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A contribution to the taxonomy of *Rhizochaete* (Polyporales, Basidiomycota)

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Abstract – *Rhizochaete* is a small genus of crust fungi that is closely related to *Phanerochaete*. A new species *Rhizochaete belizensis* is described, and three new combinations are proposed. Morphological studies and molecular sequence data from two nuclear ribosomal DNA regions (ITS and LSU) support the recognition of *R. belizensis* which is closely related to *R. radicata*. Analyses of sequence data also support the transfer of *Phanerochaete flava* to *Rhizochaete*. *Phanerochaete percitrina* from Cameroon and *Peniophora rhizomorpho-sulphurea* from India are transferred to *Rhizochaete* based on morphological studies of type specimens. *Phanerochaete rubescens* from Taiwan is placed in synonymy under *R. borneensis*. In addition, *Phanerochaete mauiensis* is redescribed and illustrated. A key to 13 accepted species of *Rhizochaete* and three morphologically similar species is presented.

Type studies / crust fungi / phlebia clade / *Phanerochaetaceae*

INTRODUCTION

Rhizochaete Gresl., Nakasone & Rajchenb. is a small, distinctive genus of crust fungi that produces hyphal cords and has a world-wide distribution. Introduced in 2004 with six species, it was distinguished from *Phanerochaete* P. Karst. by morphological and molecular characters (Greslebin *et al.*, 2004). Bianchinotti *et al.* (2005) reported that *Rhizochaete* species have perforate septal dolipore caps or parenthesomes. Recently, three species were transferred to *Rhizochaete* – *R. sulphurosa* (Bres.) Chikowski, K.H. Larss. & Gibertoni, *R. sulphurina* (P. Karst.) K.H. Larss., and *R. violascens* (Fr. : Fr.) K.H. Larss. (Chikowski *et al.*, 2016a, b).

Phylogenetic studies place *Rhizochaete* in the Phanerochaete clade (Floudas & Hibbett, 2015) or the Phanerochaetaceae Jülich (Miettinen *et al.*, 2016). Depending on the regions sequenced and the species of *Rhizochaete* and closely related taxa included in the study, *Rhizochaete* is shown to be a monophyletic or paraphyletic genus. For example, *Rhizochaete*, represented by four species, is monophyletic in Floudas & Hibbett's (2015, Fig. 1) multigene phylogenetic analyses of the Phanerochaete clade. In analysis of the ITS sequences of the Phlebiopsis subclade, however, *Rhizochaete* is paraphyletic because *Hapalopilus rutilans* (Pers.) Murrill is

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included with six *Rhizochaete* species (Floudas & Hibbett 2015, Fig. 3). Chikowski *et al.* (2016a) resolved *Rhizochaete* as monophyletic in the phylogenetic analyses of ITS sequence data that included six *Rhizochaete* species. However, with the LSU sequence dataset that included eight *Rhizochaete* species, the genus was recovered in two clades of an unresolved three-way polytomy. The two clades included the following taxa: (1) *Rhizochaete brunnea* Gresl., Nakasone & Rajchenb. *R. fouquieriae* (Nakasone & Gilb.) Gresl., Nakasone & Rajchenb., and *R. radicata* (Henn.) Gresl., Nakasone & Rajchenb. and (2) *R. americana* (Nakasone, C.R. Bergman & Burds.) Gresl., Nakasone & Rajchenb., *R. filamentosa* (Berk. & M.A. Curtis) Gresl., Nakasone & Rajchenb., *R. sulphurina, R. sulphurosa, R. violascens,* and *Phlebiopsis roumeguerii* (Bres.) Jülich & Stalpers. In contrast, in a combined ITS and LSU analyses by Miettinen *et al.* (2016, Fig. 2), seven species of *Rhizochaete* were included in a nine-way polytomy in the Phlebiopsis clade along with species of *Hapalopilus* P. Karst., *Phlebiopsis* Jülich, *Phaeophlebiopsis* D. Floudas & Hibbett, *Phlebia unica* (H.S. Jacks. & Dearden) Ginns, and *Phanerochaete lutea* (Sheng H. Wu) Hjortstam. With the addition of *rpb1* sequences, however, *Rhizochaete* (represented by three species) was resolved as a distinct subclade within the Phlebiopsis clade (Miettinen *et al.*, 2016, Fig. 3).

In this paper, we describe a new species of *Rhizochaete* from Belize and transfer three additional species to the genus based on morphological and molecular data. The circumscription of *Rhizochaete* is modified slightly to accommodate the variation observed among the species. *Rhizochaete borneensis* (Jülich) Gresl., Nakasone & Rajchenb. and *Phanerochaete mauiensis* Gilb. & Adask., which have features found in *Rhizochaete*, are redescribed and illustrated. *Phanerochaete rubescens* Sheng H. Wu, from Taiwan, is placed in synonymy under *R. borneensis*. A key to 13 accepted species in the genus and three morphological similar taxa is presented.

