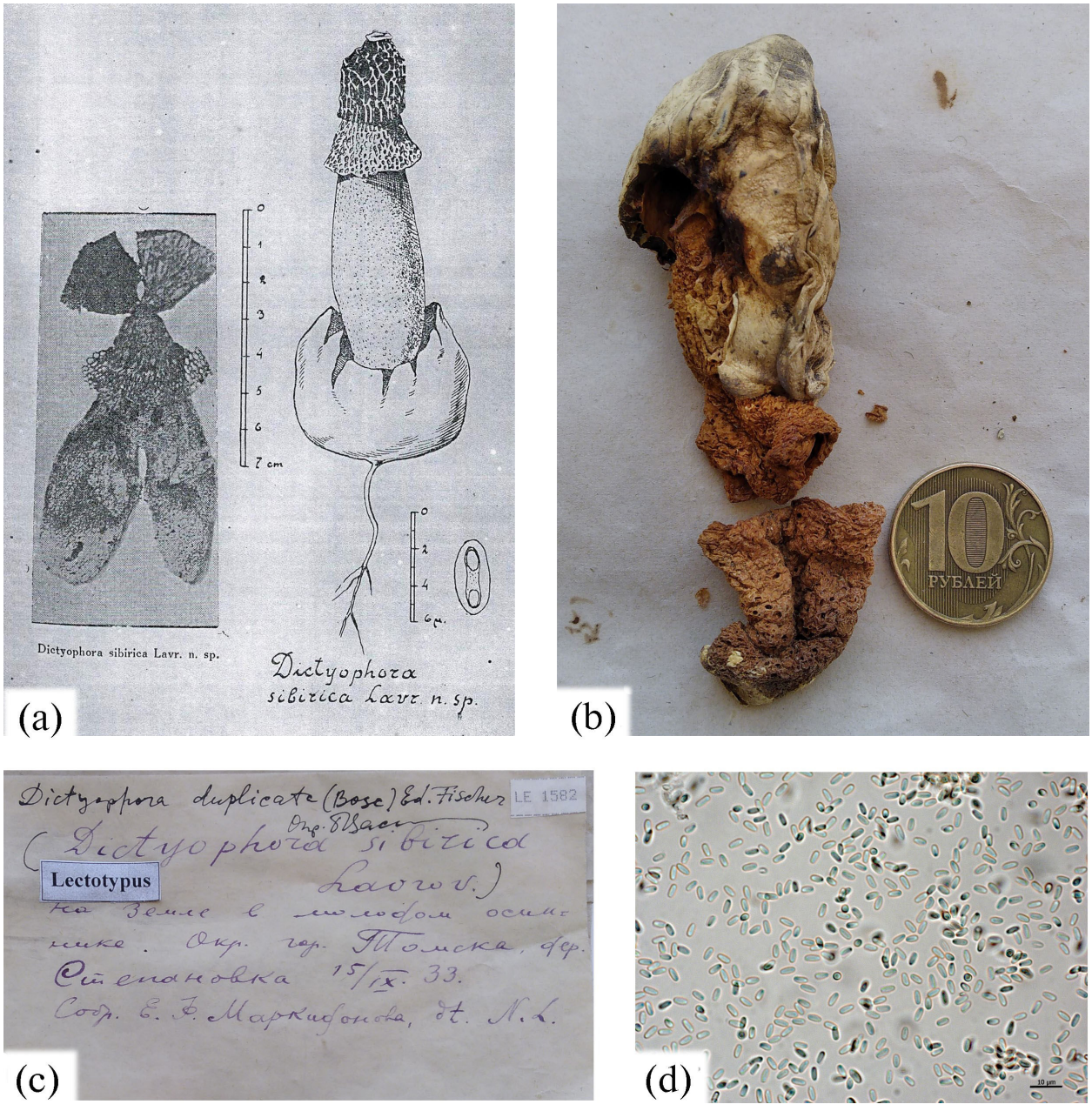

Fig. 2. The image from protologue (a), specimen (b), original label (c), and basidiospores (d) of *Dictyophora sibirica* lectotype LE 1582 (the coin diameter is 22 mm).

