# Morphological and molecular studies on *Resinicium* s. str.

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**Abstract:** *Resinicium* Pannasto is typified by *Resinicium bicolor* (Alb. & Schwein.: Fr.) Parm., (Hymenochaetales, Basidiomycota), a readily recognized and widely distributed corticioid, lignicolous species in the northern hemisphere. Five new species of *Resinicium* closely allied to *R. bicolor* from the Caribbean region are described and illustrated: ***Resinicium confertum*** Nakasone, sp. nov., ***Resinicium monticola*** Nakasone, sp. nov., ***Resinicium mutabile*** Nakasone, sp. nov., ***Resinicium rimulosum*** Nakasone, sp. nov., and ***Resinicium tenue*** Nakasone, sp. nov. In addition, *R. bicolor* and *Resinicium friabile* Hjortstam & Melo are redescribed and illustrated. Sequence analyses of the internal transcribed spacer region support the recognition of the new taxa. Further, nuclear small subunit ribosomal RNA sequence data support the recognition of two groups of *Resinicium* species: the *Resinicium* s. str. group, including *R. bicolor,* and the *Resinicium* s.l. group that includes *Resinicium furfuraceum* (Bres.) Pann. The genus *Resinicium* is redefined and a key to the *Resinicium* s. str. species is provided.

*Key words:* ITS spacer region, 18S rRNA, astrocystidia, halocystidia, *Odontia bicolor.*

**Résumé:** *Resinicium* Parmasto est caractérisé par *Resinicium bicolore* (Alb. & Schwein.: Fr.) Parm., (Hymenochaetales, Basidiomycota), un espèces lignicole, corticole aisément identifié et largement distribué dans l'hémisphère nordique. Cinq nouvelles espèces de *Resinicium* étroitement alliées au *R. bicolore* de la région des Caraïbes sont décrites et illustrées : ***Resinicium confertum*** Nakasone, sp. nov., ***Resinicium monticola*** Nakasone, sp. nov., ***Resinicium mutabile*** Nakasone, sp. nov., ***Resinicium rimulosum*** Nakasone, sp. nov., et ***Resinicium tenue*** Nakasone, sp. nov. En outre, *R. bicolore* et *Resinicium friabile* Hjortstarn & Melo ont modifié et ont illustré. Les analyses génétiques de la région transcrit interne d'espaceur soutiennent l'identification des nouveaux taxa. En outre, les donnees de la petite sous-unite de l'ARN de ribosomique nucléique soutiennent l'identification de deux groupes d'espèces de *Resinieium* : le groupe de *Resinieium* s. str., y compris le *R. bicolore,* et le groupe de *Resinicium* s.l. qui inclut le *Resinicium fuifuraceum* (Bres.) Pann. Le genre *Resinicium* est modifié et une clef aux espèces de *Resinicium* s. str. est foumie.

*Mots-clés:* la région ITS d'espaceur, l8S rRNA, astrocystidia, halocystidia, *Odontia bicolor.*

## Introduction

The genus *Resinicium* Parmasto was described in 1968 to accommodate species similar to *Phlebia* Fr. but developing capitate cystidia with an apical vesicle (halocystidia) and occurring on coniferous wood and bark. The type species is *Hydnum bicolor* Alb. & Schwein.: Fr., a striking species easily identified because of the presence of halocystidia and astrocystidia. Astrocystidia, unique to *Resinicium,* are cystidia with an apical star-like cluster of pointed, hyaline crystals. In addition to *Resinicium bicolor* (Alb. & Schwein.: Fr.) Parm., Parmasto also included *Resinicium furfuraceum* (Bres.) Parm., which has halocystidia but no astrocystidia, to the new genus. Subsequently, four new species of *Resinicium* have been described: Resinicium bisporum Stalpers (Stalpers 1976), Resinicium chiricahuaense Gilb. & Budington (Gilbertson and Budington 1970), *Resinicium friabile* Hjortstam & Melo (Hjortstam and Melo 1997), and *Resinicium luteum* Jülich (Jülich 1978). An additional six taxa were transferred to *Resinicium*: *Resinicium furfurella* (Bres.) Nakasone and *Resinicium meridionale* (Burds. & Nakasone) Nakasone (Nakasone 1990), *Resinicium granulare* (Burt) Sheng H. Wu (Wu 1990), *Resinicium pinicola* (J. Erikss.) J. Erikss. & Hjortstam (Eriksson et al. 1981), and *Resinicium saccharicola* (Burt) Nakasone (Nakasone 2000). Wu (1990) restricted *Resinicium* to species that developed astrocystidia and halocystidia with cyanophilous vesicle walls. Later, Hjortstam and Melo (1997) and Parmasto et al. (2004) recognized only four species of *Resinicium: R. bicolor, R. furfuraceum R. friabile* and *R. granulare. Resinicium bicolor, R. friabile,* and *R. saccharicola* (=*R. granulare*) develop both kinds of cystidia, whereas *R. furfuraceum* produces halocystidia only.

Genus *Resinicium* is considered to be closely related to *Phlebia* Fries and *Mycoacia* Donk because of its ceraceous texture, clavate basidia, and small, smooth, cylindrical to ellipsoid basidiospores (Parmasto 1968; Eriksson et al. 1981; Ginns and Lefebvre 1993). However, large subunit ribosomal RNA sequence data placed *R. bicolor* and related taxa in the hymenochaetoid clade and not in the polyporoid clade with *Phlebia* (Hibbett and Binder 2002). Recent studies confirm that *Resinicium* is a member of the hymenochaetoid clade (Binder et al. 2005; Larsson et al. 2004, 2006).

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Extensive collecting of corticioid fungi in the Caribbean region since 1996 produced several specimens similar to *R. bicolor* but differing in various morphological features, including basidiospore size and shape. By combining the morphological features of the basidiomes with internal transcribed spacer region DNA data, five undescribed species of *Resinicium* were discovered. The new taxa, as well as *R. bicolor* and *R. friabile*, are described and illustrated. Molecular analyses of the nuclear small subunit ribosomal RNA gene groups *Resinicium* and related species into two distinct clades: *Resinicium* s. str. and s.l. The genus *Resinicium* is redescribed, and a key to the species in *Resinicium* s. str. is presented.

## Materials and methods

### Morphological studies

Freehand sections and squash mounts of basidiomes were examined microscopically in 2% (*w/v*) KOH and 1% (*w/v*) aqueous phloxine or Melzer's reagent (Kirk et al. 2001). Sections were mounted in 0.1% (*w/v*) cotton blue in 60% lactic acid to determine cyanophily of the cell walls (Kotlaba and Pouzar 1964; Singer 1986). Drawings of microscopic features were aided with a camera lucida attachment on an Olympus BH2 compound microscope. Q is the length to width ratio of the basidiospore measurements (Kirk et al. 2001). Color descriptions were taken from Kornerup and Wanscher (1978), and herbarium designations follow Holmgren et al. (1990).

### Phylogenetic studies

#### *Taxa and outgroup selection*

The internal transcribed spacer (ITS) data set includes sequences of 25 representative *Resinicium* species generated from this study. Voucher data are provided if not listed in the "Specimens examined" section of individual species. Specimens and cultures of vouchers are available from CFMR. The strain number is followed by the GenBank accession number: *Resinicium bicolor* FP135575 DQ826533, HHB10731 DQ826534, JLLl3731 DQ826535, FP133695 DQ826536, HHB10108 DQ826537; ***R. confertum*** FP102863 DQ826538; ***R. tenue*** FP150354 DQ826539, FP150251 DQ826540; *R. friabile* FP102803 DQ826541, PR1380 DQ826542, FP150513 DQ826543, ECCO146 DQ826544, FP102983 DQ826545; ***R. rimulosum*** FP150328 DQ826546; *R. saecharicola* P102754 DQ826547, Puerto Rico, Rio Grande Municipio, Caribbean National Forest, Luquillo Mountains, El Yunque Recreation Area, 500 m, Big Tree Trail, on lower petiole of live palm, 16 June 1996, K.K. Nakasone, FP102841 DQ826548 and FP102843 DQ826549, same locale, 750-900 m, Mt. Britton Trail, on *Prestoea montana* (Graham) G. Nicholson, 21 June 1996, K.K. Nakasone; ***R. monticola*** FP102832 DQ826550, FP150061 DQ826551, FP150360 DQ826552, FP150355 DQ826553, FP150407 DQ826554, FP150332 DQ826555; ***R. mutabile*** FP102989 DQ826556, PR1366 DQ826557. *Rickenella fibula* (Bull.) Raithelh. (DQ241782, GenBank accession number) and *Rickenella mellea* (Singer & Clémençon) Lamoure (U66438) were chosen as outgroup taxa, based on previously reported results from the nuclear small subunit ribosomal RNA (nSSU rRNA) analyses (Redhead et al. 2002). An additional sequence of *R. bicolor* (DQ218310) obtained from GenBank was included also.

Previous phylogenetic studies employing the large subunit ribosomal RNA (nLSU rRNA) gene sequences placed *R. bicolor* and related taxa in the hymenochaetoid clade (Hibbett and Binder 2002; Binder et al. 2005; Larsson et al. 2004, 2006). To confirm their placement in the hymenochaetoid clade, the nSSU rRNA genes of nine *Resinicium* and allied taxa were sequenced. Specimens and cultures of vouchers are available from CFMR; collection data are provided if the specimen is not listed in the "Specimens examined" section of individual species. The strain and GenBank numbers are: *Resinicium bicolor* HHB10l08 DQ834914; *R.. chiricahuaense* JLLl4605 DQ834912, Canada, Alberta, Kananskis Valley, near Seebe, on conifer, 10 July 1967, J.L. Lowe; *R. friable* FP102983 DQ834915; *R. furfuraceum* FP101917 DQ834913, United States, Wisconsin, Door County, Toft's Point Scientific Area, on conifer, 12 August 1983, K.K. Nakasone; R. meridionale FPl10438 DQ834910, United States, Mississippi, Catfish Point, on sycamore log, 2 August 1960, P.L. Lentz, FP150352 DQ974210, Jamaica, St. Andrew Parish, Blue and John Crow Mountains National Park, Holleywell Recreation Park, along trail to waterfall, on decayed bark of hardwood, 13 June 1999, K.K. Nakasone; ***R. mutabile*** FP102989 DQ834917; *R. saccharicola* FP102754 DQ834916, see above; *Skvortzovia furfurella* (Bres.) Bononi & Hjortstam HHB3173 DQ834911, United States, Maryland, Frederick County, west of Emmitsburg, Middle Creek, on *Carya* sp., 2 September 1969, H.H. Burdsall, Jr. These 9 sequences were included in a data set with 16 representative taxa of the major subclades of the hymenochaetoid clade and two outgroup species. Taxa with their GenBank accession numbers included in the analyses are: *Basidioradulum radula* (Fr.: Fr.) Nobles AY771611; *Cyphellostereum laeve* (Fr.) D.A. Reid AY752973; *Fibrieium rude* (P. Karst.) Jülich AY654888; *Hydnoehaete duportii* (Pat.) T. Wagner & M. Fisch. AY662669; *Hydnoehaete olivacea* Cooke AY293134; *Hyphoderma praetermissum* (P. Karst.) J. Erikss. & Å. Strid AF518580; *Inonotus baumii* (Pilat) T. Wagner & M. Fisch. AY839830; *Inonotus hispidus* (Bull.: Fr.) P. Karst. U59074; *Oxyporus latemarginatus* (Durieu & Mont. ex Mont.) Donk AF082670; *Phellinus igniarius* (L.: Fr.) Quél. AF026614; *Resinicium bicolor* AF518588, AF026615; *R. meridionale* AY293142; *Rickenella fibula* AY771599; *Trichaptum abietinum* (Dicks.: Fr.) Ryvarden AF026585; *Tubulicrinis gracillimus* (D.P. Rogers & H.S. Jacks.) G. Cunn. AF518592. The outgroup taxa *Sistotrema raduloides* (P. Karst.) Donk (AY757262) and *Kavinia himantia* (Schwein.: Fr.) J. Erikss. (AY293138) are exemplars from the cantharelloid and gomphoid clades, respectively.