MATERIALS AND METHODS

Morphological studies

Thin, freehand sections from basidiomes were mounted in a drop of aqueous potassium hydroxide, KOH, (2% w/v) and aqueous phloxine (1% w/v) or Melzer's reagent (Kirk *et al.,* 2008) and examined with an Olympus BH2 compound microscope. Drawings were made with a camera lucida attachment. Cyanophily of basidiospore and hyphal walls was observed in 0.1 % cotton blue in 60% lactic acid (Kotlaba & Pouzar, 1964; Singer, 1986). Average, $\bar{x}$, basidiospore measurements were calculated from at least 30 spores, and standard deviations are given if only one specimen was measured. Standard deviations are omitted if the average of more than one specimen was calculated; number of specimens measured is given in parentheses. Q values were obtained from dividing average basidiospore length by width of at least 30 spores (Kirk *et al.,* 2008). Capitalized color names are from Ridgway (1912), and color codes follow Kornerup & Wanscher (1978). Herbarium code designations are from Index Herbariorum (Thiers, 2016). MycoBank (Robert *et al.*, 2013) and Index Fungorum (www.indexfungorum.org) were consulted frequently throughout this study.

Molecular studies

Four new ITS and one LSU sequences were generated, and 29 ITS and 25 LSU sequences of *Rhizochaete* species and related species of *Phaeophlebiopsis* D. Floudas & Hibbett, *Phanerochaete*, *Phlebiopsis,* and *Phlebia unica* were retrieved from GenBank (Benson *et al.*, 2013). We consulted Floudas & Hibbett (2015) and Chikowski *et al.* (2016a) to identify taxa in the Phanerochaetaceae to include in the dataset. *Byssomerulius corium* (Pers.) Parmasto, a member of the Byssomerulius clade and sister to the Phanerochaete clade (Floudas & Hibbett 2015) was used as the outgroup taxon. The information for these sequences is provided in Table 1. DNA extraction, amplification and sequencing followed Palmer *et al.* (2008). The ITS region was amplified with primers ITS1F (Gardes & Bruns, 1993) and ITS4 (White *et al.*, 1990). Sequences were edited with Sequencher 4.8 (Gene Codes Corp., Ann Arbor, Michigan). Newly generated sequences were deposited in GenBank (KY273029-KY273033), and the alignment was deposited in TreeBASE (SN20273). DNA sequences were aligned with MAFFT 7 (Katoh & Standley, 2013). The Q-INS-I algorithm was used to align the ITS sequences whereas the G-INS-I algorithm was used for LSU sequences. Final adjustments to the alignment were done manually with MacClade 4.08 (Maddison & Maddison, 2002). Phylogenetic analyses of the ITS and LSU dataset alone as well as a combined ITS+LSU dataset were performed using maximum likelihood (ML) and Bayesian (BY) methods. Maximum likelihood analysis was performed using RAxML black box (Stamatakis *et al.*, 2008) under the GTR model with GAMMA distributed rate heterogeneity and 100 rapid bootstrap replicates. Bayesian analysis was performed using MrBayes 3.2.6 (Ronquist *et al.*, 2012) on XSEDE through the CIPRES Science Gateway (Miller *et al.*, 2010) for 3 000 000 generations in two runs and four chains with trees sampled every 1000 generations. The burn-in period was set to 0.25. Strong support values of clades are > 90% in ML and > 0.95 posterior probabilities (PP) in BY analyses whereas moderate support values are > 65% and > 0.90, respectively.

RESULTS

Phylogenetic analyses

The combined ITS+LSU nrDNA dataset consisted of 34 ingroup sequences with a total of 1560 characters (ITS 658 characters, LSU 902 characters), including 10 of the 13 *Rhizochaete* species. There were ITS and LSU sequences for nine *Rhizochaete* species, excepting *R. violascens* with only LSU. The tree topologies obtained from the ML and BY analyses differed only with filamentosa and the flava/sulphurina clades switching positions. The BY topology is presented in Figure 1. In this tree, *Rhizochaete* was recovered in two clades with nine taxa in a strongly supported core clade and *R. violascens* with three species of *Phaeophlebiopsis* in a weakly supported sister clade. Within the core *Rhizochaete* lineage, three well-supported subclades were obtained: (1) the sulphurosa/americana/sulphurina/flava clade, (2) the radicata/belizensis/brunnea/fouquieriae clade, and (3) the filamentosa clade. In the ML tree (not shown), however, the Rhizochaete core clade had moderate support (68%) with the flava/sulphurina subclade moderately supported (71%) compared to the sulphurosa/americana/filamentosa and the radicata/belizensis/brunnea/fouquieriae subclades that had weak or no support.

Table 1. Taxa included in the phylogenetic study with voucher, locality, and GenBank accession numbers

