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Lentinoid and Polyporoid Fungi, Two Generic Conglomerates Containing Important Medicinal Mushrooms in Molecular Perspective

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ABSTRACT: Polyporoid and lentinoid fungi contain the important producers of substances having immunomodulatory, antitumoral, antiviral, and antihyperlipidemic effects. The discovery of several phylogenetic lines within the lentinoid-polyporoid continuum will help with target metabolomic analysis of species still not studied in pharmacological respects. The purpose of the present work was to increase a resolution in the lentinoid-polyporoid phylogenetic zone by means of selection of both the main representatives of *Lentinus*-related genera and poorly known/intermediate taxa such as *Lentinus suavissimus*, *Neofavolus* spp., and the resupinate part of *Polyporus* (genera *Perenniporia* and *Pachykytospora*) in the context of the basic structure of the *Polyporales* tree. The molecular phylogeny of highlighting all the polyporoid and lentinoid nodes was reconstructed using nLSU ITS rDNA and TEF datasets. The data obtained from ITS, TEF, and LSU coincide in support of core Polyporaceae of 10 clades corresponded to the generic level and 7 of these (*Cerioporus*, *Cladomeris*, *Favolus*, *Lentinus*, *Neofavolus*, *Picipes*, and *Polyporus* s.str.) contain generic units characterized by polyporoid or lentinoid morphotypes. The other 2 clades containing lentinoid taxa are outside the core *Polyporaceae*, namely *Panus* (Meruliaceae, Polyporales) and *Neolentinus* (Gloeophyllaceae, Gloeophyllales). A new genus, *Picipes*, is described and 25 new combinations are proposed.

KEY WORDS: medicinal mushrooms and fungi, *Polyporus* s.l., *Lentinus* s.l., molecular phylogeny, Polyporaceae, taxonomy

ABBREVIATIONS: BA, Bayesian; **ML**, maximum likelihood; **MP**, maximum parsimony

I. INTRODUCTION

Along with the widely distributed term polyporoid fungi, the term lentinoid fungi has been recently introduced into the current literature.[1–4] This applies to genera segregated from *Lentinus* in Pegler's sense. Both groups contain the important producers of substances having immunomodulatory, antitumoral, antiviral, and antihyperlipidemic effects (Table 1).[5–11] Further search for active producers of pharmacologically meaningful metabolites within these generic conglomerates represents a sufficient issue in medicinal mushroom science.

Beginning with Fries,[12] who described the *Lentinus* genus, the relationships of lentinoid and polyporoid fungi were obvious for various authors. Friesian establishment of *Lentinus* was based on his subtribe *Lentoscyphi* of the *Omphalina* tribe of the *Agaricus* genus.[13] Despite the declaration of affinity between *Lentinus*, *Favolus*, and *Polyporus* (*Favoli very absolute agaricini*, *Polypori autem favoloidei ab hoc genere neutiquam separari debent*[14]), a formal taxonomical position of *Polyporus* was far from *Lentinus* in the Friesian system because its large units were based on the hymenophore configuration—poroid or cellar-like in the first and truly lamellate in the second ones.

Torrend[15] was the first to adapt the Lloydian genus *Lentus* for segregation of the lentinoid element of *Polyporus*, namely *Polyporus brumalis*. Kühner[16] has emphasized the close relationships between *Lentinus variabilis* (modern name *Neolentinus cyathiformis*)

TABLE 1: Key Representatives of Medicinal Mushrooms within Lentinoid and Polyporoid Fungi

Species	Medicinal Properties
Polyporus umbellatus	Immune-modulation[5,6]
Lentinus tuber-regium	Immune-modulatory, antiviral[7]
Lentinus crinitus	Anti-inflammatory, direct antitumor[8,9]
Lentinus strigosus (= *Panus lecomtei*)	Anti-inflammatory, direct antitumor[8,9]
Lentinus lepideus (= *Neolentinus lepideus*)	Antihyperlipidemic[10]
Lentinus conchatus (= *Panus conchatus*)	Direct antitumor[11]

and the *Polyporus squamosus* group. Singer[17–19] has united *Polyporus*, *Lentinus*, and *Panus* in the family Polyporaceae, restricted to 3 polyporoid (*Polyporus*, *Pseudovafolus*, and *Mycobonia*) and 4 lamellate (*Phyllotopsis*, *Pleurotus*, *Panus*, and *Lentinus*) genera. The genus *Lentinus* this author has typified by *Lentinus lepideus* (the widely accepted typification is connected to *L. crinitus*), whereas the small-spored velutinate element of this genus he left in the *Panus*. Pouzar[20] reported that squamules at the basal portion of the stipe are amyloid both in *Polyporus* species and *Lentinus suavissimus*. Basing on Singer's classification, Stankovicová[21] showed some intermediate morphological phenomena between polyporoid and lentinoid taxa.

Concerning *Lentinus* splitting, the first related entity was the genus *Panus* described by Fries[22] with type *Panus conchatus*. A perfectly elaborated differentiation of *Lentinus* and *Panus* was made by Corner,[23] who limited the genus *Lentinus* to species with ligative skeletals, separating species with fibroid skeletals into *Panus*. In parallel, Pegler[24] re-established a large *Lentinus* with 2 subgenera, *Lentinus* and *Panus*, based on Cornerian principles. The further segregation was made by Redhead and Ginns,[25] who split from *Lentinus* 2 brown-rot genera, *Heliocybe* (the type *H. sulcata*) and *Neolentinus* (the type *N. kauffmanii*).

Furthermore, a sufficient distance between *Lentinus*, *Panus*, and *Neolentinus* was supported by karyological observation[26] and molecular studies.[3,27]

Beginning with Krüger and Gargas,[28] a congeneric nature of *Lentinus* s. str. with some representatives of large *Polyporus*, such as *P. arcularius*, *P. brumalis*, and *P. tricholoma*, [29–31] becomes obvious. Zmitrovich[32] has proposed some corresponding combinations into the genus *Lentinus*. Subsequent molecular tests of large *Polyporus*,[33,34] however, did not involve any lentinoid element; even in such a foreshortening, they allow for allocation of an independent status of the *Neofavolus* entity.[34] The molecular phylogeny shows the position of the *Panus* within merulioid lineage, not the polyporoid one.[31,35]

The purpose of the present work is to increase a resolution in the lentinoid-polyporoid phylogenetic zone by means of selection both of main section representatives of *Lentinus*-related genera and poorly known/intermediate taxa such as *L. suavissimus*, *Neofavolus* spp., and the resupinate part of *Polyporus* (genera *Perenniporia* and *Pachykytospora*) in the context of the basic structure of the *Polyporales* tree. Identification of the polyporoid-lentinoid phylogenetic zone should help researchers with target metabolomics analysis of species still not studied in pharmacological respects.

