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A new poroid species of *Resupinatus* from Puerto Rico, with a reassessment of the cyphelloid genus *Stigmatolemma*

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Abstract: A fungus with gelatinous poroid fruiting bodies was found in Puerto Rico and determined by macro- and micromorphology to be most similar to members of the lamellate agaric genus *Resupinatus.* This species is described as a new species, *Resupinatus porosus.* Phylogenetic analyses of ribosomal DNA sequences support the inclusion of this fungus in the clade containing *Resupinatus,* and indicate that this monophyletic group also includes members of *Asterotus* and the cyphelloid genus *Stigmatolemma. Resupinatus porosus* is another example of tropical poroid representatives of lamellate agaric genera. *Resupinatus* is emended to include species with poroid (*R. porosus*) or merulioid (*R. merulioides*) hymenophore as well as those with laterally stipitate (*Asterotus*) or cyphelloid (*Stigmatolemma*) fruiting bodies. Seven new combinations in *Resupinatus* are proposed to accommodate well-known species of *Stigmatolemma.*

Key words: Agarics, *Henningsomyces,* hymenophore evolution, phylogeny, *Porotheleum,* rDNA, tropical fungi

> "*Resupinatus* is an agaric genus with small to minute cupulate fruitbodies. If one takes away the gills, which may be few, one has constructed species that would find their place in the cyphellaceous genus *Stigmatolemma…*" (Donk 1966)

INTRODUCTION

Resupinatus S.F. Gray is a small genus of euagarics (Hibbett and Thorn 2001) with 49 specific and varietal epithets as of Apr 2005, excluding autonyms and invalid names (www.indexfungorum.org). Fruiting bodies of *Resupinatus* are small—a few mm to 2 cm in breadth—and generally pendent or resupinate on the undersides of rotting logs and other woody materials or herbaceous debris. Historically, members of *Resupinatus* were treated within the broad concept of *Pleurotus* (Fr.) P. Kumm. (e.g. Pilát 1935, Coker, 1944). In modern times, the genus has been characterized by a gelatinous zone in the pileus, hyaline inamyloid spores and the absence of metuloid cystidia. The genus *Hohenbuehelia* Schulzer shares the gelatinized layer and inamyloid spores, but has metuloid cystidia (Singer 1986, Thorn and Barron 1986). Singer (1986) treated the two genera as separate members of the tribe Resupinateae, family Tricholomataceae. In the Resupinateae, Singer (1986) also included three cyphelloid genera with cup-shaped fruiting bodies lacking gills, namely *Stigmatolemma* Kalchbr., *Stromatocyphella* W.B. Cooke, and *Aphyllotus* Singer. In contrast, Kühner (1980) treated *Hohenbuehelia* as a synonym of *Resupinatus,* in the tribe Resupinateae, family Pleurotaceae. Thorn and Barron (1986) showed that *Hohenbuehelia* and *Resupinatus* differ in a fundamental way-members of *Hohenbuehelia* posses a nematophagous anamorph referrable to *Nematoctonus* Drechsler, whereas *Resupinatus* species are non-nematophagous and lack a conidial anamorph. Despite this difference, Thorn and Barron (1986) treated *Hohenbuehelia* and *Resupinatus* as members of the same tribe, Resupinateae, and suggested that both genera were closely allied to *Pleurotus.*

More recent analyses of ribosomal DNA sequences (Hibbett and Vilgalys 1993, Hibbett et al 1997,

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Moncalvo et al 2000, Thorn et al 2000, Hibbett and Thorn 2001, Moncalvo et al 2002, Bodensteiner et al 2004, Binder et al 2005) have greatly clarified and changed our concepts of relationships among the pleurotoid fungi and other agarics. Thorn et al (2000) showed using sequences from nuclear rDNA that *Pleurotus* and *Hohenbuehelia* form a monophyletic group referred to as the family Pleurotaceae. Both genera are nematophagous, *Pleurotus* by toxic droplets and *Hohenbuehelia* by adhesive knobs; a single known *Hohenbuehelia* has both adhesive knobs and toxic droplets (Thorn et al 2000). Sequences from other members of the Resupinateae, including *Asterotus* Singer and *Resupinatus*, formed a monophyletic group within the Tricholomataceae sensu lato, well separated from the Pleurotaceae (Thorn et al 2000). This clade also includes species of *Stigmatolemma* (Moncalvo et al 2002, Bodensteiner et al 2004). As yet, no sequences from the other cyphelloid members of the Resupinateae, *Aphyllotus* and *Stromatocyphella*, have been available for phylogenetic analysis.

The smallest species of *Resupinatus*, such as *R. kavinii* (Pilát) M.M. Moser, form gregarious, small cups, 1–2 mm in diam, with a few reduced lamellae. Fruiting bodies of *Stigmatolemma* are minute cups, 0.1–1.5 mm in diam, gregarious or crowded on the substratum, and often surrounded by or seated in a tomentose mat of hyphae called a subiculum. Basidia line the inner surface of the cups and there are no wrinkles or lamellae. As in *Resupinatus*, the trama is fuscous and gelatinous, and the basidiospores are hyaline and inamlyloid. Romagnesi (1950, 1953, both cited in Donk 1962a) noted the similarities between *R. kavinii* (as *Scytinotopsis kavinii*) and *Stigmatolemma poriaeforme* (Pers.: Fr.) Singer (as *Solenia poriaeformis*). The generic name *Stigmatolemma* was poorly known and disused until Talbot (1956) redescribed the type species as *Porotheleum incanum* (Kalchbr.) Sacc. Up to that time, species of *Stigmatolemma* had been classified primarily in *Cyphella* (Burt 1915, Bourdot and Galzin 1928), *Porotheleum* (Cunningham 1953, Cooke 1957) or *Solenia* (Burt 1924). Singer (1962) resurrected *Stigmatolemma*, provided a modern description for the genus, and treated it as a ''reduced'' (cyphelloid) member in the tribe Resupinateae, together with *Asterotus*, *Hohenbuehelia* and *Resupinatus*. Donk (1962a) emended the genus and provided discussion of four species, *S. incanum* Kalchbr., *S. conspersum* (Pers. : Fr.) Donk, *S. taxi* (Lév.) Donk, and *S. urceolatum* (Wallr. ex Fr.) Donk.

In both *Resupinatus* and *Stigmatolemma*, the pileipellis is a loose trichodermium of coralloid-diverticulate hyphae that secrete hyaline to brownish crystalline material from fine cylindric or tapering pegs. In addition, the diverticulate elements at the cup margins in *Stigmatolemma* (see Redhead 1973) greatly resemble cheilocystidia from gill edges in *Resupinatus* (Thorn and Barron 1986). These pileipellis elements and cheilocystidia are very different from any structures found in *Hohenbuehelia.* Redhead and Nagasawa (1987) described *Resupinatus merulioides*, a species from Japan with a merulioid instead of strictly lamellate hymenophore. Other microscopic characters of this species greatly resemble the type species, *Resupinatus applicatus* (Batsch : Fr.) S.F. Gray. Redhead and Nagasawa (1987) remarked that the almost poroid hymenophore of *R. merulioides* is a unique feature within *Resupinatus*, but used the combination of gelatinized, fuscous tissues, globose, inamyloid spores, absence of metuloid cystidia and the presence of coralloid pileipellis elements with scattered tibiiform cystidioid ends as evidence for placing this species in *Resupinatus* as redefined by Thorn (1986).