Original diagnosis:

"Tota fructificatione immatura ovoidea vel subsphaeroidea 5–6 cm. diam., ab exteriore parte alba, intus gelatinosa, infra funiculos albos radiciformibus hypharum instructa. Receptaculo cylindraceo 10–20 cm. longo, 2–3 cm crasso, albo, elastico, intus inano, superne attenuato et infra volvam obducto; indusio candido vel roseolo, conico, 15–20 mm longo, basi 50–60 mm lato, retiformi, paullum (an 3–4 mm) supra inferioris pilei marginis altitudinem e stipite oriente; indusii interstitiis subrotundis vel irregulariter polygonis, in superiore indusii parte 2.5–3 mm diam., in inferiore parte 0,5–1 mm. metientibus; pileo olivaceo-virido campanulato vel subconico, 25 mm alto, basi duplo lato, cum stipitis apice limbo annuliformi recurvato conjuncto, extus cavernoso-reticulato; cavernis pilei subrhombeis 5 × 3.3 × 2 mm; sporis ellipsoideis 3–4 × 2 micr. viridis, polare 2 guttulatis, levibus; episporio 0.5–0.7 micr. crasso, hyalino".

Type collection's details: "Russian Federation, Tomsk Region, Stepanovka village near the Tomsk. 15 IX 1933. E. F. Markidonova" (LE 1582) (Lavrov, 1939).

Notes: The Stepanovka village currently is a microdistrict of Tomsk city. The distance to the point of the epitype collection in the vicinity of the Kolarovo village is about 12 km.

Description of epitype, based on fresh specimen.

Immature basidiome ovoid to subglobose, 60–70 mm diam, whitish, felted, with whitish long rhizomorph. **Mature basidiome** with white to dirty-white, cylindrical, hollow, pliant and finely porous **receptacle** (130)140–160(200) mm tall and up to 35 mm diam. **Pileus** conical 38–54 mm high, with apical perforated disc, reticulate, whitish under the gleba. **Gleba** dark greenish olive, gelatinous, with strong odor. **Indusium** 25–40(45) mm long, white, fragile, slightly lagging behind the receptacle or sticking and then often breaking with growth, with elongated to roundish pores, about 4 mm diam under the pileus, 2–2.7 mm diam in central part and becoming gradually smaller to bottom margin entire.

Basidiospores 4.0–5.0 × 1.8–2.2 µm, oblong, smooth, thin-walled, hyaline (Fig. 3c).

