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Short title: *Lentinus*, *Polyporellus*, *Neofavolus*

Phylogenetic relationships and morphological evolution in *Lentinus*, *Polyporellus* and *Neofavolus*, emphasizing southeastern Asian taxa

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Abstract: The genus *Lentinus* (Polyporaceae, Basidiomycota) is widely documented from tropical and temperate forests and is taxonomically controversial. Here we studied the relationships between *Lentinus* subg. *Lentinus* sensu Pegler (i.e. sections *Lentinus*, *Tigrini*, *Dicholamellatae*, *Rigidi*, *Lentodiellum* and *Pleuroti* and polypores that share similar morphological characters). We generated sequences of internal transcribed spacers (ITS) and

partial 28S regions of nuc rDNA and genes encoding the largest subunit of RNA polymerase II (*RPB1*), focusing on *Lentinus* subg. *Lentinus* sensu Pegler and the *Neofavolus* group, combined these data with sequences from GenBank (including *RPB2* gene sequences) and performed phylogenetic analyses with maximum likelihood and Bayesian methods. We also evaluated the transition in hymenophore morphology between *Lentinus*, *Neofavolus* and related polypores with ancestral state reconstruction. Single-gene phylogenies and phylogenies combining ITS and 28S with *RPB1* and *RPB2* genes all support existence of a *Lentinus*/*Polyporellus* clade and a separate *Neofavolus* clade. *Polyporellus* (represented by *P. arcularius*, *P. ciliatus*, *P. brumalis*) forms a clade with species representing *Lentinus* subg. *Lentinus* sensu Pegler (1983), excluding *L. suavissimus*. *Lentinus tigrinus* appears as the sister group of *Polyporellus* in the four-gene phylogeny, but this placement was weakly supported. All three multigene analyses and the single-gene analysis using ITS strongly supported *Polyporus tricholoma* as the sister group of the *Lentinus/Polyporellus* clade; only the 28S rRNA phylogeny failed to support this placement. Under parsimony the ancestral hymenophoral configuration for the *Lentinus/Polyporellus* clade is estimated to be circular pores, with independent transitions to angular pores and lamellae. The ancestral state for the *Neofavolus* clade is estimated to be angular pores, with a single transition to lamellae in *L. suavissimus*. We propose that *Lentinus suavissimus* (section *Pleuroti*) should be reclassified as *Neofavolus suavissimus* comb. nov.

Keywords: *Lentinus* sensu stricto, *Lentinus suavissimus*, multigene phylogeny, PolyPEET, taxonomy

INTRODUCTION

Lentinus Fr. is a widespread genus of wood-decaying Agaricomycetes with tough basidiocarps, hyaline spores and decurrent lamellae. Application of the generic name *Lentinus* has been

controversial (Pegler 1971, 1972, 1975, 1983a, b; Kühner1980; Corner 1981; Pegler and Young 1983; Redhead and Ginns 1985; Singer 1986). A comprehensive world monograph of *Lentinus* was published by Pegler (1983a), but this concept of the genus is polyphyletic (Hibbett and Vilgalys 1991, 1993; Hibbett et al. 1993a; Binder et al. 2005; Binder et al. 2013). *Lentinus* sensu Pegler (1983a) was subdivided into two subgenera, *Lentinus* subg. *Lentinus* and *Lentinus* subg. *Panus*, based largely on anatomy of hyphal systems and hymenophoral trama. Subgenus *Lentinus* included species with skeleto-ligative hyphae with intercalary or terminal branching, hyphal pegs (fascicles of sterile hyphae protruding from the lamellae), hymenophoral trama of descending, radiate or intermediate construction and lacking metuloids and gloecystidia, whereas subg. *Panus* included species with skeletal hyphae (thick-walled, typically unbranched), lacking hyphal pegs, with metuloids and gloecystidia and hymenophoral trama mostly of radiate construction. Subgenus *Lentinus* comprises six sections: sect. *Lentinus* sensu Pegler (eight species, including *L. crinitus* which was accepted as lectotype by Pegler), sect. *Tigrini* Pegler (six species, including *L. tigrinus*, which technically is the correct lectotype of *Lentinus* [viz. Redhead and Ginns 1985]), sect. *Dicholamellatae* Pegler (three species), sect. *Rigidi* Pegler (five species), sect. *Lentodiellum* (Murr.) Pegler (four species) and sect. *Pleuroti* Sacc. (one species), and subgenus *Panus* includes nine sections: sect. *Pulverulenti* Fr. (three species), sect. *Panus* (Fr.) Pegler (nine species), sect. *Cirrhosi* (two species), sect. *Velutini* Pegler (six species), sect. *Gigantopanus* (Corner) Pegler (one species), sect. *Squamosi* Fr. (six species), sect. *Tuberregium* (Singer) Pegler (four species), sect. *Prolifer* Pegler (four species) and sect. *Tenebrosi* Pegler (one species). The earliest acceptable lectotype by Clements and Shear (1931) for the generic name *Lentinus* technically is *L. tigrinus* (viz. Redhead and Ginns 1985), which would make *Lentinus* sect. *Tigrini* superfluous, and would require a new sectional name for *Lentinus* sect. *Lentinus*

sensu Pegler. For the sake of convenience and consistency pending a conservation, here we follow Pegler (1983a) and accept as lectotype *L. crinitus*, which is in alignment with most other classifications (see Redhead and Ginns 1985).

Alternative generic classifications of species of *Lentinus* sensu Pegler (1983a) have been proposed based on anatomy, mating systems (bipolar vs. tetrapolar), decay types (white rot vs. brown rot), nematode-trapping ability, hymenophore development, post-meiotic nuclear behavior and molecular phylogenies (Corner 1981; Redhead and Ginns 1985; Singer 1986; Hibbett et al. 1993a, b; Hibbett and Vilgalys 1993; Hibbett and Thorn 1994; Thorn et al. 2000; Hibbett and Donoghue 2011; Karunarathna et al. 2011a; Binder et al. 2013). The "lentinoid fungi" now are understood to be distributed across six genera, including *Lentinus* and *Panus* (Polyporales), *Pleurotus* and *Lentinula* (Agaricales) and *Neolentinus* and *Heliocybe* (Gloeophyllales), as outlined by Redhead and Ginns (1985) and refined by segregating *Panus* by Hibbett et al. (1993b). Excluding the five other genera listed above, in the present study "*Lentinus*" refers to *Lentinus* subg. *Lentinus* sensu Pegler, which is roughly equivalent to *Lentinus* sensu Corner (1981) and *Panus* sects. *Pleuroti* (Sacc.) Singer and *Criniti* (Sacc.) Singer, both sensu Singer (1986).

Lentinus and certain polypores have a close relationship based on their morphological characteristics. Both genera contain dimitic and amphimitic hyphal systems, cylindrical to subellipsoid and smooth inamyloid basidiospores and hyphal pegs, which place them in the Polyporaceae as traditionally defined (Corner 1981, Pegler 1983a, Gilbertson and Ryvarden, 1987). The sub-poroid hymenophore of some *Lentinus* species also suggests a possible polyporoid ancestry (Pegler 1983a). Developmental studies in *L. tigrinus* have revealed the formation of both lamellae and tangential “cross bridges”, which might be homologous to the

tangential hymenophoral elements in polypores with angular pores such as *P. arcularius* (Hibbett et al. 1993a).