II. MATERIALS AND METHODS

A. Taxon Sampling

A total of 54 specimens of polyporoid and lentinoid fungi were selected for molecular analysis. We generated a total of 17 ITS, 16 nLSU, and 16 TEF sequences for this study; 34 additional ITS sequences, 26 additional LSU sequences, and 1 additional TEF sequence of other polyporoid/merulioid genera were retrieved from GenBank based on BLAST results (http://www.ncbi.nlm.nih.gov/BLAST/). The final data set consisted of 51 ITS sequences, 17 TEF sequences, and 43 nLSU sequences.

For all analyses, the sequences of *Exidia glandulosa* retrieved from GenBank were chosen as the outgroup based on BLAST homology.

An overview of all taxa studied is given in Table 2, which shows the names of species, GenBank accession numbers, herbarium numbers, and collection particulars.

B. DNA Extraction, PCR, and Sequencing

DNA was extracted from herbarium material using 2% cetyl trimethylammonium bromide extraction buffer with the following steps of consecutive addition of the chloroform-isoamyl alcohol mixture (24:1), then isopropyl alcohol and 3 M sodium acetate solution for precipitation, 70% ethanol for washing, and finally water for dissolution. The NucleoSpin Plant II Kit (Macherey-Nagel) was used as an alternative method of DNA extraction. The ribosomal ITS1-5.8S-ITS2 region was amplified by PCR with the fungal specific primers ITS1F and ITS4B and the 28S region was amplified by PCR with the fungal specific primers LROR and LR7 (Vilgalys Laboratory; http://www.biology.duke.edu/fungi/mycolab/primers). The 1000-bp fragment of TEF1 was amplified using the primer pair EF1-983F and EF1-2212R.

For rDNA regions, the following PCR protocol was used: 1) initial denaturation at 95°C for 2 min, 2) denaturation at 94°C for 40 s, 3) annealing at 50°C for 1 min, 4) extension at 75°C for 2 min, 5) repeat for 35 cycles starting at step 2, and 6) leave at 75 °C for 10 min. For TEF1, the PCR protocol included the following steps: 1) initial denaturation at 95°C for 2 min, 2) denaturation at 95°C for 40 s, 3) annealing at 60°C for 40 s, 4) extension at 70°C for 2 min, 5) repeat for 9 cycles starting at step 2, 6) denaturation at 95°C for 45 s, 7) annealing at 50°C for 1.5 min, 8) extension at 70°C for 2 min, 9) repeat for 36 cycles starting at step 6, and 10) leave at 70°C for 10 min.

The PCR products were purified using the Fermentas Genomic DNA Purification Kit (Thermo Scientific).

Sequencing of this strand was performed with an ABI model 3130 Genetic Analyzer (Applied Biosystems) using the BigDye 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).

C. Alignments and Phylogenetic Analysis

The sequences were aligned with the web tools MAFFT (http://align.bmr.kyushu-u.ac.jp/mafft/online/server/) with Q-INS-i strategy and default settings for other options. The final alignment was corrected manually using MEGA 5.[36]

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

A MP analysis was performed using PAUP*4.0.b10.[37] One-hundred heuristic searches were conducted by stepwise addition with random sequence addition and a tree bisection-reconnection branch-swapping algorithm. One tree was held at each step during stepwise addition and the number of trees retained was limited to 100. Parsimony bootstrap analysis was performed with 1000 replicates. Gaps were treated as missing characters. Clades with only a support ≥50% were retained.

ML was run in the RAxML server (version 7.2.8; http://phylobench.vital-it.ch/raxml-bb),[38] under a GTR model with 100 rapid bootstrap replicates.

Bayesian analysis was performed using MrBayes 3.1[39] for 2 independent runs, each with 10,000,000 generations with sampling every 100 generations, with a GTR model and 4 chains. Posterior probability values ≥0.95 are considered significant.

D. Morphological Elaboration

Microscopical study of basidiomata was carried out as described by Gilbertson and Ryvarden.[40] Freehand sections and squash mounts of basidiomata were examined in Melzer's reagent, 5% KOH, and 2% Cotton Blue. Basidiome morphotypes recognized after Zmitrovich et al.[41] (see Supplement 1; http://www.researchgate.net/publication/279447216).

TABLE 2: Collections Used in This Study of ITS, nLSU, and TEF 1-Alpha Data Sets and Their Herbarium and GenBank Accession Numbers

Taxon	**Herbarium Number**	**GenBank Accession Number**		
		ITS	**nLSU**	**TEF 1-alpha**
Buglossoporus pulvinus		DQ491419		
Chlorophyllum agaricoides	AFTOL-ID 440	DQ200928	AY700187	
Datronia stereoides	Voucher Holonen	KC415179	KC415196	
Dichomitus squalens	LE 258894	KM411455	KM411471	KM411486
Dichomitus squalens	Cui9725	JQ780408	JQ780427	
Exidia glandulosa	TUFC34008	AB871761	AB871742	
Junghuhnia rhinocephala		JN710562		
Lentinus badius		GU207275		
Lentinus bertieri		GU207301		
Lentinus bertieri			AY615985	
Lentinus crinitus	LE 114683	KM411462	KR080328	KM411494
Lentinus crinitus			AY615980	
Lentinus crinitus		GU207289		
Lentinus cyathiformis		EF524038		
Lentinus cyathiformis f. *montana*	LE 3741	KM411461	KM411477	KM411492
Lentinus lepideus f. *rufescens*	LE 3792	KM411454	KM411478	KM411493
Lentinus strigosus	LE 5829	KM411451	KM411468	KM411483
Lentinus tigrinus	LE 214778	KM411459	KM411475	KM411490
Lentinus tigrinus	MUCL22821	AB478881	AB368072	
Lentinus velutinus		GQ849478		
Neofavolus mikawai	TFM:F-27416	AB735962	AB735942	
Neolentinus lepideus	LE 253834	KM411453 AB733140	KM411470	KM411485 HM536122
Neolentinus lepideus	NBRC 30750	AB733140	AB733313	
Pachykytospora wasseri	LE 814872 (typus)	KM411456	KM411472	KM411487
Pachykytospora tuberculosa		JX124705		
Panus conchatus	LE 265028	KM411463	KM434323	KM411496
Panus lecomtei	TMIC35103	JQ955726	JQ955733	
Panus similis	LE 287548	KM411466	KM411482	
Panus suavissimus	LE 202237	KM411460	KM411476	KM411491
Perenniporia kilemariensis	LE 214743 (typus)	KM411457	KM411473	KM411488
Perenniporia narymica	Dai 7016	JF706331	JF706347	
Perenniporia subacida	Dai 8224	HQ876605	JF713024	
Perenniporia valliculorum	LE 222974 (typus)	KM411458	KM411474	KM411489
Piptoporus quercinus	LE 287547	KM411464	KM411480	KM411497

