

УДК 582.284.51 : 57.063.7

© Е. А. Zvyagina,¹ А. В. Alexandrova,² Т. М. Bulyonkova³**OMPHALINA DISCOROSEA: TAXONOMICAL POSITION OF THE SPECIES**ЗВЯГИНА Е. А., АЛЕКСАНДРОВА А. В., БУЛЬОНКОВА Т. М. *OMPHALINA DISCOROSEA*:
ТАКСОНОМИЧЕСКОЕ ПОЛОЖЕНИЕ ВИДА¹ Государственный природный заповедник «Юганский», Угут, Россия² Московский государственный университет им. М. В. Ломоносова, Россия³ Институт информационных систем им. А. П. Ершова, Новосибирск, Россия¹ Yuganskiy Nature Reserve, Ugut, Russia² Lomonosov Moscow State University, Moscow, Russia³ A. P. Ershov Institute of Informatics Systems, Novosibirsk, Russia

mycena@yandex.ru

Показано высокое сходство микроморфологии образцов *Rhodocybe ulmi*, *Rh. xylophila* и *Omphalina discorosea*. Установлено, что последовательности ITS и 28S LSU образцов *O. discorosea* группируются в хорошо поддерживаемую кладу с образцами грибов рода *Arrhenia*. Обсуждается консpezifичность *Rhodocybe ulmi*, *Rh. xylophila* и *Omphalina discorosea*. Предложена новая комбинация *Arrhenia discorosea*.

Ключевые слова: Западная Сибирь, *Tricholomataceae*, *Arrhenia*, систематика.

High morphological similarity of *Rhodocybe ulmi*, *Rh. xylophila* and *Omphalina discorosea* specimens was shown. The conspecificity of this species and its systematic position in genus *Arrhenia* are confirmed by phylogenetic studies of nITS and 28S LSU datasets. A new combination, *Arrhenia discorosea*, is proposed. Descriptions are supplemented by line drawings and colored plates.

Key words: Western Siberia, *Tricholomataceae*, *Arrhenia*, taxonomy.

In the period between 2005—2010 in Western Siberia and Northern Mongolia, we collected fungi with very conspicuous features: growing on rotten wood, with omphaloid habit, pink hymenophore and pink mycelium at the base of the stipe.

Specimens were identified as *Rhodocybe ulmi* Lj. N. Vassilyeva based on morphological features. The study of the distribution showed that this species could be synonymous with *Omphalina discorosea* (Pilát) Herink et Kotl. (Petrov, 1991) and possibly had been observed before in boreal and mountain locations in Eastern Europe, Caucasus, Eastern Siberia and the Far East of Russia.

Fruitbodies had features specific both for *Rhodocybe* and for *Omphalina*, however, the concept of these two genera changed significantly in the recent decades (Lutzoni, 1997; Redhead et al., 2002; Co-David et al., 2009). For this reason, the purpose of our study was to clarify the taxonomic position of this species.

The study of literature showed that a fungus with such morphological characteristics has been described more than once under different names.

For the first time a description featuring the same characters was published by Pilát in 1934 based on a dried specimen from the Tomsk region of Siberia, as *Omphalia discorosea* Pilát.

In 1970s, three similar species were described from different regions of Russia and East Europe almost simultaneously: *Rhodocybe xylophila* Vassilkov from Caucasus (Vassilkov, 1971), *Omphalina lilaceorosea* Svrček et Kubička from Moravia (Svrček, Kubička, 1971), and *Rhodocybe ulmi* Lj. N. Vassiljeva from the Far East of Russia (Vassilyeva, 1973).

The study of morphological features of the type material of *Omphalina discorosea*, *Rhodocybe xylophila* and *Omphalina lilaceorosea*, in 1975 by J. Herink and F. Kotlaba revealed their conspecificity. The combination *O. discorosea* (Pilát) Herink et Kotl. was made formally on the basis of nomenclatural priority of *O. discorosea* Pilát (Herink, Kotlaba, 1975).

A. N. Petrov substantiated the synonymy of *Rhodocybe ulmi* and *Omphalia discorosea* in 1991. Formally, the valid name of this species should be *O. discorosea*, how-