Here, we describe a truly poroid representative of *Resupinatus* from Puerto Rico. The first collection of this species was found growing on wet wood by a mycology class of A. Perez (Univ. Interamericana at Arecibo) in the Toro Negro Commonwealth Forest at 1000 m above sea level (asl) in the Cordillera Central of Puerto Rico. Since then several other collections have been made in the Luquillo Mountains of Puerto Rico at 250–380 m asl at El Verde and the Bisley Watersheds. As a consequence of including a poroid species within *Resupinatus*, based upon phylogenetic analyses, we provide an emended description of the genus, and transfer well known species of *Stigmatolemma* to *Resupinatus.*

MATERIALS AND METHODS

Micromorphology.—Small portions of specimens of *Resupinatus* and *Stigmatolemma* were rehydrated in distilled water and then sectioned to observe micromorphological features of the hymenium, trama and pileipellis. Sections were mounted in Melzer's reagent, 0.05% (w/v) Cotton Blue in lactophenol and 2% (w/v) KOH for microscopy (Kirk et al 2001). Basidiospores were measured at 1000× magnification in Melzer's reagent. Size ranges presented are the median 80%, with extremes in parentheses. Color terms in descriptions are from Ridgway (1912). Herbarium acronyms follow Holmgren et al (1990).

DNA extraction and sequencing.—Genomic DNA was isolated from dried specimens of *R. porosus* using the E.Z.N.A. Fungal MiniPrep Kit (Omega-Biotech, Doraville, Georgia) as described in Martín and Winka (2000). The internal transcribed spacer regions of the nuclear ribosomal DNA (ITS) including the 5.8S rDNA gene were amplified using primers ITS1F and ITS4

(White et al 1990, Gardes and Bruns 1993), and the 5′ 1000-base region of the nuclear large ribosomal RNA gene (nLSU-rDNA) was amplified using primers LROR and LR5 (Vilgalys and Hester 1990). Amplifications were done using Ready-to-Go® PCR Beads (Amersham-Pharmacia Biotech, Upsala, Sweden) in a PE 9700 thermocycler (Perkin Elmer Applied Biosystems, Foster City, California), a hot start (94 C for 5 min), followed by 5 cycles of denaturation at 94 C for 30 s, annealing at 55 C for 30 s, and extension at 72 C for 1 min, then 33 cycles of 94 C for 30 s, 48 C for 30 s and 72 C for 1 min, with a final extension at 72 C for 10 min. Amplification products were cleaned using the E.Z.N.A. Clean kit (Omega Biotech) and both strands were sequenced separately using the primers listed above, plus LR3 and LR3R (Vilgalys and Hester 1990), with an ABI Prism 377 Genetic Analyzer and the ABI Prism™ BigDye™ Terminator Cycle Sequencing Ready Reaction kit with AmpliTaq®DNA Polymerase (Perkin Elmer Applied Biosystems). Sequence Navigator™ Sequence Comparison software (Perkin Elmer) was used to identify the consensus sequence from the two strands of each region sequenced.

Phylogenetic analyses.—To first verify the placement of *R. porosus* among the homobasidiomycetes, its nLSU-rDNA sequence was incorporated into the 877 taxa data matrix from Moncalvo et al (2002; downloaded from http://www.biology.duke.edu/fungi/mycolab/agaricphylogeny_start.html). Next, a data matrix of 55 nLSU-rDNA sequences (GenBank accession numbers listed in FIG. 2) was selected to represent: 1) all available sequences of *Resupinatus*, including its type species *R. applicatus* and *Stigmatolemma*; 2) putative gilled relatives of *Resupinatus*, as suggested from both traditional taxonomy (Kühner 1980, Singer 1986) and earlier molecular phylogenetic studies (Thorn et al 2000; Moncalvo et al 2000, 2002); and 3) selected poroid, cyphelloid and reduced forms that were previously shown to belong to the euagarics (Binder et al 2001, Moncalvo et al 2002, Bodensteiner et al 2004). Unfortunately, no cultures or sequences of *Stigmatolemma incanum*, the type species of *Stigmatolemma*, are available. Of these sequences, 48 were retrieved in an aligned format from http://www.biology.duke.edu/fungi/mycolab/agaricphylogeny_start.html, and sequences from *Resupinatus porosus, R. trichotis, R. applicatus, Rectipilus fasciculatus* and *Henningsomyces candidus* were manually aligned to these 48 sequences. The aligned sequence matrix was 1573 bases long including gaps, of which 747 bases where alignment was ambiguous or data were missing in one or more strains were excluded from the analyses (alignment available from TREEBase, http://www.treebase.org/, as S1363). The remaining 826 bases yielded 206 phylogenetically informative characters. Phylogenetic analyses of the 55-taxon sequence matrix employed equally-weighted parsimony (MP) in PAUP* 4.0b10 (Swofford 2003) and Bayesian Markov chain Monte Carlo (B-MCMC) statistics in MrBayes 3.1.1 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) using a Macintosh G4 computer. In addition, bootstrapped maximum likelihood (ML) analyses were conducted on 13-taxon subsets including the 10 members of the /resupinatus clade and various taxa selected as outgroups, in PAUP* 4.0b10 (Swofford 2003).

Maximum likelihood and Bayesian analyses used settings corresponding to a general reversible model of sequence evolution with allowance for some invariant sites and a gamma distribution (GTR + I + G) as suggested by hierarchical likelihood ratio tests in MrModeltest 2.0 (Posada and Crandall 1998, Nylander 2004), with the following parameter settings for execution of ML analyses in PAUP*: BaseFreq = (0.2506 0.1818 0.2938) Nst = 6 Rmat = (0.8001 6.2239 1.9635 0.8948 11.0001) Rates = gamma Shape = 0.6447 Pinvar = 0.5164; and comparable settings for MrBayes: Prset statefreqpr = dirichlet(1,1,1,1); Lset nst = 6 rates = invgamma; mcmc nchains = 4 ngen = 2 500 000 printfreq = 1000 samplefreq = 100 savebrlens = yes. Branch support for MP and ML analyses were obtained through bootstrapping with 100 replicates (for MP, each with 100 random additions of taxa), and for Bayesian analysis as the posterior probabilities calculated by MrBayes.

RESULTS

Resupinatus porosus M.P. Martín, Lodge et Thorn, sp. nov.

Species hymenophoro poroso a congeneribus diversa. Holotypus hic designatus PR-6198, *in CFMR conservatus, in Puerto Rico USA lectus.* nLSU-rDNA ex holotypus GenBank *numerus* DQ017064; ITS ex paratypus PR-5832 GenBank *numerus* DQ017063.

Pileus (FIG. 1a) convex to ungulate, astipitate and dorsally attached or attached laterally by a short pseudostipe, 5–25 (–55) mm diam × 10–15 mm tall, surface moist and hygrophanous, slightly shiny, minutely pubescent to pruinose, slightly rugulose near point of attachment, olive brown to light drab, mikado brown, chocolate brown or mahogany red (in age) near attachment to drab, dark drab, cinnamon drab, or beige toward margin, margins slightly translucent and tuberculate-striate, incised; context gelatinous, 1–3 mm deep, drab gray to beige, darkest near tubes; hymenophore poroid, tubes gelatinous, 1–5 mm in length, pores round, 2–5/mm, beige when young, then expanding (in PR-6329) to angular, 1–2/mm, with thin walls, light drab, drab, cinnamon drab to army brown, with margins slightly paler; odor and taste fungoid.