Pleurotus giganteus	CMU54-1	JQ724360	JQ724361	
Polyporus alveolaris	TUMH:50003	AB735968	AB735949	
Polyporus arcularius	Dai 6756	KC572004	KC572043	
Polyporus badius	LE 236750	KM411465	KM411481	KM411499
Polyporus brumalis	PB1	KP283491	KP283520	
Polyporus chozeniae	LE 22545		KM411479	KM411495
Polyporus grammocephalus	WD2379	AB587628	AB587619	
Polyporus melanopus	MJ132-95	KC572025	KC572066	
Polyporus pseudobetulinus	TFM:F-27626	AB587645	AB587640	
Polyporus squamosus	AFTOL-ID 704	DQ267123	AY629320	
Polyporus squamosus f. *rangiferinus*	LE 287549	KM411467		
Polyporus subvarius	WD2368	AB587643	AB587638	
Polyporus tenuiculus		KM267725		
Polyporus tubaeformis	voucher Niemela	KC572036	KC572073	
Polyporus tuberaster	Dai 4662	KC572037	KC572074	
Polyporus umbellatus	ZL-QH-2	JX110724	JX110762	
Polyporus varius	Dai 12813	KC572040	KC572077	
Serpula lacrymans	REG 383	GU187542	GU187596	
Steccherinum tenuispinum	LE 231603 (typus)	KM411452	KM411469	KM411484
Steccherinum tenuispinum		JN710599		

III. RESULTS AND DISCUSSION

A. Ten Clades in the Polyporoid-Lentinoid Continuum

The results of molecular taxonomical analysis of the lentinoid-polyporoid taxonomical continuum are presented in Figs. 1–3 (in which ITS and combined ITS+TEF+LSU phylogenies are given) and Table 3 (where all of the molecular entities are characterized).

All of the data obtained from ITS, TEF, and LSU coincide in support within core Polyporaceae of 10 clades corresponded to generic levels, and 7 of these clades contain a generic units characterized by polyporoid or lentinoid morphotypes. The remaining 2 clades containing lentinoid taxa lie outside of core Polyporaceae, namely *Panus* (Meruliaceae, Polyporales) and *Neolentinus* (Gloeophyllaceae, Gloeophyllales) (Table 3).

The consequences of molecular resolution of phylogenetic pathways in the polyporoid-lentinoid continuum seem to be sufficient. The LSU data set appears the most informative for resolution of clade interrelationships. The clade *Cerioporus* seems to be an ancient lineage in core polyporoid radiation. This unit contains fungi of polyporoid morphotype characterized by more or less inflated axial element of skeleto-binding dendrite. Such inflation can be interpreted as a residual phenomenon of physalohyphae sclerification in basically a tyromycetoid–scutigeroid morphotype. The basidiospores in all representatives included are characterized by subfusoid to subnavicular appearance. The tendency to trametization is obvious within this line (*C. varius*, *C. stereoides*, *C. mollis*).

The further phylogenetic radiation is based on *Lentinus* (including *Polyporellus*) lineage. Their representatives keep an inflation of axial element of skeleto-binding dendrite, but hyphal

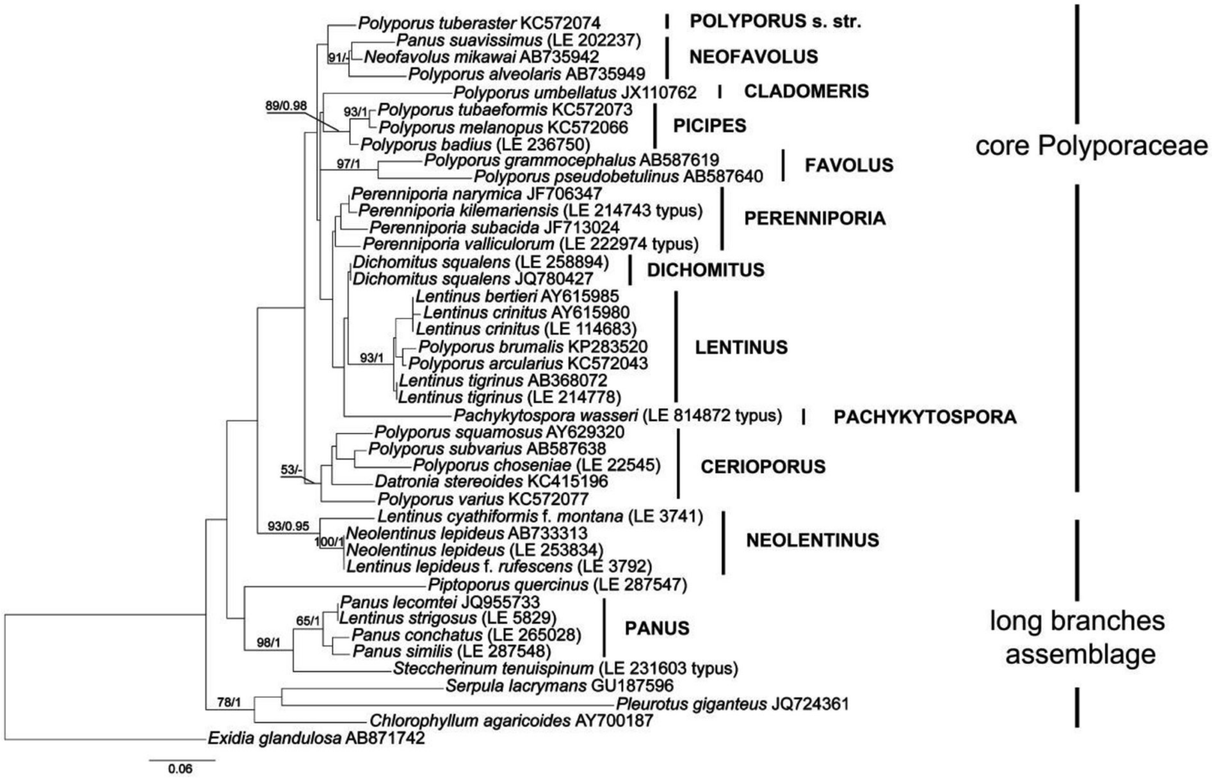

FIG. 1: The best tree obtained from the ML analysis of combined LSU data set. Bootstrap values (%) from MP and posterior probability from BY analyses are shown under and above the branches, respectively.

ramification here is more regular having dichophytic appearance as a result. The hymenophore configuration in *Lentinus* representatives varies from poroid or radially poroid in various representatives of *Polyporellus* sublineage to true lamellate with lamellae and lamellulae (*Lentinus* and *Tigrini* sublineage representatives). Numerous superficial adaptations are characteristic to tropical taxa (e.g., an upperside pillar development). The main morphogenetic tendency in tropical taxa is the substitution of protoplasma-bearing hyphae by sclerified dendrites in all tissues of basidiome. The basal *Polyporellus* sublineage can be morphogenetically connected to derivative trametoid (*Dichomitus*) and fibroporioid (*Pachykytospora*, *Perenniporia*) morphotypes. *Dichomitus* keeps micromorphological identity with the *Lentinus* lineage, whereas the *Perenniporia* lineage is characterized by basidiospore wall sclerification. The verrucose basidiospores of *Pachykytospora* represent a result of partial exospore degradation of basidiospores of the *Perenniporia* type.[42]