#### *Sequence determination and analyses*

Genomic DNA was obtained from lyophilized cultures, and the ITS region and nSSU rRNA gene were amplified and sequenced using primers as described in Greslebin et al. (2004). Sequences were manually aligned in PAUP* 4.0b10 (Swofford 2002) and MacClade 3 (Maddison and Maddison 1992) with those obtained from GenBank. The nSSU and ITS regions were analyzed separately. Sequence data sets are deposited in TreeBASE (study accession S1719, matrices M3114-5). Ambiguous sites and segments at the start and end of alignments with substantial missing data were excluded from analyses. Maximum parsimony (MP) and maximum likelihood (ML) analyses were implemented in PAUP* 4.0b10 and Bayesian analysis in MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). For the ITS region, MP analysis with the branch and bound search option was conducted with characters unordered and of equal weight, gaps treated as missing data, and maxtrees set at 2000. Bootstrap support for clades (Felsenstein 1985) was estimated from 1000 heuristic searches with as-is addition sequence, retention of one tree per replicate, TBR branch swapping, without topological constraints, nucleotides unordered, and maxtrees set to 5000. The program Modeltest 3.7 (Posada and Crandall 1998) performed nested likelihood ratio tests to determine the best model of sequence evolution. The values obtained from Modeltest were applied in ML and Bayesian analyses. ML heuristic searches were performed in PAUP* with TBR branch swapping and no topological constraints. Bayesian inference was implemented in MrBayes using the default settings except for the number of substitution types (nst) and model for among-site variation (rates) parameters. One million generations were performed, with every 1000 trees sampled. The first 2500 trees, the bumin phase, were excluded from construction of the consensus tree. Bayesian support for clades is reported as percent posterior probabilities (pp). Similar analyses were performed on the nSSU rRNA data set except that the MP analyses began with an initial heuristic search of 100 random taxon addition replicates, the retention of two shortest trees, maxtrees set to 2000. The recovered trees were used as starting trees in an heuristic search with characters unordered and of equal weight, gaps treated as missing data, and maxtrees set at 2000 to find the most parsimonious trees. Bootstrap support was estimated as described earlier except that maxtrees was set to 2000. ML and Bayesian analyses were conducted with values obtained from Modeltest following procedures described previously.

## Results

### Phylogenetic analyses

ITS sequences for 25 strains were obtained. The ITS region, consisting of the ITSl, ITS2, and 5.8S rRNA gene, is smallest in ***Resinicium confertum*** Nakasone, sp. nov. (501 base pairs (bp)), followed by ***Resinicium tenue*** Nakasone, sp. nov. and ***Resinicium rimulosum*** Nakasone, sp. nov. (506 bp), *R. friabile* (508 bp), *R. bicolor* and *R. saccharicola* (516 bp), ***Resinicium monticola*** Nakasone, sp. nov. (539 bp) and ***Resinicium mutabile*** Nakasone, sp. nov. (553 bp). The multiple sequence alignment totaled 772 bp of which 111 bp were excluded from analyses because of alignment ambiguity or missing data, and 199 bp (25.8%) were parsimony informative. In the MP analyses, 48 equally parsimonious trees of 323 steps were recovered with consistency index (CI) of 80.8%, excluding uninformative characters, and retention inaex of 94.3%. The Hasegawa-Kishino–Yano (HKY) model (Hasegawa et al. 1985) of sequence evolution with gamma-distributed rate variation was selected by Modeltest. In the subsequent ML analysis in PAUP*, the following settings obtained from Modeltest were applied: nst = 2; *t* ratio = 1.5399; rates = gamma; shape =0.4299; pinvar =0; base =(0.2617; 0.2084; 0.1988; 0.31311). In the Bayesian analysis, only the nst and rate settings were specified; default values were used for the other parameters. MP, ML, and Bayesian analyses produced congruent trees that identified eight clades corresponding to the taxa ***R. mutabile, R. monticola,*** *R. saccharicola*, *R. bicolor*, and a species group of closely related taxa consisting of *R. friabile,* ***R. tenue, R. confertum,*** and ***R. rimulosum*** (Fig. 1A). In this latter group, ***R. confertum*** and ***R. tenue*** are sister taxa, and ***R. rimulosum*** is in the basal position. The *R. saccharicola* clade was well supported with MP (90% bootstrap support), minimally supported with Bayesian inference (63% pp), but not recognized with ML analyses. The uncorrected pairwise sequence divergence values as calculated in PAUP* (data not shown) are less than 1.2% within a species and 3.8%-7.5% among *R. saccharicola*, *R. bicolor*, ***R. rimulosum, R. confertum, R. tenue*** and *R. friabile*. ***Resinicium monticola*** and ***R. mutabile*** are significantly different from each other (12.2%-12.8%) as well as from the other *Resinicium* taxa (15.7%-21.8%).

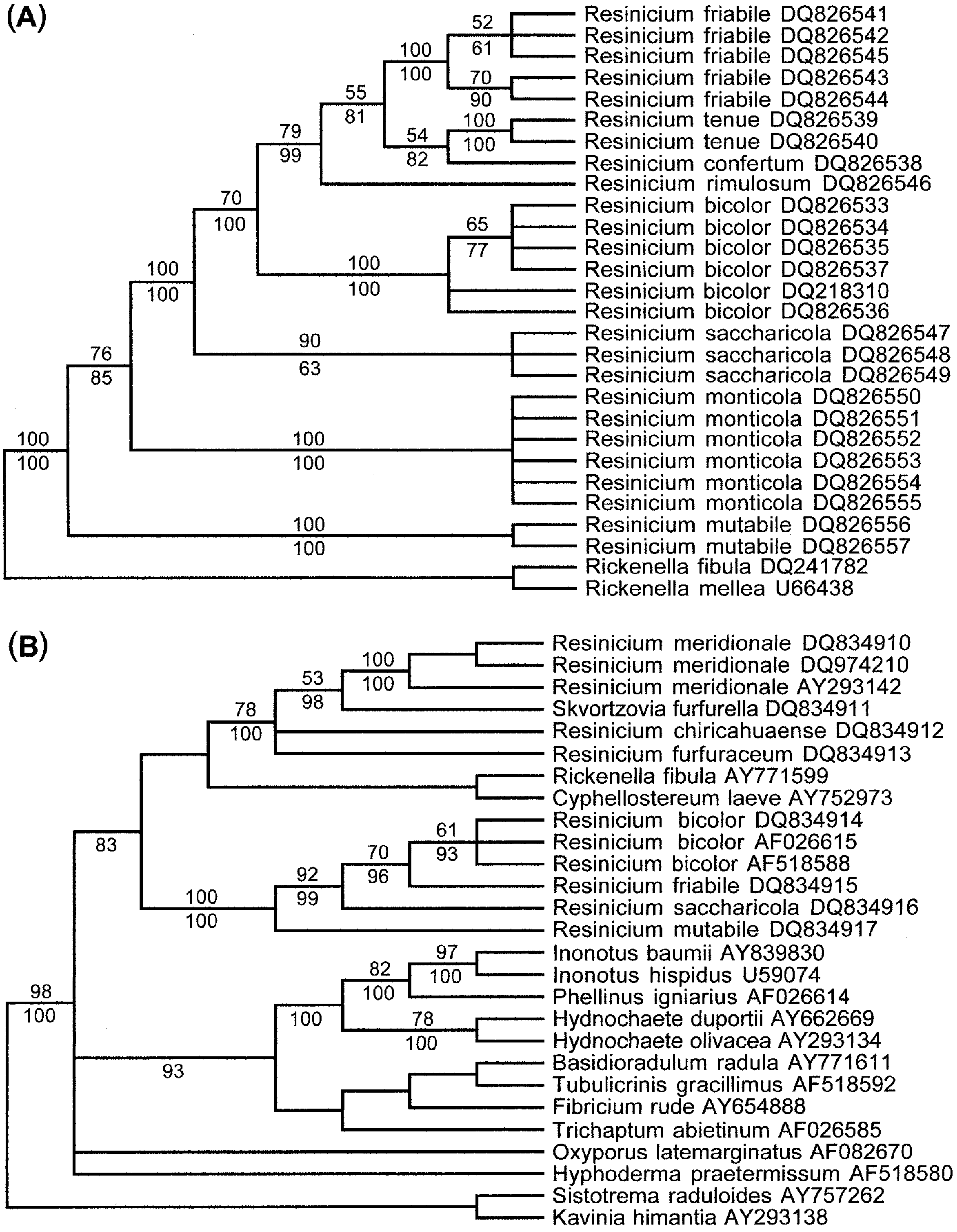
Partial sequences of the nSSU rRNA gene were obtained for nine Resinicium and allied species. The alignment consisted of 27 taxa and 1792 bp; 77 bp were excluded and 118 bp (6.5%) were parsimony informative. MP analyses recovered 9 equally parsimonious trees of 501 steps, with CI, excluding uninformative characters, of 47.8% and retention index of 65%. Modeltest selected the Tamura-Nei model (Tamura and Nei 1993) with equal base frequencies, some invariant sites, and a gamma distribution (TrNef+I+Γ) as the best-fit model of nucleotide substitution. The settings used in ML analysis were: nst = 6; base =equal; rmat = (1.000; 2.6437; 1.000; 1.000; 5.5721); rates =gamma; shape = 0.6398; pinvar = 0.6454; in Bayesian analysis, only values for nst and rates were set. In all three analyses, *Resinicium* species and allied taxa were placed in two clades (Fig. IB): (1) the *Resinicium s. str.* clade with *R. bicolor, R. friabile, R. saccharicola,* and ***R. mutabile*** (78% bootstrap support, 100% pp) and (2) the *Resinicium s.l.* clade with *R. furfuraceum, Skvortzonia furfurella, R. meridionale,* and *R. chiricahuaense* (100% bootstrap support; 100% pp).

### Morphological studies

*Resinicium* Parmasto, Consp. syst. cortic. p. 98. 1968.