Molecular studies have indicated that *Polyporus* is polyphyletic and that species of *Lentinus* and *Polyporellus* (pileate-stipitate polypores, with angular or circular pores, and relatively ephemeral fruiting bodies) form a clade (Krüger 2002; Krüger and Gargas 2004; Grand 2004, 2011; Sotome et al. 2008; Binder et al. 2013). The type species of *Polyporus* has been interpreted variously as *P. brumalis* (Clements and Shear 1931, Krüger and Gargas 2004), *P. squamosus* (Ryvarden 1978, Ryvarden and Gilbertson 1987) or *P. tuberaster* (Overholts 1953, Cunningham 1965, Singer 1986, Silveria and Wright 2005, Sotome et al. 2008). Ryvarden (1991) preferred *P. tuberaster* as lectotype of *Polyporus* while accepting *P. brumalis* as the lectotype of *Polyporellus*. For the purpose of our discussion we adopt *P. tuberaster* as type of *Polyporus* until this nomenclatural debate is settled and we accept *P. brumalis* as type of *Polyporellus*.

Six prior phylogenetic studies using different genes in *Lentinus*, *Polyporellus*, *Neofavolus* (formerly known as *Polyporus*) and related polypores are summarized (TABLE I). Five studies used sequences of the nuc rDNA internal transcribed spacer regions 1 and 2 (ITS) and 28S sequences for limited sections of *Lentinus*. Grand et al. (2011) included representative members of five sections, except section *Pleuroti* but analyzed only ITS sequences. Meanwhile, Sotome et al. (2008) used 28S, *RPB2* and *ATP6* but sampled only two sections of *Lentinus*, along with numerous polypores.

Species of *Lentinus* occur in boreal, temperate, subtropical and tropical regions (Pegler 1983a, b; Corner 1981). They play an important role in natural ecosystems as wood decomposers and show potential for seasonal food, medicine and alternative income mainly in southeastern

Asia and southern Africa (Chin 1981, Watling 1993, Mossebo 2002, Bayramoglu et al. 2006, Sysouphanthong et al. 2010, Njouonkou et al. 2013a). *Lentinus* is widely documented within southeastern Asia, including Indonesia, Thailand, Laos, Peninsular Malaysia, Borneo, Philippines, China and India (Manimohan and Leelavathy 1995, Huang 1998, Manimohan et al. 2004, Sumaiyah et al. 2007, Nazura et al. 2010, Somchai 2010, Sudirman 2010, Bolhassan et al. 2013). In Malaysia 20 species of *Lentinus* have been reported (Chipp 1921, Newsam et al. 1967, Lim 1972, Corner 1981, Pegler 1983a, Oldridge et al. 1986, Lee et al. 1995, Salmiah and Thillainathan 1998, Salmiah and Jones 2001, Noorlidah et al. 2005, Sumaiyah et al. 2007, Bolhassan et al. 2013). Seven new species of *Lentinus* have described in the past 10 y (*L. parvus, L. bambusinus, L. megacystidiatus, L. concentricus, L. roseus, L. alpacus, L. cystidiatus*), all without molecular data. However these taxa have greater resemblance to *Panus* based on reported morphological characters (Arun Kumar and Manimohan 2005, Manimohan et al. 2004, Sumaiyah et al. 2007, Karunarathna et al. 2011b, Senthilarasu et al. 2012, Drechsler-Santos 2012, Njouonkou et al. 2013b) and new sequence data that will be reported elsewhere (Seelan et al. unpubl). This study aims to assess the limits of *Lentinus* and the pattern of transitions between pores and gills. For this purpose it is necessary to sample all sections of *Lentinus* sensu Pegler and a diverse assemblage of polypores. By focusing on collections from Malaysia this study also seeks to provide a framework for taxonomic and phylogenetic studies of *Lentinus* from southeastern Asia.

MATERIALS AND METHODS

Collections.—They were made during the May-Jun 2009, 2010 rainy seasons and the Nov-Jan 2010, 2011 rainy seasons from Sabah Park in northern Borneo, Malaysia. Fruiting bodies of *Lentinus* were collected from highland and lowland dipterocarp and heath, mainly in primary and secondary forests around Kinabalu Park. *Lentinus sajor-caju* collections also were made on Gaya Island, which is about 6 km from the mainland of Kota Kinabalu, Sabah.

Locality information for the new specimens or cultures used for the DNA extraction and sequencing in this study are presented (TABLE II). All specimens of *Lentinus* were identified with reference to (Pegler 1983a) and (Corner 1981).

Additional materials were collected in the Forest Research Institute of Malaysia (FRIM) and Sungkai Wildlife Reserve Forests (PERHILITAN) in peninsular Malaysia, mainly from lowland dipterocarp forest. Specimens of *Lentinus suavissimus,* which is the only species in *Lentinus* sect. *Pleuroti* sensu Pegler (1983a) and *Neofavolus sp.* (*Polyporus alveolaris*) were collected on Chena Lakes Nature Trails, Alaska, and the Adirondack Mountains, New York). A single specimen of *Lentinus crinitus* (AJ527) was collected at Virgin Islands National Park (St John, US Virgin Islands). Specimens were dried and kept in polyethylene bags with silica gel. One specimen of *Lentinus squarrosulus* was obtained from the personal collection of Professor Yu Cheng Dai (Academy of Sciences, China). Specimens of *Polyporus arcularius* (DSH92-132), *Lentinus crinitus* (DSH92N43C) and *Lentinus tigrinus* (DSH92D787) were accessioned from the Clark University Herbarium. Additional specimens obtained from the BIOTEC Bangkok Herbarium (BBH), Thailand, and the Royal Botanical Gardens, Kew (K), UK. Duplicate specimens of Malaysian collections were deposited at the Sabah National Park Herbarium (SNP) and at the Institute for Tropical Biology and Conservation, Borneensis herbarium (BORH) at Universiti Malaysia Sabah. Two cultures of *Polyporus ciliatus* were obtained from the University of Tennessee Herbarium (TENN).

DNA extraction, PCR and sequencing.—Cultures of *P. ciliatus* were maintained 2–3 wk at 25–30 C on solid media (MEA: 20 g malt extract, 0.5 g yeast extract, 20 g agar in1 L water). When plates were covered with new mycelium, the tissue was scraped with sterile scalpels and transferred to a 1.5 mL microtube and ground with a sterile plastic pestle. In the case of specimens, a small portion of the fruiting body was ground with liquid nitrogen. Cell lysis proceeded for 1h at 65 C with the addition of 600 mL extraction buffer (50 mM EDTA, 50 mM Tris-HCl, 3% SDS, pH 8). Cell debris, polysaccharides and proteins were separated from aqueous DNA portions through two purification steps with equal volumes of phenol:chloroform (1:1) and chloroform:isoamylalcohol (24:1). Total DNA was precipitated with the addition of 3 M sodium acetate (0.1 vol.) and isopropanol (0.54 vol.) and incubated 30–60 min at −20 C. The DNA pellets were washed in 1 mL 70% EtOH, dried at 65 C for 5–15 min and resuspended in 100 mL sterile H_2O. Dilutions of the original DNA extraction, usually 1:10–1:500, were used in the polymerase chain reaction (PCR) amplification. DNA was extracted from dried specimens (approximately 0.2 g) with the EZNA Fungal DNA Kit (Omega Bio-Tek, Norcross, Georgia) and following Hosaka and Castellano (2008).