List of specimens used in phylogenetic study

Species	Herbarium	Herbarium number	DNA region	GenBank number
<i>Arrhenia auriscalpium</i> (Fr.) Fr.	DUKE TUB	Lutzoni 930731-3 TUB 011588	ITS, LSU ITS	U66428 DQ071732
<i>A. chlorocyanea</i> (Pat.) Redhead, Lutzoni, Moncalvo et Vilgalys	DUKE	Norvell 930506-4	ITS	U66456
<i>A. epichrysium</i> (Pers.) Redhead, Lutzoni, Moncalvo et Vilgalys	DAOM LE	Redhead 5223, Redhead 3140 LE 262961, Morozova 158KA05	ITS, LSU ITS	U66442 KC237880
<i>A. griseopallida</i> (Desm.) Watling	DUKE	Lutzoni and Lamoure 910824-4	ITS	U66436.1
<i>A. lobata</i> (Pers.) Kuhner et Lamoure ex Redhead	DUKE	Lutzoni and Lamoure 910824-1	ITS	U66429
<i>A. obscurata</i> (D. A. Reid) Redhead, Lutzoni, Moncalvo et Vilgalys		Lamoure L73-111 polyspore culture	ITS	U66448
<i>A. philonotis</i> (Lasch) Redhead, Lutzoni, Moncalvo et Vilgalys	DUKE	Lutzoni 930804-5	ITS, LSU	U66449
<i>A. velutipes</i> (P. D. Orton) Redhead, Lutzoni, Moncalvo et Vilgalys		Lamoure L77166h11Xh4 culture	ITS	U66455
<i>Chrysomphalina chrysophylla</i> (Fr.) Cléménçon	DUKE	Redhead 7700	ITS	U66430
<i>Clitocybe lateritia</i> J. Favre	DUKE	Lutzoni 930803-1	ITS	U66431
<i>Fayodia gracilipes</i> (Britzelm.) Bresinsky et Stangl	TUB	TUB 011585	LSU	DQ071744
<i>Lichenomphalia alpina</i> (Britzelm.) Redhead, Lutzoni, Moncalvo et Vilgalys	DUKE	Lutzoni 930816-8	ITS, LSU	U66447
<i>L. hudsoniana</i> (H. S. Jenn.) Redhead, Lutzoni, Moncalvo et Vilgalys	DUKE	Lutzoni 920728-4a	ITS, LSU	U66446
<i>L. velutina</i> (Qué.) Redhead, Lutzoni, Moncalvo et Vilgalys	DUKE	Lutzoni 930822-6	ITS	U66443
<i>Omphalina discorosea</i> (Pilát) Herink et Kotl.	LE LE LE LE LE LE LE LE LE	LE 201193 LE 18475 LE 262962 LE 262963 LE 262964 LE	ITS LSU LSU ITS LSU ITS LSU ITS LSU	KC207892 KC207887 KC207888 KC207893 KC207889 KC207894 KC207890 KC207895 KC207891
<i>O. pyxidata</i> (Bull.) Qué.		Lamoure L118h14 culture	ITS	U66450
<i>Omphalotus illudens</i> (Schwein.) Bresinsky et Besl	TUB	TUB 012155	ITS	DQ071741
<i>Rhodocybe caelata</i> (Fr.) Maire	TB	TB6995	ITS	GU384625
<i>Rh. spongiosa</i> T. J. Baroni, Largent et Aime	MCA	MCA2129	ITS	GU384628
<i>Rh. pruinosistipitata</i> T. J. Baroni, Largent et Aime	MCA	MCA1492	ITS	GU384627

Note. Classification is according to the Index Fungorum (www.indexfungorum.org). Herbarium acronyms: DAOM — Agriculture and Agri-Food Canada, Vascular Plant Herbarium; DUKE — Duke University NC, USA; LE — Komarov Botanical Institute, RU; MCA — M. Catherine Aime private herbarium; TUB — Herbarium, University of Tübingen, Germany; TB — Timothy J. Baroni private herbarium.

ever, this taxonomical position does not have a phylogenetical basis at the present time.

Materials and methods

Comparison of morphological characters of *O. discorosea* and *O. lilaceorosea* was based on the descriptions of type specimens given in the work of J. Herink and F. Kotlaba (1975). However, we didn't examine the types of the above mentioned species, but we studied the types of *Rhodocybe ulmi* (VLA M-20.441, paratype) and *Rh. xylophila*

(LE 17697, holotype) as well as the herbarium specimens of *Omphalina discorosea*: LE 201193 (Baykal region, Eastern Siberia, A. N. Petrov, 1997), LE 18475 (Altay, Western Siberia; A. E. Kovalenko, 1985), LE262965 (Altay, Western Siberia; O. V. Morozova, 2008) and our own collections made in 2005—2010 from Yugra, Western Siberia (LE 262963, LE 262964, LE 262971) and Northern Mongolia (LE 262962).

Collections were made, documented and preserved using the standard methods (Bondartsev, Singer, 1955). Macroscopic descriptions were based on the study of both fresh and dried material as well as on photographs. Dried

material was examined using standard microscopic techniques. Microstructures were observed and measured at 400 \times and at 1000 \times in squash preparations in 5% KOH, Congo Red and Melzer's reagent using a Leica light microscope. The pileipellis was examined in radial section pileus preparations. Up to 30 basidiospores, 10 cystidia and 10 elements of the pileipellis per specimen were measured to obtain descriptive statistics. A JEOL JSM-6389 LA SEM with standard procedures was used for more detailed studies of the spore surface ornamentation (Fungal., 2009).

