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STUDIES ON *OXYPORUS*. I. SEGREGATION OF *EMMIA* AND GENERAL TOPOLOGY OF PHYLOGENETIC TREE

ЗМИТРОВИЧ И. В., МАЛЫШЕВА В. Ф. ИССЛЕДОВАНИЯ РОДА *OXYPORUS*. I. ВЫДЕЛЕНИЕ РОДА *EMMIA* И ОБЩАЯ СТРУКТУРА ФИЛОГЕНЕТИЧЕСКОГО ДРЕВА

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The paper represents an introductory part of molecular-taxonomical research on the genus *Oxyporus*. The historical review of taxonomy of the genus *Oxyporus* is presented and the problems of morphological arrangements in the genus are stated. The distribution of species traditionally accommodated to *Oxyporus* over *Agaricomycetes* phylogenetic tree is revealed using nLSU dataset. The relationships between species complexes of *Oxyporus* were revealed using ITS rDNA dataset. It is shown that genus *Oxyporus* in traditional concept could be splitted into two unrelated entities, i. e. *Oxyporus* s. str. (*Hymenochaetales*) and *Emmia* (*Polyporales*). Further, it is shown that the genus *Oxyporus* has rather isolated position within the *Hymenochaetales* tree, and a new family, *Oxyporaceae*, is described here. As it appeared, the genus *Emmia* is closely related to the genera *Irpex*, *Flavodon*, *Byssomerulius*, and *Trametopsis* (*Meruliaceae*). Both revealed entities are characterized morphologically. The *Oxyporus corticola*-complex (the field of further investigation) and the group of species related to *O. populinus* are well distinguished in the genus *Oxyporus* s. str. The analysis of ITS dataset shows that the rank of such taxa as *O. borealis* and *O. schizoporoides* should be lower of species level. Two new varieties — *O. populinus* var. *borealis* and *O. populinus* var. *schizoporoides* are drawn up in the paper. The morphological elaboration of *Emmia latemarginata* and *Oxyporus populinus* is given.

Key words: *Oxyporus*, molecular taxonomy, morphology, phylogeny.

Статья представляет первую часть молекулярно-таксономического исследования рода *Oxyporus*. Представлен очерк таксономической истории рода, рассмотрены проблемы его морфологической систематики. На основе сравнительного изучения нуклеотидных последовательностей ДНК гена большой субъединицы (nLSU) изучено распределение видов традиционно выделяемого рода *Oxyporus* по филогенетическому древу *Agaricomycetes*. На основе сравнительного изучения нуклеотидных последовательностей ДНК внутренних транскрибируемых спейсеров (ITS1 и ITS2), фланкирующих ген 5.8S рибосомной ДНК/РНК, изучены взаимоотношения между видовыми комплексами рода *Oxyporus*. Показано, что род *Oxyporus* в традиционном понимании распадается на две не связанные близким родством группы: *Oxyporus* s. str. (*Hymenochaetales*) и *Emmia* (*Polyporales*). Также показано, что род *Oxyporus* занимает обособленное положение в структуре порядка *Hymenochaetales*, в связи с чем описано отдельное семейство *Oxyporaceae*. Род *Emmia* оказался близкородственным родам *Irpex*, *Flavodon*, *Byssomerulius* и *Trametopsis* (*Meruliaceae*). Оба рода охарактеризованы морфологически. В роде *Oxyporus* s. str. в свою очередь выделяются *Oxyporus corticola*-комплекс и группа видов, близких к *O. populinus*. Филогенетические исследования с использованием маркера ITS показали, что ранг таксонов *O. borealis* и *O. schizoporoides* должен быть ниже видового уровня. В связи с полученными данными номенклатурно оформлены две разновидности — *O. populinus* var. *borealis* и *O. populinus* var. *schizoporoides*. Приводятся морфологические очерки *Emmia latemarginata* и *Oxyporus populinus*.

Ключевые слова: *Oxyporus*, молекулярная таксономия, морфология, филогения.

The name *Oxyporus*[1] was established by Bourdot and Galzin (1925) for section of the genus *Coriolus*. The generic status of this entity was substantiated by Donk (1933), who characterized the genus by homogeneous context with

[1] The authors of fungal names are presented in the taxonomical part of the paper.

multilayered tubes, clampless hyphae, ovoid to subglobose spores and encrusted cystidia in many species.

The type of section was selected by Bourdot and Galzin as *Polyporus connatus*, the species known only on description by Weinmann (1826): «*Effuso-reflexus*, *seriato-confluens*; *pileo lateritio*, *velutino*, *subzonato*; *poris minutis*, *subrotundis albis… Substantia suberoso-coriacea*, *tenax*, *elastica*, *alba*, *pallida*: *odore acidulo*». Donk (1974) showed an identity of Weinmann's *P. connatus* to *Boletus populinus*, species described by Schumacher (1803) and sanctioned by Fries (1821). However, the Schumacher's type was not represented by herbarium material, too. In this connection, Ryvarden (1991) selected the neotype for *Polyporus populinus* Schum. ex Fr. as «Denmark, Fyn, Skarrup, Nov. 1860. Leg. E. Rostrup (S)».

The genus *Oxyporus* was recognized by the majority of polyporologists (Bondartsev, 1953; Donk, 1974; Ryvarden, 1978, 1991; Corner, 1987; Ryvarden, Gilbertson, 1994; Bondartseva, 1998), although Pouzar (1966) reduced this entity to part of *Rigidoporus* due to its «monomitic» context, clampless hyphae, globose-ovoid spores and the presence of encrusted cystidia. The objections to such a solution were summarized by Corner (1987) as follow: «1) A flesh of *Oxyporus* is fibrous-coriaceous with interwoven hyphae which are usually monomitic or but slightly dimitic. In *Rigidoporus* the flesh is cheesy-coriaceous to waxy and, in its pileate species, more or less distinctly dimitic with radiating, longitudinal skeletal hyphae. 2) The dissepiments are not agglutinated in *Oxyporus* as they are in most species typical of *Rigidoporus*. 3) *Oxyporus* lacks the ventricoso-acute and smooth cystidia of hymenial origin which are present in most species of *Rigidoporus*. 4) The pileus of *Oxyporus* lacks the firm, determinate, more or less palisade-like hymenioderm of *Rigidoporus*…».