Three regions were sequenced, including those encoding the internal transcribed spacers (ITS = ITS1 + 5.8S + ITS2) and partial large subunit of 28S nuclear ribosomal RNA (28S) and subunit 1 of RNA polymerase II (*RPB1*) (TABLE II). The ITS (approx. 600–700 bp, including 157 bp 5.8S rRNA coding region) was amplified with the primer pair ITS-1F/ITS4 (White et al. 1990, Gardes and Bruns 1993) and the partial 28S region (approx. 1300 bp) was amplified with the primer pair LR0R/LR7 (Vilgalys and Hester 1990). For ribosomal DNA markers this PCR protocol was used: (i) initial denaturation at 95 C for 2 min, (ii) denaturation at 94 C for 45 s, (iii) annealing at 50 C for 1 min 10 s, (iv) extension at 72 C for 2 min, (v) repeat for 34 cycles starting at step 2, (vi) leave at 72 C for 10 min (Binder et al. 2010). Sequencing primers for ITS and 28S were the same used for PCR and in the case of 28S with two additional internal primers: LR3R and LR5 (Vilgalys and Hester 1990). A part of the *RPB1* gene between conserved domains A and C of *RPB1* (approx. 1400 bp) was amplified with the primer pair RPB1-Af and RPB1-Cr (Stiller and Hall 1997, Matheny et al. 2002). In some cases the primer RPB1-2.2f (Binder et al 2010) was used as an alternative to RPB1-Af, producing a slightly shorter product (approx. 1000 bp). Additional sequencing primers were: RPB1-2f, RPB1-2.1f, RPB1-2.2f and RPB1-2.1r (Frøslev et al. 2005).

For *RPB1* the following touchdown PCR protocol was used: (i) initial denaturation at 94 C for 2 min, (ii) denaturation at 94 C for 40 s, (iii) annealing at 60 C for 40 s (minus 1 C per cycle), (iv) extension at 72 C for 2 min, (v) repeat for nine cycles starting at step 2, (vi) denaturation at 94 C for 45 s, (vii) annealing at 53 C for 1 min 30 s, (viii) extension at 72 C for 2 min, (ix) repeat for 36 cycles starting at step 6, (x) leave at 72 C for 10 min. The amplification products for all markers were sequenced with BigDye 3.1 terminator sequencing chemistry (Applied Biosystems, Foster City, California) and run on an Applied Biosystems 3130 Genetic Analyzer at Clark University or analyzed by Macrogen Inc. Rockville, Maryland.

Sequence alignment and phylogenetic analyses.—In addition to the sequences generated here, 72 were retrieved from GenBank and come mainly from Sotome et al. (2013) and Binder et al. (2013). Accession numbers of ITS, 28S, *RPB1* and *RPB2* sequences used in the analysis are provided (SUPPLEMENTARY TABLE I). Sequences were aligned with either MUSCLE 3.8 (Edgar 2004), in the case of protein-coding genes, or PRANK 130820 (Loytynoja and Goldmann 2008) for the ITS sequences, becausee it has been shown to outperform most other alignment algorithms for aligning ITS sequences (Nagy et al. 2012). MUSCLE was launched with default parameters, whereas in the case of PRANK we selected the +F option. The alignments were manually corrected with MacClade 4.08 (Maddison and Maddison 2002; http://macclade.org/). Overly variable intron regions from the *RPB1* and *RPB2*

alignments were excluded. For the combined datasets each marker was aligned separately and then concatenated in MacClade. Four datasets were assembled for the phylogenetic analyses (Figs. 1, 2; SUPPLEMENTARY FIGS.1, 2), and single-gene phylogenies provided (SUPPLEMENTARY FIGS. 3–6).

Phylogenetically informative indels in the ITS alignment were recoded as a matrix of binary characters and were appended to the end of the concatenated matrix for the Bayesian analyses. Indels were coded with the simple indel coding algorithm (Simmons and Ochoterena 2000) using the gapcode.by script (http://www.bioinformatics.org/~rick/software.html).

Two phylogenetic analyses were performed in all the datasets: (i) Maximum likelihood analyses (ML) were run in RAxML 7.2.8 (http://phylobench.vitaleit.ch/raxmlebb/index.php; Stamatakis et al. 2008) under the GTRGAMMA model with 100 rapid bootstrap replicates. (ii) Bayesian analyses (BI) were run with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) at the Cipres Science Gateway (Miller et al 2010; http://www.phylo.org/) for 10 000 000 generations, under a GTR model, modeling rate heterogeneity by a discrete gamma distribution. MrBayes was launched with two runs with four chains each and trees were sampled every 100 generations. For both ML and BI we partitioned the dataset into single genes and estimated a partitioned model with unlinked model parameters between the partitions. The recoded indels were modeled with the likelihood model for binary characters implemented in MrBayes. The burn-in was determined by checking the convergence of log-likelihood values in Tracer 1.5 (Rambaut and Drummond 2007), and the first 30 000 trees from each run were discarded. The remaining 140 000 trees were used to compute a 50% majority rule consensus tree and estimate posterior probabilities (PP) with the SumTrees script of the Dendropy package (Sukumaran and Holder 2010). Convergence of log likelihood scores (−Ln) was assessed with TRACER 1.4 (Rambaut and Drummond 2007) and stationarity was assumed when a stable equilibrium value was reached (Ronquist and Huelsenbeck 2003). Individual nodes were considered well supported when ML bootstrap values (BS) were at least 70% and when PP values were at least 0.95.

Ancestral state reconstruction (ASR).—To reconstruct the evolution of hymenophoral transitions within the *Lentinus* and *Neofavolus* clades, we used parsimony and ML optimization, implemented in MESQUITE 2.75 (Maddison and Maddison 2011). Hymenophoral forms within *Lentinus*, *Neofavolus* and other remaining core polyporoid members were assigned as discrete unordered character states: Odontoid and tuberculate (outgroup) = 0, circular pores = 1, daedaleoid = 2, angular pores = 3, lamellate = 4, sub-poroid lamellae = 5 and round to angular pores = 6 (SUPPLEMENTARY TABLE II). Character coding 5 represents the sub-poroid construction that arises from the base of

the stipe, which was considered as an important character to differentiate *L. tigrinus* and *L. suavissimus*. Meanwhile, coding 6 represents polymorphic characters within *Trametes villosa*, *T. polyzona*, *Datronia scutellata* and *P. tricholoma*. All character coding was produced based on Ryvarden (1991).

Ancestral states were estimated with 1000 rooted trees drawn randomly from the post burn-in tree pool derived from the MrBayes analysis of the four-gene 99 taxa dataset. In MESQUITE, the option TRACE CHARACTER OVER TREES was selected to reconstruct ancestral character states assuming an Mk1 class model and unordered characters. Parsimony reconstructions were optimized with the MOST PARSIMONIOUS RECONSTRUCTIONS (MPR) option.

RESULTS

Seventy new sequences were generated: 31 (ITS), 19 (28S) and 20 (*RPB1)*. Single-gene phylogenies from ML analyses of the ITS, 28S, *RPB1* and *RPB2* datasets indicated no strongly supported conflict, and are provided (SUPPLEMENTARY FIGS. 3–6). Phylogenetic relationships among members of the *Lentinus* and *Neofavolus* clades were estimated with three multigene datasets, ITS+28S+*RPB1*+*RPB2*, ITS+28S+*RPB2* and ITS+28S+*RPB1*, and an ITS only dataset. ML and BI trees generated from all analyses were largely congruent; only the ML tree topologies are illustrated here, and conclusions are based primarily on the topology of the best tree from the ML analysis of the combined ITS+28S+*RPB1*+*RPB2* dataset (FIG. 1). A detailed analysis of relationships in the *Neofavolus* clade was produced using ITS alone (FIG. 2). A comparative overview of the different datasets used for the phylogenetic analyses is provided (TABLE III), and the alignments were deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S16854). Most available sequences from GenBank for *Lentinus* and *Neofavolus* were included (SUPPLEMENTARY TABLE I), except an ITS sequence deposited by Grand et al. (2011) GU207275 labeled as *Lentinus badius*, which was placed in the core polyporoid clade but not in the *Lentinus* group in preliminary analyses (not shown).