Species	*Isolate no.*	*Locality Country: State*	*GenBank accession no.*	
			ITS	*LSU*
Phaeophlebiopsis caribbeana	FD442	USA: Virgin Islands*	KP135416	–
	HHB-6990	USA: Florida	KP135415	KP135243
Phaeophlebiopsis ignerii	FD425	USA: Virginia	KP135418	–
Phaeophlebiopsis peniophoroides	FP150577	USA: Hawaii	KP135417	KP1352730
Phanerochaete affinis	KHL11839	Sweden	EU118652	EU118652
Phanerochaete conifericola	OM7749-7	Finland	KP135173	–
Phanerochaete ericina	HHB2288	USA: North Carolina	KP135167	KP135247
Phanerochaete laevis	FD206	USA: Massachusetts	KP135152	–
	HHB15519	USA: Alabama	KP135149	KP135249
Phanerochaete rhodella	FD18	USA: Massachusetts	KP135187	KP135258
Phanerochaete velutina	LE298547	Russia	KP994360	KP994385
Phlebia unica	KHL11786	Sweden	EU118657	EU118657
Phlebiopsis crassa	KKN86	USA: Arizona	KP135394	KP135215
	MAFF420737	Japan	AB809163	AB809163
Phlebiopsis flavidoalba	KHL13055	Costa Rica	EU118662	EU118662
Phlebiopsis gigantea	FBCC315	Finland	LN611131	LN611131
Rhizochaete americana	FP102188	USA: Illinois	KP135409	KP135277
	HHB2004	USA: Georgia	AY219391	AY219391
Rhizochaete belizensis	FP150712	Belize	KP135408	KP135280
Rhizochaete brunnea	MR11455	Argentina	AY219389	AY219389
Rhizochaete filamentosa	FP105240	USA: Indiana	KP135411	AY219393
	HHB3169	USA: Maryland	KP135410	KP135278
Rhizochaete flava	PR3148	Puerto Rico	KY273029	–
	PR1141	Puerto Rico	KY273030	KY273033
Rhizochaete fouquieriae	KKN121	USA: Arizona	AY219390	GU187608
Rhizochaete radicata	FD123	USA: Massachusetts	KP135407	KP135279
	FD338	USA: Massachusetts	KP135406	–
	HHB1909	USA: North Carolina	AY219392	AY219392
Rhizochaete sulphurina	DLL2014-176	USA: Idaho	KY273032	–
	HHB5604	USA: Montana	KY273031	GU187610
Rhizochaete sulphurosa	KHL16087	Brazil	KT003523	–
	URM85028	Brazil	KT003521	KT003517
	URM87190	Brazil	KT003522	KT003519
Rhizochaete violascens	KHL11169	Norway	–	EU118612
Byssomerulius corium	FP102382	USA: Wisconsin	KP135230	KP135007

* U.S. Virgin Islands is a U.S. Territory.

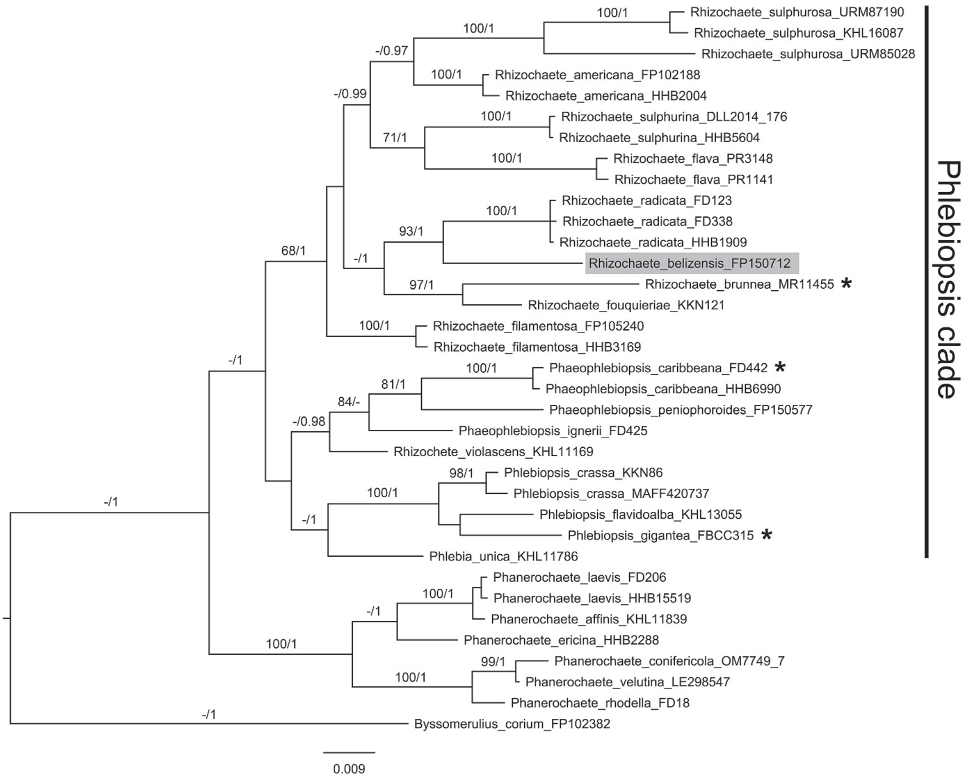

Fig. 1. Bayesian consensus tree based on combined ITS+LSU nrDNA sequences. Support values along branches are from Maximum likelihood bootstrap (≥ 65%) and Bayesian analyses (PP ≥ 0.95), respectively. A dash indicates ML bootstrap value < 65%. Generic types are indicated by an asterisk (*) and new species is highlighted.

With ITS sequences alone, *Rhizochaete* was recovered as a strongly supported monophyletic genus by ML and BY analyses, 96% and 0.96, respectively, but the Phlebiopsis clade was paraphyletic (trees not shown). In comparison, analyses of the LSU dataset found the Phlebiopsis clade moderately supported (70%) with ML analysis or strongly supported (0.99) with BY analysis but resolved *Rhizochaete* as paraphyletic in clades with little or no support (trees not shown).