The contents of the genus *Oxyporus* was initially limited by *Oxyporus corticola*, *O. latemarginatus*, *O. obducens*, *O. philadelphi*, *O. populinus*, *O. ravidus*, *O. similis* (Donk, 1933, 1966; Bondarzew, Singer, 1941; Ryvarden, 1972). Later, some newly described species were added to this genus: *O. borealis* (Jenssen, Ryvarden, 1985), *O. lilaceus* (Corner, 1987), *O. sinensis* (Zeng, 1992), *O. schizoporoides* (Spirin, Zmitrovich, 2003), *O. macroporus* (Dai et al., 2004), *O. neotropicus* (Ryvarden, 2004), *O. ginkgonis* (Dai, Wang, 2005), *O. andinus*, *O. brunneus* (Iturriaga, Ryvarden, 2010), *O. fragilis* (Laessøe, Ryvarden, 2010), and some others. Parallelly, some critical reviews were undertaken, where *O. similis* was reduced to *O. obducens* (Vampola, 1992a), *O. ravidus* and *O. phellodendri* were introduced in synonymy of *O. corticola* (Vampola, 1992b), and *O. lilaceus* was designated as dubious species (Hattori, 2001).

The molecular data of last decades confirmed a sufficient taxonomical distance between *Oxyporus* and *Rigidoporus* (Kaewchai et al., 2010) and showed a position of *O. populinus* and *O. corticola* complexes in the *Hymenochaetales* (Larsson et al., 2006). During the molecular analysis of *Phanerochaete*-related genera, Greslebin et al. (2004) showed that *O. latemarginatus*, *Irpex* and *Lopharia* coincide in a same cluster, but such a position and sequence identity were not discussed by the authors on the reason of highlighting their scope on relationships of the phanerochaetoid taxa.

Moreover, a new genus *Emmia* was described for *O. latemarginatus* on the sum of morphological features (Zmitrovich et al., 2006). Till now, this genus was not precisely tested in a molecular perspective, and such a testing is main purpose of the present work.

The second purpose is testing of status of two little-known taxa, *O. schizoporoides*, described some years ago due to stable morphological pattern and *O. borealis*, collected repeatedly in the Kirov and Leningrad regions of Russia.

The third purpose of this paper is clarification of position of *Oxyporus* on the phylogenetic tree of *Agaricomycetes*. The analysis of taxa relationships in *O. corticola*-complex we planning as the following paper of the opening series.

Materials and methods

Taxa selection. The presentation of general structure of *Agaricomycetes* tree was undertaken with introducing of such taxa as *Cantharellus cibarius*, *Sistotrema oblongisporum* (*Cantharellales*); *Phallus impudicus* (*Phallales*); *Hyphodontia pallidula*, *Pseudochaete tabacina*, *Resinicium bicolor*, *Rickenella mellea*, *Schizopora paradoxa*, *Trichaptum abietinum* (*Hymenochaetales*), *Athelia arachnoidea* (*Amylocorticiales*); *Boletus edulis*, *B. aereus* (*Boletales*); *Agaricus bisporus*, *Jaapia argillacea*, *Lichenomphalia umbellifera*, *Tricholoma fulvum* (*Agaricales*); *Russula emetica* (*Russulales*); *Corticium roseum* (*Corticiales*); *Gloeophyllum sepiarium* (*Gloeophyllales*); *Artolenzites elegans*, *Daedaleopsis confragosa*, *Fomes fomentarius*, *Lentinus tigrinus*, *Polyporus squamosus*, *Trametes conchifera*, *T. gibbosa*, *T. pubescens*, *T. versicolor* (*Polyporales—Polyporaceae*); *Australohydnum dregeanum*, *Bjerkandera adusta*, *Byssomerulius corium*, *Ceriporia excelsa*, *C. reticulata*, *Cerrena unicolor*, *Diplomitoporus flavescens*, *Flavodon flavus*, *Gloeoporus dichrous*, *Irpex lacteus*, *Leptoporus mollis*, *Panus conchatus*, *Phanerochaete sordida*, *Phlebia tremellosa*, *Trametopsis cervina* (*Polyporales—Meruliaceae*). An original rDNA sequences of *Oxyporus schizoporoides*, *O. borealis*, and '*Oxyporus*' *latemarginatus* were introduced in analysis together with GenBank sequences of *O. populinus* and *O. corticola*.

Taxon sampling. A total of 9 specimens of the mycological herbarium of the Komarov Botanical Institute (LE) were considered for molecular analysis: *Byssomerulius corium* (LE 241938), *Ceriporia exelsa* (LE 247365), *Flavodon flavus* (LE 295997), '*Oxyporus*' *latemarginatus* (LE 254427), '*Oxyporus*' *latemarginatus* (LE 254426), '*Oxyporus*' *latemarginatus* (LE 222701), *O. schizoporoides* (LE 208262 — typus), *O. borealis* (LE 295998), *Trametes pubescens* (LE 262759).

Additional sequences of other species were retrieved from GenBank (http://www.ncbi.nlm.nih.gov/Genbank/): 28 ITS sequences and 53 LSU sequences, including *Sistotrema oblongisporum* AY647210 (ITS sequence) and *Cantharellus cibarius* AY041157, JX030441 (LSU sequences) chosen as outgroups.