Single-gene phylogenies and phylogenies combining ITS and 28S with *RPB1* or *RPB2* genes all support existence of a *Lentinus*/*Polyporellus* clade and a separate *Neofavolus* clade (FIGS. 1, 2; SUPPLEMENTARY FIGS. 1–6). *Polyporellus* (represented by *P. arcularius, P. ciliatus* and *P. brumalis*) nested within a paraphyletic assemblage of species representing *Lentinus* subg. *Lentinus* sensu Pegler (1983) excluding *L. suavissimus*. *Lentinus tigrinus* appears as the sister group of *Polyporellus* in the four-gene phylogeny, but this placement is weakly supported (FIG. 1). All three multigene analyses and the single-gene analyses using ITS and *RPB2* strongly support *Polyporus tricholoma* as the sister group of *Lentinus*/*Polyporellus*; only 28S fails to support this placement (*P. tricholoma* was not sampled for *RPB1*; SUPPLEMENTARY FIG. 4).

Five sections of *Lentinus* sensu Pegler (1983) are represented in the *Lentinus*/*Polyporellus* clade: sections *Rigidi* (*L. squarrosulus, L. polychrous, L. sajor-caju*), *Lentodiellum* (*L. scleropus, L. striatulus*), *Lentinus* (*L. crinitus, L. swartzii, L. bertieri*), *Dicholamellatae* (*L. badius*) and *Tigrini* (*L. tigrinus*). However *Lentinus* sect. *Pleuroti*, represented by *L. suavissimus* (= *Neofavolus suavissimus*), is strongly supported as a member of the *Neofavolus* clade in all multigene and single-gene analyses (except the single-gene analysis of *RPB2*, which did not include *L. suavissimus*) (FIGS. 1, 2; SUPPLEMENTARY FIGS. 1–6). All datasets with appropriate sampling place *L. suavissimus* as the sister group of *N. mikawai* (FIGS. 1, 2; SUPPLEMENTARY FIGS. 1–6). Results from the ITS+28S+*RPB1*+*RPB2* dataset are in general agreement with analyses of Grand et al. (2004, 2011) and Sotome et al. (2008).

A single-gene phylogeny of the *Neofavolus* group was constructed with 33 ITS sequences, including 20 sequences from Sotome et al. (2013), focusing on the position of *L. suavissimus* (= *N. suavissimus*, which was not sampled by Sotome; FIG. 2). The ML analysis provides strong bootstrap support for monophyly of 10 individuals of *L. suavissimus* (FIG. 2).

However the *L. suavissimus* group is divided into two distinct lineages with a strong geographic pattern; one includes collections from Tennessee, New York and Quebec, and the other includes collections from France, Germany, Russia and Alaska (FIG.2). In addition three unidentified collections of *Neofavolus* from New York and Massachusetts were placed as a paraphyletic assemblage, with a nested clade of Japanese collections of *N. alveolaris* and *N. cremeoalbidus* from Sotome et al. (2013). The topology of the *Neofavolus* clade is consistent in the ITS and multigene analyses (FIGS. 1, 2).

Ancestral-state reconstruction suggests a complex pattern of transitions between round pores, angular pores and lamellae. Under ML the pattern of hymenophoral transitions is largely equivocal (results not shown). Under parsimony the ancestral hymenophoral configuration for the *Lentinus*/*Polyporellus* clade is estimated to be circular pores, with independent transitions to angular pores and lamellae (FIG. 1). The ancestral state for the *Neofavolus* clade is estimated to be angular pores, with a single transition to lamellae in *L. suavissimus* (= *N. suavissimus*).

TAXONOMY

Neofavolus suavissimus (Fr.) J. S. Seelan, Justo and Hibbett, comb. nov.

MycoBank MB810089

Lentinus suavissimus Fries., Synopsis Generis Lentinorum 13. 1836. Basionym.

≡ *Pocillaria suavissima* (Fr.) Kuntze, *Revisio generum plantarum* 2: 866 (1891)

≡ *Hemicybe suavissima* (Fr.) P. Karst.: 249. 1897.

≡ *Panus suavissimus* (Fr.) Singer, Lilloa 22: 274. 1951.

= *Lentinus anisatus* Henn., Verhandlungen des Botanischen Vereins der Provinz Brandenburg 39: 95. 1898.

Notes. Four individuals of *L. suavissimus* (L09791624, L09791625, TMI18871, DSH2011) conformed to Pegler's (1983) description of the species. However one collection of *L. suavissimus* differed from the description in Pegler as follows: Fruiting bodies of collection

ADD7 were slightly larger than those reported for *L. suavissimus* by Pegler (pileus 3–8 cm diam, stipe 1–3 cm × 5–8 mm in ADD7, vs. pileus 0.5–5 cm diam, stipe 0.5–2 cm × 4–6 mm). The pileus of ADD7 was white when fresh, whereas Pegler (1983) reported that pileus of *L. suavissimus* is yellow to tawny ochraceous (FIG. 3A, B). The pale appearance of ADD7 might be due to rain. In addition the stipe base is red in ADD7, which has not been noted in *L. suavissimus* (FIG. 3A).

Lentinus suavissimus is uncommon, but it has been widely reported (sometimes under the synonyms *Poccularia haematopus* [Berk.] Kuntze, *Panellus haematopus* [Berk.] Murr. and *Lentinus haematopus* Berk.) in North America, including Canada (Ontario, Quebec, Saskatchewan) and USA (Maine, Michigan, New Hampshire, New York, North Carolina, Tennessee, Vermont, Virginia) (Murrill 1915, Kauffman 1918, Mains et al. 1939, Bigelow, 1959, Bigelow and Barr 1962, Miller and Manning 1976, Pomerleau 1980, McNeil 2006), Europe, including Austria, Czech Republic, Denmark, Estonia, Finland, France, Germany, Latvia, Norway, Poland and Sweden (Pilát, 1946, Pegler 1983a, Knudsen et al. 2012), and Japan (Kobayashi 2007). The precise locality of LE127 is not known (but might be Russia). Specimen DSH2011 from Alaska represents a significant westward range extension for the species in North America.

Specimens examined. UNITED STATES. New York: Adirondack mountains, 44°06′45″N 73°55′26″W, 800 ft. On dead wood, 15 Oct 2012, Jaya Seelan (ADD7); Alaska: Fairbanks, on dead branch, 06 Jul 2011, David Hibbett, (DSH2011); GERMANY: Bayern: Pensenberg. On dead branch, 24 Aug 1960, Donk, MA (L0791625).CZECH REPUBLIC: Boheman, Sobeslav, South of Bohemia. On dead log, 06 Aug 1958, Kotlaba, F (L0791624). JAPAN. Mount Otyonosen, Tottori. On fallen branch, 02.10.1994, Nagasawa, E (TMI18871).