Basidiomes resupinate, effuse, up to 650 μm thick, soft, membranous, subceraceous or ceraceous, white, yellow to light brown; hymenophore grandinioid, spinose, papillose or tuberculate, rarely smooth or farinaceous; mycelial cords sometimes present in substrate; margin undifferentiated. Hyphal system monomitic with nodose-septate or simple-septate generative hyphae. Subicular hyphae agglutinated or not, often bearing acicular, refractive, nonstaining spines apically encrusted with a cluster of hyaline crystals. Astrocystidia present in hymenium, occasionally embedded in subiculum and aculeus trama. Halocystidia usually present, walls of vesicles and interior bulbs may be cyanophilous. Hyphidia sometimes present in hymenium. Basidia cylindri-

**Fig. 1.** (A) Strict consensus of 48 most-parsimonious trees based on the ITS sequences of *Resinicium* s. str. species. *Rickenella fibula* and *Rickenella mellea* are the outgroup taxa. (B) Strict consensus of 9 most-parsimonious trees based on sequences from the nSSU rRNA gene region for *Resinicium* and other species from the hymenochaetoid clade. *Sistotrema raduloides* and *Kavinia himantia* are the outgroup taxa. In both trees, bootstrap support values are positioned above, and posterior probabilities below the branches.



cal to clavate, often with a median constriction, 4-sterigmate. Basidiospores ellipsoid to cylindrical, Q = 1.4-2.2(-2.4), thin-walled, smooth, sometimes cyanophilous, not reacting with Melzer's reagent. Fruiting on wood and bark of angiosperms and gymnosperms and grass culms.

The genus *Resinicium* is redescribed to include additional information on basidiome texture, hymenophore variation and color, hymenial elements, and substrate preferences. Most species possess nodose-septate hyphae; the exception is *R. Saccharicola*, which has simple-septate hyphae with rare clamp connections. The genus is restricted to species that produce astrocystidia, the only consistent character found in all accepted species. Astrocystidia found in the hymenium are primarily ventricose-rostrate with an acute or bulbous apex that is encrusted with pointed calcium oxalate crystals arranged in a star-like manner. Encrusted spines developed on the subicular hyphae of some species appear to be a reduced form of astrocystidia. For scanning electron micrographs of astrocystidia and crystal clusters, see Keller (1985) and Connolly and Jellison (1995).

Halocystidia are sphaero-pedunculate structures with a small, apical bulb enclosed by a larger vesicle that is initially filled with dark yellow, resin-like material. Wu (1990) was the first to report that the vesicle walls were cyanophilous. In several species the walls of the interior apical bulb also are cyanophilous. Ultrastructure micrographs of halocystidia in *R. bicolor* show that the outer vesicle wall is more electron-dense than the wall of the interior apical bulb (Clémençon 2004). Although present in most species of Resinieium, halocystidia are absent in ***R. monticola*** and ***Resinicium mutabile*** Nakasone, sp. nov. ***Resinicium mutabile*** develops a different kind of cystidium with an undifferentiated stalk that supports an apical vesicle but lacks an interior apical bulb.

*Resinicium furfuraceum*, one of the original species in *Resinicium*, lacks astrocystidia; thus, it is excluded from *Resinicium* s.str. as defined here, in Hjortstam (1998), and Wu (1990).

TYPE: *Resinicium bicolor* (Alb. & Schwein.: Fr.) Parmasto

**Key to the species in *Resinicium* s. str.**

1. Hyphae simple septate, with scattered single clamp connections.. ......... *R. saccharicola* (see Nakasone (2000) for a description and illustration)

1. Hyphae mostly nodose septate, clamp connections abundant. ............................................ 2

2*a*. Halocystidia rare or absent. .......................................................................... 3

2*b*. Halocystidia numerous. ............................................................................... 4

3*a*. Basidiome tuberculate to papillose, white to yellow. ............................................ ***R. monticola***

3*b*. Basidiome spinose, brown. ..................................................................... *R. mutabile*

4*a*. Basidiospores cylindrical to narrowly ellipsoid, Q = 1.7-2.4. ........................................... *R. bicolor*

4*b*. Basidiospores ellipsoid, Q = 1.4-1.6 ..................................................................... 5

5*a*. Basidiomes subceraceous to ceraceous ........................................................... 6

5*b*. Basidiomes soft to subceraceous. ..................................................................... 7

6*a*. Basidiomes strongly rimose, white to yellow ........................................... ***R. rimulosum***

6*b*. Basidiomes rarely with cracks, yellow to yellowish brown ........................................ *R. friabile*

7*a*. Basidiomes soft to subceraceous, aculei single, up to 100 μm long ...................................... ***R. tenue***

7*b*. Basidiomes soft to membranous, aculei aggregated, up to 1 mm long. ................................. ***R. confertum***

## Species descriptions

*Resinicium bicolor* (Alb. & Schwein.: Fr.) Parmasto, Consp. syst. cortic. p. 98. 1968. Figures 2-4 and 14

≡ *Hydnum bicolor* Alb. & Schwein., Consp. fung. lusat. p. 270. 1805.

≡ *Hydnum bicolor* Alb. & Schwein.: Fr., Syst. mycol. 1: 417. 1821.

≡ *Acia bicolor* (Alb. & Schwein.: Fr.) P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 5: 42. 1879.

≡ *Odontia bicolor* (Alb. & Schwein.: Fr.) Quél., Enchir. fung. p. 195. 1886.

≡ *Odontia bicolor* (Alb. & Schwein.: Fr.) Bres., Ann. Mycol. 1: 87. 1903.

≡ *Mycoacia bicolor* (Alb. & Schwein.: Fr.) Spirin & Zmitr., Novosti Sisto Nizsh. Rast. 37: 183. 2004.

=*Hydnum subtile* Fr., Syst. mycol. 1: 425. 1821 (sec. Bresadola 1903).

≡ *Hydnum ochroleucum* var. subtile (Fr.) Pers., Mycol. eur. 2: 186. 1825.

≡ *Acia subtilis* (Fr.) P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 5: 42. 1879.

≡ *Odontia subtilis* (Fr.) Quél., Fl. mycol. France p. 435. 1888.

*Kneiffia subgelatinosa* Berk. & Broome, Ann. Mag. Nat. Hist. ser. 4, 15(85): 32. 1875.

≡ *Odontia subgelatinosa* (Berk. & Broome) Cooke & Quél., Clav. syn. hymenomyc. eur. p. 206. 1878.
=*Hydnum serratum* Peck, Rep. State Bot. New York State Museum 50: 112. 1898.
=*Hydnum balsameum* Peck, Bull. New York State Mus. Nat. Hist. 75: 15. 1904.
=*Hydnum echinosporum* Velen., České houby p. 745. 1922 (sec. Cejp 1928).

Basidiomes resupinate, widely effuse, up to 15 cm × 7.5 cm, adnate, not separable, thin, subceraceous or ceraceous, rarely soft, farinaceous, papillose to spinose, area between aculei 90-300 µm thick, smooth, continuous, fertile, pale yellow (4A3), orange white (5A2), greyish orange [5B(3-4)], pale orange (5A3), or brownish orange (5C4), with scattered cracks; mycelial cords sometimes present in decayed substrate; hymenophore composed of conical to cylindrical aculei, 140-1000 µm x 100-300 µm, 3-6 aculeilrnm, single or aggregated, smooth or farinaceous, tapering to an acute or blunt fimbriate sterile apex, aculei sometimes prostrate, with multiple smaller aculei developing linearly along its length; margins gradually or abruptly thinning out, appressed, finely farinaceous or spinose, concolorous with hymenophore. Hyphal system monomitic, generative hyphae regularly nodose septate. Aculei composed of wholly or partially agglutinated hyphae in a central core, often with embedded halocystidia, enclosed by subhymenial and hymenial layers, at apex hyphae cylindrical or tapered; tramal hyphae 1.5-4.5 µm in diameter, nodose septate, infrequently branched, walls hyaline, thin or up to 1 µm thick, smooth or coated with dark-brown mucilaginous materials. Subiculum 60-250 µm thick, composed of moderately dense to densely compact, partially agglutinated subicular hyphae arranged parallel to substrate, often with embedded halocystidia and astrocystidia; subicular hyphae (1.5-)2-4.5 µm in diameter, nodose septate, moderately branched, walls hyaline, thin, and smooth, often developing acerose spines, 6 µm × 0.5 µm, apically encrusted with a cluster of hyaline crystals. Subhymenium up to 36 µm thick, a somewhat agglutinated tissue; subhymenial hyphae 1.5-3.5 µm in diameter, nodose septate, short-celled, frequently branched, walls hyaline, thin, and smooth. Hymenium composed of hyphidia, halocystidia, astrocystidia, and basidia. Hyphidia rare to scattered, filamentous, tapered or knobby at apex, up to 20 µm × 2.5 µm, clamped at base, walls thin, hyaline, smooth. Halocystidia numerous in the hymenium, subiculum and aculeus trama, sphaeropedunculate, (16-)18-30(-40)µm × 3.5-5.5 µm tapering to 1-3 µm in diameter at base, with a basal clamp connection, apical bulb 7-11 µm in diameter enclosed by a vesicle, 12-30 µm in diameter, empty or filled with resinous, hyaline to dark-yellow material, walls hyaline, thin, smooth, vesicle walls cyanophilous. Astrocystidia rare to numerous in hymenium and subiculum, aculeate or ventricose-rostrate, (13-)18-25 µm × (2.5-)3-4 µm, tapering to 1-2 µm in diameter at base with a basal clamp connection, walls hyaline, thin, smooth, tapered at apex or with a small spherical bulb 2–3 µm in diameter, encrusted with a dense, stellate cluster of hyaline crystals 12-15 µm in diameter. Basidia clavate to cylindrical, often with a median constriction, (13-)15-22 µm x 4.5-6 µm, tapering to 1.5-2.5 µm in diameter at base with a basal clamp connection, walls hyaline, thin, smooth, 4-sterigmate, sterigmata slender and up to 5-6 µm long. Basidiospores rare to numerous, cylindrical to narrowly ellipsoid, (4.5-)5.5-7.2(-8) µm × (2.5-)2.9-3.5 µm, Q = 1.7-2(-2.4), walls hyaline, thin, smooth, cyanophilous, not reacting in Melzer's reagent.

HABITAT: Wood and bark of angiosperms and gymnosperms.

DISTRIBUTION: Europe, India, Japan, Korea, Canada, United States.

REPRESENTATIVE SPECIMENS EXAMINED: See Supplementary data.[1]

TYPE MATERIAL EXAMINED: Great Britain. Scotland, Tayside, Glamis, on fir, April 1874, Herb. Berkeley, K(M)60l06 (K, holotype of *Kneiffia subgelatinosa*). Germany. Ad ligna abietine, ex Herb. Link, F49570 (S, holotype of *Hydnum bicolor*). United States. New York: North Elba, on balsam fir, 15 September, C.H. Peck (NYS, holotype of *Hydnum balsameum*); Adirondack Mts., Ampersand Pond, on spruce (wood), September, C.H. Peck (NYS, holotype of *Hydnum serratum*; isotype NY 00776149).