The crown group is presented by independent lineages *Polyporus* s. str., *Neofavolus*, *Cladomeris*, *Picipes*, and *Favolus*. It is possible that more ancient lineage of the crown group is *Cladomeris* represented by one sclerotium-forming species of grifoloid morphotype (*C. umbellatus*). This species is characterized by predominance of protoplasm-bearing hyphae with inflated axial segments. The substitution of protoplasm-bearing hyphae by sclerified dendrites with inflated axial element is characteristic to *Picipes* lineage (=*Polyporus melanopus* group), uniting fungi of the polyporoid morphotype with small pores, blackish stipe cuticle, and tendency to trametization. Generative hyphae in *P. badius* are devoid of clamps, whereas all of the other representatives bear the fibulate hyphae. The basidiospores in both *Cladomeris* and *Picipes* lines are cylindric. The lineage *Polyporus* s. str. (*P. tuberaster*) is connected

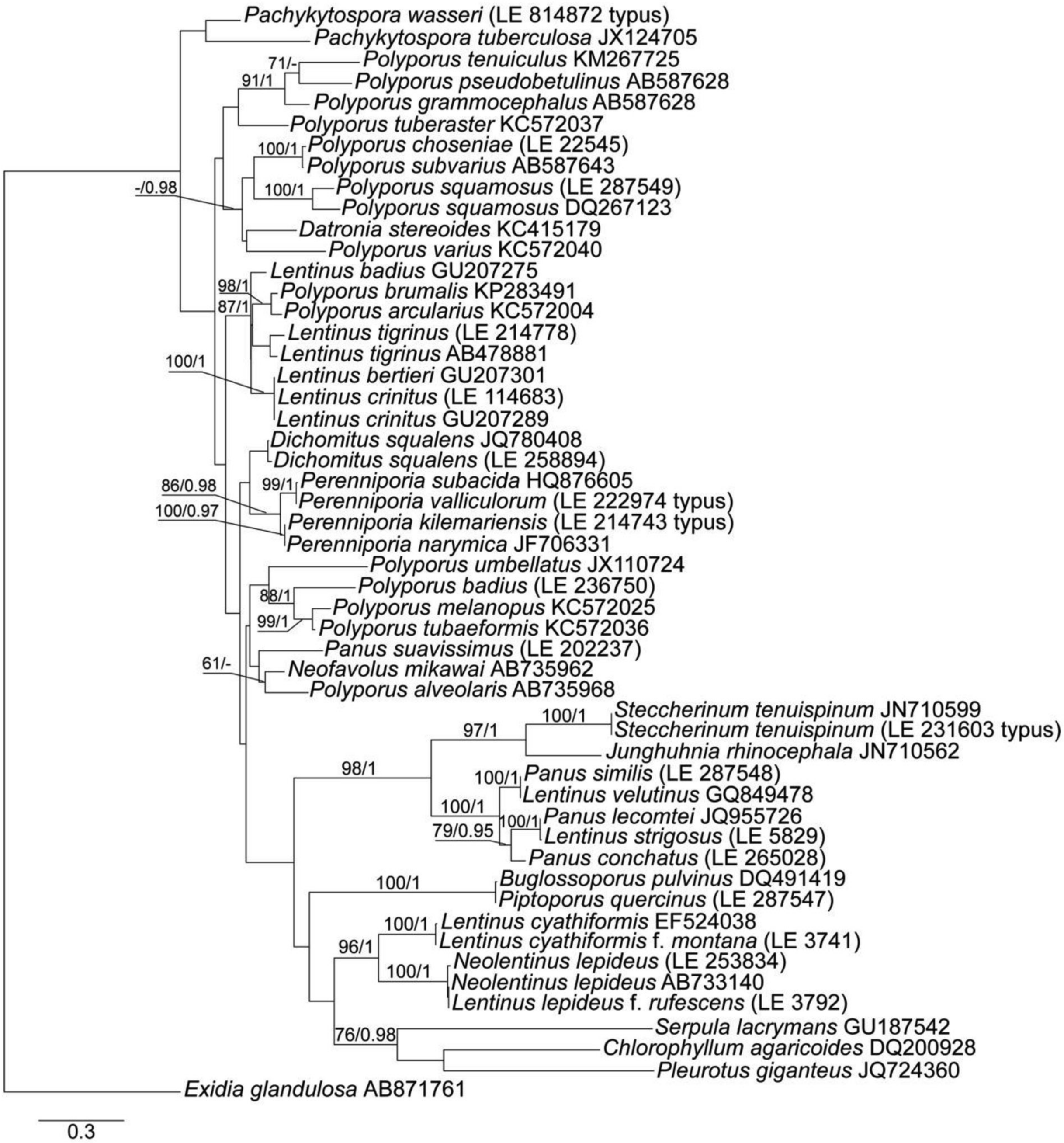

FIG. 2: The best tree obtained from the ML analysis of ITS data set. Bootstrap values (%) from MP and posterior probability from BY analyses are shown under and above the branches, respectively.

to *Cladomeris* by other way: this is sclerotium-forming polypore with sclerified dichophytic skeletals and elongated spores due to large subcellular pores. The characters' patterns of *Favolus* and *Neofavolus* allow characterize them as certain scraps of lines to trametization (*Favolus*) and lentination (*Neofavolus suavissimus*) of *Picipes*-like morphotypes. Some *Favolus* representatives are devoid of clamps. The basidiospores in *Neofavolus* and *Favolus* are cylindric, like those of *Picipes* representatives.