DISCUSSION

Relationships between the agaricoid genus *Lentinus* and certain polypores have long been suspected based on anatomical features (Corner 1981, Pegler 1983a) and phylogenetic analyses with scattered sampling of both genes and species (Hibbett et al. 1993, Tage Roland 2001, Krüger et al. 2008, Sotome et al. 2008, Grand et al. 2011, Sotome et al. 2013). The present study includes the most comprehensive phylogenetic analysis of *Lentinus* so far, with a focus on southeastern Asian taxa. Most species of *Lentinus* subg. *Lentinus* sensu Pegler (1983a) form a monophyletic group along with the pileate-stipitate *Polyporellus* (FIG. 1), but *Lentinus suavissimus* is not in this group; the new combination *Neofavolus suavissimus* is proposed. Relationships among the species of *Polyporellus*,which form a strongly supported clade, and *Lentinus* sects. *Lentinus, Rigidi, Lentodiellum, Dicholamellatae* and *Tigrini* sensu Pegler are not well resolved (FIG. 1). The taxonomic disposition of the *Lentinus*/*Polyporellus* clade will await improved phylogenetic resolution, perhaps from genomic analyses (complete genomes are available for *L. tigrinus* and *P. arcularius*). If the topology of the four-gene tree is upheld, one option would be to combine *Polyporellus* into *Lentinus*. In the meantime we discuss *Lentinus* and *Polyporellus* as separate genera.

There have been parallel transformations between angular pores and sub-poroid lamellae in the *Lentinus*/*Polyporellus* clade and the *Neofavolus* clade (FIG. 1). In *Neofavolus* the topology suggests one most parsimonious reconstruction, implying derivation of sub-poroid lamellae from angular pores (FIG. 1). The hymenophore of *N. suavissimus* is sub-poroid only at the apex of the stipe, whereas in *L. tigrinus* the hymenophore is sub-poroid across the entire width of the pileus (FIG. 1; Hibbett et al. 1993a). These structural differences reflect the convergent origins of sub-poroid lamellae from poroid ancestors in *Neofavolus* and the *Lentinus*/*Polyporellus* clade (Pegler 1983a, Hibbett et al. 1993a).

The precise pattern of transformations in hymenophore configurations in the *Lentinus*/*Polyporellus* clade is not well resolved, in part due to uncertainty about the branching order at the base of the clade. *Polyporus tricholoma*, which is reported as having circular or angular pores, is strongly supported as the sister group of the *Lentinus*/*Polyporellus* clade. The most parsimonious reconstruction of character states suggested that the plesiomorphic condition for the *Lentinus/Polyporellus* clade is to have circular pores (FIG. 1, SUPPLEMENTARY FIG. 7). On some tree topologies, a single transition from circular to angular pores is reconstructed in the lineage leading to *P. arcularius* and *P. brumalis*, but in other trees these two species do not form a monophyletic group (FIG. 1, SUPPLEMENTARY FIG. 7). In all trees the species of *Lentinus* other than *L. tigrinus* form a clade (albeit weakly supported), which implies a single transition to wholly lamellate hymenophores. The sub-poroid hymenophore of *Lentinus tigrinus* is morphologically intermediate between lamellae and angular pores, but the precursor to the wholly lamellate condition in the *Lentinus/Polyporellus* clade is uncertain.

Relationships of *Lentinus* sect. *Dicholamellatae*.—Pegler (1983a) placed three species in section *Dicholamellatae: L. araucariae*, *L. brunneofloccosus* and *L. badius.* Manimohan et al. (2004) and Njouonkou et al. (2013) described *L. cystidiatus* and *L. dicholamellatus* respectively as members of this section. However morphological features reported for *L. cystidiatus* (cheilocystidia and absence of hyphal pegs) suggest that it is probably a *Panus* and ITS sequence data from a specimen identified as *L. dicholamellatus* (TENN060790) suggest that it is in fact *L. sajor-caju*, which will be discussed in a forthcoming study focused on the *L. sajor-caju* complex (Seelan et al. unpubl).

Morphological characters distinguishing sect. *Dicholamellatae* include a verrucose-squamose pileal surface, wide-angled skeleto-ligative hyphae and non-inflated generative

hyphae, radiate hymenophoral trama, abundant hyphal pegs, often dichotomously furcate hymenophore, without true lamellulae, ellipsoid to cylindrical spores and large basidia (17–20 × 3.5–4.5 μm). Species of section *Dicholamellatae* exhibit metavelangiocarpic development, with a universal veil eventually reduced to verrucose squamules, which differs from the gymnocarpic development represented in other *Lentinus* species like *L. squarrosulus*, *L. sajor-caju*, *L. tigrinus*, *L. striatulus*, *L. scleropus*, *L. bertieri*, *L. swartzii* and *L. polychrous*. *Lentinus araucariae* is similar to *L. badius*, except that it has subdistant and furcating lamellae.

Section *Dicholamellatae* is represented here by four isolates that form a strongly supported group (FIG.1). Isolate JS0094 from Borneo is macromorphologically similar to *L. araucariae* as described in Pegler (1983a) (FIG. 3E, F). The pilea surface was thin and with subdistant, dichotomizing lamellae compared to other *L. badius* collections. However microscopic characters of this isolate conform to the description of *L. badius* and were indistinguishable from those of the isolate JSKT5858 from peninsular Malaysia (FIG. 3G, H). All four specimens of section *Dicholamellatae* had abundant hyphal pegs. Pegler (1983a) reported that *L. badius* contains more abundant hyphal pegs than *L. araucariae*.

The isolates of Borneo and peninsular Malaysia form a sister clade to the two isolates from Thailand. Isolate PU00436 was identified as *L. araucariae* in the herbarium collection, but it matches Pegler's description of *L. badius*. We examined the holotype of *L. araucariae* (PC, New Caledonia); none of the collections from this study match the holotype. Thus at present we find evidence of at least two species that conform morphologically to Pegler's concept of *L. badius,* one in Malaysia and another in Thailand.

Pegler placed into synonymy with *L. badius* the names *Agaricus verrucarius* Berk. (West Bengal, Darjeeling), *Lentinus inquinans* Berk. (Nepal), *Lentinus brevipes* Cooke (Malay

Peninsula, Perak), *Lentinus fuscus* Lloyd (Singapore), and *Lentinus inverseconicus* (Vietnam), and he placed into synonymy with *L. araucariae*, the name *Panus verruciceps* Hongo (from Papua New Guinea). Pegler reported that the type locality of *L. badius* (synonym *Panus badius*) is in the Philippines. Meanwhile the type locality for *L. araucariae* is recorded from New Caledonia and this species is mainly restricted to Australasia and Sabah, Malaysia. Resolving the species of section *Dicholamellatae* will require additional sampling from across the geographic range of *L. badius* and *L. araucariae*, including as many type specimens as possible.

Relationships of Lentinus *sect.* Rigidi.—Section Rigidi comprises *L. sajor-caju*, *L. squarrosulus* and *L. polychrous* according to Pegler (1983a). Pegler (1983a) placed *L. sajor-caju* as the type species for section *Rigidi*. Section *Rigidi* is represented by four isolates of each species.

Lentinus sajor-caju is the only species reported in the section that has an annulus and gills with abundant hyphal pegs. Meanwhile *L. squarrosulus*, which has a slender stipe, and *L. polychrous*, which has a short, thick stipe, lack an annulus (Corner 1981, Pegler 1983a). Grand (2011) and Sotome et al. (2008) said that this section was poorly resolved due to lack of sampling. Our study suggests that the section *Rigidi* is monophyletic. The combined four-gene phylogeny moderately supported the monophyly of *L. sajor-caju*, *L. squarrosulus* and *L. polychrous* as in Pegler's classification. *Lentinus sajor-caju* forms a clade that is sister to a clade containing *L. squarrosulus* and *L. polychrous* (FIG. 1).