***Resinicium confertum*** Nakasone, sp. nov. Figures 5 and 15.

*Differt a* R. friabili *et* R. tenui *basidiomatibus mollibus membranaeeis, aeuleis aggregatis, et basidiosporis majoribus,* (4.5-)5-6(-7) *µm* × 3.2-3.5(-4) µm, *a* R. saccharicola *fibulatis hyphis.* Holotype: Puerto Rico, Aguas Buenas Municipio, Route 156, near Aguas Buenas, Cerro de Teza, on decorticate hardwood, 23 June 1996, K.K. Nakasone, FP102863 (BPI, isotype CFMR).

ETYMOLOGY: *confertus,* Latin, crowded, referring to the aggregated aculei.

REMARKS: *Resinicium bicolor* is a common white-rot decay fungus found throughout the north temperate region. It causes a root and butt rot of living trees (Domanski 1976; Nobles 1953). Basidiomes are often associated with a species of single-celled green alga (Poelt and Jülich 1969; Eriksson et al. 1981; Breitenbach and Kranzlin 1986). Over 200 collections of *R. bicolor* were examined from Asia, Europe, and North America. Although the specimens were variable in texture, thickness, and size and abundance of aculei, a consistent feature was the basidiospores with Q ≥ 1.7. The cylindrical to narrowly ellipsoid basidiospores distinguish *R. bicolor* from other species discussed herein *Resinicium bicolor* has been studied by ecologists and forest pathologists. Recent studies have focused on *R. bicolor* as a biological control agent for *Heterobasidion annosum* (Holmer and Stenlid 1997) and its interaction with other decay fungi of spruce stumps (Woods et al. 2(05). Although rarely associated with herbarium specimens, mycelial cords produced by *R. bicolor* are of interest to ecologists studying the foraging habits of basidiomycetes (Zakaria and Boddy 2002) and the translocation of calcium and minerals (Connolly and Jellison 1995; Connolly et al. 1999).

Bresadola (1903) examined an original Schweinitz speci-

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[1] Supplementary data for this article are available on the journal Web site (http://canjbot.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5176. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

men of *Hydnum bicolor* from the Link Herbarium at Berlin. Although Link's herbarium was destroyed during World War II (B. Hein, personal communication, 2005), a piece of this specimen was found in Bresadola's herbarium at Stockholm. On the packet in Bresadola's hand is written "Ex Herb. Link, exempl. von Schweintz!" This specimen is accepted as the type of *H. bicolor.* Although tiny, the specimen is in excellent condition with numerous astrocystidia, halocystidia, basidia, and basidiospores of average size, 6.57 µm × 3.24 µm Q = 2.03. Bourdot and Galzin (1928) described two forms of *Odontia bicolor.*, forma *capitata* and forma *filicina.* Specimens of *O. bicolor* forma *capitata* from Paris were found to be conspecific with *R. bicolor.*

Bresadola (1903) stated that the *H. subtile* specimen at Uppsala is conspecific with the type of *H. bicolor* in Link's herbarium. There is a specimen of *Hydnum subtile* from Sweden collected by Fries in the Uppsala herbarium that could be the specimen Bresadola saw. This specimen is *R. bicolor* and is in fairly good condition though no basidia were observed. The cylindrical basidiospores are rare but typical, average size 5.82 µm 2.88 µm, Q = 2.0. However, this specimen might not be the holotype of *H. subtile* because it does not agree with the protologue in several key aspects. The specimen is brown and fruiting on bare, decayed wood, whereas the protologue describes the fungus as whitish or subhyaline and growing on bark of *Betula.* Nevertheless, I accept Bresadola's synonymy.

The holotype of *Kneiffia subgelatinosa* (Berk. & Broome) at Kew is a small collection in poor condition. The specimen is smooth with only several small aculei with mostly collapsed hyphae and several astrocystidia and halocystidia; no basidiospores were observed. Nonetheless, this specimen is likely to be *R. bicolor* as synonymized by Reid and Austwick (1963).

The type specimen of *Hydnum balsameum* Peck, is a large collection in good condition with numerous halocystidia and astrocystidia. It is conspecific with *R. bicolor,* though it has a farinaceous texture and brown aculei. The narrowly ellipsoid basidiospores are rare, averaging 5.2 × 2.9 µm, Q = 1.8. Similarly, the type specimen of *Hydnum serratum* Peck, is in good condition with aculei of various sizes and microscopic features typical for *R. bicolor.* The numerous, cylindrical basidiospores in this collection average 6.5 × 3.1 µm Q = 2.07. Thus, I concur with Miller (1934), Brown (1935), and Gilbertson (1962), who considered *H. balsameum* and *H. serratum* conspecific with *R. bicolor.*

*Hydnum acutum* Pers. was synonymized with *H. subtile* by Fries (1828, p. 140). However, the type of *H. acutum* at Leiden (No. 910.262-2) is conspecific with *Hydnum pachyodon* Pers. (≡ *Spongipellis pachyodon* (Pers.) Kotl. & Pouzar), according to notes by M.A. Donk and L. Romell. *Hydnum echinosporum* Velen. was placed in synonymy with *O. bicolor* by Cejp (1928).

Reports of *R. bicolor* from Hawaii (Gilbertson and Adaskaveg 1993; Gilbertson and Hemmes 1997; Gilbertson et al. 2002) and Taiwan (Lin and Chen 1990; Wu 1990), and *O. bicolor* from New Zealand (Cunningham 1959) and South Africa (Talbot 1958) should be referred to *R. friabile.* Basidiome resupinate, effused, closely appressed, thin to thick, soft, membranous, fragile, at first minutely odontoid with finely porose areas between aculei, 60-500 µm thick between aculei, in mature areas light orange (5A4) to greyish orange (5B4) or Light Buff (Ridgway 1912), cracking deeply between aculei or aculei clusters in well-developed areas exposing a white, felty context; hymenophore composed of aculei up to 1 mm × 200 µm, at first conical then cylindrical, single or fused into clusters, 3-5 aculei per mm or 1-2 clusters per mm, apices at first penicillate then rounded, smooth, blunt, aculeus clusters with multiple rounded apices; margins indeterminate, gradually thinning out, raised and farinaceous to granulose, white to pale cream, with smaller, rounded aculei.

Hyphal system monomitic, generative hyphae regularly nodose septate. Aculei composed of a central core of partially agglutinated hyphae enclosed by thin subhymenial and hymenial layers, at apex terminal hyphae not differentiated. Subiculum up to 500 µm thick, with mostly collapsed, indistinct hyphae; subicular hyphae 2-4.5 µm in diameter, nodose septate, moderately branched, often collapsed or disintegrated, walls hyaline, thin, smooth, often developing refractive, acicular spines, 3-8 µm × 0.5-1 µm with an apical cluster of hyaline crystals, up to 6 µm in diameter. Subhymenium up to 20 µm thick, somewhat agglutinated; subhymenial hyphae 1.5-3 µm in diameter, nodose septate, frequently branched, vertically arranged, short-celled, walls thin, hyaline, smooth. Hymenium a palisade of halocystidia, astrocystidia, and basidia. Halocystidia numerous, sphaeropedunculate, 16-25 µm × 3.5-5 µm, tapering to 2 µm in diameter at base, with a basal clamp connection, apical bulb 8-12 µm in diameter and enclosed by a globose vesicle up to 20 µm in diameter, empty or containing nonstaining, resinouslike material, walls hyaline, thin to slightly thick, smooth, vesicle wall cyanophilous. Astrocystidia abundant, ribiform to lecythiform, 10-20 µm × 1-3 µm, with a basal clamp connection, walls hyaline, thin, smooth, apical bulb 3-5 µm in diameter, encrusted with a star-like cluster of hyaline crystals up to 11 µm in diameter. Basidia clavate, 10-16 µm × 4-5.5 µm, tapering to 2 µm in diameter at base, nodose septate at base, walls hyaline, thin, smooth, 4-sterigmate. Basidiospores ellipsoid, (4.5-)5-6(-7) µm × 3.2-3.5(-4) µm, Q = 1.53, walls thin, hyaline, smooth, acyanophilous, not reacting in Melzer's reagent.

HABITAT: Wood and bark of angiosperms.

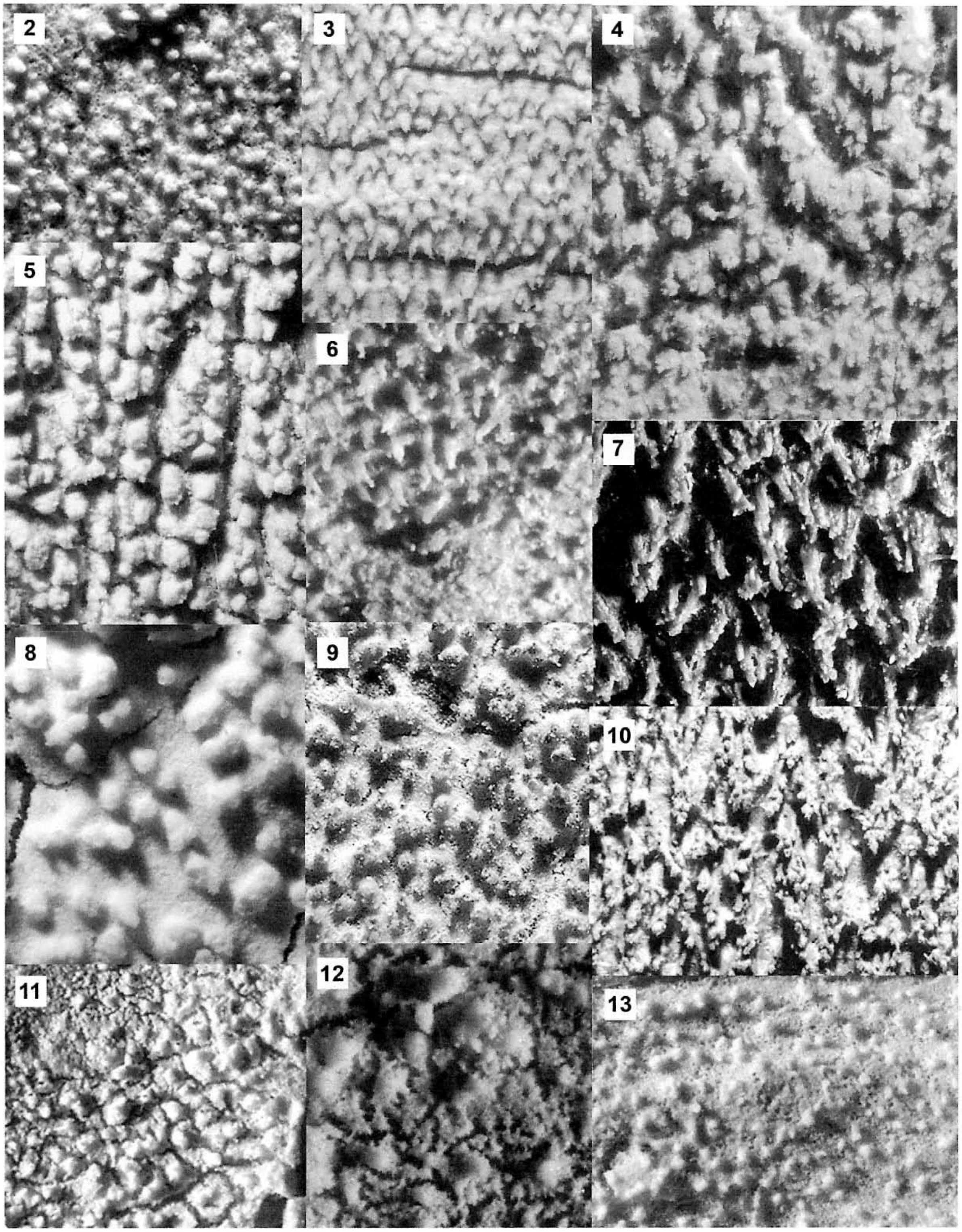
DISTRIBUTION: Puerto Rico.