The final data sets consisted of 37 ITS sequences and 58 LSU sequences.

Collections used in this study of ITS and nLSU datasets, their herbarium and GenBank accession numbers

Taxon	Herbarium number	GenBank accession number
	ITS	
Australohydnum dregeanum		AF 479669
Bjerkandera adusta		AF 455468
Byssomerulius corium	LE 241938	KF 856504
Ceriporia excelsa	LE 247365	KF 856503
C. reticulata		EU 118613
Cerrena unicolor		JQ 031127
Diplomitoporus flavescens		FN 907908
Flavodon flavus		JN 710543
Fomes fomentarius		HQ 189535
Gloeoporus dichrous		JQ 673109
Hyphodontia pallidula		DQ 340317
'*Irpex*' *flavus*	LE 295997	KF856505
I. lacteus		AY 569565
Lentinus tigrinus		DQ 056860
L. tigrinus		AF 516517
Leptoporus mollis		EU 402584
Lichenomphalia umbellifera		JF 908503
Oxyporus borealis	LE 295998	KF 856502
O. corticola		KC 176675
'Oxyporus' latemarginatus		FN 252852
'Oxyporus' latemarginatus		GU 062267
'Oxyporus' latemarginatus	LE 254427	KF 856500
'Oxyporus' latemarginatus	LE 222701	KF 856498
'Oxyporus' latemarginatus	LE 254426	KF 856499
O. populinus		FN 907910
O. schizoporoides	LE 208262 (type)	KF 856501
Panus conchatus		JN 710579
Phanerochaete sordida		AY 219378
Phlebia tremellosa		GU 062266
Polyporus squamosus		HQ 439363
Pseudochaete tabacina		JQ 279610
Schizopora paradoxa		AF 145571
Sistotrema oblongisporum		AY 647210
Trametes pubescens	LE 262759	HQ 435851
T. pubescens		AY 684173
Trametopsis cervina		JN 165020
Trichaptum abietinum		AY 781273
	nLSU	
Agaricus bisporus		DQ 071710
Artolenzites elegans		FJ 372714
Athelia arachnoidea		GU 187557
Boletus aereus		KF 030339
B. edulis		HQ 161848
Bjerkandera adusta		JQ 388758
		AB 733334
Byssomerulius corium		AY 586640
Cantharellus cibarius		AY 041157
		JX 030441
Ceriporia excelsa	LE 247365	KF 856506
C. reticulata		EU 118614
Cerrena unicolor		FJ 821525
		FJ 821524
Corticium roseum		AY 463401
Daedaleopsis confragosa		AJ 406547
Diplomitoporus flavescens		GU 566005

Continued table

Taxon	Herbarium number	GenBank accession number
Flavodon flavus	LE 295997	KF 856510
Fomes fomentarius		AF 261538
Gloeophyllum sepiarium		HM 536061
Gloeoporus dichrous		DQ 679919
		FJ 496709
Hyphodontia pallidula		AJ 406594
Irpex lacteus		FJ 471545
		HM 008937
		EU 522839
Jaapia argillacea		GU 187581
Lentinus tigrinus		AF 518627
Lenzites gibbosa		FJ 890419
Leptoporus mollis		EU 402510
		AY 293195
Lichenomphalia umbellifera		AF 261445
		GU 811045
Oxyporus corticola		KC 176682
'Oxyporus' latemarginatus	LE 254427	KF856507
	LE 254426	KF856508
'Oxyporus' populinus		AJ 406467
O. populinus		AY 059064
O. schizoporoides	LE 208262 (type)	KF 856509
Panus conchatus		AY 616004
Phallus impudicus		AY 152404
Phanerochaete sordida		FJ 471566
		HM 008938
		GQ 470659
Phlebia tremellosa		AY 293200
Polyporus squamosus		AF 135181
Pseudochaete tabacina		JQ 279626
Resinicium bicolor		AY 586709
Rickenella mellea		U 66438
Russula emetica		AF 325305
Schizopora paradoxa		AJ 406463
Sistotrema oblongisporum		GQ 162819
Trametes conchifera		KC 503510
T. pubescens		JN 164811
T. versicolor		AB 604944
Trametopsis cervina		JN 164796
Trichaptum abietinum		AF 518659
Tricholoma fulvum		AY 207309

Taxa studied are given in Table, which shows the names of species, GenBank accession numbers, herbarium numbers, and collection specification.

DNA extraction, PCR and sequencing. DNA was extracted using AxyPrep™ Multisource Genomic DNA Miniprep Kit (Axygen Biosciences, California, USA) under consideration of the manufacturer's recommendations. The ribosomal ITS1—5.8S—ITS2 region was amplified by PCR with the fungal specific primers ITS1F and ITS4B (http://www. biology.duke.edu/fungi/mycolab/primers.htm) and 28S region was amplified with the fungal specific primers LROR and LR7 (http://www.biology.duke.edu/fungi/mycolab/primers.htm). The PCR products were purified using Fermentas Genomic DNA Purification Kit (Thermo Scientific). Sequencing was performed with ABI model 3130 Genetic Analyzer (Applied Biosystems) using BigDyeTM Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems) with the same primers. 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.

Alignments and phylogenetic analysis. Sequences were aligned using web tools: MAFFT (http://mafft.cbrc.jp/alignment/server/) with Q-INS-i option. Ambiguously aligned portions of ITS-regions or multiple base gaps were excluded from alignment for further analysis. The final alignment was corrected manually using MEGA 5 (Tamura et al., 2011).

Phylogenetic reconstructions were performed with maximum likelihood (ML) and Bayesian (BA) analyses.

Maximum likelihood was performed using RA×ML server, v.7.2.8 (http://http://phylobench.vital-it.ch/raxml-bb/; Stamatakis et al., 2008), under GTR model with one hundred rapid bootstrap replicates.