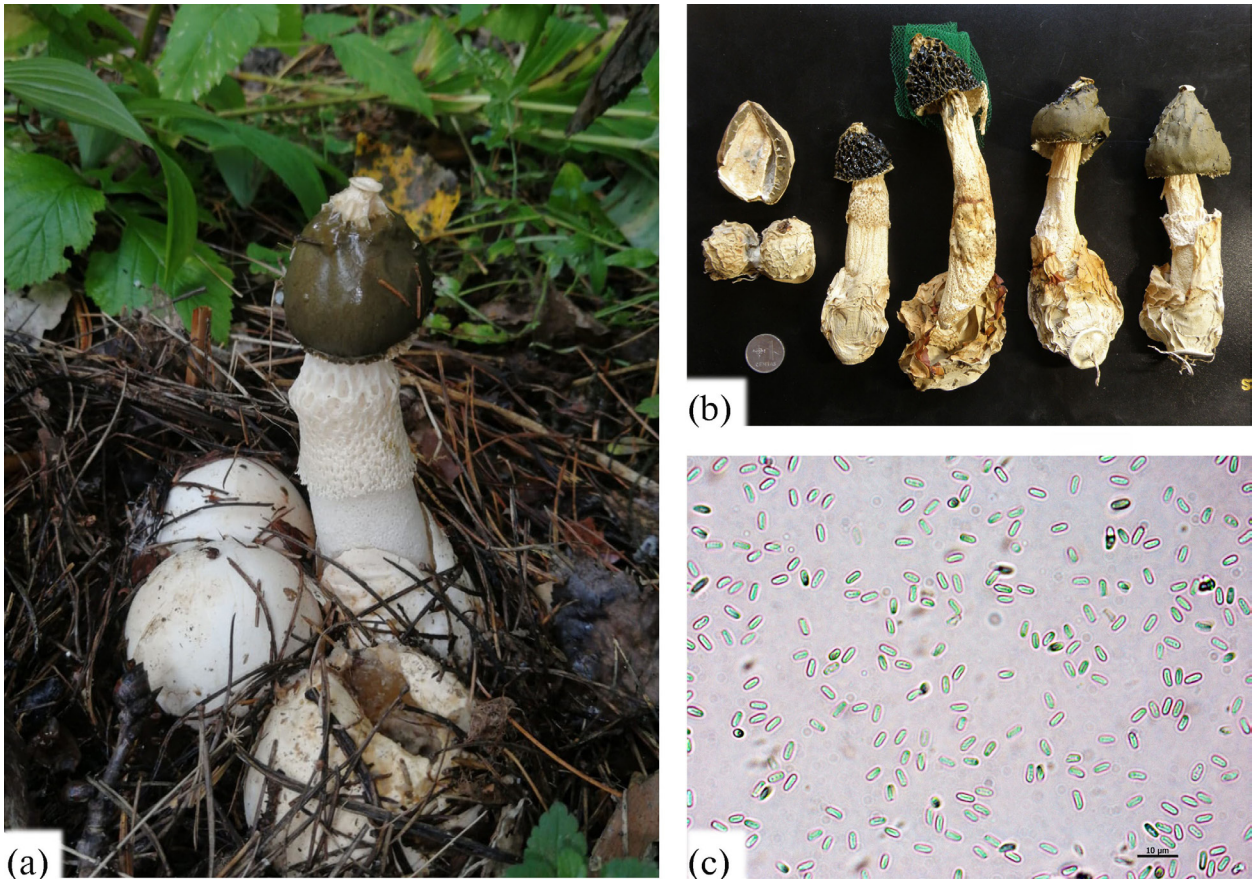

Fig. 3. The fresh basidiomes (a), dried basidiomes (b) and basidiospores (c) of *Phallus sibiricus* epitype LE F-348635 (the coin diameter is 18.75 mm).

Epitype collection's details: "Russian Federation, Tomsk Region, Tomsky District, vicinities of Kolarovo village, 56°21'00.0"N, 84°57'00.0"E, mixed forest with *Pinus sylvestris, P. sibirica, Betula pendula, Populus tremula,* and *Padus avium, Sorbus sibirica, Lonicera tatarica* in undergrowth, on litter and humified wood near. 27 VIII 2022. N. N. Kudashova, S. I. Gashkov, V. N. Stepanov" (LE F-348635; ITS GB OR712348, tef1-α OR727902, ATP6 OR727901). Abundant fructification with the more 50 basidiomes (Fig. 3a).

The epitype specimen agrees with the Lavrov's original description of *Dictyophora sibirica*.

Additional specimens examined.

"Novosibirsk Region, Novosibirsk City, the territory of the Central Siberian Botanical Garden of the Siberian Branch of the Russian Academy of Sciences, 54°49'12"N, 83°06'36"E, planting of *Quercus* spp., on soil. 29 VII 2017. D. V. Ageev" (LE F-348632; ITS GenBank MK965097). Unripened basidiome on the egg stage and destroyed mature basidiome.

"Krasnoyarsk Territory, Kuraginsky District, 1 km northwest from Zharovsk village, edge of the forest, 53°46'48"N, 93°53'24"E, on soil and litter under *Picea* sp. 18 VIII 2016. I. Yu. Krom" (LE F-348633; ITS GB OR708542). Unripened basidiomes on the egg stage.

"Irkutsk Region, Irkutsk city, the right bank of the Irkut river, near the mouth of the Kaya river, the territory of the «Angara» resort, 52°17'24"N, 104°14'24"E, thickets of shrubs in a *Pinus*-dominated forest, on soil. 11 IX 2019. I. V. Enushchenko" (LE 324109; ITS GB OR708543).

"Republic of Buryatia, Tunkinsky District, vicinities of Arshan village, on soil. 25 VIII 2019. E. S. Kurlov" (YuR 3715; ITS GB OR708544). Unripened basidiomes on the egg stage.

Sequencing of the ITS1-5.8S-ITS2 region resulted in a sequence identical to that of the *Phallus ultraduplicatus* holotype (GenBank KJ591584). The morphological description of *Phallus ultraduplicatus* (Adamčík et al., 2015) coincides with the protologue of *Dictyophora sibirica* as well as with the epitype and additional specimens.

Thus, the morphological and genetic identity of *Phallus ultraduplicatus* and *P. sibiricus* type material has been demonstrated. According to the principle of priority stated in the Article 11.4 of the International Code of Nomenclature (Turland et al., 2018), it is necessary to maintain *P. sibiricus* as the valid name for the taxon and consider *P. ultraduplicatus* as a synonym.

Taxonomic conclusion

According to H. Kreisel (1996), the genus *Dictyophora* was included in *Phallus* s. l. So, we introduce the following new combination. Since we consider *Phallus ultraduplicatus* is adequately treated as a synonym of the *P. sibiricus*.

Phallus sibiricus (Lavrov) Rebriev, **comb. nov.**

Basionym: ≡ *Dictyophora sibirica* Lavrov, 1936, in Trudy Biologicheskogo nauchno-issledovatel`skogo instituta 2: 46.

= *Phallus ultraduplicatus* X.-D. Yu, W. Lv, S. X. Lv, Xu H. Chen et Qin Wang, 2015, Crypt. Mycol. 36(2): 146.

Mycobank: MB 850579.

We designate as epitype the following collection: LE F-348635.

Mycobank: MB 254698.

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