***Resinicium confertum*** is characterized by a soft, extensively cracked basidiome of aggregated, fused aculei and ellipsoid basidiospores. Although known only from one collection, the holotype displays the complete range of hymenophore development from thin, developing areas with small conical aculei to thick, mature areas with aggregated aculei. The broader basidiospores and soft, membranous basidiome of ***R. confertum*** distinguish it from *R. bicolor* and ***R. tenue.*** *Resinicium saccharicola* has basidiospores of similar shape and size to ***R. confertum*** but lacks clamp connections. Compared to ***R. confertum,*** *R. friabile* has slightly shorter basidiospores as well as basidiomes with a distinctly subceraceous to ceraceous texture.

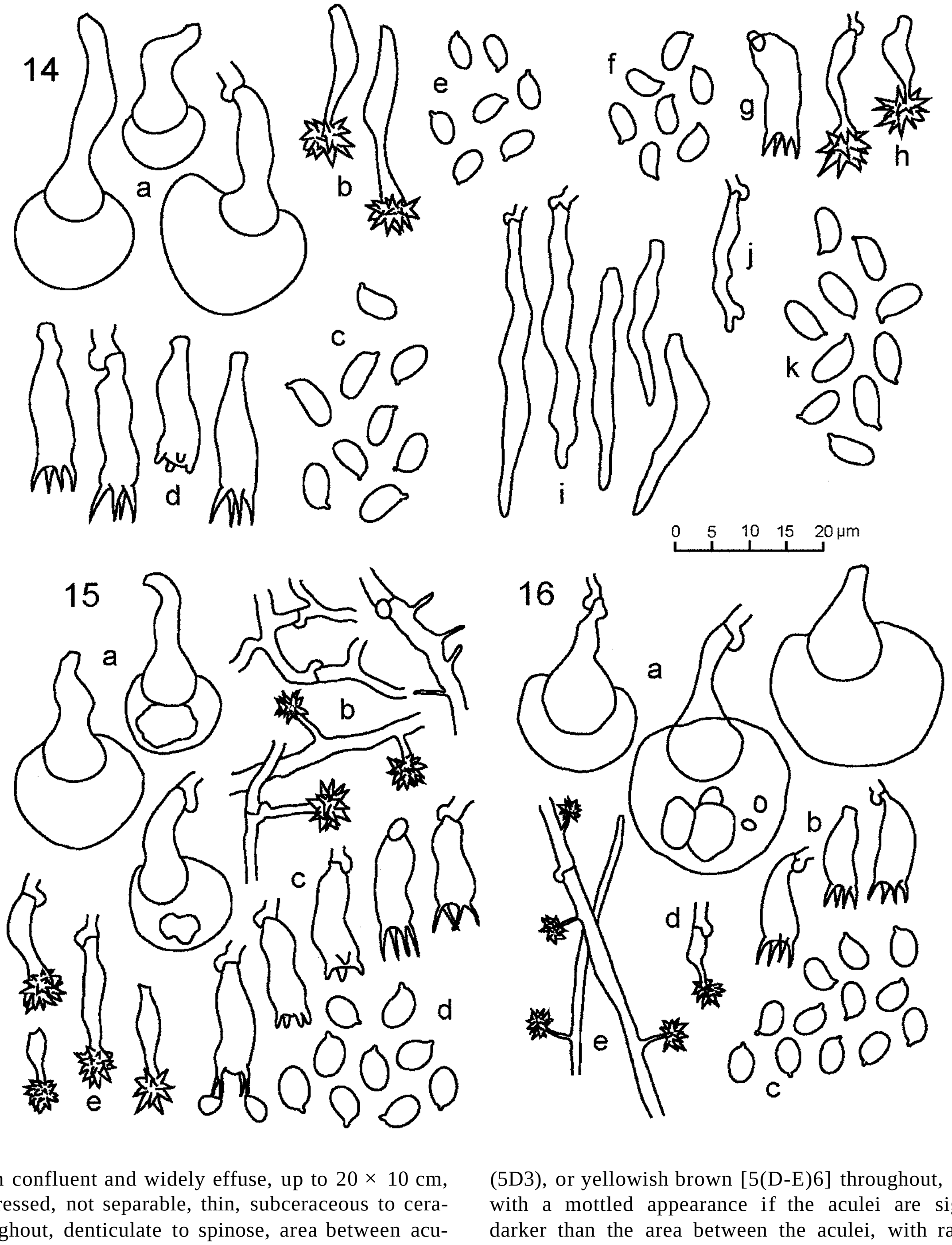
***Resinicium friabile*** Hjortstam & Melo, Mycotaxon 65: 324. 1997. Figures 6, 7, and 16

Basidiomes resupinate, beginning as small circular

**Figs. 2-13.** Hymenophore of *Resinicium* species. **Fig. 2.** *Resinicium bicolor* US0265450. **Fig. 3.** *Hydnum serratum* holotype. **Fig. 4.** *Resinicium bicolor* US0265398. **Fig. 5.** ***Resinicium confertum*** holotype FP102863. **Figs. 6 and 7.** *Resinicium friabile* holotype K(M)60l03. **Fig. 8.** ***Resinicium monticola*** holotype FPI50360. **Figs. 9 and 10.** ***Resinicium mutabile*** holotype FP102989. **Figs. 11 and 12.** ***Resinicium rimulosum*** holotype FP150328. **Fig. 13.** ***Resinicium tenue*** holotype FP 150354. Scale bar =1 mm for Figs. 2-11, scale bar =0.5 mm for Fig 12.



**Figs. 14-16.** Microscopic elements of *Resinicium* species. Fig. 14. *Resinicium bicolor,* from holotype of *Hydnum serratum*: (*a*) halocystidia, (*b*) astrocystidia, (*c*) basidiospores, (*d*) basidia; *R. bicolor* from US0265398: (*e*) basidiospores; *R. bicolor* from PC0088661 : (*f*) basidiospores, (*g*) basidium, (*h*) astrocystidia; *R. bicolor* from EWR117: (*i*) terminal hyphae from apex of aculei, (*j*) hyphidium from hymenium; *R. bicolor* from Galzin 21139: (*k*) basidiospores. Fig. 15. ***Resinicium confertum***, from holotype FP102863: (*a*) halocystidia, (*b*) subhymenial hyphae with spines, some with apical encrustations; (*c*) basidia; (*d*) basidiospores, (*e*) astrocystidia from hymenium. Fig. 16. *Resinicium friabile,* from FP102803: (*a*) halocystidia, (*b*) basidia, (*c*) basidiospores, (*d*) astrocystidium; *R. friabile* from Wu 9704-70: (*e*) subicular hyphae bearing encrusted spines.



patches then confluent and widely effuse, up to 20 × 10 cm, closely appressed, not separable, thin, subceraceous to ceraceous throughout, denticulate to spinose, area between aculei up to 180 µm thick, smooth, subfelty, farinaceous, stringy or porose, rarely fibrillose, light yellow (4A4), greyish yellow (4B4), to pale yellow (4A3), greyish brown (5D3), or yellowish brown [5(D-E)6] throughout, sometimes with a mottled appearance if the aculei are significantly darker than the area between the aculei, with rare cracks; hymenophore composed of aculei 200-1000 µm × 150-200 µm, (3-)4–7 aculei per millimetre, at first conical to cylindrical, evenly and widely distributed, then becoming aggregated and fused, smooth or with short lateral knobs, apices acute, entire, fimbriate or tufted, sometimes lighter in color than base; margins indistinct, gradually or abruptly thinning out, adnate, appressed, white, finely farinaceous.

Hyphal system monomitic, generative hyphae regularly nodose septate. Aculei composed of agglutinated hyphae and embedded halocystidia in a central core enclosed by subhymenial and hymenial layers, with astrocystidia scattered in hymenium; apex sterile, composed of obtuse or tapered terminal hyphae; tramal hyphae 1.5--4.5 µm in diameter, nodose septate, infrequently branched, walls hyaline, thin to slightly thickened, smooth. Subiculum up to 60 µm thick, a densely compact, more or less vertically arranged tissue composed of agglutinated, collapsed, indistinct hyphae and embedded halocystidia; subicular hyphae 1.5-3 µm in diameter, nodose septate, moderately branched, walls hyaline, thin, smooth, developing refractive, acicular spines, up to 14 µm × 1.5 µm, apically encrusted with a cluster of hyaline crystals. Subhymenium up to 30 µm thick, a compact and agglutinated tissue; subhymenial hyphae 1.5-3.5 µm in diameter, nodose septate, short-celled, frequently branched, walls hyaline, thin, smooth. Hymenium composed of halocystidia, astrocystidia, and basidia. Halocystidia numerous in the hymenium, subiculum and aculeus trama, sphaeropedunculate, 16-27 µm × 3.5-5 µm, tapering to 1.5-3 µm in diameter at base, with a basal clamp connection, apical bulb 4-15 µm in diameter and enclosed by a vesicle, 8-27 µm in diameter, empty or filled with opaque, resinous, hyaline to dark yellow material, walls hyaline, thin, smooth, apical bulb and vesicle walls cyanophilous. Astrocystidia rare to numerous in hymenium and subiculum, aculeate to lageniform, 7-14 µm × 1.5-3 µm, tapering to 1–1.5 µm in diameter at base, with a basal clamp connection, walls hyaline, thin, smooth, sometimes with a small apical bulb, 2-3 µm in diameter, encrusted with a dense, stellate cluster of hyaline crystals. Basidia cylindrical to clavate, 10-15(-20) µm × 4-5.5 µm, with a short stalk 1-3 µm in diameter, with a basal clamp connection, walls hyaline, thin, smooth, 4-sterigmate. Basidiospores rare to numerous, ellipsoid, (4-)4.5-5.5 µm × (2.5-)3-3.5 µm, Q = 1.4 - 1.6, walls hyaline, thin, smooth, cyanophilous, not reacting in Melzer's reagent.

HABITAT: Wood and bark of angiosperms and gymnosperms.