Bayesian analysis was performed using MrBayes 3.1 (Ronquist, Huelsenbeck, 2003) for two independent runs, each with 2 000 000 generations with GTR model and four chains with sampling every 10 generations for ITS and 1 000 000 generations with F81 model and four chains with sampling every 10 generations for LSU. Posterior probability (PP) value ≥0.95 are considered as significant.

Morphological elaboration. Microscopical study of basidiomata was carried out as described by Gilbertson and Ryvarden (1986). Freehand sections and squash mounts of basidiomata were examined in the Melzer's reagent, 5 % KOH and 2 % Cotton Blue.

Results and discussion

LSU dataset (Fig. 1). The data obtained show that the genus *Oxyporus* in traditional sense breaks up to two unrelated entities — type-containing one, which forms a pure clade into *Hymenochaetales* (*O. populinus*-complex, *O. corticola*), and '*Oxyporus*' *latemarginatus* forming own clade into *Polyporales*; the latter corresponds to genus *Emmia* (Zmitrovich et al., 2006).

The genera *Flavodon*, *Irpex*, *Byssomerulius*, and *Trametopsis* appeared to have been neighboring groups of *Emmia*. The neighboring groups of *Oxyporus* s. str. were *Shizopora* and *Trichaptum* — both not intermixing with *Oxyporus*-containing clade. The LSU-information showed a minimal distance between *O. populinus* and *O. schizoporoides*.

ITS dataset (Fig. 2). The ITS data corresponds well to nLSU dataset. Because the *Agaricomycetes* tree was removed in this analysis, the *Lichenomphalia* (agaricoid clade) was attracted to *Hymenochaetales*. The *Oxyporus* s. str. appeared as an independent lineage, but more informative LSU-dataset nevertheless builds it in the *Hymenochaetales* tree and the divergence in trichotomy *O. populinus*—*O. borealis*—*O. shizoporoides* appeared to be lower of species level. The position of '*Oxyporus*' *latemarginatus* in clade neighboring to *Irpex* — *Flavodon* keeps in ITS-phylogeny on the level of independent entity. Also, both *Byssomerulius* and *Trametopsis* are related to these genera with formation of common superclade.

Discussion. The genus *Emmia* according to previous idea was adapted to '*Oxyporus*' *latemarginatus*; the second member, *Ceriporia metamorphosa*, was added by V. A. Spirin after elaboration of their general concept (Zmitrovich et al., 2006). The differences between *Oxyporus* and *Emmia* in their hyphal system and hyphal structure were highlighted: pseudodimitic with sharp-angle branching pattern in *Oxyporus* and monomitic with rectangular branching pattern in *Emmia*. Besides, the hyphae in *Emmia* are faintly amyloid. Basidia in *Oxyporus* are club-shaped and devoid of medial constriction, whereas basidia in *Emmia* are constricted. The spores in *Emmia* are abundant in microscopic preparations — this feature was highlighted by Belorussian mycologist Emma Komarova, the person in which honor the genus was named. Basidiome development in *Emmia*, contrary to *Oxyporus*, excludes the formation of pileate processes in the cases of lateral attachment of the basidiome initials; in such cases the cushion-like formations with large flower-like pores are developing. The molecular data strongly supports an independent generic status of '*Oxyporus*' *latemarginatus* and its position within phanerochaetoid/phlebioid (not hymenochaetoid) fungi.

Concerning family status of the grouping which includes the *Byssomerulius*-clade, there are controversial opinions, varying from splitter's '*Byssomerulius*-family' (Larsson, 2007) to uncertain 'Residual polyporoid clade' (Binder et al., 2014). In our opinion, the groups which form 'residual polyporoid clade', despite of a certain degree of rotation, in all the configurations are rooted to *Phlebia*-containing clade which corresponds to *Meruliaceae* pool. Our configuration of the *Meruliaceae* tree is characterized by three main radiations: 1) *Cerrena*-clade: *Cerrena*, *Diplomitoporus*, *Panus*, etc.; 2) *Byssomerulius*-clade: *Byssomerulius*, *Ceriporia* (presumably, heterogeneous), *Emmia*, *Gloeoporus*, *Irpex*, *Flavodon*, *Leptoporus*, *Trametopsis*, etc.; 3) *Phlebia*-clade: *Australohydnum*, *Bjerkandera*, *Phanerochaete*, *Phlebia*, etc.

The core-*Oxyporus* clade is nested in the hymenochaetoid cluster on nLSU-phylogeny, whereas ITS-phylogeny takes the oxyporoid clade out from hymenochaetoid tree. The consensus 5.8S and nLSU data obtained by Larsson et al. (2006) suggests that *Oxyporus* represents a basal clade of the *Hymenochaetales* without close relationships to its other groups. Our two datasets well correspond to such a position. In our opinion, this group represents an independent family of the *Hymenochaetales*.

As we already mentioned, the structure of *O. corticola*-complex could be subject for a separate elaboration. In the present paper, we tested only two species which gravitate to *O. populinus*, namely *O. borealis* and *O. schizoporoides*. The ITS-phylogeny shows that divergence of both taxa from *O. populinus* has not come yet to a species level and all three taxa represent rather an ecotypes (sensu Zmitrovich et al., 2011) of a single polymorphic species (trans-cortical on living trees of *O. populinus*-morphotype, prostrate corticolous of *O. schizoporoides*-morphotype and trans-cortical on oligotrophic substrates of *O. borealis*-morphotype).

Taxonomy. Below follows a taxonomical mounting of the revealed phylogenetic situation: a new family and nomenclatural combinations as well as morphological elaboration of the genus *Emmia* and *O. populinus*-group.