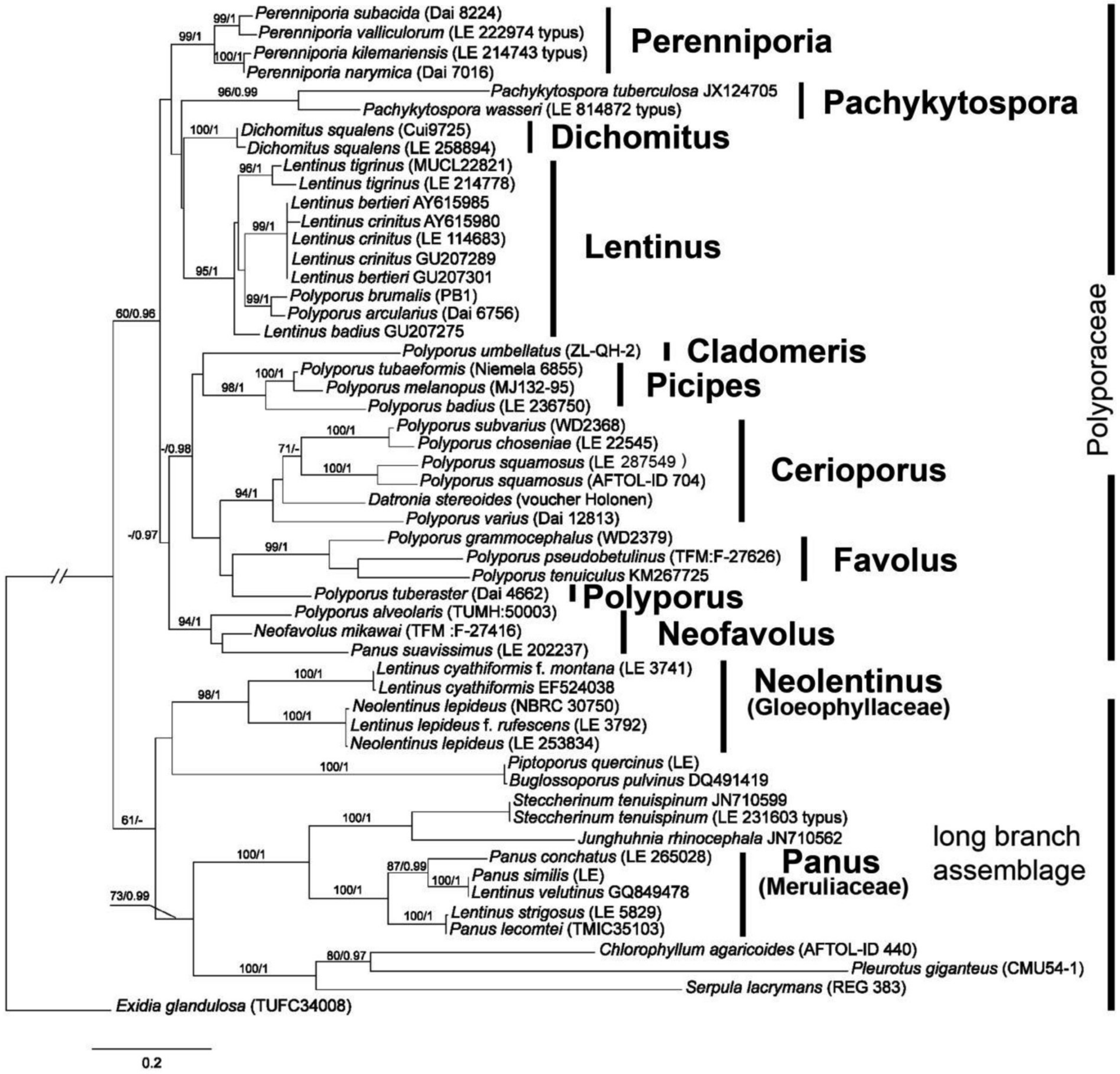

FIG. 3: The best tree obtained from the ML analysis of combined TEF–ITS–LSU data set. Bootstrap values (%) from MP and posterior probability from BY analyses are shown under and above the slash, respectively.

The consensus dataset indicates multiple origins of polyporoid and lentinoid morphotypes, the phylogenetically derivative nature of lentinoid and resupinate poroid morphotypes, as well as the tendency of transformation of skeleto-binding dendrites into fibrohyphae massifs in long-lived basidiomes.

The taxonomical consequences of such a resolution are also diverse. In particular, the genus *Lentinus* s. str. has to include the *Polyporus arcularius* group. The corresponding combinations were made by Zmitrovich[32]; however, the name *Lentinus ciliatus* (Fr.) Zmitr. would be rejected as invalid and replaced by the new correct name. Another matter is final recognition of heterogeneity of the remaining *Polyporus*. Until now, the *Polyporus* conglomerate has been kept as widely known and corresponding

TABLE 3: Phylogenetic Overview of the Polyporoid-Lentinoid Continuum

Clade Name	Phylogeny Supporting Characteristics	Morphological Characterization
Core polyporoid phylogenetic radiation		
_Cerioporus_*	ITS (–/0.98); LSU (53/–); combined (94/1)	Polyporoid to trametoid; dimitic with inflated axial skeletals and arboriform branching; basidiospores fusoid, with navicular tendency, or humpbacked
_Cladomeris_*	Combined (100/1)	Polyporoid – grifoloid; subdimitic with inflated axial hyphae and ±dichophytic branching; basidiospores subcylindric
Dichomitus	Combined (100/1)	Trametoid to fibroporioid; dimitic with inflated axial skeletals and dichophytic branching; basidiospores fusoid, smooth, thin-walled
_Favolus_*	ITS (71/–); LSU (97/1); combined (99/1)	Polyporoid – favoloid; dimitic with uninflated axial element and arboriform branching; basidiospores with fusoid or navicular tendency
_Lentinus_*/**	ITS (87/1); LSU (93/1); combined (95/1)	Lentinoid or polyporoid; dimitic with inflated axial element ±dichophytic branching; basidiospores subcylindric
_Neofavolus_*/**	LSU (91/–); combined (94/1)	Polyporoid (favoloid) or lentinoid; dimitic with uninflated axial element and rare; ±dichophytic branching; basidiospores subcylindric
Pachykytospora	combined (96/0.99)	Fibroporioid; dimitic with inflated axial skeletals and arboriform branching; basidiospores fusoid-elliptical, with ridged exosporium
Perenniporia	ITS (86/0.98); combined (99/1)	Trametoid to fibroporioid; dimitic with inflated axial skeletals and arboriform branching; basidiospores truncate, smooth, thick-walled
_Picipes_*	ITS (88/1); LSU (89/0.98); combined (98/1)	Polyporoid without sclerotium; dimitic or trimitic with uninflated axial skeletals and active dichophytic branching; basidiospores cylindric, <10 μm long
_Polyporus s.str._*	Combined (100/1)	Polyporoid arising from sclerotium; dimitic with uninflated axial skeletals and moderate dichophytic branching; basidiospores fusoid, >10 μm long
Merulioid phylogenetic radiation		
Panus**	ITS (98/1); LSU (98/1); combined (100/1)	Lentinoid; dimitic with fibrohyphae (uninflated with collapsed appendages); basidia < 30 μm long; basidiospores subcylindric; white-rot fungi
Gloeophyllales phylogenetic radiation		
Neolentinus**	ITS (96/1); LSU (93/0.95); combined (98/1)	Lentinoid; dimitic with fibrohyphae (uninflated with collapsed appendages); basidia > 30 μm long; basidiospores with navicular or fusoid tendency; brown-rot fungi

Bootstrap values (%) from MP and posterior probability from BY analyses are shown below and above the slash, respectively.

*Entity unites species of polyporoid (including favoloid) morphotype.

**Entity unites species of lentinoid morphotype.

*/**Entity unites species both of polyporoid and lentinoid morphotypes.

TABLE 4: Diagnostic Key to Genera of Polyporoid and Lentinoid Fungi

I. Sclerohyphae unbranched at the maturity (fibrohyphae) – uninflated with collapsed appendages; their abundant terminations in the hymenium are recognized as pseudocystidia. Hymenophore lamellate.