Taxonomy

Rhizochaete Gresl., Nakasone & Rajchenb., emended

Basidiome effused, loosely adnate, pellicular to membranous, fragile, readily detached; hymenial surface smooth to tuberculate, yellow, orange, brown, *olivaceous or violaceous*, usually turning red to purple in KOH solution, *occasionally with no reaction or turning dark brown*; margin fimbriate to fibrillose, often with hyphal cords that typically turn red to violet in KOH *but sometimes with no reaction*. *Hyphal system* monomitic; generative hyphae regularly clamped or primarily simple-septate with scattered clamps. *Subiculum* composed of non-agglutinated, loosely arranged hyphae often encrusted with small, discrete, insoluble crystal clusters and coated with small, particulate, yellow, resinous-like material that dissolves readily in KOH. *In one species* (*R. percitrina*) *with large masses of yellow, resinous-like material that dissolves readily in KOH embedded in trama. Cystidia* usually present, cylindrical to subfusiform, thin to thick-walled, encrusted *or smooth*. *Basidia* clavate to subcylindrical, 4-sterigmate. *Basidiospores* cylindrical to ellipsoid, up to 6 × 4 µm, walls hyaline, thin to slightly thickened, smooth, acyanophilous, not reacting to Melzer's reagent. On wood and bark of angiosperms and gymnosperms, associated with a white rot-decay.

Typus: *Rhizochaete brunnea* Gresl., Nakasone & Rajchenb.

The circumscription of *Rhizochaete* is slightly modified (indicated by italicized text) to include variation observed in the basidiome and hyphal cord reaction to KOH solution and the distribution and form of the resinous-like material in the context. Consult Greslebin *et al.* (2004) for a more detailed description and discussion of the genus. In the key below, *Phanerochaete galactites* (Bourdot & Galzin) J. Erikss. & Ryvarden, *Ceraceomyces cystidiatus* (J. Erikss. & Hjortstam) Hjortstam, and *P. mauiensis* are included for they resemble some species of *Rhizochaete*.

Key to the species of *Rhizochaete* and similar taxa

1\. Hyphae primarily simple-septate with scattered clamps 2
1\. Hyphae regularly clamped 12

  2\. Cystidia with thin or slightly thickened walls, < 1 µm thick 3
  2\. Cystidia with distinctly thick walls, > 1 µm thick 8

3\. Hymenium turning purple, pink or red in KOH 4
3\. Hymenium not reacting or darkening to orange or brown in KOH 5

  4\. Subiculum yellow, cystidia 30-45 × 4-5.5 µm .... *R. sulphurosa*
  4\. Subiculum brown, cystidia 30-60 × 5-7 µm .... *R. filamentosa*

5\. Basidiomes white, cream to yellowish brown, hyphal cords white, basidiospores 2-2.5 µm diam .... *Phanerochaete galactites*
5\. Basidiomes yellow to brownish orange, hyphal cords yellow to yellowish brown, basidiospores 2.2-3.6 µm diam 6

  6\. Basidiomes bright yellow, unchanged in KOH, basidiospores 2.2-3 µm broad, from Central Africa .... *R. percitrina*
  6\. Basidiomes yellow to brownish orange, darkening in KOH, basidiospores 2.8-3.6 µm broad 7

7\. Basidia 30-40 µm long, basidiospores 3.8-4.7 µm long, from India .... *R. rhizomorphosulphurea*
7\. Basidia 15-25 µm long, basidiospores 4.3-5.8 µm long, from Central and South America .... *R. flava*

  8\. Cystidia usually < 50 µm long 9
  8\. Cystidia usually > 50 µm long 10

9\. Basidiomes red in KOH, cystidia heavily encrusted with hyaline crystals, from Asia .... *R. borneensis*
9\. Basidiomes unchanged in KOH, cystidia smooth, from Africa .... *R. percitrina*

  10\. Basidiomes cream to buff, hyphal cords absent .... *Phanerochaete mauiensis*
  10\. Basidiomes dull orange, dull yellow, or yellowish brown, hyphal cords present 11

11. Subiculum mustard yellow to brown, cystidia usually > 60 µm long, spores > 4 µm long, found worldwide .... *R. radicata*
11. Subiculum yellow, cystidia usually < 60 µm long, spores < 4 µm long, from Belize .... *R. belizensis*
    12. Cystidia absent or rare .... *R. violascens*
    12. Cystidia abundant 13
13. Cystidia cylindrical, up to 250 µm long with thick walls, basidia 40-60 µm long, from Argentina .... *R. brunnea*
13. Cystidia up to 100 µm long with thin walls, basidia ≤ 40 µm long 14
    14. Basidiospores 3-4 µm broad, from southern Arizona .... *R. fouquieriae*
    14. Basidiospores usually ≤ 3 µm broad 15
15. Basidiomes dingy white to violaceous, from North Europe .... *Ceraceomyces cystidiatus*
15. Basidiomes yellow, brown, or olive brown 16
    16. Basidiomes olive brown to yellowish brown, cystidia ≤ 60 µm long, from eastern North America .... *R. americana*
    16. Basidiomes bright to dull yellow, cystidia > 60 µm long, from western North America and North Europe .... *R. sulphurina*

Species descriptions

Rhizochaete belizensis Nakasone, K. Draeger & B. Ortiz, ***sp. nov.*** **Fig. 2**

MycoBank No.: MB818007

Diagnosis: *Rhizochaete belizensis* is most similar to *R. radicata* but differs in having shorter basidiospores, average size 3.5-3.6 × 2.5-2.6 µm, and shorter cystidia, usually < 60 µm long.