Lentinus sajor-caju revealed wide variation in morphological features in collections from different areas (Pegler 1983a). According to Pegler (1983a), 26 synonyms of *L. sajor-caju* have been reported in prior classifications. Two isolates (SNP24989, JS0056) from Borneo form a clade that is sister to a clade containing two isolates (FRI62056, TENN59793) from peninsular Malaysia and Thailand respectively. The Bornean isolates, from the mainland (JS0056) and Gaya

Island (SNP24989), are morphologically different based on the pileus shape. The pileus of isolate JS0056 is larger (7–9 cm) diam compared to isolate SNP24989, which is 3–5 cm diam. Both isolates had abundant hyphal pegs and an annulus. Isolate SNP24989 had a lobed margin (FIG. 3I), which is not present in isolate JS0056 (FIG. 3J). It is not clear whether these morphological variations correspond to species limits.

Lentinus polychrous resembles *L. badius* based on their pilea surface (squamules and warts present as in *L. badius*) and forked hymenophore. However *Lentinus polychrous* has dimitic to trimitic hyphal construction, rarely forking lamellae and a reduced number of hyphal pegs, which is different from *L. badius*, which has dimitic hyphal construction, strongly forking lamellae and abundant hyphal pegs, and explains why this species was not placed by Pegler (1983a) in section *Dicholamellatae*. *Lentinus polychrous* often has distinctive coloration (ochraceous to brown) on the pileus surface with scattered squamules as described in Pegler (1983a), which we observed in some of the herbarium specimens or fresh materials from Indonesia (AR618), Thailand and Malaysia.

L. polychrous has a pileus surface that resembles chamois leather in both color and texture, which contrasts with dark brown lamellae with a reddish or purplish tint, according to Pegler (1983a). This morphological character was observed in isolate AH00024 from Thailand. Meanwhile isolate KM141387 from Thailand did not have the reddish lamellae but it had a greenish to dark brown pileus and rusty brown lamellae. Isolate JS0054 from Borneo had light to cream brown pileus with scattered squamules as in *L. badius* (FIG. 3K).

Lentinus tigrinus is reported frequently in tropical regions especially in southeastern Asia (Sumaiyah et al. 2007, Dulay et al. 2012, Bolhassan et al. 2013). Pegler (1983a) reported that *L. tigrinus* has essentially a north temperate distribution. He also added that this species often is

confused with *L. squarrosulus*, which is mainly found in paleotropical and Australasian regions. The main cause of confusion between *L. tigrinus* (section *Tigrini*) and *L. squarrosulus* (section *Rigidi*) is their similar scabrous pilea surfaces (FIG. 3L). Grand et al. (2011) generated an ITS phylogeny and performed mating studies of section *Lentinus* emphasizing *L. tigrinus*, confirming that it has only a Eurasian and north temperate distribution.

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LEGENDS

FIG. 1. Phylogenetic relationships of members of the *Lentinus* and *Neofavolus* clades inferred from 28S, ITS, *RPB1* and *RPB2* sequences. Topology from ML analysis. Support values along branches are from ML bootstrap (≥ 70) and BI analyses (PP ≥ 0.95) respectively. Symbols on branches indicate transitions in hymenophoral form estimated with parsimony. Sections of *Lentinus* sensu Pegler (1983) are indicated. Hymenophore character states occurring within *Lentinus*, *Polyporellus* and *Neofavolus* are illustrated.

FIG. 2. ML analysis of the ITS dataset of the *Neofavolus* clade. Support values along branches are from ML bootstrap (≥ 70) and BI analyses (PP ≥ 0.95) respectively.

FIG. 3. *Neofavolus suavissimus (= L. suavissimus).* A, B. *Neofavolus suavissimus* from Adirondack Park, New York (ADD7, Photo by Jaya Seelan). C, D. Sub-poroid hymenophore in young basidiocarp (Photo by Jiri Lastuvka, Bohemia). E, F. *Lentinus badius* from Borneo (JS0094). G, H. *Lentinus badius* from Peninsular Malaysia (JSKT5858). I. *Lentinus sajor-caju* from mainland Borneo (SNP24989). J. *Lentinus sajor-caju* from Gaya Island (JS0056). K. *Lentinus polychrous* from Borneo (JS0054). L. *Lentinus squarrosulus* (BORHF0009).

FOOTNOTES

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TABLE I. Major molecular systematic studies for *Lentinus*, *Polyporellus* and related polypores showing the numbers of species and individual (in parentheses) samples

Lentinus subg. *Lentinus*/ section[a]	Hibbett et al. (1993)	Rolen, Tage (2001)	Krüger et al. (2008)	Sotome et al. (2008)	Grand et al. (2011)	Sotome et al. (2013)	This study
Lentinus	1(1)	3 (60)			3(31)		3(8)
Tigrini	1(1)	1(1)	1(7)	1(1)	2(31)	1(1)	1(2)
Dicholamellatae					1(1)		1(4)
Rigidi				3(4)	2(3)		3(12)
Lentodiellum		2(4)			2(2)		2(2)
Pleuroti							1(10)
Related genera							
Polyporellus	1(1)		6(56)	3(7)	4(12)	1(1)	4(9)
Neofavolus	1(1)		1(1)			3(15)	3(18)
Other Polyporales	6(6)		17(19)	27 (64)		12 (20)	40(50)
Gene (s)	ITS, LSU	ITS, LSU	ITS, LSU	LSU, *rpb2*, *ATP6*	ITS	ITS, LSU	ITS, LSU, *rpb1*, *rpb2*

[a] Section *Lentinus* includes (*L. bertieri*, *L. crinitus* and *L. swartzii*); section *Tigrini* includes *L.tigrinus* and *L. glabratus*; section *Rigidi* includes *L. polychrous*, *L. sajor-caju* and *L. squarrosulus*, section *Dicholamellatae* includes *L. badius* and section *Lentodiellum* includes *L. striatulus* and *L. scleropus*. *Polyporellus* group includes *Polyporus arcularius*, *P. brumalis*, *P. ciliatus* and *P. tricholoma*.

TABLE II. Taxon sampling, geographic location, specimen-voucher information and GenBank accession numbers

Species	Specimen voucher/cultures	Location	GenBank accession number		
			ITS	nLSU	*RPB1*
Lentinus badius	JS0094	Crocker Range Park, Borneo	KP283478	KP283512	KP325691
L. badius	JSKT5858	Sungkai, Perak, Peninsular Malaysia	KP283479	KP283513	KP325690
L. badius	DED07668	Phuket, Thailand	KP283480	KP283518	KP325692
L. badius	PU00436	Nakhon Ratchasima, Thailand	KP283481		
L. crinitus	DSH9243C	Costa Rica	KP283495	KP283523	KP325687
L. crinitus	AJ527	St John, US Virgin Islands		KP283521	KP325688
L. polychrous	AH00024	Phang-Nga, Thailand	KP283485		
L. polychrous	JS00054	Malungong, Borneo	KP283486		
L. polychrous	KM141387	Thailand	KP283487	KP283514	
L. sajor-caju	FRI62056	FRIM, Peninsular Malaysia	KP283492	KP283509	KP325677
L. sajor-caju	SNP24989	Gaya Island, Borneo	KP283493	KP283510	KP325678
L. sajor-caju	JS0056	Kinabalu Park, Borneo	KP283494	KP283511	KP325679
L. squarrosulus	CUI6513	Yunnan, China	KP283482	KP283516	KP325680
L. squarrosulus	FRIM4180	Pahang, P. Malaysia	KP283483	KP283517	KP325682
L. squarrosulus	BORHF0009	Sorinsim, Borneo	KP283484	KP283515	KP325681
L. tigrinus	DSH92D787	North Carolina, USA	KP283488		KP325689
L. suavissimus	ADD7	Adirondacks State Park, NY, USA	KP283501	KP283527	KP325694
L. suavissimus	LE0791625	Germany	KP283500		
L. suavissimus	TENN19955	Great Smoky Mountain National Park, TN, USA	KP283504		
L. suavissimus	TENN11096	Great Smoky Mountain National Park, TN, USA	KP283505	AY615970	
L. suavissimus	TENN13225	Great Smoky Mountain National Park, TN, USA	KP283503		
Species	Specimen voucher/cultures	Location	GenBank accession numbers		
			ITS	nLSU	*RPB1*