Pileipellis (FIG. 1b) a loose cutis of tangled, tubular-coralloid hyphae with thin walls, 2.5–4.0 (–5.0) µm diam, with tapering or cylindrical branchlets 3–6 (–10) µm long by 0.5–2.0 µm diam, heavily encrusted with brownish and highly refractive materials that gradually dissolve in KOH; trama a gelatinized, loose tangle of predominantly ascendant hyphae with

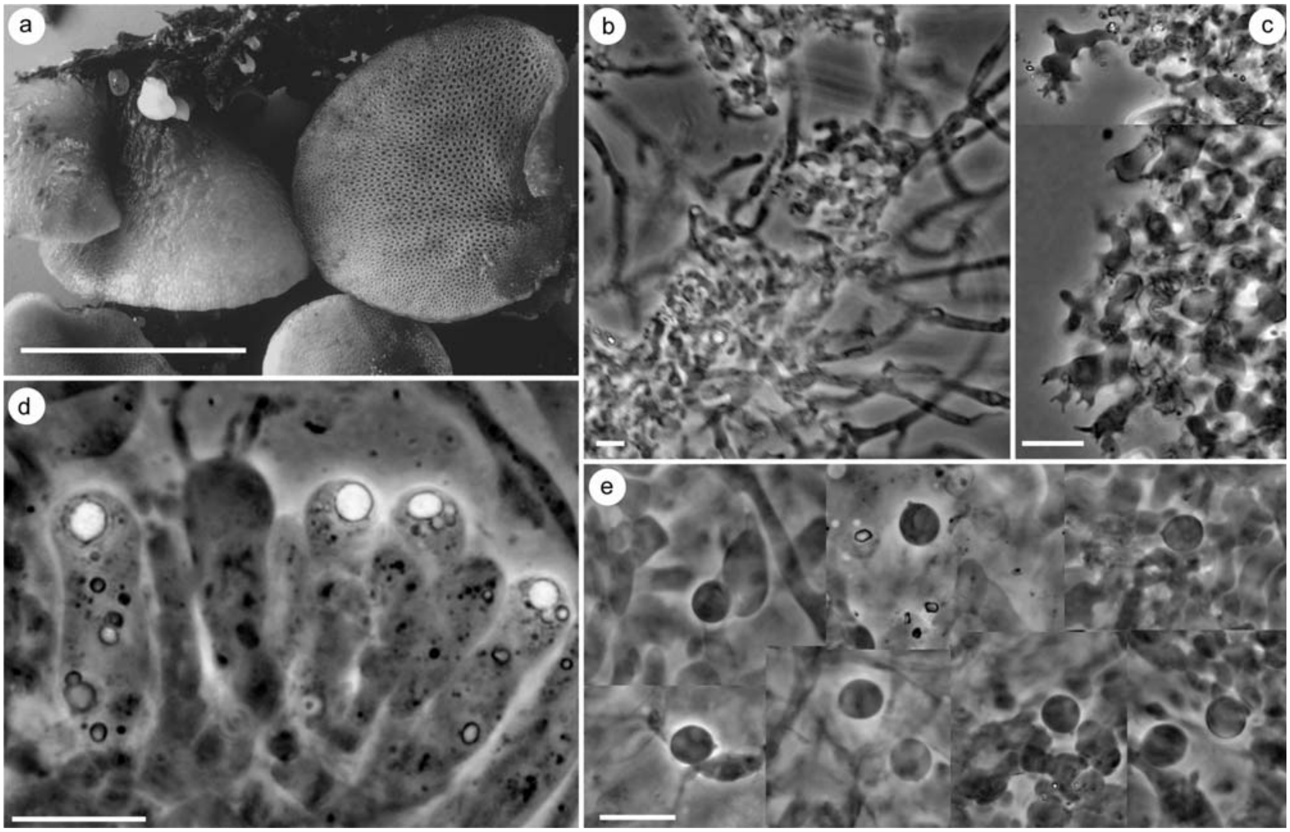

FIG. 1a–e. *Resupinatus porosus*: holotype, PR 6198 (a–c), and PR 6329 (d–e). a) Fruiting bodies, several turned over to show poroid hymenophore (scale bar 1 cm), b) scalp of pileipellis, showing coralloid cutis elements and tubular hyphae of underlying gelatinous zone, c) dissepiment fringe of diverticulate cheliocystidia-like elements, d) clavate basidioles and one mature basidium, e) basidiospores on pileipellis scalp. Scale bars: a = 1 cm, b–e = 10 μm.

clamps and thin, smooth walls, 1.5–4.0 (–5.0) μm diam, basal layer 100–150 μm deep, darker, denser and with predominantly horizontally arranged hyphae, continuous with hymenophoral trama; hymenophoral trama 20–350 μm broad, dense, with parallel hyphae (1.5–) 2.5–3.0 (–5.0) μm diam in a gelatinous matrix; subhymenium compact and brownish, about 5 μm deep, of short blocky cells 4–10 × 1.5–4.0 μm; pleurocystidia and metuloid pseudocystidia lacking; dissepiments resembling cheilocystidia, clavate-acanthophysoid or coralloid, 7–30 × 2–7 μm, with multiple tapering diverticulae 0.5–2.0 μm long by 0.2–0.5 μm diam, often bearing granular to crystalline encrustation (FIG. 1c); hymenium a dense palisade of clavate basidioles 15–20 × 5–6 μm; basidia clavate, 4-spored, 22–26 (–30) × 5.5–6.5 (–7.5) μm (FIG. 1d); basidiospores white in print, globose or subglobose, hyaline, inamyloid, smooth, thin-walled, 4.6–5.4 (–5.8) × 4.0–5.0 (–5.2) μm (FIG. 1e).

Specimens examined. USA. PUERTO RICO: Municipio de Orocovis, near Biology House, Toro Negro Community Forest, Cordillera Central, 18°9′10″N, 66°32′8″W, elev. 1000 m, in subtropical lower montane wet forest, on white-rotted wood, 6 Nov 1999, *A. Pérez*, PR-5832 (CFMR, MA-Fungi 52656, DK); Municipio de Luquillo, Bisley Tower Trail, the Bisley Watersheds, Caribbean National Forest, Luquillo Mts., 18°19′N, 65°48′W, elev. 350 m, on log, 14 Jun 2000, *L. Lopez, B. Ortiz, D.J. Lodge & D. Winter*, PR-6198 (HOLOTYPE, CFMR; ISOTYPES MA-Fungi 52657, UPRRP); same location, 18°18′25″N, 65°44′24″W, elev. 250 m, in subtropical wet forest, on rotting palm trunk (*Prestoea montana* [Graham] Nicholson), 16 Jul 2002, *S.A. Cantrell*, PR-6329 (CFMR, MA-Fungi, TRTC, NY, DAOM); same location, habitat, and collectors, 27 Aug 2002, PR-6329.1 (CFMR, NY, K); Municipio de Río Grande, El Verde Research Area, intersection of Quebrada Prieta and main trail, Caribbean National Forest, Luquillo Mts., 18°19′30.5″N, 65°48′57″W, elev. 380 m, in subtropical wet forest, on large fallen tree trunk of *Dacryodes excelsa* Vahl. (Burseraceae), 22 Sep 2000, *D.J. Lodge*, PR-6267 (CFMR, DK).

Comments. This species greatly resembles *Resupinatus applicatus* in both micromorphology and macromorphology, with the exception of its poroid hymenophore. In this regard it is similar to *Panellus pusillus* (Pers.) Burds. & O.K. Miller, a poroid