POLYPORALES

MERULIACEAE

Emmia Zmitr., Spirin et V. Malysheva, Mycena 6: 33, 2006. — *Rigidoporus* subgen. *Neooxyporus* Pouzar, 1966 nomen dissonum.

Basidiomes annual, orbicular, soft and fragile. Hymenophore tubular, one-layered, tubes firstly reticulate, later elongated, with thin dissepiments and large mouths,

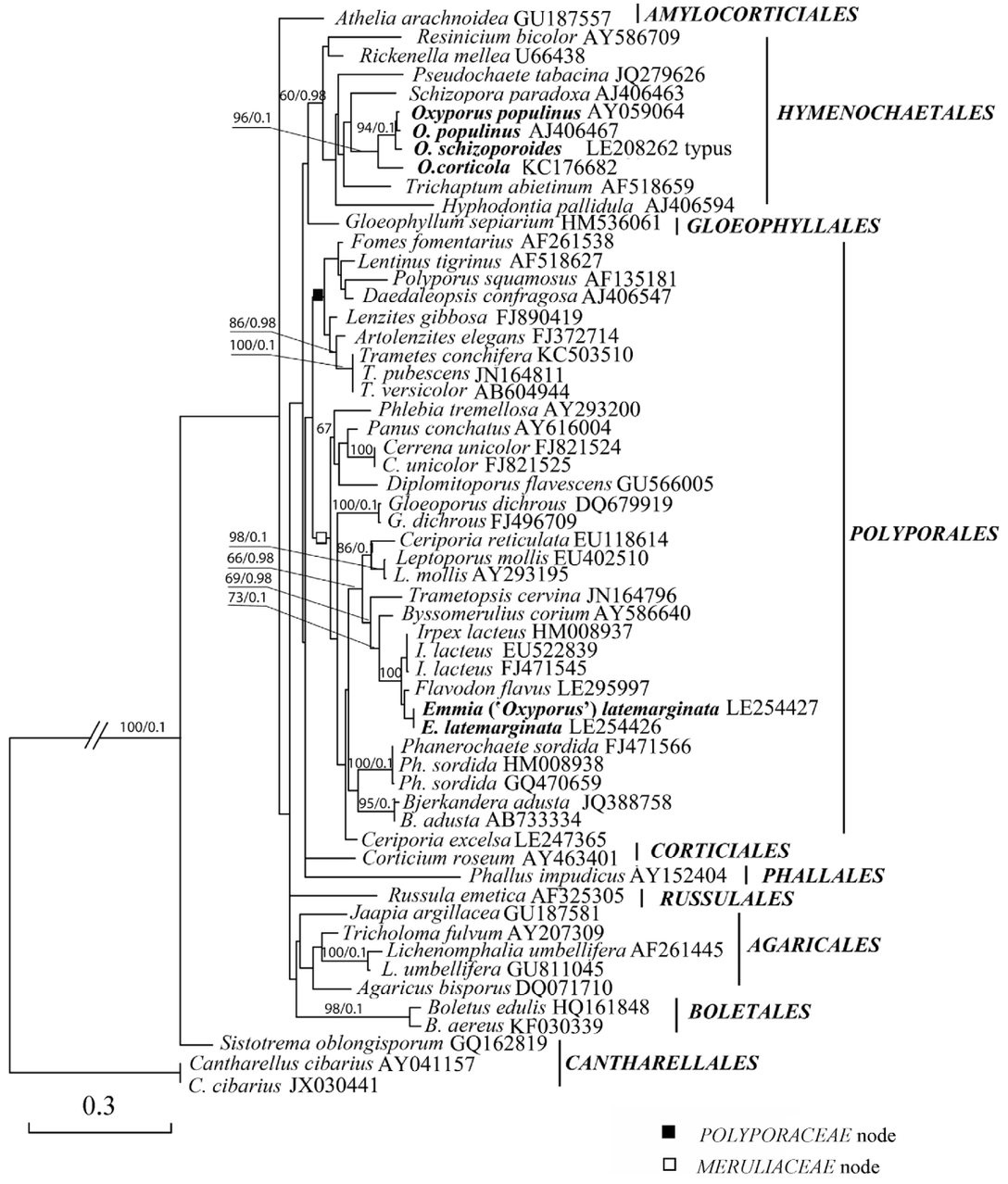

Fig. 1. Phylogenetic rooted tree showing distribution of members of traditionally limited genus *Oxyporus* within radiation of *Agaricomycetes* obtained from the Maximum Likelihood analysis of the nLSU dataset. Bootstrap values (%) from Maximum Likelihood analyses ≥50 and Posterior probability from Bayesian analysis ≥0.95 are shown over the branches. The representatives of the *Oxyporus*-conglomerate are given in bold face.

soft-waxy. Tube trama subparallel. Hyphal system monomitic; hyphae clampless, thin-walled in tubes, with thickened walls in subiculum, slightly amyloid. Cystidia present as leptocystidia, thin-walled, cylindrical, naked or faintly encrusted. Basidia clavate, 4-spored, efibulate, with shallow medial constriction. Basidiospores ellipsoid to short-cylindrical, often abundant, cyanophilous.

T y p u s: *Polyporus latemarginatus* Durieu et Mont., 1856 (monotypic).

Saprotrophic. Causes a white rot.