The collected material is deposited in the Mycological Herbarium of Komarov Botanical Institute (LE).

We used 24 sequences of 28S large subunit nuclear ribosomal gene (28S LSU) region of omphalinoid and clitocyboid taxa to determine the generic affiliation of our specimens. The internal transcribed spacer of nuclear ribosomal gene (ITS) data set of 12 sequences was used to determine intrageneric relationships of *O. discorosea*. The specimens and sequences used in this study are listed in Table.

DNA was extracted from air-dried herbarium specimens using the NucleoSpin Plant II Kit (Macherey-Nagel).

Polymerase chain reaction protocol: 1 μ l of DNA was combined with 19 μ l of the PCR mix containing Taq polymerase buffer, 50 mM MgCl₂, dNTP, H₂O, Hot Start Taq polymerase and ITS1F and ITS4B primers for ITS (Gardes, Bruns, 1993), LR3R and LR7 for 28S LSU (Vilgalys, Hester, 1990). The amplifications of ITS and LSU were made using the same protocol: 35 cycles with the following parameters: denaturation at 94 °C (3 min), annealing at 51 °C (1 min), extension at 72 °C (2 min). PCR products were purified with the AxyPrep PCR Clean-up Kit.

Sequencing reaction was set up with the same primer combination as the one used for PCR reaction. The sequencing of this strand was performed with the ABI model 3130 Genetic Analyzer (Applied Biosystems) using the BigDye™ Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems). The raw data were processed using Sequencing Analysis 5.3.1 (Applied Biosystems). All sequences were deposited in GenBank with accession numbers given in Table 1. Sequences were edited with Seqman Pro 7.1.0 (2006).

Alignment ITS. We followed M. Lutzoni (1997), found the most similar sequences using BLAST (Altschul et al., 1990), added them to alignment in pairs or groups and aligned manually. The alignment was segmented into indel-rich and indel-poor regions by eye. Indel-rich regions were excluded from the alignment by identifying flanking regions, ideally without any gaps and ambiguity. Big insertions in ITS2 in *Lichenomphalia* group were also excluded.

Alignment LSU. The 28S LSU region was aligned in MEGA4 (Tamura et al., 2007) using CLUSTALW (Higgins et al., 1994) with gap opening penalty 5, gap extension penalty 2 and corrected manually. Ambiguity aligned regions were excluded from alignment.

Maximum likelihood (ML) and Maximum parsimony (MP) analyses were performed in PAUP version 4.0b10 (Swofford, 2002).

Results and discussion

Morphological study

Images of the fruiting body are shown in Fig. 1, and of microstructures in Fig. 2.

Fruiting body of all samples omphalinoid; pileus surface brown or grayish-brown when moist, ochre when dry, edge translucent-striate, silky or ingrown-fibrous, finely scaly, hygrophanous. Lamellae decurrent, not distant, of different length, dark rose, sometimes with darker edge. Stem central or eccentric, brown, thick-fleshed, in some specimens smooth, in some covered with pink felt, with bright pink mycelium at base. Substrate: rotten wood of deciduous trees. Macromorphological characters and ecology fully fit the description of *O. discorosea* (Herink, Kotlaba, 1975).

Pileipellis a cutis of 5–9 μ m thick encrusted hyphae, with clamps. Subpellis hyphae thinner and not encrusted. In the specimens LE 262962 from Northern Mongolia and LE 262964 from Western Siberia superficial hyphae, have thin, sparse growths, perpendicular to the surface.

Spores 6–9(10) \times (3)4–6 μ m, ellipsoid, dacryoid, inamyloid, rough with granular contents. Photographs obtained with a scanning electron microscope show distinct surface roughness (Fig. 3). The roughness is already apparent in immature spores seated on basidia and becomes more pronounced in fully-formed breakaway spores. Spores of the specimen from Northern Mongolia are slightly angled, which is typical for the genus *Rhodocybe*. We also observed some variation in the spore surface character from almost smooth to distinctly rough, and according to E. M. Bulakh (personal communication) it can be almost smooth on SEM images.

Basidia 25–30 μ m, tetrasporic. In the sample LE 262964 we encountered bisporic basidia. Sterigmata about 4 μ m long.

In the hymenophore of LE 262964, LE 262963, LE 18475, and LE 201193 there were abundant cystidia or cystidia-like curved cells on the lamellae edge sized 18–42 \times 12 μ m. In the samples LE 17697 (*Rhodocybe xylophila* Vassilkov holotype) and LE 262962 from Northern Mongolia, LE 262964, LE 262971 from Western Siberia such structures were rare. In LE 18475, LE 262964, LE 262963 we observed long (35–150 \times 2–5 μ m) hair-like structures at lamellae edges, possibly a fungus parasite; in the remaining samples, including the type, such structures were not seen.