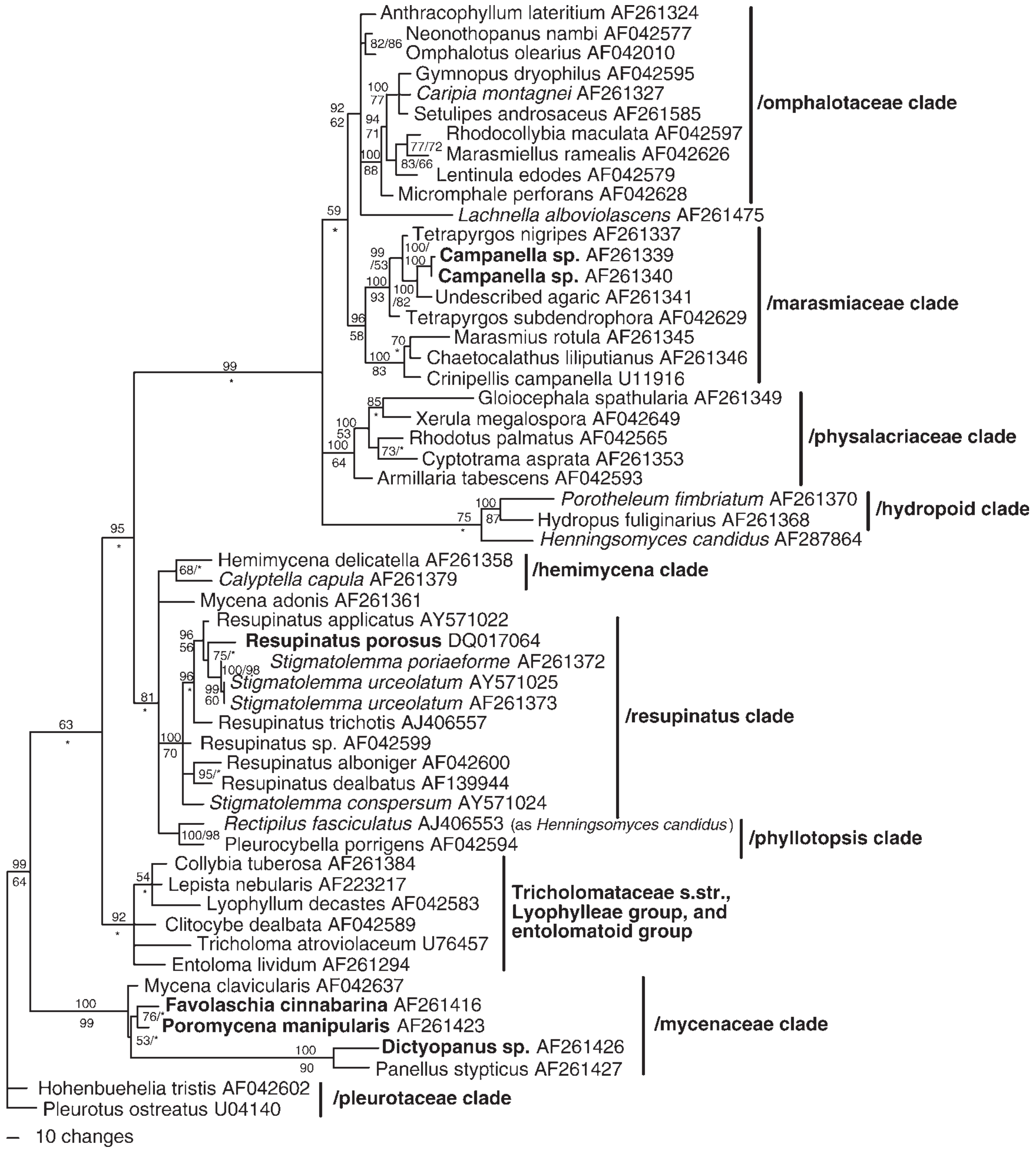

FIG. 2. Majority rule consensus tree from Bayesian analysis of 55 taxa. Numbers above branches indicate posterior probabilities estimated from a B-MCMC analysis. Numbers below branches are bootstrap supports estimated from parsimony bootstrapping (only values >50% are shown). Asterisks indicate branches that are not found in the strict consensus tree of parsimony analysis. Two clades recovered only in MP analyses were *Anthracophyllum* with (*Neonothopanus, Omphalotus*) (62% bss) and *Lachnella* with *Henningsomyces* (70% bss). Poroid taxa are labeled in bold, cyphelloid and reduced forms in italic, and gilled forms in plain text. The tree was rooted with *Pleurotus* (in MrBayes) or with *Pleurotus* and *Hohenbuehelia* (MP in PAUP*). Clades are labeled following Moncalvo et al (2002).

species of a predominantly lamellate genus, which greatly resembles the lamellate *P. stypticus* (Bull.: Fr.) P. Karst. except for hymenophoral arrangement (Jin et al 2001).

Phylogenetic analyses.—In all analyses, including the 879-taxon analysis (data not shown), *Resupinatus porosus* was placed within the /resupinatus clade of Moncalvo et al (2002). MP and B-MCMC analyses of the 55-taxa data matrix support the monophyly of the *Resupinatus* clade (100% bayesian posterior probability [pp] and 70% bootstrap support [bss], FIG. 2) and suggest paraphyly of *Resupinatus* with respect to *Stigmatolemma*, in agreement with results

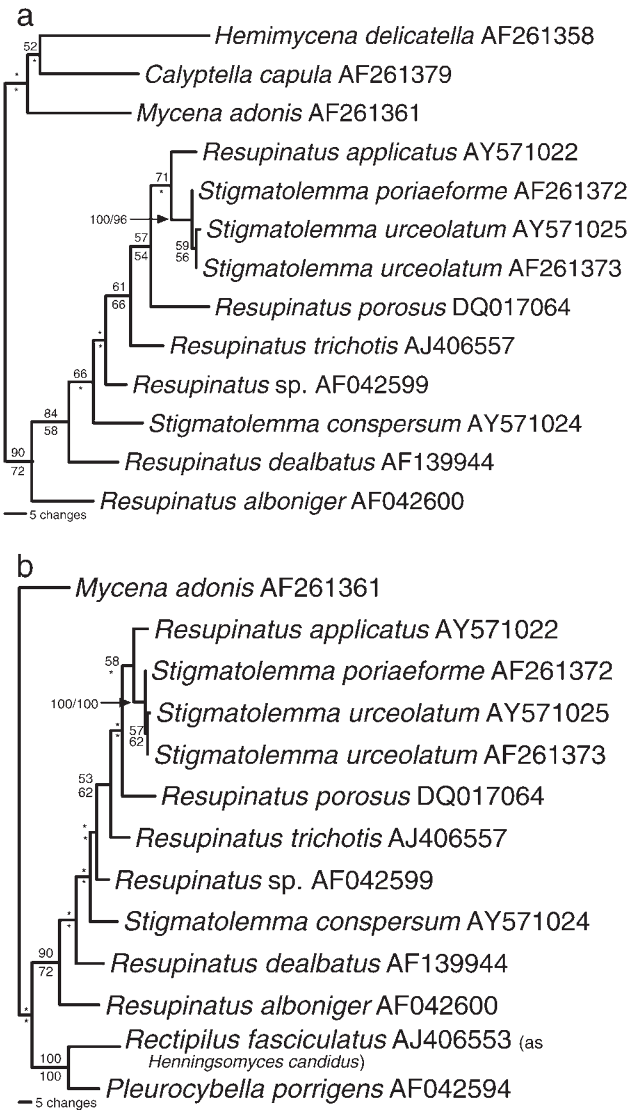

FIG. 3. Impact of outgroup choice on topology of the /resupinatus clade. a) One of two most parsimonious trees found in an heuristic search with 100 random additions of taxa when *Mycena adonis* and the /hemimycena clade were chosen as outgroup; length = 206 steps; CI = 0.704; RC = 0.421; 60 parsimony-informative characters. b) Single most parsimonious tree found in an heuristic search with 100 random additions of taxa when *Mycena adonis* and the /phyllotopsis clade were chosen as outgroup; length = 203 steps; CI = 0.704; RC = 0.435; 65 parsimony-informative characters. Numbers above nodes are bootstrap support (%) from parsimony-based analysis with 100 replicates, each with 100 random additions of taxa; numbers below branches are bootstrap support (%) from a Maximum Likelihood analysis with 100 replicates and settings of BaseFreq = (0.2506 0.1818 0.2938), Nst = 6, Rmat = (0.8001 6.2239 1.9635 0.8948 11.0001), Rates = gamma, Shape = 0.6447, Pinvar = 0.5164, equivalent to the GTR + I + G model of evolution (Nylander 2004). Asterisks indicate nodes with less than 50% bootstrap support (i.e. nodes that collapse in a majority-rule consensus tree).

obtained in an analysis of a larger data set of 879 species of homobasidiomycetes (data not shown). MP analysis yielded 44 equally parsimonious trees in 17 different tree-islands (Maddison 1991) (tree length = 1211; consistency index = 0.324). The topology of the tree resulting from B-MCMC analysis was similar to that of the MP trees except at deeper nodes (FIG. 2). The /resupinatus clade appeared in all Bayesian (FIG. 2) and ML (data not shown) analyses within a clade of weak support that included *Mycena adonis*, *Hemimycena delicatella, Calyptella capula, Rectipilus fasciculatus*, and *Pleurocybella porrigens.* Various sets of these five taxa were used to root the *Resupinatus* clade in 13-taxon MP and ML analyses in order to verify relationships within the clade. All analyses indicated paraphyly of *Resupinatus* with respect to *Stigmatolemma*, which appears to be derived from within a monophyletic *Resupinatus* (FIG. 3, and data not shown). *Stigmatolemma conspersum*, a species with multiple cyphelloid cups on a raised subiculum (Agerer 1978, Bodensteiner et al 2004), did not cluster with the other species of *Stigmatolemma*, but appeared basal within the /resupinatus clade (FIGS. 2, 3).