Emmia latemarginata (Durieu et Mont.) Zmitr., Spirin et V. Malysheva, Mycena 6: 33, 2006. — *Polyporus latemarginatus* Durieu et Mont., 1856. — *Oxyporus latemarginatus* (Durieu et Mont.) Donk, 1966; *Poria ambigua* Bres., 1897; *P. excurrens* var. *macrostoma* Speg., 1899; *P. geoderma* Speg., 1899; *Irpex cornescens* Lloyd, 1915; *Polyporus cokeri* Murrill, 1920; *Poria lacerata* Murrill, 1920; *P. roseitingens* Murrill, 1920; *P. salicina* Murrill,

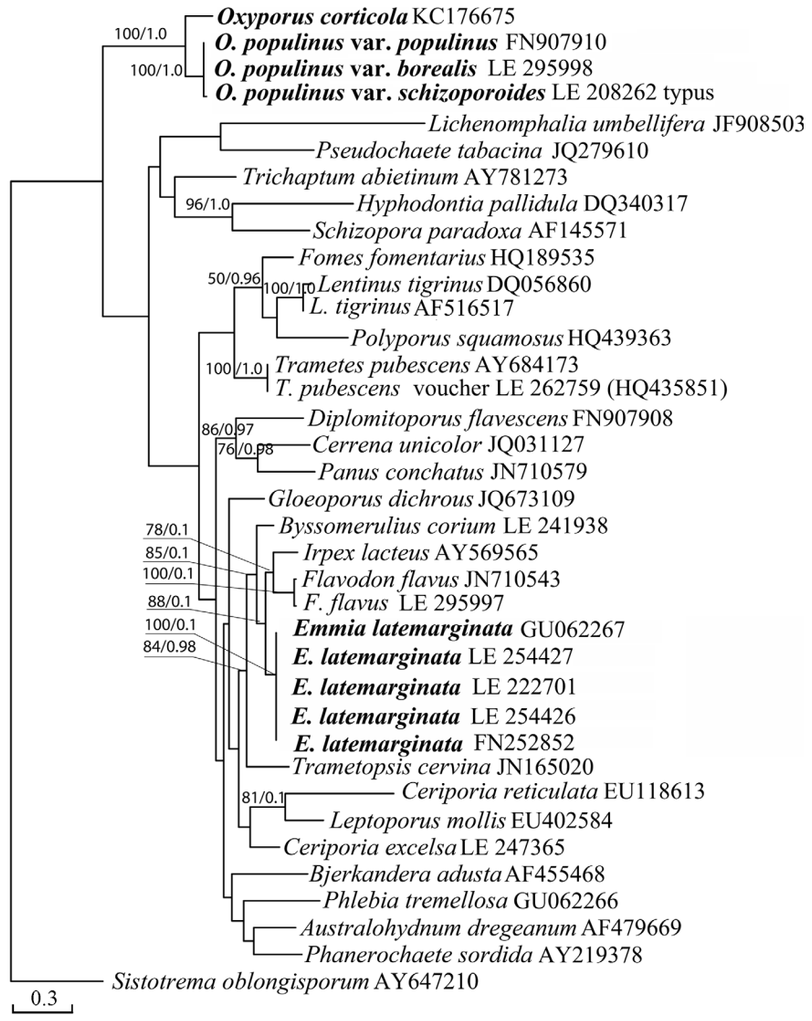

Fig. 2. Phylogenetic tree which reflects of species relationships within *Oxyporus* and related taxa based on sequences of the nrITS1–5.8S–ITS2 region. The rooted tree was constructed with the Maximum Likelihood analysis. Bootstrap values (%) from Maximum Likelihood analyses ≥50 and Posterior probability from Bayesian analysis ≥0.95 are shown over the branches. The representatives of the *Oxyporus*-conglomerate are given in bold face.

1920; *Leptoporus zilingianus* Pilát, 1934; *Poria consobrinoides* Pilát, 1936; *P. reticulatomarginata* Pilát, 1936; ?*Leptoporus werneri* Pilát, 1939 (Fig. 3, *a*, *b*).

Basidiomes annual, orbicular, prostrate or cushion-like, merging with stalactite-like or nodulose formations up to 15 cm in diam. and 2—15 mm thick, soft and fragile, readily separable; white to cream, sometimes with rosaceous or grayish tints, on last stages can be isabelline to ochraceous; soaked when fresh, spongy at drying. Margin wide, sterile, white, fimbriate to film. Hymenophore tubular, one-layered, tubes firstly reticulate, later elongated, angular or flower-like, with thin dissepiments and large mouths, soft-waxy, 0.5—3 per mm.

Hyphal system monomitic. Hyphae simple-septate, 3—8 μm in diam., thin-walled in tubes, with thickened walls in subiculum, faintly amyloid, with slightly inflated segments. Cystidia present as leptocystidia, rare to abundant, 20—30×4.5—6 μm, thin-walled, cylindrical or slightly utriform, naked or faintly apically encrusted. Basidia in small clusters, clavate with clear medial constriction, 4-spored, without clamp at the base. Basidiospores abundant obovoid to short-cylindrical, (5.0)5.5—7.5(8.0)× 3—4.2 μm, thin-walled, inamyloid, cyanophilous, with small droplets in a cytoplasm.

Through the world on frondose, rarely coniferous wood. Saprotrophic. Causes a white rot. Having a high biological activity, the fungus seems to be a perspective subject for biotechnological studies.

Material examined: '*Poria ambigua*' Bres. — Russia, Novosibirsk Region, Novosibirsk, on Betula pendula, 7 09 1935, leg. B. I. Kravtsev, det. A. Pilát, Exsicc. Ser. «Hymenomycetes Sibiriae» (LE 25370); USA, New York, Fish Creek, on beech, 8 10 1959, leg. J. L. Lowe, R. L. Gilbertson, N. Y. State University college of forestry, N 11673 (LE 210059); '*Oxyporus latemarginatus*' — Russia, Samara Region, Zhiguli, on fallen Acer platanoides, 27 07 2000, leg. V. F. Malysheva (LE 209715); Russia, Astrakhan Region, Astrakhansky Reserve, on fallen

Fig. 3. The representatives of taxa related to *Oxyporus* in traditional sense: *a*, *b* — nodulose and cushion-like ecotypes of *Emmia latemarginata* (photo N. V. Psurtseva, V. F. Malysheva); *c*, *d* — leptosomic and eurisomic ecades of *Oxyporus populinus* var. *populunus* (photo I. V. Zmitrovich, G. Yu. Konechnaya); *e* — *O. populinus* var. *borealis* (LE 295998; photo V. F. Malysheva, I. V. Zmitrovich); *f* — *O. populinus* var. *schizoporoides* (type specimen; photo V. F. Malysheva). Scale bar — 1 cm.