Stipe surface a thin layer of thick encrusted hyphae, identical to those on the surface of the cap, with a layer of thin smooth hyphae underneath.

Phylogenetic study

We used phylogenetic analysis of 28S LSU dataset for determination the generic affiliation of our specimens.

For performing the ML analysis of 28S LSU data set, the TIM + I + G model with $-\ln L = 1476.1097$ was chosen based on AIC in Modeltest 3.8 (Posada, 2006)



Fig. 1. *Arrhenia discorosea*: basidiomes (1a–1d — LE 262962; 2a, 2b — LE 262971; 3 — general view).

using the ModelTest Web Server (<http://darwin.uvigo.es>). ML analysis resulted in one tree with the score of 1471.44249.

A heuristic search was conducted with the following conditions: characters were unordered and weighted equally; the starting tree was obtained via stepwise addition; addition sequence was random, the number of trees retained was limited to 100; the branching-swapping algorithm was tree-bisection reconnection (TBR), one tree was held at each step during stepwise addition. Bootstrap analyses were performed using heuristic search with 1000 replicates. Gaps were treated as «missing». Of the 660 total characters 598 characters were constant, 34 characters were parsimony-informative, 28 variable characters were parsimony-uninformative.

Heuristic search revealed the 100 most parsimonious trees with a length of 117, a consistency index (CI) of 0.6068, a retention index (RI) of 0.7278, and a homoplasy index (HI) of 0.3932. We used a Bootstrap 50 % majority-rule consensus tree.

The topology of ML and MP 50 % majority-rule consensus tree of the 28S LSU data set was the same. The well supported clade *Arrhenia* (98 %) contained *Arrhenia* from GenBank and a branch of five *Omphalina discorosea* sequences. Other omphalinoid and clitocyboid taxa were placed in the outgroup (Fig. 4, a).

Because *Arrhenia epichysium* (Pers.) Redhead, Lutzoni, Moncalvo et Vilgalys and *Omphalina discorosea* have very similar morphology and ecology and only differ in the fruitbody color, we needed delimitation between these spe-

cies. To achieve this we used phylogenetic analysis of ITS region, as it is the most appropriate method to tell species apart.

The MP analysis of the ITS region was performed with heuristic search options. Characters were unordered and weighted equally; the starting tree was obtained via stepwise addition; the addition sequence was random, the number of trees retained was limited to 100; the branching-swapping algorithm was tree-bisection reconnection (TBR), one tree was held at each step during stepwise addition. Bootstrap analyses were performed using heuristic search with 1000 replicates. Gaps were treated as «missing». Of the 420 total characters, 333 were constant, 39 were parsimony-informative and 48 variable characters were parsimony-uninformative.

Based on the aligned sequences, heuristic searches revealed the 100 most parsimonious trees with a length of 115, a consistency index (CI) of 0.8957, a retention index (RI) of 0.8723, and a homoplasy index (HI) of 0.1043.

For ML analysis of the ITS region the best model K80(K2P) + I with $-\ln L = 1160.6927$ was selected by AIC in Modeltest 3.8 (Posada, 2006). ML analysis yielded five trees with the score of the best tree (1159.80338). The topology of ML and MP Bootstrap 50 % majority-rule consensus tree based on the ITS data was the same. The branch of *O. discorosea* was well supported (Fig. 4, b).

Comparison of microscopical characters shows that the structure of the pileus and stipe surfaces, size of basidia and spores are identical in all specimens studied, including the type specimens.

However, the spores, in contrast to the descriptions of *O. discorosea* (Pilát, 1934), *Rhodocybe xylophila* (Vassilkov, 1971), *Omphalina lilaceorosea* (Svrček, Kubička, 1971) are not smooth like in *Omphalina* and *Arrhenia*, but distinctly rough (Fig. 3), as stated in the description of *Rhodocybe ulmi* (Vassilyeva, 1973) and look like spores of the genus *Rhodocybe* (Baroni, 1981). Variation in the spore surface character on SEM images from angulate to smooth suggests that the thin spore wall could wrinkle during preparation. It could be a reason of the differences in the original diagnoses.

In addition, there are curved cystidia-like basidium-sized cells in the hymenophore of the studied specimens, including the type of *Rh. xylophila*. However, in all the original diagnoses, the authors note that there are no cystidia (Svrček, Kubička, 1971; Vassilkov, 1971; Vassilyeva, 1973; Herink, Kotlaba, 1975).