The other cyphelloid or reduced taxa used in this study were placed in the /omphalotaceae clade (*Caripia montagnei*), /hydropoid clade (*Porotheleum fimbriatum*), /phyllotopsis clade (*Rectipilus fasciculatus*), and /hemimycena clade (*Calyptella capula*); *Henningsomyces candidus* and *Lachnella alboviolascens* were clustered by MP (but not B-MCMC) analyses in a weakly supported clade of uncertain affinities. Poroid taxa are found in the /tetrapyrgoid clade (*Campanella* spp.), /resupinatus clade (*R. porosus*), and /mycenaceae clade (*Poromycena manipularis* and *Favolaschia cinnabarina*).

Redeterminations of specimens and Genbank accessions.— *Stigmatolemma poriaeforme* and *S. urceolatum* are strongly supported as monophyletic (100% pp and 98% bss in the 55-taxon analyses) but distinct taxa (FIG. 2). One sequence of *Stigmatolemma urceolatum* (AF261373) was derived from a culture that had been tentatively identified as *Henningsomyces puber* (Rom. ex W.B. Cooke) D.A. Reid, but the voucher specimen (HHB 3534sp, CFMR) was borrowed by RGT and re-identified on the basis of morphology as *Stigmatolemma urceolatum.* This sequence was reported by Moncalvo et al (2002) as cyphelloid HHB3534sp and is listed in Genbank as Cyphellaceae HHB3534sp. Sequences AY571025 (and also AY571062, not included in these analyses) are based on a collection (RGT 8509008/01 = DAOM 212665) originally misidentified by RGT as *S. poriaeforme* and redetermined as *Stigmatolemma urceolatum* on the basis of morphology by RGT during this study. These sequences were reported as *S. poriaeforme* by Bodensteiner et al (2004) and are listed in Genbank as *S. poriiforme* (AY571025) and *S. poriaeforme* (AY571062). The voucher specimen for the sequence of *Stigmatolemma poriaeforme* AF261372 was examined by RGT and confirmed by morphology as that species.

The two sequences retrieved from GenBank as *Henningsomyces candidus* did not cluster together, leading us to believe that one or both were misidentified. The first of these (AJ406553) clusters with the gilled fungus *Pleurocybella porrigens* (100% pp, 96% bss) whereas the second (AF287864) weakly clustered with the /hydropoid clade (75% pp) or with another cyphelloid species, *Lachnella alboviolascens* (70% bss), as depicted by Genbank numbers in FIG. 2. The voucher specimen for AF287864 (T-156 = DAOM 195432a; packet filed in DAOM as *Hohenbuehelia angustata*, the predominant portion of the collection) was re-examined by RGT and confirmed to be *Henningsomyces candidus*. In other studies, this sequence of *Henningsomyces candidus* clustered with Genbank accession AJ406539 (Hibbett and Binder 2002, Bodensteiner et al 2004, Binder et al 2005, as *Rectipilus fasciculatus*); this misidentification is apparently the result of transposition of sequences or DNAs of G.E. Langer 4485 (voucher is *Rectipilus fasciculatus*, but sequence AJ406539 is *Henningsomyces candidus*) and G.E. Langer 4482 (voucher is *Henningsomyces candidus*, but sequence AJ406553 is *Rectipilus fasciculatus*) (M. Binder, personal communication). The corrected names are used (FIGS. 2 and 3). The true *Henningsomyces candidus* (and *Henningsomyces/Rectipilus* clade A of Bodensteiner et al 2004) cannot be placed with certainty, but may be an ally of the /omphalotaceae and /physalacriaceae clades (FIG. 2; Binder et al 2005), whereas *Rectipilus fasciculatus* (and *Henningsomyces/Rectipilus* clade B of Bodensteiner et al 2004) is a member of the /phyllotopsis clade (FIG. 2; Binder et al 2005, as *Henningsomyces candidus*).

DISCUSSION

The discovery of a poroid *Resupinatus* species provides a remarkable example of extreme plasticity in the hymenophoral arrangement in a group of euagarics, the /resupinatus clade. This clade contains species with gilled (e.g. *Resupinatus alboniger* [Pat.] Singer and *R. dealbatus* [Berk.] Singer), meruloid (*R. merulioides*), poroid (*R. porosus*), and cyphelloid (*Stigmatolemma*) hymenophores. In this clade, both the poroid and cyphelloid habits appear to be derived from gilled ancestors (FIG. 2). A more detailed examination of the hymenophore evolution in this clade is still hampered by our limited taxon sampling.

A sister group for the *Resupinatus* clade could not be unambiguously determined in this or other molecular phylogenetic studies in the euagarics (Moncalvo et al 2000, Thorn et al 2000, Moncalvo et al 2002, Bodensteiner et al 2004, Binder et al 2005). Here, ML and B-MCMC analyses suggest that members of the *Hemimycena* clade, *Mycena adonis*, *Pleurocybella porrigens*, and *Rectipilus fasciculatus* are all possibly closely related to the *Resupinatus* clade (FIGS. 2, 3), however, these relationships are not supported by MP analyses. Weak support for a similar sister group relationship was also recorded by Bodensteiner et al (2004, their FIG. 3) by using MP analyses, which placed *Calyptella* (*Hemimycena* clade) sister to *Resupinatus*. A recent study using weighted parsimony ratchet analysis of a 656-taxon matrix of Homobasidiomycetes suggested, without bootstrap support, that *Arrhenia* may be sister to the /resupinatus clade (Binder et al 2005). Here, whatever the choice and size of outgroup, *Resupinatus* was paraphyletic and a gilled hymenophore was more likely to be the ancestral state of the clade (FIGS. 2, 3).

A similar pattern indicating that cyphelloid or poroid species have arisen from lamellate ancestors has been shown in several other groups of euagarics, notably in the Mycenaceae, Physalacriaceae, Omphalotaceae, Marasmiaceae, and the /hemimycena clade (Moncalvo et al 2002). Within the /mycenaceae clade, the predominantly tropical poroid genera *Favolaschia, Poromycena*, and *Dictyopanus* all appear to be derived from lamellate fungi (FIG. 2, Jin et al 2001, Moncalvo et al 2002). In the Marasmiaceae clade, the poroid genus *Campanella* also appears to be derived (FIG. 2; *Tetrapyrgos* spp. and the unidentified collection JMCR.34, which probably represents an undescribed taxon, are all gilled). The cyphelloid *Calyptella capula* appears derived within the reduced but lamellate genus *Hemimycena*, and the reduced agaric *Caripia montagnei* (suggested to be related to the stereoid genera *Cymatoderma, Skepperiella*, and *Cotylidia* by Singer 1986) is derived within the lamellate clade of *Micromphale* and *Gymnopus* (FIG. 2; Moncalvo et al 2002). Similar conclusions can be drawn from the study of Bodensteiner et al (2004). Although there appears to be widespread support among the current taxon sample for derivation of reduced, cyphelloid or poroid forms from lamellate ones, there is no support for a series by which poroid forms were derived from cyphelloid ones that were in turn derived form lamellate taxa. Although it is apparent that a poroid hymenophore provides greater surface area for spore production than a lamellate one (particularly when the lamellae are widely spaced, as they often are in *Resupinatus*), and that loss of lamellae is a natural consequence of reduction in fruiting body size beyond a certain point, it is not obvious to us why both of these evolutionary trends are more common in the humid tropics than in temperate regions, as they appear to be.