Fraxinus sp., 22 10 2009, leg Yu. A. Rebriev, det. I. V. Zmitrovich (LE 287082); Russia, Rostov Region, Kalininsky village, on fallen log of Acer sp., 06 10 2006, leg. N. V. Psurtseva, det. I. V. Zmitrovich (LE 254426, 254427); Russia, Orel Region, Peredovik village vicinities, on fallen log of Populus tremula, 14 06 2009, leg. S. V. Volobuev, det. I. V. Zmitrovich, S. V. Volobuev (LE 284610); Russia, Pskov Region, Bashovo, 11 07 2000, leg. E. S. Popov, det. I. V. Zmitrovich (LE 222701).

OXYPORACEAE

Zmitr. et V. Malysheva familia nova (MB 806128). — *Polyporaceae* tribus *Oxyporeae* Bondartsev et Singer, Ann. Mycol. 39: 62, 1941.

Basidiomata annua perenniesque, *pileata ad resupinata et late prostrata. Hymenophorum tubulare*, *unistratosum vel multistratosum. Tubuli primo cupuliformes*, *deinde porrigentes*, *crassimarginatae*, *fibrosae. Systema hypharum pseudodimiticum. Hyphae efibulatae*, *tenuitunicatae ad crassitunicatae*, *inamyloideae*, *in hymenophoro intricatae. Pseudocystidia adsunt vel desunt*, *crassitunicata*, *apicaliter incrustata vel nuda. Leptocystidia tenuitunicata*, *fusoidea*, *apice incrustata. Basidia clavata sine constriction mediale*, *tetrasporifera*, *basi efibulata. Sporae ovoideae ad subglobosae*, *tenuitunicatae*, *inamyloideae et acyanophilae. Ad lignum putredum arborum frondosarum et coniferarum. Putredinem albidae provocant*.

Type: *Oxyporus* (Bourdot et Galzin) Donk, 1933.

Basidiomes annual or perennial, pileate to resupinate and widely prostrate. Hymenophore tubular, one-layered to multilayered. Tubes initially cup-shaped, later of normal appearance, rather thick-walled, tough-fibrous. Hyphal system pseudodimitic. Hyphae simple-septate, thin-walled to thick-walled, inamyloid, in tube trama densely interwoven. Pseudocystidia, if present, thick-walled, cylindrical, with or without an apical incrustation. Leptocystidia hyphoid to fusoid, apically encrusted. Basidia clavate, without a medial constriction, 4-spored, without a basal clamp. Basidiospores ovoid to subglobose, inamyloid, acyanophilous to cyanophilous. On living and fallen deciduous or coniferous wood. Causes a white rot.

This newly described family of the *Hymenochaetales* is comparable to the *Schizoporaceae* in certain aspects as pseudoskeletal fibroid hyphae, ovoid sporae, encrusted cystidia, tough-fibrous consistency of basidiomes, but differs in their lacking of clamp-connections and trametoid to fibroporioid basidiomes with elongated tubes. It is probable that family is monotypic, but position of *Leucophellinus* Singer should be precisely tested.

Oxyporus (Bourdot et Galzin) Donk, Med. Bot. Mus. Herb. Rijksuiver. Utrecht 9: 202, 1933. — *Coriolus* sect. *Oxyporus* Bourdot et Galzin, 1925.

Description — as it was given for the family *Oxyporaceae* (see above). There are two species complexes, related to 1) *O. populinus*, and 2) *O. corticola*. The core part of the first one we describe herein.

Oxyporus populinus (Schumach.: Fr.) Donk, Med. Bot. Mus. Herb. Rijksuiver. Utrecht 9: 202, 1933. — *Boletus populinus* Schumach., 1803; *Polyporus connatus* Weinm., 1826; *Trametes secretanii* Otth, 1866; *Polyporus cremeus* Bres. ex Lloyd, 1915; *Oxyporus borealis* G. M. Jenssen et Ryvarden, 1985; *O. schizoporoides* Zmitr. et Spirin in Spirin et Zmitr., 2003 (Fig. 3, *c—f*).

Basidiomes annual to perennial, pileate to resupinate and forming marginal pseudopilei, as a rule imbricate and laterally fused with forming of patches up to 50 cm in diam., but in some cases solitary. Single pilei 2—6(20) cm in diam. and 0.5—5 cm thick, corioloid to trametoid with widely decurrent base, conchate to triquetrous in section. Upperside tomentose to glabrous, but in some cases squalid to obscurely hispid, ivory-cream to pale buff, darkening with the age; often overmossed. Context ivory to cream and tawny, initially cheese-tough, later suberous, azonate or faintly zonate. Hymenophore tubular, concolorous to the context, one- to multilayered (2—4 mm each layer), with indistinct sterile strata. Pore surface cream colored to pale ochraceous (ochre rufescent), the pores thick- to thin-walled, circular to slightly angular, (2)5—7 per 1 mm.

Hyphal system pseudodimitic. Generative hyphae 2.0—3.5 μm in diam., simple-septate, thin-walled, hyaline, densely interwoven in tube trama; pseudoskeletal hyphae 2.8—5 μm in diam., thick-walled, hyaline. Pseudocystidia 15—35×5—12 μm, cylindrical to clavate, thick-walled, apically encrusted. Leptocystidia 15—20× ×3—5 μm, hyphoid or fusoid, apically encrusted. Basidia 8—17×4—5.7(7) μm, clavate, 4-spored, without a basal clamp. Basidiospores 3.5—5.5×2.5—4.5 μm, ovoid to subglobose, thin-walled, inamyloid, cyanophilous, as a rule with large subapical lipid globule.