Cheilocystidia as such are characteristic of both *Arrhenia epichysium* and *Rhodocybe caelata* (Fr.) Maire, which are very close to *Omphalina discorosea* morphologically. Encrusted hyphae of the pileipellis are characteristic both of *Arrhenia* and *Rhodocybe*, clamps may be present or absent in both (Barony, 1981; Elborne, 2008).

Thus, the micro-morphological features of the specimens can be interpreted in two ways, as similar to the characters of either *Arrhenia* or *Rhodocybe*.

Phylogenetic analysis of LSU and ITS data sets shows that our specimens are nested in the *Arrhenia* clade (Fig. 4) and form an independent well-supported branch.

Therefore, the specimens represent an independent species belonging to the genus *Arrhenia*. Below we give the description of the new combination.

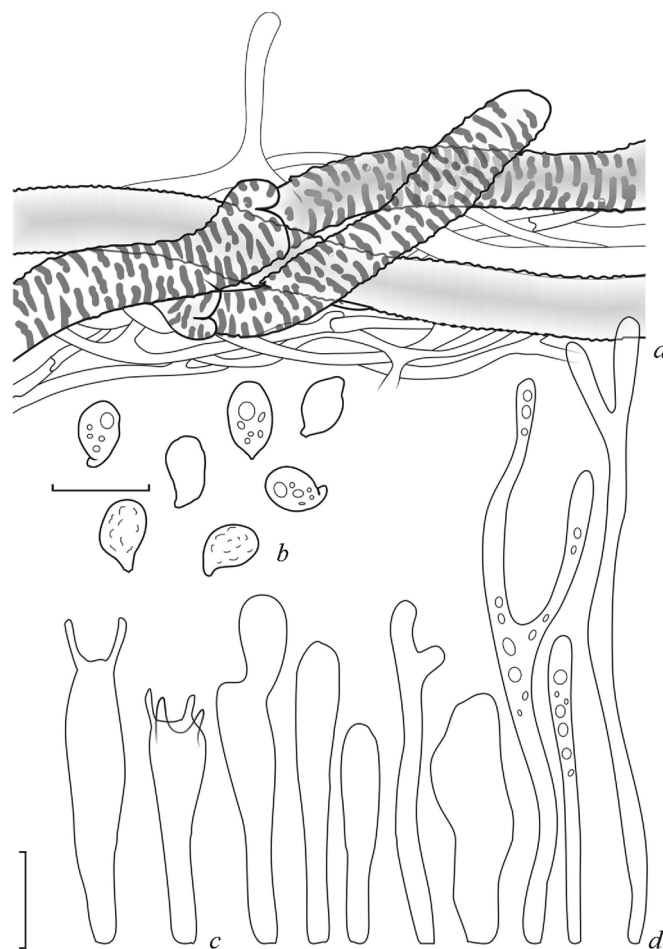


Fig. 2. *Arrhenia discorosea*: a — pileipellis; b — spores; c — basidia; d — hair-like structures at lamellae edge. Scale bar — 10 μm .

***Arrhenia discorosea* (Pilát) Zvyagina, Alexandrova et Bulyonkova comb. nov. (MB 805197).**

Basionym: *Omphalia discorosea*, Pilát, Bull. trimest. Soc. mycol. France 49(3—4): 278, 1934 («1933»).

Synonymy: *Rhodocybe xylophila* Vassilkov, Mikol. Fitopatol. 5(4): 384, 1971; *Omphalina lilaceorosea* Svrček et Kubička, Česká Mykol. 25(4): 93, 1971; *Rhodocybe ulmi* Lj. N. Vassiljeva, Agarik. shlyapochn. griby Primorsk. kraja: 112, 1973; *Omphalina discorosea* (Pilát) Herink et Kotl., Česká Mykol. 29(3): 163, 1975.

Iconography: Svrček et Kubička, Česká Mykol. 25(4): 93, 1971 (ut *Omphalina lilaceorosea*); Lj. N. Vassiljeva, Agarik. shlyapochn. griby Primorsk. kraja: 112, 1973 (ut *Rhodocybe ulmi*); Herink et Kotl., Česká Mykol. 29(3): 163, 1975 (ut *Omphalina discorosea*).