Type: Belize, Cayo District, Blue Hole National Park, Hummingbird Loop Trail, on decorticate hardwood, 15 November 2001, K.K. Nakasone, FP150712 (holotype CFMR). GenBank accession numbers: KP135408 (ITS) and KP135280 (LSU).

Basidiome resupinate, widely effused, loosely adnate, up to 700 µm thick, pellicular, soft, fragile, with hyphal cords; hymenial surface smooth, fragile, readily flaking off, orange white (5A2), turning violaceous, Pale Pinkish Buff, or Light Buff in KOH; context byssoid, white next to substrate, then light yellow [3A(4-5)], Lemon Chrome or Strontium Yellow just under hymenium; margin adnate, thinning out, subfelty, sterile, darker than hymenium, orange grey (5B2) or Chamois, becoming cordonic. Hyphal cords up to 2 mm diam, dark mustard yellow, yellowish brown (5D8), or brown (6D7), turning violaceous in KOH.

Hyphal system monomitic; generative hyphae simple-septate with rare single clamps. *Subiculum* up to 600 µm thick, an open, non-agglutinated, loosely interwoven tissue; subicular hyphae 3.5-7 µm diam, occasionally ampullate up to 9 µm diam, simple-septate with rare, single clamp connections, moderately branched, sometimes with H-connections, walls hyaline, thin to 2.2 µm thick, heavily coated with small, particulate, yellowish brown material that readily dissolves in 2% KOH and encrusted with coarse, insoluble hyaline crystals. *Subhymenium* up to 70 µm thick, a moderately dense, non-agglutinated tissue of upright, short-celled hyphae, subhymenial hyphae 3-5 µm diam, simple-septate, much branched, walls hyaline, thin, coated with small, particulate, yellowish brown material that readily dissolves in KOH. *Hymenium* up to 60 µm thick, a dense palisade of cystidia and basidia.

Cystidia subfusiform, rarely clavate, with a subacute or obtuse apex, 40-60(-75) × 8-9.5 µm, up to 13 µm diam including crystals, simple-septate at base, protruding or enclosed, sometimes with secondary septa, walls hyaline, slightly thickened or up to 2.2 µm thick, upper half lightly to heavily encrusted with hyaline, insoluble crystals. *Basidia* narrowly clavate, 17-25 × 4.2-5.5(-5.8) µm, simple-septate at base, 4-sterigmate, walls hyaline, thin, coated with particulate, yellowish brown material that readily dissolves in 2% KOH. *Basidiospores* ellipsoid to broadly ellipsoid, (2.9-)3-4(-4.2) × 2.2-3 µm, $\bar{x}$ (2) = 3.5-3.6 × 2.5-2.6 µm, Q = 1.3-1.5, walls hyaline, thin, smooth, acyanophilous, not reacting in Melzer's reagent.

Habitat and distribution: On bark and wood of angiosperms in Belize.

Additional specimens examined: Belize, Cayo District, Mountain Pine Ridge, Five Sisters Lodge, along Nature Trail, on decayed hardwood, 19 November 2001, K.K. Nakasone, FP150806 and FP150811 (CFMR).

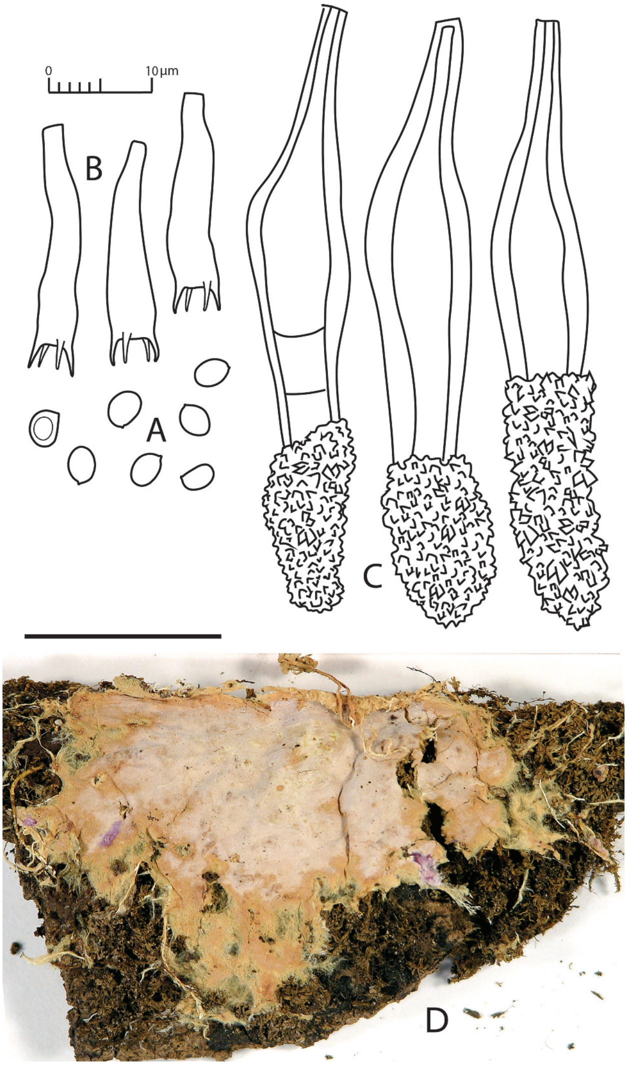

Fig. 2. *Rhizochaete beliziensis* (FP150806, paratype). **A.** Basidiospores. **B.** Basidia. **C.** Cystidia. **D.** Basidiome with hyphal cords (from FP150811, paratype). Scale bar = 20 mm.