- A. Basidia <30 μm at maturity. Basidiospores cylindric. Cause a white rot. ... *Panus*.
- B. Basidia >30 μm at maturity. Basidiospores with navicular or fusoid tendency. Cause brown-rot. ... *Neolentinus.*

II. Sclerohyphae sympodially branched. Pseudocystidia none. Hymenophore lamellate, cellar, or poroid.

- A. Axial element of skeleto-binding dendrite is recognizable owing to its inflation.
  - 1. Hyphal system subdimitic, sclerohyphae absent in hymenophorla trama. Basidiomes of grifoloid morphotype. Basidiospores subcylindric. ... *Cladomeris*.
  - 2. Hyphal system dimitic, sclerohyphae present in hymenophoral trama. Basidiomes of polyporoid, trametoid, or lentinoid morphotypes.
    - α. Basidiomes of polyporoid or trametoid morphotype. Basidiospores fusoid, with navicular tendency, or humpbacked. ... *Cerioporus*.
    - β. Basidiomes of lentinoid or polyporoid morphotype. Basidiospores subcylindric. ... *Lentinus*.
- B. Axial element of skeleto-binding dendrite uninflated.
  - 1. Sclerohyphae dichophytic. Basidiomes of polyporoid morphotype.
    - α. Sclerohyphae moderately branched. Basidiospores fusoid, >10 μm long. Basidiomata arising from sclerotium. ... *Polyporus*.
    - β. Sclerohyphae strongly branched. Basidiospores cylindric, <10 μm long. Sclerotium absent. ... *Picipes*.
  - 2. Sclerohyphae arboriform. Basidiomes of polyporoid, favoloid, or lentinoid morphotype.
    - α. Sclerohyphae regularly branched. Basidiospores with fusoid or navicular tendency. Basidiomes of polyporoid or favoloid morphotype. ... *Favolus*.
    - β. Sclerohyphae rarely branched. Basidiospores subcylindric. Basidiomes of favoloid or lentinoid morphotype. ... *Neofavolus.*

to the everyday patrimonial generic concept,[43–45] although the micromorphological diversity within this genus was discussed by some authors.[46–50] The discovery of an independent lineage, which includes the *Polyporus* type (*Polyporus tuberaster*), raised a problem of restoration of old and establishing of new names for remaining lineages: *Cerioporus* (type *P. squamosus*), *Cladomeris* (type *P. umbellatus*), *Favolus* (type *P. brasiliensis*), and *Neofavolus* (type *P. alveolaris*). The last lineage also includes lentinoid elements such as *L. suavissimus*. Such rearrangement successfully solves a problem of *Datronia*. This trametoid unit joins in polyporoid *Cerioporus*.

The revealing of several phylogenetic lines within the lentinoid-polyporoid continuum undoubtedly will help with target metabolomic analysis of species still not studied in pharmacological respects.

B. Diagnostic Key to Genera of Polyporoid and Lentinoid Fungi

A diagnostic key to genera of polyporoid and lentinoid fungi is presented in Table 4.

C. Taxonomical Catalogue of Polyporoid and Lentinoid Fungi

The catalogue presented in Table 5 reflects the view of the *Polyporus* s.l.–*Lentinus* s.l. conglomerate on a molecular perspective. Therefore, some nomenclatural innovations are given here. An enlarged version of the taxonomical catalogue of polyporoid and lentinoid fungi, which includes a synonymy of all of the taxa, is presented in Supplement 2 (http://www.researchgate.net/publication/279447065).

TABLE 5: Taxonomical Catalogue of Polyporoid and Lentinoid Fungi

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POLYPORALES

POLYPORACEAE

CERIOPORUS Quél., Ench. Fung.: 167, 1886.

Type: *Boletus squamosus* Huds., 1778.

Cerioporus admirabilis (Peck) Zmitr. et Kovalenko comb. nov. (MB 812034). – Bas.: *Polyporus admirabilis* Peck, Bull. Torrey Bot. Cl. 26: 69, 1899.

Cerioporus choseniae (Vassilkov) Zmitr. et Kovalenko comb. nov. (MB 812035). – Bas.: *Piptoporus choseniae* Vassilkov, Nov. Sist. Nizsch. Rast. 4: 244, 1967 [ut '*chozeniae*'];

Cerioporus corylinus (Mauri) Zmitr. et Kovalenko comb. nov. (MB 812036). – Bas.: *Polyporus corylinus* Mauri, Giorn. Arc. Roma 54: 3, 1818.

Cerioporus hygrocybe (M. Pieri et B. Rivoire) Zmitr. et Kovalenko comb. nov. (MB 812269). – Bas.: *Polyporus hygrocybe* M. Pieri et B. Rivoire, Bull. Soc. Mycol. France 121: 10, 2005.

Cerioporus leptocephalus (Jacq.) Zmitr. et Kovalenko comb. nov. (MB 812037). – Bas.: *Boletus leptocephalus* Jacq., Miscell. austriac. 1: 142, 1778 [*Polyporus leptocephalus* Jacq.: Fr., 1821].

Cerioporus meridionalis (A. David) Zmitr. et Kovalenko comb. nov. (MB 812038). – Bas.: *Leucoporus meridionalis* A. David, Bull. Soc. Mycol. France 88: 301, 1972.

Cerioporus mollis (Sommerf.) Zmitr. et Kovalenko comb. nov. (MB 812039). – Bas.: *Daedalea mollis* Sommerf., Suppl. Fl. Lapp.: 271, 1826.

Cerioporus rhizophilus (Pat.) Zmitr. et Kovalenko comb. nov. (MB 812040). – Bas.: *Polyporus rhizophilus* Pat., J. Bot. 8: 219, 1894.

Cerioporus squamosus (Huds.) Quél., Enchir. Fung.: 166, 1886.

Cerioporus squamosus (Huds.) Fr. f. ***rangiferina*** (Bolton) Zmitr. et Kovalenko comb. et stat. nov. (MB 812607). – Bas.: *Boletus rangiferinus* Bolton, Hist. fung. Halifax 3: 138, 1790.

Cerioporus stereoides (Fr.) Zmitr. et Kovalenko comb. nov. (MB 812041). – Bas.: *Polyporus stereoides* Fr., Observ. mycol. 2: 258, 1818.

Cerioporus varius (Pers.) Zmitr. et Kovalenko comb. nov. (MB 812042). – Bas.: *Boletus varius* Pers., Observ. mycol. 1: 85, 1796 [*Polyporus varius* Pers.: Fr., 1821].

Cerioporus vassilievae (Thorn) Zmitr. et Kovalenko comb. nov. (MB 812047). – Bas.: *Polyporus vassilievae* Thorn, Karstenia 40(1−2): 185, 2000.

Provisional position: *Datronia scutellata* (Schwein.) Gilb. et Ryvarden, Mycotaxon 22: 364, 1985; *D. decipiens* (Bres.) Ryvarden, Mycotaxon 33: 308, 1988.

CLADOMERIS Quél., Enchir. fung.: 167, 1886.

Type: *Boletus umbellatus* Pers., 1801.

Cladomeris umbellata (Pers.) Quél., Enchir. fung.: 167, 1886.

FAVOLUS Fr., Elench. 1: 44, 1828.

Type: *Merulius daedaleus* Link, 1789.