Specimens examined: Caucasus, Republic of Georgia, Lagodekhsy nature reserve, Shromskoye ravine, bank of river, mixed broadleaf forest, on rotten trunk of *Ulmus*, 4 10 1951, coll. and det. B. P. Vassilkov (*Rhodocybe xylophila* holotype, LE 17697). — Western Siberia, Altay region, Altaysky nature reserve, Teletskoye lake, valley of Kyga river, mixed taiga, on dry dead wood, 19 08 1985, coll. and det. A. E. Kovalenko (LE 18475). Altay region, Barnaul, South-Siberian Botanical Garden, on dry dead wood, 28 07 2008, coll. Yu. K. Novozhylov, det. E. F. Ma-

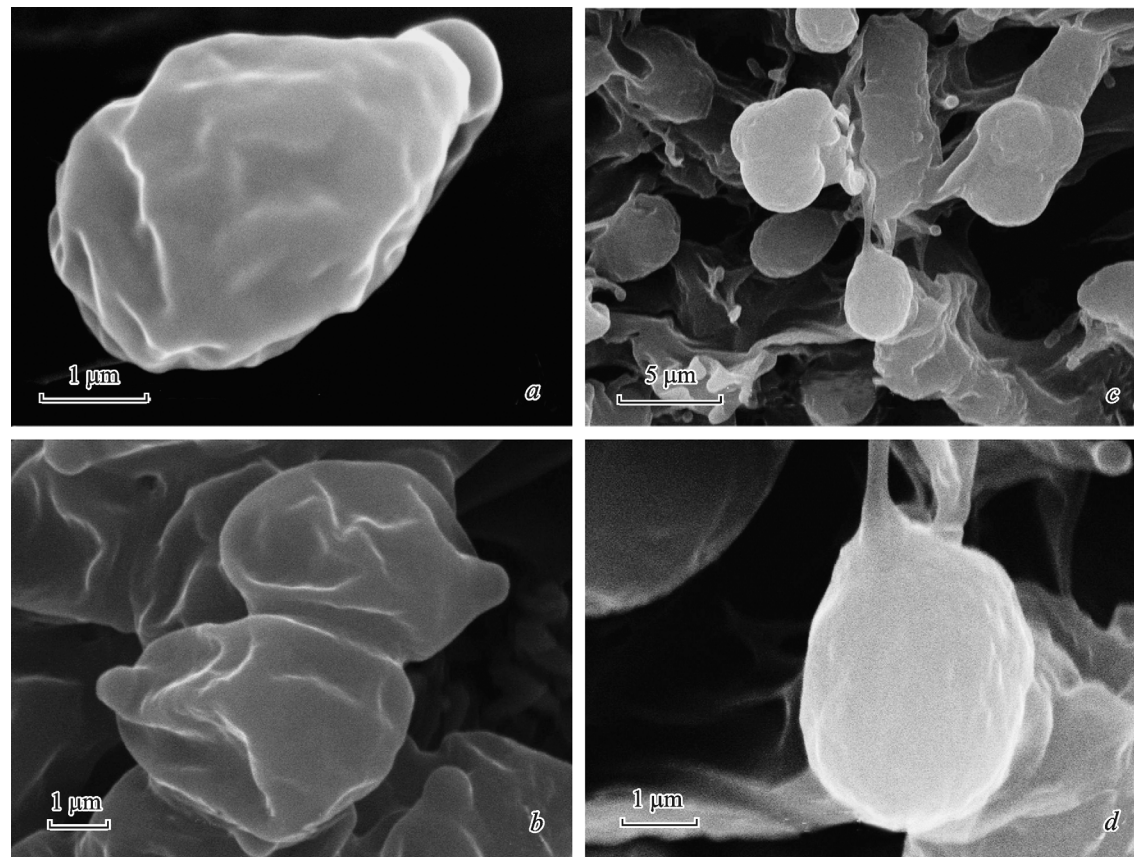


Fig. 3. *Arrhenia discorosea*. SEM photo of spores: *a* — LE 262962; *b–d* — LE 262963.