Rhizochaete belizensis is characterized by a fragile, soft, pale-colored basidiome with mustard yellow hyphal cords, simple-septate generative hyphae, thick-walled subfusiform cystidia, and small, broadly ellipsoid basidiospores. Compared to *R. belizensis, R. radicata* has typically longer basidiospores, 3.5-5 µm long, and longer cystidia, 60-100(-115) µm long, whereas *R. borneensis*, from Asia, has slightly larger basidiospores, 4-5 × 2.8-3.2 µm. Sequence analyses of the combined ITS and LSU show that *R. belizensis* is a distinct species that is sister to *R. radicata* (Fig. 1). Floudas & Hibbett (2015) were the first to show that *R. belizensis*, as *Rhizochaete* sp. FP150712, was closely related to *R. radicata* in their ITS and multigene analyses.

Rhizochaete borneensis (Jülich) Gresl., Nakasone & Rajchenb., *Mycologia* 96: 267 (2004) **Fig. 3**

= *Phanerochaete rubescens* Sheng H. Wu, *Mycological Research* 102: 1131 (1998).

Basidiomes resupinate, effused, thin, soft, membranous to pellicular; hymenial surface smooth, greyish yellow [4B(4-5)], turning red-violet in KOH; context tomentose, bright orange yellow (4A7); margin adnate with bright orange yellow (4A7) hyphal cords, turning red-violet in KOH.

Hyphal system monomitic; generative hyphae simple-septate with rare single clamps. Subiculum a loosely organized, non-agglutinated tissue; subicular

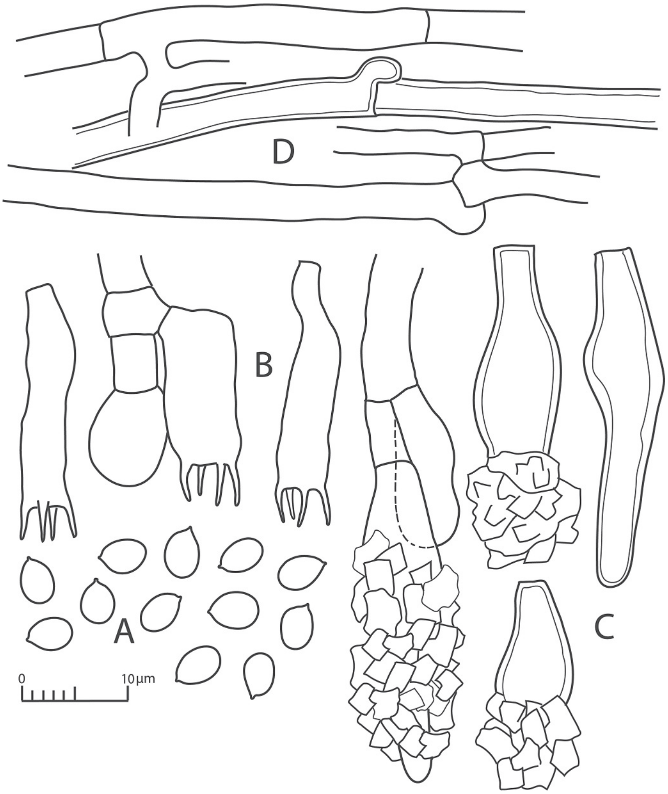

Fig. 3. *Phanerochaete borneensis* (Jülich 78-2157, holotype). **A.** Basidiospores. **B.** Basidia. **C.** Cystidia. **D.** Subicular hyphae.

hyphae 2-5 µm diam, simple-septate, moderately branched, sometimes with H-connections, walls hyaline, thin to slightly thickened, coated with small, yellow material that dissolves in KOH. *Subhymenium* slightly thickened. *Hymenium* a palisade of cystidia and basidia. *Cystidia* enclosed or slightly protruding, subfusiform to conical with an obtuse apex, 20-35(-50) × 7-8 µm, up to 12 µm diam including encrustations, simple-septate at base, walls hyaline, slightly thickened, encrusted at apex or upper half with coarse, insoluble, hyaline crystals, sometimes slightly dextrinoid. *Basidia* clavate to broadly cylindrical, (16-)20-30(-37) × 5-8 µm, simple-septate at base, 4-sterigmate, walls hyaline, thin to slightly thickened, smooth. *Basidiospores* broadly ellipsoid, 4-5 × 2.8-3.3 µm, walls hyaline, thin to slightly thickened, smooth, not reacting in Melzer's reagent.

Habitat and distribution: On decayed wood in Borneo and Taiwan.

Type specimen examined: Malaysia, Borneo, Sarawak State, Gunung Mulu National Park, Camp 1, 16 March 1978, W. Jülich 78-2157 (L, holotype).

Descriptions: Jülich (1980), Wu (1998, as *P. rubescens*).

Rhizochaete borneensis is characterized by a grayish yellow basidiome and yellow hyphal cords that turn red to violet in KOH, simple-septate hyphae, short, thick-walled, encrusted cystidia, and broadly ellipsoid basidiospores. *Rhizochaete radicata* is similar to *R. borneensis* but has longer cystidia, (40-)60-100(-115) µm long and slightly narrower basidiospores, 2.2-3 µm diam. In contrast, the cystidia in *R. percitrina*, from Cameroon, are short and thick-walled but smooth. Although we were not able to examine the holotype of *P. rubescens*, as described by Wu (1998), it is morphologically indistinguishable from *R. borneensis*. In addition, these taxa occur in the same subtropical-tropical region of Asia.