Favolus albostipes (Ryvarden et Iturr.) Zmitr. et Kovalenko comb. nov. (MB 812043). – Bas.: *Polyporus albostipes* Ryvarden et Iturr., Mycologia 95: 1071, 2003.

Favolus acervatus (Lloyd) Sotome et T. Hatt., Fungal Div. 58: 254, 2013.

Favolus biskeletalis (Corner) Zmitr. et Kovalenko comb. nov. (MB 812044). – Bas.: *Polyporus biskeletalis* Corner, Beih. Nova Hedwigia 78: 57, 1984.

F. brasiliensis (Fr.) Fr., Linnaea 5: 511, 1830 [*Daedalea brasiliensis* Fr., 1821].

Favolus elongoporus (Drechsler-Santos et Ryvarden) Zmitr. et Kovalenko comb. nov. (MB 812045). – Bas.: *Polyporus elongoporus* Drechsler-Santos et Ryvarden, Syn. Fung. 25: 39, 2008.

TABLE 5: (Continued)

F. emerici (Berk. ex Cooke) Imazeki, Bull. Tokyo Sci. Mus. 6: 95, 1943.

Favolus ianthinus (Gibertoni et Ryvarden) Zmitr. et Kovalenko comb. nov. (MB 812046). – Bas.: *Polyporus ianthinus* Gibertoni et Ryvarden in Gibertoni, Ryvarden et Cavalcanti, Syn. Fung. 18: 53, 2004.

F. philippinensis Berk., London J. Bot. 1: 148, 1842.

F. pseudobetulinus (Murashk. ex Pilát) Sotome et T. Hatt., Fungal Div. 58: 260, 2013.

F. roseus Lloyd, Mycol. Writ. 7: 1157, 1922.

F. spathulatus (Jungh.) Lév., Ann. Sci. Nat. Bot. (ser. 3) 2: 203, 1844.

Favolus udus (Jungh.) Zmitr. et Kovalenko comb. nov. (MB 812076). – Bas.: *Polyporus udus* Jungh., Tijdskr. Nat. Gesch. Physiol. 7: 289, 1940.

LENTINUS Fr., Syst. Orbis Veg. 1: 77, 1825.

Type: *Agaricus crinitus* L., 1763.

Lentinus alpacus Senthil. et S. K. Singh in Senthilarasu, Sharma et Singh, Mycotaxon 121: 70, 2013.

Lentinus anastomosans Rick, Lilloa 2: 310, 1938.

Lentinus anthocephalus (Lév.) Pegler, Bull. Jard. Bot. Natn. Belg. 41: 280, 1971.

Lentinus araucariae Har. et Pat., J. Bot. 17: 11, 1903.

Lentinus arcularius (Batsch) Zmitr., Int. J. Medicinal Mushrooms 12(1): 88, 2010.

Lentinus atrobrunneus Pegler, Bull. Jard. Bot. Natn. Belg. 41: 275, 1971.

Lentinus badius (Berk.) Berk., London J. Bot. 6: 491, 1847.

Lentinus baguirmiensis Pat. et Har., Bull. Soc. mycol. France 24: 14, 1908.

Lentinus bambusinus T. K. A. Kumar et Manim., Mycotaxon 92: 119, 2005.

Lentinus bertieri (Fr.) Fr., Syst. Orbis Veg. 1: 77, 1825.

Lentinus brumalis (Pers.) Zmitr., Int. J. Medicinal Mushrooms 12(1): 88, 2010.

Lentinus brunneofloccosus Pegler, Bull. Jard. Bot. Natnl Belg. 41: 278, 1971.

Lentinus calyx (Speg.) Pegler, Kew Bull. Add. Ser. 9: 32, 1983.

Lentinus cladopus Lév., Ann. Sci. Nat. Bot. (Ser. 3) 2: 174, 1844.

Lentinus concavus (Berk.) Henn. in Engler et Prantl, Nat. Pflfam. 1: 224, 1900.

Lentinus concentricus Karun., K. D. Hyde et Zhu L. Yang in Karun., Yang, Zhao, Vellinga, Bahkali, Chukeatirote et K. D. Hyde, Mycol. Progr. 10(4): 395, 2011.

Lentinus concinnus Pat., Bull. Soc. Mycol. France 8: 47, 1892.

Lentinus connatus Berk., London J. Bot. 1(3): 145, 1842.

Lentinus crinitus (L.) Fr., Syst. Orbis veg. 1: 77, 1851.

Lentinus dicholamellatus Manim. in Manim., Divya, Kumar, Vrinda et Pradeep, Mycotaxon 90(2): 312, 2004.

Lentinus flexipes (Fr.) Zmitr. et Kovalenko comb. nov. (MB 812268). – Bas.: *Polyporus flexipes* Fr., Linnaea 5: 515, 1830.

Lentinus glabratus Mont. in La Sagra, Cuba Pl. Cell.: 424, 1842.

Lentinus longiporus (Audet, Boulet et Sirard) Zmitr. et Kovalenko comb. nov. (MB 812110). **–** Bas.: *Polyporus longiporus* Audet, Boulet et Sirard in Boulet, Les Champignons des Arbres de l'Est de l'Amérique du Nord: 530, 2003.

Lentinus megacystidiatus Karun., K. D. Hyde et Zhu L. Yang in Karun., Yang, Zhao, Vellinga, Bahkali, Chukeatirote et K. D. Hyde, Mycol. Progr. 10(4): 393, 2011.

Lentinus nigroosseus Pilát, Ann. Mycol. 34: 122, 1936.

Lentinus polychrous Lév., Ann. Sci. Nat. Bot. (Ser. 3) 2: 175, 1844.

Lentinus retinervis Pegler, Kew. Bull. Add. Ser. 9: 30, pl. 1b, 1983.

Lentinus roseus Karun., K. D. Hyde et Zhu L. Yang in Karun., Yang, Zhao, Vellinga, Bahkali, Chukeatirote et K. D. Hyde, Mycol. Progr. 10(4): 392, 2011.

Lentinus sajor-caju (Fr.) Fr., Epicr.: 393, 1838.

Lentinus sclerogenus Sacc., Nuov. Giorn. Bot. Ital. 23: 230, 1916.

Lentinus squarrosulus Mont., Ann. Sci. Nat. Bot. (ser. 2) 18: 21, 1842.

Lentinus striatulus Lév., Ann. Sci. Nat. Bot. (Ser. 3) 5: 120, 1846.

Lentinus stupeus Klotzsch, Linnaea 8: 480, 1833 [ut '*stupens*'].

Lentinus substrictus (Bolton) Zmitr. et Kovalenko comb. nov. (MB 812111). – Bas.: *Boletus substrictus* Bolton, Hist. fung. Halifax, App.: 170, 1792.

Lentinus swartzii Berk., Hook. London J. Bot. 2: 632, 1843.

Lentinus tigrinus (Bull.) Fr., Syst. Orbis Veg.: 78, 1825.

Lentinus tuber-regium (Fr.) Fr., Syn. generis Lentinus: 3, 1836.

Lentinus umbrinus H. W. Reichardt, Verh. Zool.-Bot. Ges. Wien 16: 375, 1866.