DISTRIBUTION: China, Taiwan, Vietnam, Japan, New Zealand, Puerto Rico, United States (Florida, Hawaii), Mexico, Belize, Ecuador, Brazil, Uruguay, South Africa.

TYPE SPECIMENS EXAMINED: Brazil. São Paulo State: reg. Santos, Ubatuba, Ihla Anchieta, (on decorticated wood), 17 January 1987, L. Ryvarden 24159 (K(M)60103, holotype); (on decorticated wood), 17-18 January 1987, L. Ryvarden 24168 (K(M)60104, paratype); on palm, 2 February 1987, K. Hjortstam 16770 (K(M)60105, paratype).

REMARKS: *Resinicium friabile* has a wide distribution and is the only *Resinicium* species known from the southern hemisphere. More than 50 specimens were examined from the tropical to temperate regions of Asia, the Americas, and Africa. Its highly variable hymenophore presents special challenges for identification for aculei may be well developed, as in the holotype, to odontoid in thin, developing specimens. A consistent feature is the presence of embedded halocystidia in the ceraceous subiculum and aculeus trama that are easily observed when the apical vesicles are filled with dark yellow, resinouslike substances. Typically, halocystidia are more numerous and prominent than astrocystidia, which are often scarce and inconspicuous. Although frequently misidentified as *R. bicolor, R. friabile* has ellipsoid basidiospores that are distinct from the cylindrical basidiospores typical of *R. bicolor.* The Q value of *R. friabile* ranges from 1.4-1.6 whereas that of *R. bicolor* is 1.7-2.2. In addition, *R. bicolor* has larger basidia and astrocystidia and a north temperate distribution.

Additional descriptions and illustrations of *R. friabile* are available in Hjortstam and Melo (1997), as *Odontia bicolor* in Cunningham (1959), and as *R. bicolor* in Lin and Chen (1990), Maekawa (1993), and Wu (1990). Reports of *R. bicolor* from South Africa (Talbot 1958), New Zealand (Cunningham 1959), Taiwan (Wu 1990), and Hawaii (Gilbertson and Adaskaveg 1993; Gilbertson and Hemmes 1997; Gilbertson et al. 2002) should be attributed to *R. friabile.* In Japan, both *R. bicolor* and *R. friabile* occur, though most of the specimens cited by Maekawa (1993) are *R. friabile.*

REPRESENTATIVE SPECIES EXAMINED: See Supplementary data[1].

***Resinicium monticola*** Nakasone, sp. nov. Figures 8 and 17

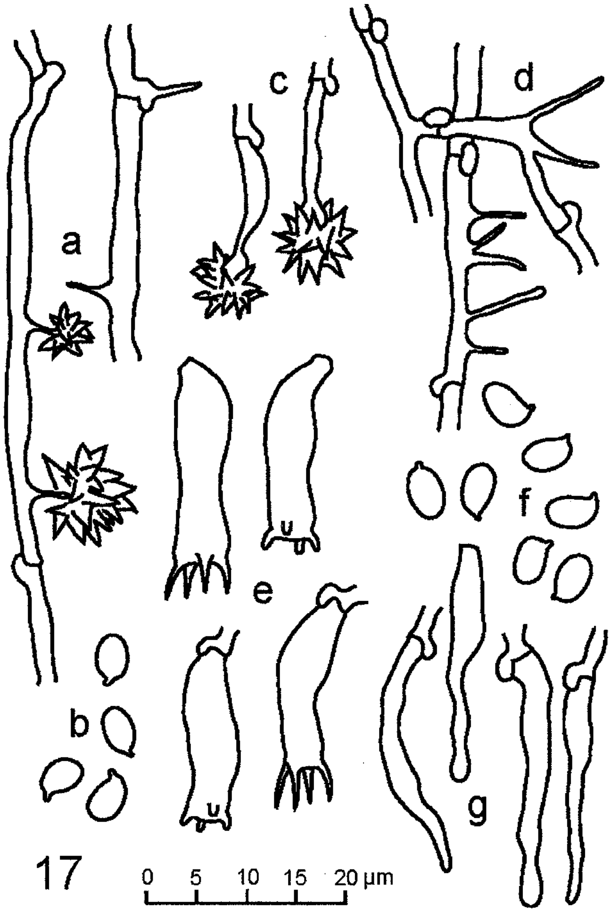
*Differt* a R. bicolori *et* R. friabili *basidiomatibus mollibus vel subceraceis, aculeis tuberculatis, aculeis et subiculis crystalliz plenis, astrocystidiis abundis, halocystidiis absentibus, basidiis raro, basidiosporis ellipsoideis, 4.8-5.5(-6) µm × 2.8-3.2 µm.* Holotype: Jamaica, Saint Andrew Parish, Blue Mountains and John Crow Mountains National Parks, Hollywell Recreation Park, along Waterfall Trail, on corticate hardwood, 13 June 1999, K.K. Nakasone, FP150360 (BPI, isotype CFMR, 11).

ETYMOLOGY: *Mons,* Latin, mountain + *-cola,* Latin, dweller, referring to its mountainous habitat.

Basidiomes resupinate, widely effused, thin to moderately thick, adherent, closely appressed, adherent, not easily separable, soft to subceraceous, membranous, tuberculate, area between tubercules 100-650 µm thick, smooth, felty, even, white, yellowish white [(2--4)A2] or pale yellow (4A3), rarely developing cracks; hymenophore composed of short conical, broad tubercules up to 180 µm × 300 µm, 3-6 tubercules per millimetre, single or fused, apex with a single, or occasionally, multiple points, obtuse, smooth or rarely bristly, often translucent; margins distinct, abrupt, white, smooth or gradually thinning out, finely farinaceous.

Hyphal system monomitic, generative hyphae regularly nodose septate. Tubercules filled with crystal clusters, at apex astrocystidia, cystidia, and hyphidia visible; cystidia capitate, 20–40 µm × 2–4 µm, tapering to 2-3 µm in diameter at base, with a basal clamp connection, apical bulb 3-6 µm in diameter, walls hyaline, thin, smooth, acyanophilous; hyphidia cylindrical to subulate, occasionally knobby or slightly enlarged at apex, 20-27 µm × 2-3 µm in diameter, clamped at base, walls hyaline, thin, smooth. Subiculum 80-550 µm thick, composed of crystal clusters and agglutinated hyphae embedded in mucilaginous material that dissolves in KOH but not in lactophenol cotton blue; subicular hyphae 1.5-3 µm in diameter, nodose septate, frequently

**Fig. 17.** ***Resinicium monticola,*** from holotype FP150360: (*a*) subicular hyphae with bare or encrusted spines, (*b*) basidiospores, (*c*) astrocystidia from hymeniuin; from FP150061: (*d*) subicular hyphae with denuded spines, (*e*) basidia; from FP150332: (*f*) basidiospores, (*g*) hyphidia from apices of aculei.



branched, often collapsed and indistinct, walls hyaline, thin, smooth, with refractive, acicular spines, up to 10 µm × 1 µm, bearing an apical cluster of crystals up to 12 µm in diameter. Subhymenium up to 25 µm thick, indistinct, obscured from numerous crystal clusters; subhymenial hyphae 1.5-3 µm in diameter, nodose septate, frequently branched, short-celled, walls hyaline, thin, and smooth. Hymenium composed of astrocystidia and basidia. Astrocystidia aculeate to lageniform, 10–30 µm × 1.5–4(–6) µm, tapering to 1-1.5 µm in diameter at base, with a basal clamp connection, walls hyaline, thin, smooth, at apex a small spherical bulb 2-4 µm in diameter, encrusted with a dense, stellate cluster of hyaline crystals, up to 15 µm in diameter. Basidia rare, cylindrical, often with a median constriction, 16-25 µm × 5-6 µm, tapering to 2-2.5 µm in diameter at base, with a basal clamp connection, walls hyaline, thin, smooth, 4-sterigrnate. Basidiospores rare, ellipsoid, 4.8-5.5(-6) µm × 2.8-3.2 µm, Q = 1.6-1.7, sometimes developing a short, narrow peg, walls hyaline, thin, smooth, acyanophilous, not reacting in Melzer's reagent.

HABITAT: : Bark and wood of angiosperms.

DISTRIBUTION: Jamaica, Puerto Rico.

SPECIMENS EXAMINED: See Supplementary data[1].

REMARKS: ***Resinicium monticola*** is characterized by soft to subceraceous, white to pale yellow basidiomes with small tubercules, numerous crystal clusters throughout the subiculum and tubercular trama, astrocystidia, and ellipsoid basidiospores but lacking halocystidia. The crystal clusters are the dominant component of the basidiome context and obscure all other microscopic features. Basidia and basidiospores are rare or absent in most collections. This is the only species that lacks true halocystidia or cystidia bearing an apical vesicle.

***Resinicium mutabile*** Nakasone, sp. nov. Figures 9, 10, and 18

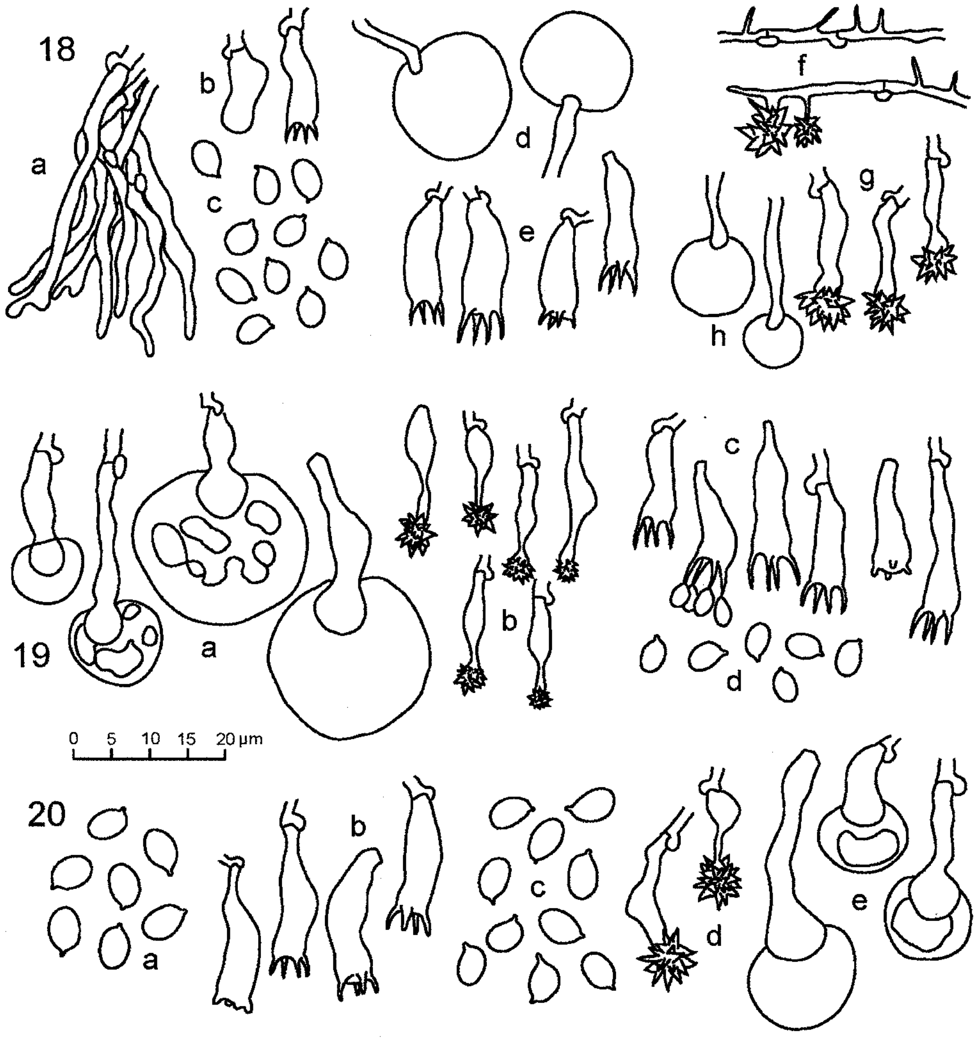
*Differt a* **R. monticola** *aculeis cylindricis, gracilibis, aggregatis, brunneis; halocystidiis absentibus; vesicularis in tramarum aculeis inclusis, globosis, aureis; basidiis raro, basidiosporis ellipsoideis, (4.5-)5-5.5 µm × 3-3.5(-4) µm.* Holotype: Puerto Rico, Rio Grande Municipio, Caribbean National Forest, El Verde Field Station, on well-decayed decorticate angiosperm, 28 June 1996, K.K. Nakasone, FP102989 (BPI, isotype CFMR, UPRRP).