Rhizochaete flava (Burt) Nakasone, K. Draeger & B. Ortiz, ***comb. nov.***

MycoBank No.: MB818015

≡ *Coniophora flava* Burt, Annals Missouri Botanical Garden 4: 261 (1917).

≡ *Peniophora flava* (Burt) D.P. Rogers & H.S. Jacks., Farlowia 1: 278 (1943).

≡ *Phanerochaete flava* (Burt) Nakasone, Burds. & Lodge, Mycologia 90: 132 (1998).

Basidiospores ellipsoid to narrowly ellipsoid, 4.3-5.5(-5.8) × 2.8-3.2 µm, $\bar{x} = 4.8 \pm 0.4 \times 3 \pm 0.1$ µm, Q = 1.6 ± 0.1, walls hyaline, thin, smooth, acyanophilous, not reacting in Melzer's reagent.

Specimens examined: Puerto Rico, Rio Grande Municipio, Luquillo Mountains, Caribbean National Forest, El Verde Research Area, trail to Sonadora, on decorticate hardwood branch, 20 May 1993, D.J. Lodge, M. Boyd, & L. Fish, PR1141 (CFMR); log on ground, 4 June 1998, K.K. Nakasone, FP150195 (CFMR). Isabela Municipio, Guajataca Commonwealth Forest, First camp, Verada Nueva Trail, on decayed branch, 22 January 1996, D.J. Lodge & M. Harrington, PR3148 (CFMR).

Description and illustration: Nakasone *et al.* (1998).

Rhizochaete flava is a typical member of this genus except that its hymenium and hyphal cords do not turn red or purple in KOH but darken to brown instead. Molecular data also support the transfer of *R. flava* into *Rhizochaete* where it is in a clade with *R. sulphurosa* and *R. sulphurina* (Fig. 1). It can be confused with *R. sulphurosa* which has similar basidiome and basidiospore features, but *R. sulphurosa* has narrower cystidia, 4-6 µm diam, and hymenium and hyphal cords that turn purple in KOH.

Multiple attempts were made to sequence the ITS of different *R. flava* strains, but only PR3148 was successful. The previous ITS sequence of *R. flava* in GenBank (AY219358) by de Koker *et al.* (2003) was based on a mix-up of the specimen and culture, PR-3147, which is *Microporellus obovatus* (Jungh.) Ryvarden.

Rhizochaete percitrina (P. Roberts & Hjortstam) Nakasone, ***comb. nov.*** **Fig. 4**

MycoBank No.: MB818016

≡ *Phanerochaete percitrina* P. Roberts, Kew Bulletin 55: 821 (2000).

Basidiome effused, thin, up to 250 µm thick, loosely adnate, fragile, soft, pellicular to membranous with hyphal cords; hymenial surface smooth to farinaceous, pale yellow (3A3), light yellow [(2-3)A(4-5), 4A(4-5)] with scattered light orange (5A4) areas, no color change in KOH; margin appressed, fibrillose to cordonic, concolorous with hymenium, no color change in KOH.

Hyphal system monomitic; generative hyphae simple-septate. *Subiculum* up to 200 µm thick, a non-agglutinated tissue of loosely arranged hyphae, more or less

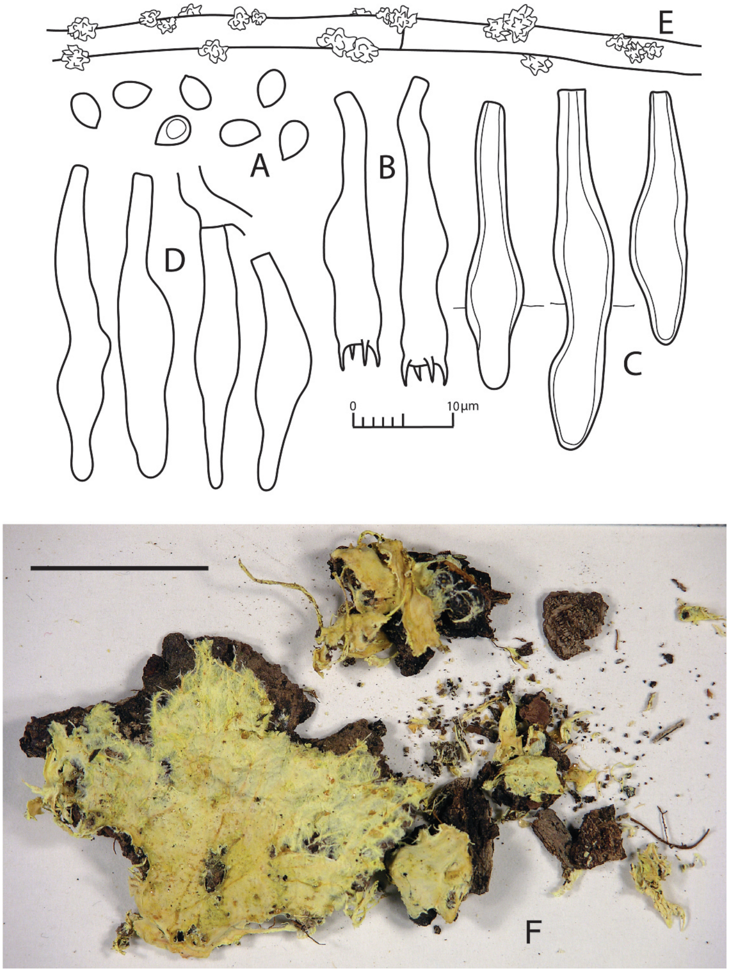

Fig. 4. *Phanerochaete percitrina* (K(M) 50164, holotype). **A.** Basidiospores. **B.** Basidia. **C.** Cystidia with thickened walls. **D.** Cystidia with thin walls (from K(M)50165, paratype). **E.** Encrusted subicular hypha. **F.** Basidiome with hyphal cords. Scale bar = 20 mm.

