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 merulloid (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 possess a nematophagous anamorph referrible 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.

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, Aphyllopus 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 Stigmatolemmata 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 inamylloid. Romagnesi (1950, 1953, both cited in Donk 1962a) noted the similarities between R. kavinii (as Seytinotopsis kavinii) and Stigmatolemmata 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 Stigmatolemmata 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 Stigmatolemmata, 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 Stigmatolemmata (see Redhead 1973) greatly resemble chelisocystidia from gill edges in Resupinatus (Thorn and Barron 1986). These pileipellis elements and chelisocystidia are very different from any structures found in Hohenbuehelia. Redhead and Nagasawa (1987) described Resupinatus meruloides, a species from Japan with a meruloid 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. meruloides is a unique feature within Resupinatus, but used the combination of gelatinized, fuscous tissues, globose, inamylloid spores, absence of metuloid cystidia and the presence of coralloid pileipellis elements with scattered tibiiform cystidiod 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. Capitalized 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 Martin 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 EZ.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 (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-taxa sequence matrix employed equally-weighted parsimony (MP) in PAUP*: 4.0b10 (Swoford 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 (Swoford 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) Nat = 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 M.P. Martı́n, Lodge et Thorn, paratypus PR-5832 GenBank DQ017064; ITS ex holotypus GenBank numerus DQ017064; ITS ex paratypus PR-5832 GenBank numerus DQ017063.

Pileus (Fig. 1a) convex to unglculate, 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, makado 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 wails, 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 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′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 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
*Resupinatus* was placed within the /resupinatus clade of Moncalvo et al (2002). MP and B-MCMC analyses of the 55-taxon 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 *Stigmatoloma*, in agreement with results 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, Hemimyccena delicatella, Calypella capula, Rectipilus fasciatus, 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 fasciatus), 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 (AF261358) 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 cyphellaceae HHB3534sp and is listed in Genbank as S. poriaeforme by Bodensteiner et al (2004) and are listed in Genbank as S. poriaeforme.

**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).
The discovery of a poroid *Henningsomyces candidus* and *Rectipilus fasciculatus* 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, *Lachnellia 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 by morphology as that species. The voucher specimen for AF287864, the predominant portion of the collection, was re-examined by RGT and confirmed by morphology as that species. The corrected names are used (FIG. 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 /phylloptosis 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. meruloides*), 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, *Myccena 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 636-taxon matrix of Homobasidiomycetes suggested, without boot-strap support, that *Arrenia* 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 *Dictyopus* 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; *Tetraphysos* spp. and the unidentified collection JMR.34, which probably repre-sents an undescribed taxon, are all gilled). The cyphelloid *Calyptella capula* appears derived within the reduced but lamellate genus *Hemimycena*, and the reduced agaric *Caripta montagnei* (suggested to be related to the stereoid genera *Gymnopus, Skelliperiella,* and *Cotylidia* by Singer 1986) is derived within the lamellate clade of *Micromphale* and *Gymnoporus* (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 (2002) have combined within the cyphelloid genus Resupinatus S.F. Gray, Nat. Arr. Brit. Pl. 1:617. 1821 phylogenetically incorrect to distinguish the gilled genera (or, frequently, higher taxa) on the basis of hymenophoral arrangement—lamellate, poroid or cyphelloid species formerly classified in Omphalina. Therefore, 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 Resupinatus S.F. Gray, Nat. Arr. Brit. Pl. 1:617. 1821 phylogenetically incorrect to distinguish the gilled genera (or, frequently, higher taxa) on the basis of hymenophoral arrangement—lamellate, poroid or cyphelloid species formerly classified in Omphalina. Therefore, it has also been shown recently that it was phylogenetically incorrect to distinguish the gilled genera (or, frequently, higher taxa) on the basis of hymenophoral arrangement—lamellate, poroid or cyphelloid 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**


- *Stigmatolemma* Kalchbr., Grevillea 10:104. 1882
- *Calathinus* Quél., Ench. Fungorum 46. 1886
- *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 "ramecales 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 in-correctly 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 (synonyms) 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.

Pleurotopis (Henn.) Earle (1909) and Ureolus 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. Pleurotopis Henn., basionym for Pleurotopis 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). *Urecesus* Velen. was described with a single species, *U. sambucinus*, which is also a synonym of *Hohenbuehelia cyphelliformis* (Thorn 1986). *Phyllostremella* 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 *Stromatosephyra*).

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

Basionym *Solenia hyalinus* 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 poriaformis** (Pers.: Fr.) Thorn, Moncalvo & Redhead, comb. nov.

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

= *Stigmatolemma poriaformis* (Pers.: Fr.) Singer, Sydowia 15:52. 1962


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*), Redhead (1973, as *Stigmato-lemna poriaformis*), 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 *poriaformis* 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 “*poriformis*” or “*poriformis,*” we follow Art. 60G.1(b) (referred to in Art. 60.8) that allows the complicating 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.


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

For descriptions and illustrations 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: 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 *Phaeoglabrutochicha farinacea*), Reid (1975, as *Stigmatolemma farinacea*), and Redhead (1973, as *Stigmatolemma poriaformis*). This taxon is characterized by gregarious, grayish, globose to vase-shaped fruiting
bodies 0.5–1.5 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.


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


As indicated previously by Donk (1959, 1962a), the descriptions and illustration of *Peziza poroides* 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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