This study clearly shows that the delimitation of genera (or, frequently, higher taxa) on the basis of hymenophoral arrangement—lamellate, poroid or cyphelloid—is artificial and non-phylogenetic. Similarly, it has also been shown recently that it was phylogenetically incorrect to distinguish the gilled genus *Cortinarius* from its secotioid or hypogeous relatives in *Thaxterogaster* and *Hymenogaster* (Peintner et al 2001), and most species of the latter genera have been subsequently synonymized with *Cortinarius* (Peintner et al 2002). Likewise, Redhead et al (2002) have combined within the cyphelloid genus *Arrhenia* a number of centrally stipitate and lamellate species formerly classified in *Omphalina*. Therefore, we propose the following emended description of *Resupinatus*, and the necessary new combinations to accommodate species of *Stigmatolemma* within a more broadly defined and monophyletic *Resupinatus*.

TAXONOMY

Resupinatus S.F. Gray, Nat. Arr. Brit. Pl. 1:617. 1821

≡ *Agaricus* [familia] *Resupinatus* Nees, Syst. Pilze 197. 1816, *nom. invalid.*

= *Phyllotus* P. Karst., Bidr. Känn. Finl. Nat. Folk 32:xiv, 92. 1879

= *Stigmatolemma* Kalchbr., Grevillea 10:104. 1882

= *Calathinus* Quél., Ench. Fungorum 46. 1886

= *Scytinotopsis* Singer, Ann. Mycol. 34:335. 1936, *nom. invalid. nud.*

= *Asterotus* Singer, Mycologia 35:161. 1943

Saprotrophic, non-nematophagous, on decaying wood, bark, or herbaceous debris; fruiting bodies cupulate and pendent or pleurotoid to laterally pseudostipitate (with stipe not clearly differentiated from the pileus); hymenophore smooth (in cyphelloid taxa), lamellate, merulioid or poroid; lamellae or wrinkled folds (if present) radiating from point of attachment in pendent species, often few in number; pileipellis a loose trichodermium of coralloid-diverticulate hyphae that secrete hyaline to brownish crystalline material from fine cylindric or tapering pegs, resembling a ''rameales structure'' (Singer 1986); hymenophoral and pileus trama of fuscous, gelatinized hyphae; hymenophoral trama regular to interwoven; subhymenium poorly distinguished but usually more deeply pigmented than the trama or hymenium; hymenium without metuloid pseudocystidia but frequently with fusoid cheilocystidia with diverticulate, incrusted tips; basidioles clavate, basidia 2- or 4-spored; basidiospores hyaline, inamyloid, elliptical, globose, or stauriform; all hyphae with simple clamp connections; pigments present, frequently intraparietal and incrusting.

The generic synonymy is revised herein to include some names that have been listed previously as synonyms of *Resupinatus* and some that have incorrectly been synonymized with other genera, but exclude some others that have incorrectly been listed as synonyms. When Gray (1821) published the generic name *Resupinatus*, he included a single species, *R. applicatus* (Batsch: Fr.) S.F. Gray and attributed the name to [Nees von] ''Esenbeck'' (sic). Hence, the authorship of the generic name has been variously cited, e.g. as ''(C. Nees) ex S.F. Gray'' (Donk 1962b), ''Nees ex S.F. Gray'' (Singer 1986), and ''S.F. Gray'' (Horak 1968). *Agaricus* [''Familia''] *Resupinatus* Nees is an invalid name published as a misplaced family name within a tribe in a genus, in violation of ICBN Article 33.7 (Greuter et al 2000). The name *Resupinatus* is to be attributed solely to S.F. Gray, as is correctly listed in appendix IIIA (Greuter et al 2000) in the treatment of *Pleurotus*. *Resupinatus* S.F. Gray being a monotypic name, the one included species is the holotype (Art. 9.1, 10.1). Consequently, the generic names *Phyllotus* P. Karst. and *Calathinus* Quél. were nomenclaturally superfluous when published since both were published without designation of types and they both included the holotype of *Resupinatus*. They are automatically typified by *Agaricus applicatus* Batsch: Fries (ICBN Articles 52.1, 52.2 and 7.5, Greuter et al 2000). In these cases, application of the rules alleviates back-and-forth arguments over the correct typification of these names, and makes both automatic synonyms (typonyms) of *Resupinatus*, as previously indicated by Singer (1962, for *Phyllotus*) and Thorn and Barron (1986, for *Calathinus*). *Asterotus* was first indicated as a synonym of *Resupinatus* by Singer (1975) and this conclusion is supported by phylogenetic analyses that place its type species within a monophyletic *Resupinatus* (FIG. 2). We add *Stigmatolemma* to the list of synonyms of *Resupinatus*, and make the appropriate new combinations below.

Pleurotopsis (Henn.) Earle (1909) and *Urceolus* Velen. (1939) are excluded from *Resupinatus* and placed in synonymy with *Hohenbuehelia* in accordance with Singer (1986) contrary to his earlier listing (Singer 1975). The lectotype of *Marasmius* sect. *Pleurotopsis* Henn., basionym for *Pleurotopsis* Earle (1909) selected by Donk (1951) is *Marasmius spodoleucus* Berk. & Broome, which corresponds with the type indication by Earle (1909) and Singer (1942) for the taxon at the generic level as well. This species was placed in synonymy with *Agaricus cyphelliformis* Berk. by Singer (in Donk 1962b), who then classified it as a *Resupinatus*. However, it is now considered to be a *Hohenbuehelia*, *H. cyphelliformis* (Berk.) Miller (in Thorn 1986). *Urceolus* Velen. was described with a single species, *U. sambucinus*, which is also a synonym of *Hohenbuehelia cyphelliformis* (Thorn 1986). *Phyllotremella* Lloyd (1920) has been treated as both a *Resupinatus* (Horak 1968) and a *Hohenbuehelia* (Singer 1986). Its taxonomic position remains unresolved.

Resupinatus conspersus (Pers.: Fr.) Thorn, Moncalvo & Redhead, comb. nov.

Basionym *Peziza conspersa* Persoon Mycol. Eur. 1:271. 1822

≡ *Stigmatolemma conspersum* (Pers.: Fr.) Donk, Persoonia 2:339. 1962

For descriptions and illustrations, see Bourdot and Galzin (1928, p. 163, as *Cyphella grisella*), Breitenbach and Kränzlin (1986, p. 204), and Agerer (1978).

Resupinatus huia (G. Cunn.) Thorn, Moncalvo & Redhead, comb. nov.

Basionym *Solenia huia* G. Cunn. Trans Roy. Soc. N.Z. 81:179. 1953

≡ *Stigmatolemma huia* (G. Cunn.) W.B. Cooke, Sydowia Beih. 4:128, 1961, nom. inval., Art. 33.2

For descriptions and illustrations, see Cunningham (1953, 1963, as *Stromatoscypha*).

Resupinatus hyalinus (Singer) Thorn, Moncalvo & Redhead, comb. nov.

Basionym *Stigmatolemma hyalinum* Singer, Fieldiana, Bot. 21:43. 1989

For a description, see Singer (1989).

Resupinatus incanus (Kalchbr.) Thorn, Moncalvo & Redhead, comb. nov.

Basionym *Stigmatolemma incanum* Kalchbr., Grevillea 10:104. 1882

For a description and illustration, see Talbot (1956, as *Porothelium incanum*).

Resupinatus poriaeformis (Pers.: Fr.) Thorn, Moncalvo & Redhead, comb. nov.