L. suavissimus	TENN13316	Quebec, Canada	KP283502		
L. suavissimus	TENN11330	France	KP283498	AY615969	
L. suavissimus	TENN11129	France	KP283499		
L. suavissimus	LE127	Russia	KP283497		
L. suavissimus	DSH2011 (AL57)	Fairbanks, AK, USA	KP283496	KP283525	KP325693
Polyporus arcularius	DSH92-132	Taman Negara, Pahang, P. Malaysia	KP283489	KP283522	KP325686
Polyporus brumalis	PB4 (EP4)	Worcester, MA, USA	KP283490	KP283519	KP325685
Polyporus brumalis	PB1	Newton hill, MA, USA	KP283491	KP283520	
Polyporus ciliatus	TFB10167 (SP3)	Roskilde Amt, Denmark			KP325684
Polyporus ciliatus	TFB7480 (SP28)	Finland			KP325683
Neofavolus sp.	MA672	Worcester, MA, USA	KP283506	KP283524	KP325696
Neofavolus sp.	ADD5	Adirondacks State Park, NY, USA	KP283508		
Neofavolus sp.	SAV10	Savoy Mountain, Massachusetts, USA	KP283507	KP283526	KP325695

Abbreviations: JS, author's collection number; DED, PU, AH, Biotech Bangkok herbarium; SNP, Sabah National Park herbarium; BORHF, BORNEENSIS herbaria collections; LE, Leiden Herbarium; SAV, MA, ADD, EP,PB, DSH, AJ, Clark University Herbaria collections (different letters indicate different collectors or area collected); SP, Culture collection from University of Tennessee Herbarium (TENN); CUI, Collection from Professor Yu Cheng Dai (Academy of Sciences, China); FRI, Forest Research Institute of Malaysia (FRIM) Herbaria; K(M), Royal Botanical Garden Kew, London.

TABLE III. Phylogenetic datasets used in this study

Dataset	Ingroup sequences	Outgroup	Parsimony-informative characters (including gap)	Aligned length (bp)
nLSU+ITS+*rpb1*+*rpb2*	40 *Lentinus*/ *Polyporellus* taxa and 59 other Polyporales	*Dendocorticium sulphurellum* and *Lopharia cinerascens* (Polyporales)	3728	6402
nLSU+ITS+*rpb1*	40 *Lentinus*/*Polyporellus* taxa and 58 other Polyporales	*Dendocorticium sulphurellum* and *Lopharia cinerascens* (Polyporales)	2334	4553
nLSU+ITS+*rpb2*	37 *Lentinus*/*Polyporellus* taxa and 58 other Polyporales	*Dendocorticium sulphurellum* and *Lopharia cinerascens* (Polyporales)	2272	5025
ITS	10 *L. suavissimus* taxa, 18 *Neofavolus* and 5 *Favolus* taxa	*Favolus brasilliensis*(Polyporales)	238	711

= Sectional type

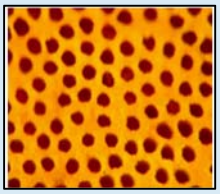
= Generic type

Hymenophore type

3 Lamellae

2 Subporoid lamellae

1 Angular pores



0 Circular pores

Lentinus squarrosulus **BORHF0009 Borneo**
Lentinus squarrosulus **CUI6513 China**
Lentinus squarrosulus **FRIM4180 Peninsular Malaysia**
Lentinus squarrosulus AB478883 Japan
Lentinus polychrous **AH00024 Thailand**
Lentinus polychrous **JS0054 Borneo**
Lentinus polychrous AB478882 Thailand
Lentinus polychrous **KM141387 Thailand**
Lentinus sajor-caju **FRI62056 Peninsular Malaysia**
Lentinus sajor-caju TENN59793 Thailand
Lentinus sajor-caju **SNP24989 Borneo**
Lentinus sajor-caju **JS0056 Borneo**
Lentinus swartzii TRMO194 Costa Rica
Lentinus swartzii TRMO166 Costa Rica
Lentinus crinitus **DSH92N43C Costa Rica**
Lentinus crinitus **AJ527 St. John USA**
Lentinus crinitus TFB9145 Florida USA
Lentinus crinitus TENN59372 Dominican Republic
Lentinus bertieri TENN59781 Dominican Republic
Lentinus bertieri TENN59770 Dominican Republic
Lentinus badius **PU00436 Thailand**
Lentinus badius **DED07668 Thailand**
Lentinus badius **JS0094 Borneo**
Lentinus badius **JSKT5858 Peninsular Malaysia**
Lentinus striatulus **GU207311 Costa Rica**
Lentinus scleropus **GU207310 Mexico**
Polyporus brumalis **EP4 Massachusetts USA**
Polyporus brumalis FJ596883 Great Smoky Mountain, USA
Polyporus brumalis **PB1 Massachusetts USA**
Polyporus arcularius **DSH92132 Peninsular Malaysia**
Polyporus arcularius TENN56447 Costa Rica
Polyporus arcularius WD2138 Japan
Polyporus ciliatus **TFB10167 Denmark**
Polyporus ciliatus **TFB7480 Finland**
Lentinus tigrinus **DSH92D787 North Carolina, USA**
Lentinus tigrinus TENN9093 Louisiana USA
Polyporus tricholoma TENN56503 Puerto Rico
Microporus xanthopus Cui8242
Microporus affinis LE269654
Daedaleopsis confragosa WD747
Lignosus rhinocerus PEN94
Coriolopsis gallica RLG7630sp
Coriolopsis trogii RLG4286sp
Earliella scabrosa PR1209
Fomes fomentarius DAOM129034
Pachykytospora tuberculosa JX124705
Coriolopsis cf. *byrsina* FP105050sp
Amauroderma rugosum ML56
Cryptoporus volvatus DAOM211791
Ganoderma sp.
Ganoderma tsugae AFTOL-ID771
Ganoderma lucidum WD565
Coriolopsis cf. *caperata* CR22
Perenniporia medulla-panis Cui3274
Dichomitus squalens MN929
Donkioporia expansa P-188
Datronia mollis RLG6304sp
Polyporus leprieurii TENN10489
Polyporus varius WD2347
Pseudofavolus cucullatus TENN8744
Pseudofavolus cucullatus TENN11221
Polyporus squamosus AFTOL-ID704
Datronia scutellata RLG9584T
Echinochaete russiceps TFM-F24255
Polyporus umbellatus WD719
Polyporus tuberaster DAOM7997B
Polyporus badius WD2341
Polyporus tubiformis WD1939
Polyporus melanopus DAOM212269
Polyporus dictyopus TENN59385
Polyporus udus WD1878
Favolus acervatus TFM-F27345 Japan
Favolus acervatus TFM-F14764 Japan
Favolus acervatus WD2351 Japan
Favolus emerici TFM-F21697 Japan
Favolus roseus PEN33 Malaysia
Favolus brasiliensis INPA241452 Brazil
Neofavolus cremeoalbidus TUMH50009 Japan
Neofavolus cremeoalbidus TUMH50008 Japan
Neofavolus alveolaris TUMH50003 Japan
Neofavolus alveolaris WD2358 Japan
Neofavolus sp. **SAV10 Massachusetts USA**
Neofavolus sp. **MA672 Massachusetts USA**
Neofavolus sp. **ADD5 New York USA**
Lentinus suavissimus **ADD7 New York USA**
Lentinus suavissimus AY615970 USA
Lentinus suavissimus **DSH2011 Fairbanks, Alaska USA**
Neofavolus mikawai TFM-F27417 Japan
Neofavolus mikawai TUMH50005 Japan
Trametes sanguinea PRSC95
Trametes cubensis TJV93 213sp
Trametes elegans FP105679sp
Trametes maxima OH189sp
Trametes versicolor FP135156sp
Trametes hirsuta RLG5133T
Trametes villosa FP71974R
Trametes polyzona BKW004
Lopharia cinerascens FP105043sp
Dentocorticium sulphurellum T609