ETYMOLOGY: *mutabilis,* Latin, changeable, referring to the color of the basidiome.

Basidiomes resupinate, widely effused, up to 15 cm × 5 cm, thin, following the contours of the substrate, soft to subceraceous, odontoid to spinose, area between aculei up to 300 µm thick, smooth, porose to farinaceous, occasionally reflective, overall color a mottled greyish orange (5B3), brownish orange (5C4), or light brown [5D(4-5)], often entire aculei or just the apices darker than smooth areas between aculei; fine cracks developing on drying to expose a soft, finely farinaceous context; hymenophore composed of slender, cylindrical aculei up to 1 mm × 300 µm, 2-6 aculei per mm, arranged linearly or aggregated into tubercules with multiple apices, sometimes occurring singly, with smooth or knobby sides, apices acute or obtuse, bristly, sometimes covered by a dark brown, refractive, resinous substance; margins indistinct, gradually thinning out, pulverulent, white or abrupt with short aculei, occasionally with mycelia cords.

Hyphal system monomitic, generative hyphae regularly nodose septate. Aculei composed of a core tissue of partially agglutinated, hyaline to yellow hyphae and embedded golden brown vesicles enclosed by subhymenial and hymenial layers, apex sterile, comprised of slightly differentiated, cylindrical to tapering, unbranched terminal hyphae, 1.5-2 µm in diameter. Subiculum up to 280 µm thick, composed of crystal clusters, dark golden brown vesicles up to 20 µm in diameter, and collapsed, indistinct hyphae; subicular hyphae 1.5-3 µm in diameter, nodose septate, frequently branched, walls hyaline, thin, smooth, often bearing acicular, refractive spines with a terminal cluster of hyaline crystals. Subhymenium up to 40 µm thick, filled with stellate crystal clusters; subhymenial hyphae 1.5-2.5 µm in diameter, nodose septate, frequently branched, short-celled, walls hyaline, thin, smooth. Hymenium composed of astrocystidia, cystidia, and basidia often embedded in resinous material. Astrocystidia numerous, cylindrical with an apical bulb or narrowly lageniform, 13-20 µm × 2-3 µm, tapering to 1.5-

**Figs. 18-20**. Microscopic elements of Resinicium species. Fig. 18. ***Resinicium mutabile***, from holotype FP102989: (*a*) hyphidia from aculeus apex, (*b*) basidia, (*c*) basidiospores; from HHB7146: (*d*) vesiculate cystidia; from HHB7168: (*e*) basidia; from PR1366: (*f*) subicular hyphae with denuded or encrusted spines; (*g*) hymenial cystidia; (*h*) vesiculate cystidia. Fig. 19. ***Resinicium rimulosum***, from holotype FP150328: (*a*) halocystidia, (*b*) astrocystidia, (*c*) basidia, (*d*) basidiospores. Fig. 20. ***Resinicium tenue***, from FP150386: (*a*) basidiospores, (*b*) basidia; from holotype FP150354: (*c*) basidiospores, (*d*) astrocystidia, (*e*) halocystidia.



2 µm in diameter at base, with a basal clamp connection, walls hyaline, thin, smooth, at apex with a spherical bulb, 2-4 µm in diameter, encrusted with a stellate cluster of hyaline crystals up to 25 µm in diameter. Cystidia numerous, with a slender stalk, 1-3.5 µm in diameter, clamped at base, walls hyaline, thin, smooth, apex undifferentiated, obtuse, enclosed by a dark golden yellow, resinouslike, globose vesicle, 6-20 µm in diameter. Basidia rare, clavate to cylindrical with a median constriction, 11-16 µm × 3.5-6 µm tapering to 1.5-2 µm in diameter at base, with a basal clamp connection, walls hyaline, thin, smooth, 4-sterigmate. Basidiospores rare, ellipsoid, (4.5-)5-5.5 µm × 3-3.5(-4) µm, Q = 1.42-1.65, walls hyaline, thin, smooth, acyanophilous, not reacting in Melzer's reagent.

HABITAT: Wood of angiosperms.

DISTRIBUTION: Belize, Puerto Rico, United States (Florida, Hawaii).

SPECIMENS EXAMINED: See Supplementary data1.

REMARKS: ***Resinicium mutabile*** is characterized by thin, mottled, light brown basidiomes with aggregated aculei, a soft or subceraceous texture, numerous stellate crystal clusters throughout the subiculum and aculeus trama, astrocystidia, cystidia with a globose vesicle, and ellipsoid basidiospores. Basidia and basidiospores are absent in many collections. The vesicle-bearing cystidia superficially resemble true halocystidia but the stalk is undifferentiated and lacks an interior apical bulb. The mottled basidiome is a result of the dark brown aculei protruding above a yellow basal layer. ***Resinicium mutabile*** is most similar to ***R. monticola*** for they both produce ellipsoid basidiospores, astrocystidia, and lack true halocystidia. They are readily differentiated by the color of the basidiomes and morphology of aculei and cystidia.

### ***Resinicium rimulosum*** Nakasone, sp. nov. Figures 11, 12, and 19

*Differt* a R. friabili *basidiomatibus albidis rimosis, a* R. conferto *et* R. tenui *basidiosporis minoribus.* Holotype: Jamaica, Saint Andrew Parish, Cinchona Botanical Gardens, along trail to Moree's Gap, on bark of dead hardwood, 12 June 1999, K.K. Nakasone, FP150328 (BPI, isotype CFMR, D).

ETYMOLOGY: *rimulosus*, Latin, minutely cracked, referring to the cracked hymenophore.

Basidiome resupinate, effuse, beginning as small, irregular patches, confluent, closely appressed, thin, subceraceous, odontoid, white to yellowish white (4A2), area between aculei up to 180 µm thick, reticulate to porose with numerous cracks; hymenophore composed of short, conical aculei, up to 150 µm × 140 µm, 4-6 aculei per mm, smooth, single or occasionally fused at base, apex acute, terminating to a single point; margins indistinct, gradually thinning out, white, finely farinaceous.

Hyphal system monomitic, generative hyphae regularly nodose septate. Aculei composed of a central core of agglutinated hyphae and embedded halocystidia enclosed by thin subhymenial and hymenial layers, at apex terminal hyphae slightly tapered. Subiculum 70-150 µm thick, composed of a dense layer of agglutinated, often indistinct hyphae and embedded halocystidia; subicular hyphae 2.5-5 µm in diameter, nodose septate, frequently branched, often irregularly inflated, walls hyaline, thin to slightly thickened, smooth. Subhymenium indistinct, up to 20 µm thick, partially agglutinated; subhymenial hyphae 1.8-3 µm in diameter, nodose septate, short-celled, frequently branched, walls hyaline, thin, smooth. Hymenium a palisade of halocystidia, astrocystidia, and basidia. Halocystidia numerous, sphaeropedunculate, 13-25(-35) µm × 2.5-5 µm, tapering to 2-3 µm in diameter at base, with a basal clamp connection, apical bulb 5-9 µm in diameter enclosed by a vesicle, 10-25 µm in diameter, walls hyaline, thin to slightly thickened, smooth, walls of apical bulb and vesicle cyanophilous. Astrocystidia numerous, aculeate to lageniform, 11-22 µm × (2.5-)3-4 µm, tapering to 1-1.5 µm in diameter at base, with a basal clamp connection, walls hyaline, thin, smooth, apex acute or with a small spherical bulb, 1.5-2.5 µm in diameter, encrusted with a stellate cluster of hyaline crystals, up to 12 µm in diameter. Basidia clavate or cylindrical with a median constriction, 11-22 µm × 4-5 µm, tapering to 1.5-2 µm in diameter at base, with a basal clamp connection, walls hyaline, thin, smooth, 4-sterigmate, sterigmata up to 5 µm long, slender, arcuate at maturity. Basidiospores scattered, ellipsoid, 4-4.8(-5) µm × (2.5-)2.8-3(-3.5) µm, Q = 1.5, walls hyaline, thin, smooth, acyanophilous, not reacting in Melzer's reagent.

HABITAT: Wood and bark of angiosperm.

DISTRIBUTION: Jamaica.

REMARKS: ***Resinicium rimulosum*** is characterized by white to pale yellow, rimose, subceraceous basidiomes with small aculei and small, ellipsoid basidiospores. It is most similar to *R. friabile* which has basidiospores of the same size but basidiomes that are darker brown, more ceraceous, and only occasionally cracked. The basidiomes of ***R. confertum*** and ***R. rimulosum*** are extensively cracked; however, in ***R. confertum*** the basidiospores are slightly larger, aculei aggregated and fused, and basidiomes soft and fragile. Compared to ***R. tenue,*** the basidiospores in ***R. rimulosum*** are smaller and the basidiome more extensively cracked.

### ***Resinicium tenue*** Nakasone sp. nov. Figs. 13 and 20

*Differt a* R. conferto *et* R. friabili *basidiomatibus mollibus, basidiosporis paulo latior (4.5-)5.5--6 µm × (3-)3.5-4 µm, et a R. saccharicola fibulatis hyphis.* Holotype: Jamaica, St. Andrew Parish, Blue Mountains and John Crow Mountains National Parks, Hollywell Recreation Park, along Waterfall Trail, on wood and bark of angiosperm, 13 June 1999, K.K. Nakasone, FP 150354 (BPI; isotype CFMR, D).

ETYMOLOGY: *tenuis*, Latin, thin, referring to the thin basidiomes.