Basionym *Peziza anomala* [var.] *poriaeformis* Persoon, Syn. Fung.: 656. 1801

≡ *Stigmatolemma poriaeforme* (Pers.: Fr.) Singer, Sydowia 15:52. 1962

≡ *Stigmatolemma poriaeforme* (Pers.: Fr.) W.B. Cooke, Sydowia Beih. 4:128. 1961, comb. invalid., Art. 33.3

For descriptions and illustrations, see Bourdot and Galzin (1928, p. 163, as *Cyphella*), Burt (1924, as *Solenia*), Coker (1921, as *Solenia*), Cunningham (1953, as *Solenia*; 1963, as *Stromatoscypha*), and Agerer (1978). Descriptions by Cooke (e.g. 1961, 1989, as *poroides*) are far too broad and include all species treated here. This species is primarily distinguished from *R. urceolatus* by its cupulate fruiting bodies that are imbedded in a dense and tomentose subiculum, but many mycologists including ourselves have misapplied this name to specimens of *R. urceolatus*.

Note on etymology and orthography. We retain the unusual orthography of the species epithet *poriaeformis* that was the original spelling (once the dipthong æ is corrected to ae, Art. 60.6) of Persoon, De Candolle and Fries and used by virtually all subsequent authors, including Donk (1962a). Although Article 60.8 of the International Code of Botanical Nomenclature (Greuter et al 2000) appears to suggest that the compound should be ''corrected'' to read ''*poriiformis*'' or ''*poriformis*,'' we follow Art. 60G.1(b) (referred to in Art. 60.8) that allows the compounding form ''ae'' for etymological reasons, i.e., indicating the origin of the name, being a reference to the genus *Poria* (''*Poria*-shaped'') rather than *porus* (''pore-shaped''), and it also serves to distinguish it from the near-homonym, *S. poriforme* (P. Henn.) W.B. Cooke, following Art. 53.3.

Resupinatus taxi (Lév.) Thorn, Moncalvo & Redhead, comb. nov.

Basionym *Cyphella taxi* Lév. Ann. Sci. nat (Bot.) II 8:336. 1837

≡ *Stigmatolemma taxi* (Lév.) Donk, Persoonia 2:342. 1962

For descriptions and ilustrations see Burt (1915, as *Cyphella cupulaeformis*), Coker (1921, as *C. cupulaeformis*), Donk (1962a) and Gilbertson and Blackwell (1987).

Resupinatus urceolatus (Wallr. ex Fr.: Fr.) Thorn, Moncalvo & Redhead, comb. nov.

Basionym *Solenia urceolata* Wallr. ex Fr. Elench. Fung. II: 28. 1828, non *Peziza urceolata* Vahl, Fl. Dan. 6(17):10. 1790

≡ *Stigmatolemma urceolatum* (Wallr. ex Fr.) Donk, Persoonia 2:341. 1962

= *Stigmatolemma farinaceum* (Kalchbr. & Cooke) D.A. Reid, Contr. Bolus Herb. 7:22. 1975 (as ''*farinacea*'')

≡ *Cyphella farinacea* Kalchbr. & Cooke Grevillea 9:18. 1880

For descriptions and illustrations, see Bourdot & Galzin (1928, as *Cyphella urceolata*), Donk (1962a), Breitenbach and Kränzlin (1986, p. 206), Talbot

(1956, as *Cyphella farinacea*), Cooke (1961, as *Phaeoglabrotricha farinacea*), Reid (1975, as *Stigmatolemma farinacea*), and Redhead (1973, as *Stigmatolemma poriaeforme*). This taxon is characterized by gregarious, grayish, globose to vase-shaped fruiting bodies 0.3–1.5 mm in diam, externally farinaceous with short, incrusted hairs, subiculum sparse and wispy or lacking, and globose to subglobose basidiospores 4.5–6.0 µm in diam. This species has frequently been confused with *Resupinatus poriaeformis*, which differs in that fruiting bodies are seated in a distinct, white to grayish, felty to membranous subiculum, resembling a crustose lichen.

Excluded species.—*Stigmatolemma fimbriatum* (Pers. : Fr.) Pouzar, Ceska Mykol. 12:27. 1958

This is *Porotheleum fimbriatum* (Pers.) Fr. and is frequently treated as *Stromatoscypha fimbriatum* (Pers. : Fr.) Donk. Donk (1951) coined the generic name *Stromatoscypha* to replace *Porotheleum* (Fr. : Fr.) Fr. (1836), a later homonym of *Porothelium* Eschw. (1824) under the ICBN rules effective in 1951. However, with earlier starting dates for fungi instituted in the 1981 International Code of Botanical Nomenclature (Voss et al 1983), *Porotheleum* Fr. (1818) is the valid and correct name for this genus, and *Stromatoscypha* is an obligate synonym.

Stigmatolemma poriforme (Henn.) W.B. Cooke, Sydowia Beih. 4:128. 1961 (as “*poriformis*”)

Basionym *Cyphella poriformis* Henn., Engl. Bot. Jahrb. 21:85. 1897

This species is too poorly known from available descriptions to advocate transferring it to *Resupinatus*.

Stigmatolemma porioides (Alb. & Schwein. : Fr.) W.B. Cooke, Mem. NY Bot. Gard. 49:168. 1989 (as “*poroides*”)

As indicated previously by Donk (1959, 1962a), the descriptions and illustration of *Peziza porioides* by Albertini and Schweinitz (1805, p. 327 and Tab. VI f. 5) and Fries (1823, p. 111) clearly indicate that this is a synonym of *Porotheleum fimbriatum*, not *Resupinatus poriaeformis*.

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LITERATURE CITED

Agerer R. 1978. *Lachnella-Crinipellis, Stigmatolemma-Fistulina*: zwei Verwandtschaftsreihen? Zeitschr Mykol 44:52–70.

Albertini IB, Schweinitz LD. 1805. Conspectus fungorum in Lusatiae superioris agro Niskiensi crescentium. Lipsiae: Sumptibus Kummerianus, 376 p., XII pl.

Binder M, Hibbett DS, Larsson KH, Larsson E, Langer E, Langer G. 2005. The phylogenetic distribution of resupinate forms across major clades of mushroom-forming fungi (Homobasidiomycetes). Systematics Biodiversity 3:113–157.

———, ———, Molitoris HP. 2001. Phylogenetic relationships of the marine gasteromycete *Nia vibrissa*. Mycologia 93:679–688.

Bodensteiner P, Binder M, Moncalvo JM, Agerer R, Hibbett DS. 2004. Phylogenetic relationships of cyphelloid homobasidiomycetes. Mol Phyl Evol 33:501–515.

Bourdot H, Galzin A. 1928. Hyménomycètes de France. Sceaux, France: M. Bry. 761 p.

Breitenbach J, Kränzlin F. 1986. Fungi of Switzerland. Vol. 2. Non gilled fungi. Lucerne, Switzerland: Verlag Mykologia. 412 p.

Burt EA. 1915. The Thelephoraceae of North America III. Ann. Missouri Bot Gard 1:357–382.

———. 1924. The Thelephoraceae of North America XIII. Ann. Missouri Bot. Gard. 11:1–36.

Coker WC. 1921. Notes on the Thelephoraceae of North Carolina. J. Elisha Mitch Sci Soc 36:146–196.

———. 1944. The smaller species of *Pleurotus* in North Carolina. J. Elisha Mitch Sci Soc 60:71–95.

Cooke WB. 1957. The Porotheleaceae: *Porotheleum*. Mycologia 49:680–693.

———. 1961. The cyphellaceous fungi: a study in the Porotheleaceae. Beih. Sydowia 4:1–144, I–XX.

———. 1989. The cyphelloid fungi of Ohio. Mem NY Bot Gdn 49:158–172.

Cunningham GH. 1953. Thelephoraceae of New Zealand, Part I. Subfamily Cyphelloideae. Trans Roy Soc NZ 81:165–188.