Section: *Rigidi*

Section: ***Lentinus***

Section: ***Dicholamellatae***

Section: ***Lentodiellum***

Polyporellus

Section: ***Tigrini***

Polyporellus

Remaining *Polyporus* and additional genera

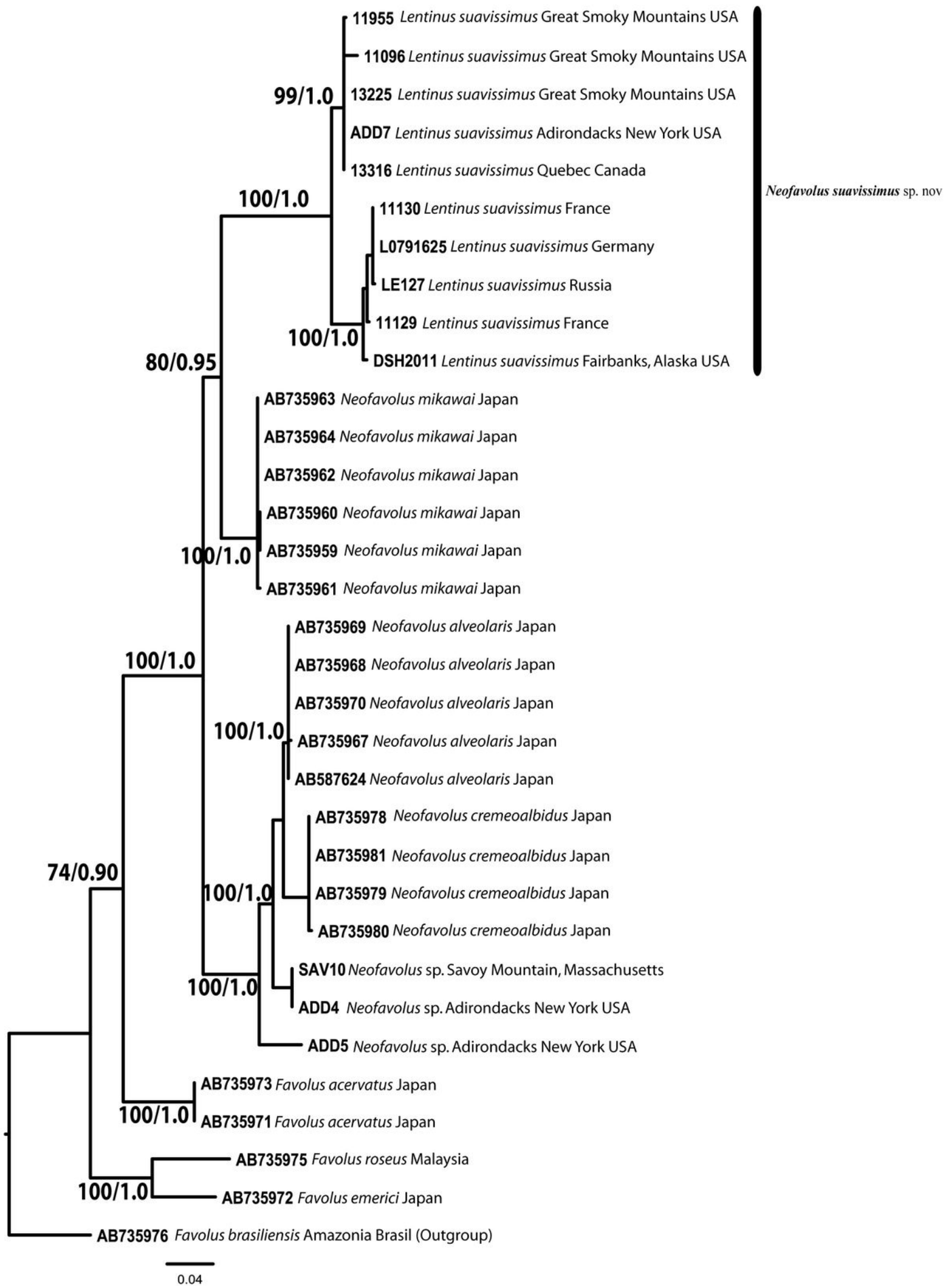
Favolus

Neofavolus

Section: ***Pleuroti***

Outgroup

0.05


11955 Lentinus suavissimus Great Smoky Mountains USA
11096 Lentinus suavissimus Great Smoky Mountains USA
99/1.0
13225 Lentinus suavissimus Great Smoky Mountains USA
ADD7 Lentinus suavissimus Adirondacks New York USA
13316 Lentinus suavissimus Quebec Canada
100/1.0
11130 Lentinus suavissimus France
L0791625 Lentinus suavissimus Germany
LE127 Lentinus suavissimus Russia
11129 Lentinus suavissimus France
100/1.0
DSH2011 Lentinus suavissimus Fairbanks, Alaska USA
Neofavolus suavissimus sp. nov
80/0.95
AB735963 Neofavolus mikawai Japan
AB735964 Neofavolus mikawai Japan
AB735962 Neofavolus mikawai Japan
AB735960 Neofavolus mikawai Japan
100/1.0
AB735959 Neofavolus mikawai Japan
AB735961 Neofavolus mikawai Japan
AB735969 Neofavolus alveolaris Japan
100/1.0
AB735968 Neofavolus alveolaris Japan
AB735970 Neofavolus alveolaris Japan
100/1.0
AB735967 Neofavolus alveolaris Japan
AB587624 Neofavolus alveolaris Japan
AB735978 Neofavolus cremeoalbidus Japan
AB735981 Neofavolus cremeoalbidus Japan
74/0.90
100/1.0
AB735979 Neofavolus cremeoalbidus Japan
AB735980 Neofavolus cremeoalbidus Japan
SAV10 Neofavolus sp. Savoy Mountain, Massachusetts
100/1.0
ADD4 Neofavolus sp. Adirondacks New York USA
ADD5 Neofavolus sp. Adirondacks New York USA
AB735973 Favolus acervatus Japan
100/1.0
AB735971 Favolus acervatus Japan
AB735975 Favolus roseus Malaysia
100/1.0
AB735972 Favolus emerici Japan
AB735976 Favolus brasiliensis Amazonia Brasil (Outgroup)
0.04


A
08/15/2012
B
08/15/2012
C
D
E
F
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