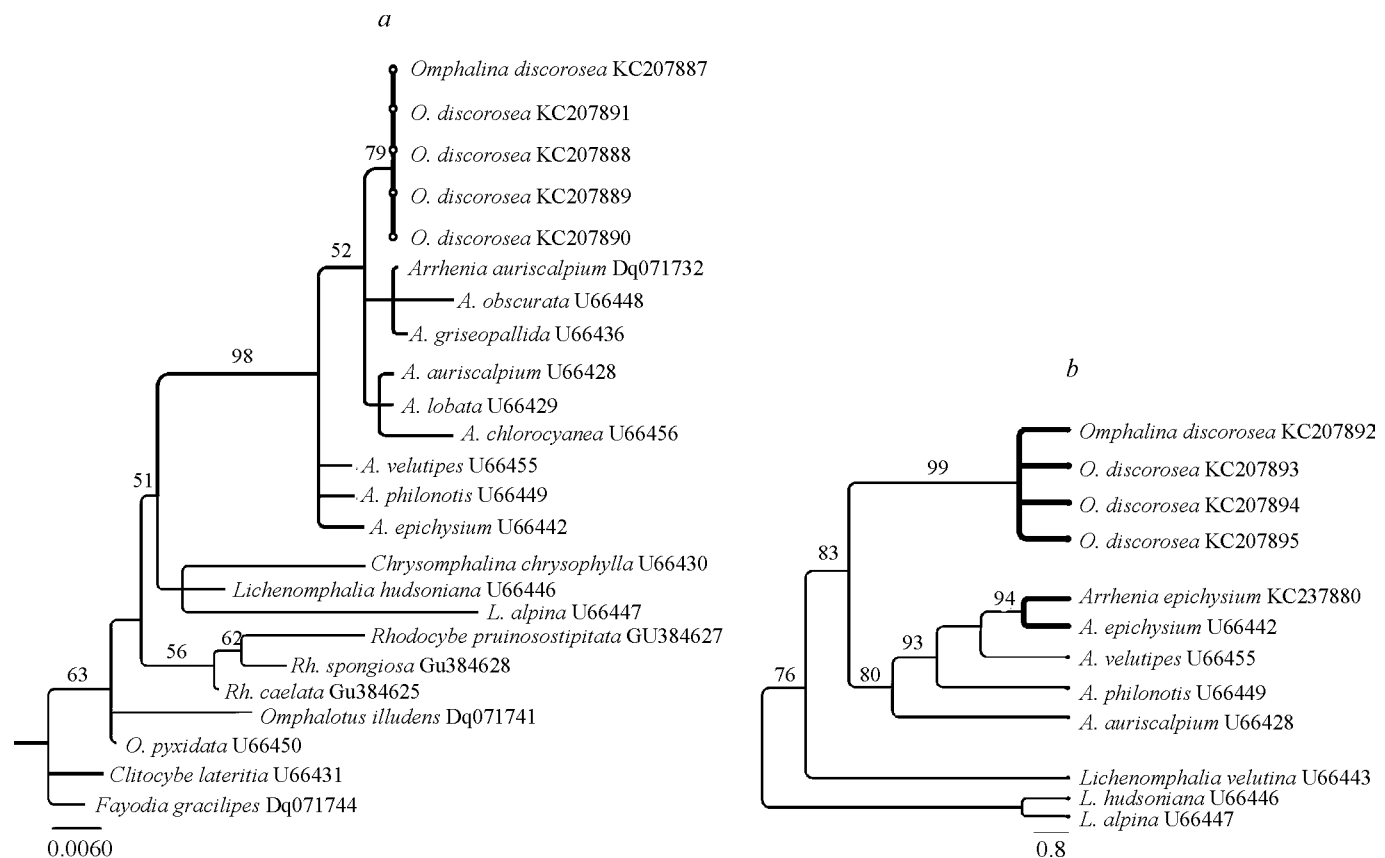


Fig. 4. ML trees based on LSU (*a*) and ITS (*b*) data with bootstrap support of MP 50 % majority-rule consensus tree above branches.

lysheva (LE 262965). Yugra, Yugansky nature reserve, Aymagromsy river basin, mixed taiga, on dead wood of *Populus tremula*, 15 08 2007, coll. and det. E. A. Zvyagina (LE 262964). Yugra, Yugansky nature reserve, Maliy Yugan river basin, mixed taiga, on dead wood of *Populus tremula*, 10 07 2008, coll. and det. E. A. Zvyagina (LE 262971). Yugra, Khanty-Mansiyskiy district, Shapsha village vicinities, mixed taiga, on dead wood of *Populus tremula*, 18 08 2010, coll. and det. T. Yu. Svetasheva (LE 262963). — Eastern Siberia, Baykal region, Bargusinskaya valley, alder thickets in ravine, on dead wood of *Populus tremula*, 06 08 1997, coll. and det. A. N. Petrov (LE 201193). — Northern Mongolia, West-Khentee, Selenge Aimak, Mandal Sum, Research station Khonin Nuga, Hangra lake, lowland *Larix*—*Betula* forest, on fallen trunk of *Populus*, 20 08 2008, coll. and det. A. V. Alexandrova (LE 262962). — Far East, Primorsky region, Khualaza vicinities, on fallen trunk of *Ulmus*, 22 08 1963, coll. and det. Lj. N. Vassiljeva (*Rhodocybe ulmi* paratype VLA M-20.441).

Comments. Another lignicolous species, *Arrhenia epichysium*, differs from *A. discorosea* in the dark blue tint of basidiocarps. *Omphalina demissa* (Fr.) Quél. is smaller, terricolous, purplish lilac, later developing a carmine tint, with distant lamellae and large (10—13 × 6.5 μm) spores (Romagnesi, 1942). *Arrhenia discorosea* could be confused with a lignicolous *Rhodocybe*. *Rhodocybe lignicola* Singer has angulate spores (Vassilkov, 1971). *Rh. paurii* T. J. Baroni, J.-M. Moncalvo, R. P. Bhatt et S. L. Stephenson is pleurotoid.