Basidiomes resupinate, widely effuse, up to 6 cm × 4 cm, thin, closely appressed, adherent, soft to subceraceous, odontoid to grandinioid, white, yellowish white [(3-4)A2], or greyish brown [(5-6)D3], area between aculei even, up to 100 µm thick, smooth, felty to finely porose, with scattered cracks; hymenophore of short conical or cylindrical aculei 70-110 µm × 43-110 µm, 4-6 aculei per mm, terete or slightly compressed, single, evenly colored, apex acute, occasionally penicillate; margins indistinct, gradually thinning out, white, finely farinaceous.

Hyphal system monomitic, generative hyphae regularly nodose septate. Aculei composed of a core of vertically arranged hyphae and embedded halocystidia enclosed by thin subhymenial and hymenial layers; apex sterile, comprised of astrocystidia and cylindrical, unbranched terminal hyphae, 2-3 µm in diameter. Subiculum 40-70 µm thick, an indistinct tissue of agglutinated, often collapsed hyphae, sometimes arranged in parallel, with scattered embedded halocystidia; subicular hyphae 2-4.5 µm in diameter, nodose septate, sparsely to frequently branched, walls hyaline, thin, smooth, with refractive, acicular spines developed perpendicularly from hyphae, up to 8 × 1 µm, apically encrusted with a small cluster of stellate crystals. Subhymenium up to 30 µm thick, somewhat agglutinated with an open texture; subhymenial hyphae 1.2-2.5 µm in diameter, nodose septate, frequently branched, short-celled, often collapsed, walls hyaline, thin, smooth. Hymenium composed of halocystidia, astrocystidia, and basidia. Halocystidia numerous, sphaeropedunculate, 10-25(-30) µm × 2.5-5 µm, tapering to 1.5-3 µm in diameter at base, with a basal clamp connection, apical bulb 5-8 µm in diameter, enclosed by a vesicle 8-12 µm in diameter, walls hyaline, thin, smooth, apical bulb and vesicle walls cyanophilous. Astrocystidia abundant, aculeate to lageniform, sometimes flexuous, 12-25 µm × 3-4 µm, tapering to 1.5-2 µm in diameter at base, with a basal clamp connection, walls hyaline, thin, smooth, at apex with a small spherical bulb 1.5-3 µm in diameter, encrusted with a stellate cluster of hyaline crystals, up to 10 µm in diameter. Basidia often difficult to observe, clavate, sometimes with a short, narrow stalk, (12-)16-20 µm × 4.5-5 µm, tapering to 2-3 µm in diameter at base, clamped at base, walls hyaline, thin, smooth, 4-sterigmate. Basidiospores ellipsoid, (4.5-)5-6 µm × (3-)3.5-4 µm, Q = 1.4-1.47, sometimes developing a short peg, walls hyaline, thin, smooth, acyanophilous, not reacting in Melzer's reagent.

HABITAT: Wood and bark of angiosperms.

DISTRIBUTION: Jamaica.

SPECIMENS EXAMINED: See Supplementary data[1].

REMARKS: ***Resinicium tenue*** is characterized by thin, grandinioid to odontoid basidiomes with felty to finely porose areas among the aculei, halocystidia, astrocystidia, and ellipsoid basidiospores. The basidiospores of ***R. tenue*** are similar to those found in *R. saccharicola*, ***R. confertum*** and *R. friabile*, However, hyphae are simple septate in *R. saccharicola*, and the aculei are soft and aggregated in ***R. confertum***. *Resinicium friabile* has a more ceraceous basidiome, larger aculei, and slightly narrower basidiospores compared to ***R. tenue. Resinicium tenue*** appears to be restricted to Jamaica in contrast to *R. friabile* which is widely distributed.

Taxa excluded from *Resinicium* s.str.

*Resinicium bisporum* Stalpers, Persoonia 9(1): 145. 1976. Transferred to *Mycoaciella* (Eriksson et al. 1978) and *Phlebia* (Nakasone 2002), *R. bisporum* is placed in the phleboid clade in a recent phylogenetic study using nLSU rRNA (Larsson et al. 2004).

*Resinicium chiricahuaense* Gilbertson & Budington, Mycologia 62(4): 674. 1970. Although transferred to *Phlebia* (Wu 1990), *R. chiricahuaense* is a member of the hymenochaetoid clade. Based on nLSU rRNA gene data, it belongs in the *Resinicium* s. str. clade (Larsson et al. 2006), whereas the nSSU rRNA data place it in the *Resinicium* s.l. clade (Fig. 1B).

*Resinicium furfuraceum* (Bres.) Parmasto, Consp. syst. cortic. 98. 1968. This is one of the original species in *Resinicium*, but nSSU and nLSU rRNA data show that it belongs in the *Resinicium* s. str. clade (Fig. 1B; Larsson et al. 2006).

*Resinicium furfurellum* (Bres.) Nakasone, Mycol. Mem. 15: 284. 1990. Currently the type of the monotypic genus *Skvortzovia* (Hjortstam and Bononi 1987), *R. furfurellum* was transferred to *Jacksonomyces* (Wu and Chen 1992). With nSSU and nLSU rRNA gene data, this species is shown to belong in the *Resinicium* s.l. clade (Fig. 1B; Larsson et al. 2006).

*Resinicium luteum* Jülich, Persoonia 9(4): 468. 1978. Although transferred to *Phlebia* by Wu (1990), examination of the isotype specimen at Kew, K(M)1131787, revealed that *R. luteum* is conspecific with *Mycoacia meridionalis* Burds. & Nakasone. The holotype specimen at L is apparently lost (P.AJ. Audiffred, personal communication, 2000).

*Resinicium meridionale* (Burds. & Nakasone) Nakasone, Mycol. Mem. 15: 285. 1990. Originally described in *Mycoacia* (Burdsall and Nakasone 1981), *R. meridionale* is clearly in the *Resinicium* s.l. clade as shown by analyses of the nSSU and nLSU rRNA sequence data (Fig. 1B; Larsson et al. 2006).

*Resinicium pinicola* (J. Erikss.) J. Erikss. & Hjortstam, Corticiaceae North Europe 6: 1271. 1981. First published as a *Mycoacia* species (Eriksson 1949), Larsson et al. (2006) showed with nLSU rRNA gene sequence data that *R. pinicola* is a member of the *Resinicium* s.l. clade.

*Resinicium praeteritum* (H.S. Jacks. & Dearden) Ginns & Lefebvre, Mycol. Mem. 19: 138. 1993. Originally described as a *Corticium* species (Jackson and Dearden 1949), examination of the holotype specimen at TRTC, no. 52743, suggests that *R. praeteritum* is not allied to *Resinicium* despite the development of capitate cystidia. The membranous to pellicular basidiome and larger, slender clavate basidia, 25-32 µm x 4-5.5 µm, suggest that it may have affinities to *Ceraceomyces* Jülich.

## Discussion

The Caribbean region supports a diversity of *Resinicium* species closely allied to *R. bicolor*, the well-known north temperate species. Five new taxa from this region can be differentiated by basidiome texture, hymenophore configuration, basidiospore shape and size, and presence or absence of halocystidia. Q, the length to width ratio of the basidiospore measurement, is useful for distinguishing *Resinicium* species. ITS sequence data support the recognition of five new *Resinicium* species as well as three previously described taxa. Furthermore, results from morphological and molecular data presented herein necessitated the modification of the generic circumscription of *Resinicium*. Wu's (1990) proposal to limit Resinicium to taxa with astrocystidia and halocystidia with cyanophilous walls is too restrictive whereas Parmasto's (1968) original concept is too broad.

Resinicium s. str. as defined here consists of eight species, *R. bicolor*, ***R. confertum***, *R. friabile*, ***R. monticola***, ***R. mutabile***, ***R. rimulosum***, *R. saccharicola*, and *R. tenue*. The single feature shared by all in this group is astrocystidia, a unique structure in the basidiomycetes. Astrocystidia are found in the hymenium and sometimes are embedded in the subiculum and aculeus trama. The apically encrusted spines developed on subicular hyphae of many species appear to be a reduced form of astrocystidia. The hymenophore is varied, from smooth, farinaceous, grandinioid, spinose, papillose to tuberculate. Most species produce clamp connections and are saprophytic on angiosperms or gymnosperms. The exception is *R. saccharicola*, in which the hyphae are simple septate and preferred substrates are herbaceous stems, grass culms, and palm petioles (Nakasone 2000). Halocystidia are present in all members of this genus except ***R. monticola*** and ***R. mutabile.*** The latter species produces vesiculate cystidia that are different from halocystidia. *Resinicium friabile* has the widest distribution and *R. bicolor*, the best known species, is limited to the northern temperate region.

The ITS sequence data provide strong support for the recognition of the eight morphological species. The size of the ITS region shows an interesting trend. ***Resinicium monticola*** and ***R. mutabile***, distantly related to each other and the other species, have the largest ITS region, 539 bp and 553 bp, respectively. Morphologically, these species are the most divergent in that they lack true halocystidia. The smallest ITS regions, 501-508 bp, are found in ***R. confertum***, *R. friabile*, ***R. tenue***, and ***R. rimulosum***. These species are similar in micromorphology with basidiospores of similar shape and size, but differ in basidiome texture. *Resinicium bicolor* and *R. saccharicola* have an ITS region of intermediate size, 516 bp.

Hjortstam (1998) and Wu (1990) recognized the morphological heterogeneity of the species in *Resinicium* when they separated the taxa into two groups: *Resinicium* s. str. and s.l. Molecular data support this separation because the nSSU rRNA data presented herein show that *Resinicium* and allied taxa cluster into two distinct clades. *Resinicium* s. str. includes *R. bicolor* and closely related species that produce astrocystidia, whereas species in the *Resinicium* s.l. clade lack astrocystidia. Species included in *Resinicium* s.l. are *R. meridionale, R. chiricahuaense, R. furfuraceum, R. pinicola,* and *Skvortzovia furfurella.* The generic placement for these species is unclear. For example, Nakasone (1990) transferred *Mycoacia meridionalis* and *Odontia furfurella* Bres. to *Resinicium,* but other authors (Hjortstam and Melo 1997; Parmasto et al. 2004) prefer to keep the former species in *Mycoacia* and the latter in *Skvortzovia.* Similarly, the status of *R. chiricahuaense* is questionable because nLSU rRNA data places it in the *Resinicium* s. str. clade (Larsson et al. (2006) and the nSSU rRNA data in the *Resinicium* s.l. clade (Fig. 1B). Molecular and morphological studies are underway to resolve the systematics of the species in *Resinicium* s.l.

The Caribbean basin is a well-known biodiversity hotspot for vertebrate and plant species (Myers et al. 2000). Although the fungi are not as well-known, several studies suggest that this region also supports a high diversity of basidiomycetes. Summarizing several years of research, Lodge et al. (2002) found that 22%, or 71 taxa, of the mushroom species identified from the Greater Antilles were new to science. Thus, the high diversity of *Resinicium* species in the Caribbean region is not surprising.

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