Lentinus villosus Klotzsch, Linnaea 8: 479, 1833.

Lentinus vossii (Kalchbr.) Zmitr. et Kovalenko comb. nov. (MB 812112). – Bas.: *Polyporus vossii* Kalchbr., Verh. zool.-bot. Ges. Wien 29: 689, 1879.

Lentinus zeyheri Berk., Hook. London J. Bot. 2: 514, 1843.

NEOFAVOLUS Sotome et T. Hatt., Fungal Div. 58(1): 249, 2013.

Type: *Merulius alveolaris* DC., 1815.

Neofavolus alveolaris (DC.) Sotome et T. Hatt., Fungal Div. 58(1): 250, 2013.

N. cremeoalbidus Sotome et T. Hatt., Fungal Div. 58(1): 250, 2013.

N. mikawai (Lloyd) Sotome et T. Hatt., Fungal Div. 58(1): 251, 2013.

Neofavolus suavissimus (Fr.) Zmitr. et Kovalenko comb. nov. (MB 812026). – Bas.: *Lentinus suavissimus* Fr., Meth. Grund. Mod. Pflanzensoziol.: 13, 1836.

Provisional position: *Lentinus lamelliporus* Har. et Pat., Bull. Mus. Nat. Hist. 8: 131, 1902.

PICIPES Zmitr. et Kovalenko gen. nov. (MB 812027)

= *Melanopus* Pat., 1887 in Donk's (1960) typification. Nomen ambiguum.

Basidiomata annual, stipitate, of polyporoid morphotype. Pilei infundibiliform, covered with hard cuticle, without scales, smoke gray to castaneous or deeply brown. Stipe covered with brownish to black cuticle. Pores small (more than 5 per mm). Hyphal system dimitic with uninflated both corioiloid and fibrous skeletals; the last ones are subsolid. Clamps present or absent. Basidiospores cylindric, smooth, hyaline. On wood of frondose and coniferous trees causing a white rot.

Type: *Boletus badius* Pers., 1801.

Etymology: *piceus* – covered by tar, *pes* – stipe. This term refers to *Polyporus picipes* Fr. and substitutes the name *Melanopus* Pat. nom. ambig. based on *Polyporus melanopus* Sw.: Fr.

A numerous branched skeletals with uninflated axial elements, numerous subsolid fibrohyphae in combination with small pores and dark-colored stipe cuticle are characteristic for the genus.

Picipes badius (Pers.) Zmitr. et Kovalenko comb. nov. (MB812028). – Bas.: *Boletus badius* Pers., Syn. Meth. Fung. 2: 253, 1801.

TABLE 5: (Continued)

Picipes melanopus (Pers.) Zmitr. et Kovalenko comb. nov. (MB812029). – Bas.: *Boletus melanopus* Pers., Tent. Disp. Meth. Fung.: 70, 1797 [*Polyporus melanopus* Pers.: Fr., 1821].

Picipes tubaeformis (P. Karst.) Zmitr. et Kovalenko comb. nov. (MB812030). – Bas.: *Polyporellus varius* subsp. *tubaeformis* P. Karst., Meddn Soc. Fauna Fl. Fennica 9: 69, 1882.

POLYPORUS [Mich.] Fr., Syst. Mycol. 1: 341, 1821.

Type: *Polyporus tuberaster* Jacq. ex Pers. per Fr., 1821.

Polyporus tuberaster (Jacq. ex Pers.) Fr., Syst. Mycol. 1: 347, 1821.

MERULIACEAE

PANUS Fr., Syst. Mycol. 1: 396, 1821.

Type: *Agaricus conchatus* Bull., 1787.

Panus ciliatus (Lév.) T. W. May et A. E. Wood, Mycotaxon 54: 148, 1995.

Panus conchatus (Bull.: Fr.) Fr., Epicr.: 397, 1838.

Panus fasciatus (Berk.) Singer, Agaricales mod. Tax. 2nd ed.: 172, 1962.

Panus hookerianus (Berk.) T. W. May et A. E. Wood, Mycotaxon 54: 148, 1995.

Panus lecomtei (Fr.) Corner, Beih. Nova Hedw. 69: 90, 1981.

Panus similis (Berk. et Broome) T. W. May et A. E. Wood, Mycotaxon 54: 148, 1995.

Panus strigellus (Berk.) Chardon et Toro, Monogr. Univ. Porto Rico Ser. B 2: 315, 1934.

Panus tephroleucus (Mont.) T. W. May et A. E. Wood, Mycotaxon 54: 148, 1995.

Panus velutinus (Fr.) Overh., J. Dept Agric. Porto Rico 14: 353, 1930 non Fr., 1838.

Provisional position: *Lentinus martianoffianus* Kalchbr. in Thüm., Bull. Mosk. Obshch. Ispyt. Prir. 52: 144, 1877; *L. hirtiformis* Murrill, N. Am. Fl. 9: 293, 1915; *L. courtetianus* Har. et Pat., Bull. Mus. Hist. Nat. Paris 15: 88, 1909.

GLOEOPHYLLALES

GLOEOPHYLLACEAE

NEOLENTINUS Redhead et Ginns, Trans. Mycol. Soc. Japan 26(3): 357, 1985.

Type: *Lentinus kaufmannii* A. H. Sm., 1946.

Neolentinus adhaerens (Alb. et Schwein.) Redhead et Ginns, Trans. Mycol. Soc. Japan 26(3): 357, 1985.

Neolentinus cirrhosus (Fr.) Redhead et Ginns, Trans. Mycol. Soc. Japan 26(3): 357, 1985.

Neolentinus cyathiformis (Schaeff.) Della Maggiora et Trassinelli, Index Fungorum 171: 1, 2014.

Neolentinus dactyloides (Cleland) Redhead et Ginns, Trans. Mycol. Soc. Japan 26(3): 357, 1985.

Neolentinus kauffmanii (A. H. Sm.) Redhead et Ginns, Trans. Mycol. Soc. Japan 26(3): 357, 1985.

Neolentinus lepideus (Fr.) Redhead et Ginns, Trans. Mycol. Soc. Japan 26(3): 357, 1985.

Neolentinus lepideus* f. *rufescens (A. N. Petrov) Zmitr. et Kovalenko comb. nov. (MB 812274). – Bas.: *Lentinus lepideus* f. *rufescens* A. N. Petrov, Mikol. Fitopatol. 21(1): 38, 1987.

Neolentinus pallidus (Berk. et M. A. Curtis) Redhead et Ginns, Trans. Mycol. Soc. Japan 26(3): 357, 1985.

Neolentinus papuanus (Hongo) Redhead et Ginns, Trans. Mycol. Soc. Japan 26(3): 357, 1985.

Neolentinus ponderosus (O. K. Mill.) Redhead et Ginns, Trans. Mycol. Soc. Japan 26(3): 357, 1985.

Neolentinus sulcatus (Berk.) F. Rune, Mycol. Res. 98(5): 543, 1994.

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