Acknowledgements

We wish to thank Tatyana Svetasheva, Olga Morosova, Eugene Popov, Ekaterina Malysheva, Vera Malysheva for their great help in molecular work, specimen loans and valuable comments. Sincere thanks to Dr. A. E. Kovalenko team at the mycology lab of Komarov Botanical Institute for creating a hospitable and friendly atmosphere. The work was partly supported by the grant RSF N 14-50-00029.

REFERENCES

- Altschul S. F., Gish W., Miller W., Myers E. W., Lipman D. J. Basic local alignment search tool // *J. Mol. Biol.* 1990. Vol. 215. P. 403—410.
- Baroni T. J. A revision of the genus *Rhodocybe* (Agaricales) // *Nova Hedwigia*. 1981. H. 67. 196 p.
- Bondartsev A. S., Singer R. A guide to collecting of high basidial fungi for scientific study // *Proc. of Komarov Botanical Institute*. 1950. Vol. 2, N 6. P. 499—572 (in Russ.).
- Co-David D., Langeveld D., Noordeloos M. E. Molecular phylogeny and spore evolution of Entolomataceae // *Persoonia*. 2009. Vol. 23. P. 147—176.
- Elborne S. A. *Arrhenia* Fr. // *Funga Nordica*. 1st ed. / Eds H. Knudsen, J. Vesterholt. Copenhagen: Nordsvamp, 2008. P. 226—234.
- Fungal Biodiversity // CBS Laboratory Manual. Ser. 1 / Eds P. W. Crous et al. Utrecht, Netherlands: CBS, 2009. P. 270.
- Gardes M., Bruns T. D. ITS primers with enhanced specificity for Basidiomycetes: application to identification of mycorrhizae and rusts // *Mol. Ecol.* 1993. Vol. 2. P. 113—118.
- Herink J., Kotlaba F. What is *Rhodocybe xylophila* Vasil'k. and *Omphalina lilaceorosea* Svr. et Kub.? // *Česká Mykol.* 1975. Vol. 29. P. 157—166.
- Higgins D., Thompson J., Gibson T., Thompson J. D., Higgins D. G., Gibson T. J. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice // *Nucl. Ac. Res.* 1994. Vol. 22. P. 4673—4680.
- Lutzoni F. M. Phylogeny of lichen- and non-lichen-forming omphalinoid mushrooms and the utility of testing for combinability among multiple data sets // *Systemat. Biol.* 1997. Vol. 46, N 3. P. 373—406.
- Petrov A. N. Synopsis of macromycetes flora of the Baikal region. Novosibirsk: Nauka, Siber. Dep., 1991. 81 p. (in Russ.).
- Pilát A. Additamenta ad floram Sibirae Asiae orientalis mycolgicam. Pars secunda // *Bull. trimest. Soc. mycol. France*. 1934 («1933»). Vol. 49. P. 256—339.
- Posada D. ModelTest Server: a web-based tool for the statistical selection of models of nucleotide substitution online // *Nucl. Ac. Res.* 2006. Vol. 34. P. W700—W703.
- Redhead S. A. Phylogeny of Agarics: Partial systematic solutions for core omphalinoid genera in the Agaricales (Euagarics) // *Mycotaxon*. 2002. Vol. 83. P. 19—57.
- Romagnesi H. Quelques points de taxonomie. I. Sur un groupe particulier d'Omphalina // *Bull. Soc. Mycol. France*. 1942. Vol. 58. P. 81—87.
- SeqMan Pro 7.1.0. Lasergene Evolution Suite. Software Suite for Sequence Analysis. [Electronic resource]. DNASTAR Inc., Madison, WI, USA. 2006.
- Svrček M., Kubička J. *Omphalina lilaceorosea* spec. nov. // *Česká Mykol.* 1971. Vol. 25. P. 193—196.
- Swofford D. L. PAUP* 4.0b10: Phylogenetic analysis using parsimony (*and other methods) [Electronic resource]. Sunderland, Massachusetts: Sinauer, 2002.
- Tamura K., Dudley J., Nei M., Kumar S. MEGA4: Molecular evolutionary genetics analysis (MEGA) software vers. 4.0 // *Mol. Biol. Evol.* 2007. Vol. 24. P. 1596—1599.
- Vassilkov B. P. A new species of agaric fungi in the Transcaucasus // *Mikologiya i fitopatologiya*. 1971. Vol. 5. P. 384—385 (in Russ.).
- Vassilyeva L. N. Agarics and Boletes (Agaricales) of the Primorsk region. Leningrad: Nauka, 1973. 331 p. (in Russ.).
- Vilgalys R., Hester M. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species // *J. Bacteriol.* 1990. Vol. 172. P. 4238—4246.

Received 22 III 2014