———. 1963. The Thelephoraceae of Australia and New Zealand. New Zealand DSIR Bulletin 145:1–358.

Donk MA. 1951. The generic names proposed for Hymenomycetes. Reinwardtia 1:199–220.

———. 1959. Notes on ‘Cyphellaceae’—I. Persoonia 1:25–110.

———. 1962a. Notes on ‘Cyphellaceae’—II. Persoonia 2:331–348.

———. 1962b. The generic names proposed for Agaricaceae. Beih Nova Hedw 5:1–320.

———. 1966. A reassessment of the Cyphellaceae. Acta Bot Neerl 15:95–101.

Earle FS. 1909. The genera of the North American gill fungi. Bull. NY Bot. Gdn. 5:373–451.

Fries EM. 1823. Systema Mycologicum. Vol. II. Gryphiswaldiae: Ernesti Mauritii. 621 p.

Gardes M, Bruns TD. 1993. ITS Primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Molec. Ecol. 2:113–118.

Gilbertson RL, Blackwell M. 1987. Notes on wood-rotting fungi on junipers in the Gulf Coast Region. II. Mycotaxon 28:369–402.

Gray SF. 1821. A natural arrangement of British plants. Vol. 1. London: Baldwin, Cradock and Joy. 824 p.

Greuter W, McNeill J, Barrie FR, Burdet HM, Demoulin V, Filgueiras TS, Nicolson DH, Silva PC, Skog JE, Trehane P, Turland NJ, Hawksworth DL, eds. 2000. International Code of Botanical Nomenclature (Saint Louis Code). Adopted by the Sixteenth International Botanical Congress St. Louis, Missouri, July-August 1999. Regnum Veg. 138:1–474.

Hibbett DS, Binder M. 2002. Evolution of complex fruiting-body morphologies in homobasidiomycetes. Proc. Roy. Soc. (London) B 269:1963–1969.

———, Pine EM, Langer E, Langer G, Donoghue M. 1997. Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. Proc. Natl. Acad. Sci. USA 94:12002–12006.

———, Thorn RG. 2001. Homobasidiomycetes. In: McLaughlin DJ, McLaughlin EG, Lemke PA, eds. Systematics and Evolution, Part B. Berlin, Germany: Springer-Verlag: The Mycota vol VII: 121–168.

———, Vilgalys R. 1993. Phylogenetic relationships of the Basidiomycete genus *Lentinus* inferred from molecular and morphological characters. Syst Bot 18:409–433.

Holmgren PK, Holmgren NH, Barnett LC. 1990. Index Herbariorum, Part I. 8th ed. Regnum Vegetabile 120:1–693.

Horak E. 1968. Synopsis generum Agaricalium (Die Gattungstypen der Agaricales). Beitr. Kryptogamenflora Schweiz 13:1–741.

Huelsenbeck JP, Ronquist F. 2001. MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics (Oxford) 17:754–755.

Jin J, Hughes KW, Petersen RH. 2001. Phylogenetic relationships of *Panellus* (Agaricales) and related species based on morphology and ribosomal large subunit DNA sequences. Mycotaxon 79:7–21.

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. Dictionary of the Fungi. 9th ed. Wallingford, UK: CAB International. 655 p.

Kühner R. 1980. Les Hyménomycètes agaricoïdes, Numéro spécial du Bulletin de la Société Linnéene de Lyon Société Linnéene de Lyon, Lyon. 1027 p.

Lloyd CG. 1920. Mycological Notes 64. Mycological Writings 6:985–1029.

Maddison DR. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Syst. Zool. 40:315–328.

Martín MP, Winka K. 2000. Alternative methods of extracting and amplifying DNA from lichens. Lichenologist 32:189–196.

Moncalvo JM, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R. 2000. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. Syst Biol 49:278–305.

———, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC, Hofstetter, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsson S, Clemencon H, Miller OK, Jr. 2002. One hundred and seventeen clades of euagarics. Mol Phylog Evol 23:357–400.

Nylander JAA. 2004. MrModeltest v2. Program distributed by the author Evolutionary Biology Centre, Uppsala University.

Peintner U, Bougher NL, Castellano MA, Moncalvo JM, Moser MM, Trappe JM, Vilgalys R. 2001. Multiple origins of sequestrate fungi related to *Cortinarius* (Cortinariaceae). Amer J Bot 88:2168–2179.

———, Horak E, Moser M, Vilgalys R. 2002. *Rozites*, *Cuphocybe* and *Rapacea* are taxonomic synonyms of *Cortinarius*: New combinations and new names. Mycotaxon 83:447–451.

Pilát A. 1935. *Pleurotus* Fries. In: Kavina C, Pilát A, eds. Atlas des champignons de l'Europe. Prague, Czechoslovakia: Musée National à Prague. Vol. 2, fasc. 6-16. 193 p.

Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818.

Redhead SA. 1973. Epistolae mycologicae I. Some cyphelloid basidiomycetes from British Columbia. Syesis 6:221–227.

———, Lutzoni F, Moncalvo JM, Vilgalys R. 2002. Phylogeny of agarics: partial solutions for core omphalinoid genera in the Agaricales (euagarics). Mycotaxon 83:19–57.

———, Nagasawa E. 1987. *Resinomycena japonica* and *Resupinatus merulioides*, new species of Agaricales from Japan. Can J Bot 65:972–976.

Reid DA. 1975. Type studies of the larger Basidiomycetes described from South Africa. In: Schelpe EACLE, ed. Contributions from the Bolus Herbarium No. 7. Rondebosch, South Africa: University of Capetown. 255 p.

Ridgway R. 1912. Color standards and color nomenclature. Washington, DC: Publ. by the author. 43 p, 53 pl.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics (Oxford) 19:1572–1574.

Singer R. 1942. A monographic study of the genera *Crinipellis* and *Chaetocalathus*. Lilloa 8:441–534.

———. 1962. The Agaricales in modern taxonomy. 2nd ed. Weinheim, Germany: J Cramer 915 p.

———. 1975. The Agaricales in modern taxonomy. 3rd ed. Vaduz, Liechtenstein: J Cramer 912 p.

———. 1986. The Agaricales in modern taxonomy. 4th ed. Koenigstein, Germany: Koeltz Scientific Books. 981 p.

———. 1989. New taxa and new combinations of Agaricales (Diagnoses fungorum novorum Agaricalium IV). Fieldiana Botany 21:1–133.

Swofford D. 2003. PAUP*: Phylogenetic analysis using parsimony (*and other methods). Version 4. Sunderland, Massachusetts: Sinauer.

Talbot PHB. 1956. The cyphelloid fungi of South Africa. Bothalia 6:465–487.

Thorn RG. 1986. The ''*Pleurotus silvanus*'' complex. Mycotaxon 25:26–66.

———, Barron GL. 1986. *Nematoctonus* and the tribe Resupinateae in Ontario, Canada. Mycotaxon 25: 321–453.

———, Moncalvo JM, Reddy CA, Vilgalys R. 2000. Phylogenetic analyses and the distribution of nematophagy support a monophyletic Pleurotaceae within the polyphyletic pleurotoid-lentinoid fungi. Mycologia 92: 241–252.

Velenovsky J. 1939. Novitates Mycologicae. Prague: Ludvik Soucek. 211 p.

Vilgalys R, Hester M. 1990. Rapid genetic identification of mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J Bacteriol 172: 4238–4246.

Voss EG, Burdet HM, Chaloner WG, Demoulin V, Hiepko P, McNeill J, Nicolson DH, Rollins RC, Silva PC, Greuter W, eds. 1983., International Code of Botanical Nomenclature, adopted by the thirteenth International Botanical Congress, Sydney, August 1981. Regnum Vegetabile 111:1–472.

White TJ, Bruns TD, Lee SB, Taylor JW. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, et al, eds. PCR Protocols: a guide to methods and applications. San Diego, California: Academic Press. p 315–322.