On living and fallen deciduous wood (Acer, Aesculus, Alnus, Betula, Castanea, Celtis, Cornus, Corylus, Crataegus, Eucalyptus, Fagus, Fraxinus, Juglans, Malus, Platanus, Padus, Populus, Robinia, Quercus, Salix, Sambucus, Sorbus, Tilia, Ulmus). Causes a white rot.

A polymorphic species which modal ecotype is imbricate formation developed along bark cracks of living trees of Acer platanoides, Aesculus hippocastanum, Populus nigra, etc. The pilei in such ecotype are faintly tomentose to glabrous, overmossed and the tubes are stratose.

Oxyporus populinus* var. *borealis (G. M. Jenssen et Ryvarden) Zmitr. et V. Malysheva var. et comb. nov. (MB 806129). — Bas.: *Oxyporus borealis* G. M. Jenssen et Ryvarden, Trans. Brit. Mycol. Soc. 84: 546, 1985; ?*Polyporus connatus* Weinm., 1826 (Fig. 3, *e*).

Basidiomes annual (or biannual), pileate. Pilei 1—3(12) cm in wide and 0.2–0.8 cm thick, corioloid with widely decurrent base, conchate in section. Upperside villose to hispid, ivory-cream to ochre rufescent; without mosses or algae cover. Context ivory to cream, homogeneous corky-suberous. Hymenophore tubular, concolorous to the context, one- to two-layered with prominent sterile strate. Pore surface cream colored to ochre rufescent, the pores thick-walled, circular to slightly angular, 2—5 per 1 mm.

Hyphal system pseudodimitic. Generative hyphae 2.0—3.5 μm in diam., simple-septate, thin-walled, hyaline, densely interwoven in tube trama; pseudoskeletal hyphae 2.5—4 μm in diam., thick-walled, hyaline. Pseudocystidia 15—35×4—8 μm, cylindrical to clavate, thick-walled, apically encrusted. Leptocystidia not seen. Basidia 8—17×5—7 μm, clavate, 4-spored, without a basal clamp. Basidiospores 4—4.5 μm, subglobose, thin-walled, inamyloid, acyanophilous.

Material examined: Russia, Leningrad Region, Nizhnesvirsky Reserve, on fallen Salix sp., 09 08 1997, leg. I. V. Zmitrovich, det. L. Ryvarden (LE 203761). — Russia, Kirov Region, Kirov, on stump of Acer platanoides, 10 09 2012, leg. A. A. Shirokikh, det. I. V. Zmitrovich (LE 295998).

This leptosomic oligotrophic pileate ecotype was mentioned in north or middle taiga forest growing on fallen birch long. The combination of corioloid habitus with rufescent-brown hispid upperside is highly characteristic for this ecotype and in certain details it coincides with Weinmann's description of his *Polyporus connatus*.

Oxyporus populinus* var. *schizoporoides (Zmitr. et Spirin) Zmitr. et V. Malysheva var. et comb. nov. (MB 806130). — Bas.: *Oxyporus schizoporoides* Zmitr. et Spirin in Spirin et Zmitr., Karstenia 43: 77, 2003 (Fig. 3, *f*).

Basidiomes perennial, resupinate and forming marginal pseudopilei, up to 50 cm in extent. Context creamish to tawny, floccose, up to 1 mm thick. Hymenophore tubular, up to 2 mm thick, obscurely stratose, with indistinct sterile strata. Pore surface cream colored to pale ochraceous, the pores thick- to thin-walled, circular to sinuose and lacerate, (4)5—6(7) per 1 mm.

Hyphal system pseudodimitic. Generative hyphae 2.5—3.0 μm in diam., simple-septate, thin-walled, hyaline, densely interwoven in tube trama; pseudoskeletal hyphae 2.5—3.5 μm in diam., thick-walled, hyaline. Pseudocystidia not seen. Leptocystidia 16—17.5×3.5—5 μm, hyphoid or fusoid, apically encrusted. Basidia 15.2—17×4.5—5.5 μm, clavate, 4-spored, without a basal clamp. Basidiospores 4.2—4.9(5.1)×(2.8)3—4 μm, ovoid to subglobose, thin-walled, inamyloid, cyanophilous, with oil-rich content.

Material examined: Russia, St. Petersburg, Rzhevka, on dying Populus suaveolens, 14 06 2000, leg. I. V. Zmitrovich (LE 208262 — typus); Rostov Region, Veshenskaya, on dry Populus sp., 07 11 2003, leg. Yu. A. Rebriev, det. I. V. Zmitrovich (LE 287253, 227967, 227978); Orel Region, Spasskoye-Lutovinovo vicinities, on fallen branch of frondose tree in oak-birch forest, 10 05 2009, leg. et det. S. V. Volobuev (LE 269764); Laos, Tat Kuang Si National park, on fallen wood, 02 12 2013, leg. O. N. Ezhov, det. I. V. Zmitrovich (LE 269784).

This resupinate corticolous ecotype appears in various world regions and can be easily allocated due to its prostrate basidiomes with nodular pseudopilei at the margin. The surface of pseudopilei can be overmossed. It is probable that further revision of *O. corticola*-complex is capable to give an additional material on this element.

Residual species need molecular testing: *O. andinus* Iturr. et Ryvarden, *O. brunneus* Iturr. et Ryvarden, *O. cuneatus* (Murrill) Aoshima, *O. fragilis* Læssøe et Ryvarden, *O. neotropicus* Ryvarden, *O. subpopulinus* B. K. Cui et Y. C. Dai.

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