parallel to substrate, and large masses of dark yellow, resinous-like material that dissolves in KOH; subicular hyphae 2.5-5 µm diam, sometimes inflating up to 7 µm at septa, simple-septate, sparsely to moderately branched, often developing H-connections, walls hyaline, thin to 1.5 µm thick, smooth to heavily encrusted with small, discrete clusters of insoluble, hyaline crystals. *Subhymenium* slightly thickening, up to 40 µm thick, a compact, non-agglutinated tissue of short-celled, upright hyphae; subhymenial hyphae 2.2-4.5 µm diam, simple septate, moderately branched, walls hyaline, thin, smooth. *Hymenium* up to 40 µm thick, a dense palisade of cystidia and basidia. *Cystidia* inconspicuous, cylindrical to subfusiform, rarely moniliform, occasionally with one or more adventitious septa, 22-35 × 3.5-6 µm, simple septate at base, enclosed or protruding up to 15 µm, walls hyaline, thin or up to 1 µm thick toward base, smooth. *Basidia* narrowly clavate, often slightly constricted, usually with a distinct stalk, 23-30 × 4.3-5.8 µm, simple-septate at base, walls hyaline, thin or up to 0.7 µm thick at base, smooth, 4-sterigmate. *Basidiospores* ellipsoid, often containing a single oil-like globule, 3.5-4.3 × 2.2-3 µm, $\bar{x}$ (2) = 3.7-4.1 × 2.4-2.5 µm, Q = 1.5-1.7, walls hyaline, thin, smooth, acyanophilous, not reacting in Melzer's reagent.

Habitat and distribution: On decayed wood in Cameroon.

Type specimen examined: Cameroon, South West Province, Korup National Park, Science Camp, on rotten log, 3 April 1997, P. Roberts K837, K(M)50164 (K, holotype).

Additional specimens examined: Cameroon, South West Province, Korup National Park, trail to Rengo Rock, on rotten branch, 8 April 1997, P.J. Roberts K966, K(M)50165 (K); trail from Rengo Camp to Erat, on very rotten wood, 2 May 1996, P.J. Roberts K380, K(M)58811 (K).

Description and illustration: Roberts (2000).

Phanerochaete percitrina is characterized by fragile, bright yellow, pellicular basidiomes with hyphal cords, subicular hyphae encrusted with small clusters of hyaline crystals, cylindrical to subfusiform cystidia, and small, ellipsoid basidiospores. There is some variation in the specimens cited above. For example, Roberts (2000) described and illustrated cylindrical basidiospores, 3.5-4.5(-6) × 2-2.5(-3) µm, Q = 1.8-2.2, which are narrower than those observed in this study. Distinctly thick-walled basidia and cystidia were observed in the holotype whereas embedded, clavate cystidia were observed only in specimen K(M)50165.

Phanerochaete percitrina is transferred to *Rhizochaete* because of its fragile, pellicular basidiomes, yellow hyphal cords, and small, ellipsoid basidiospores. These are character traits found in most *Rhizochaete* species; however, *R. percitrina* also displays characters that are unique or unusual in the genus. For example, in the subiculum it produces large masses of dark yellow resinous-like material that dissolves in KOH instead of tiny, yellow, resinous-like particles coating the hyphae in other species of *Rhizochaete*. Unlike most species in the genus, *R. percitrina* and *R. flava* do not develop encrusted cystidia nor do their hymenia turn red or purple in KOH. Thick-walled basidia are present in *R. brunnea* and sometimes in *R. percitrina*. Sequence data are needed to determine the phylogenetic relationship between *R. percitrina* and other *Rhizochaete* species.

Rhizochaete rhizomorphosulphurea (B.K. Bakshi & Suj. Singh) Nakasone, ***comb. nov***. **Fig. 5**

MycoBank No.: MB818017

≡ *Peniophora rhizomorphosulphurea* B.K. Bakshi & Suj. Singh, Indian Forester 92: 567 (1966).

Basidiome resupinate, widely effused, 5 × 2 cm (isotype at DAOM), up to 500 µm thick, membranous to subceraceous when fresh, on drying becoming pellicular, soft, fragile, readily cracking and detaching from the substrate; hymenial surface smooth, sulfur yellow when fresh then drying to light orange (5A2), greyish orange (5B4), Light Ochraceous-Buff, Warm-Buff, Chamois, or Honey Yellow, turning slightly darker in KOH; context byssoid, white next to substrate, then light yellow [3A(4-5)], Lemon Chrome or Strontium Yellow just under hymenium; margin adnate, thinning out, fibrillose to cordonic, white, yellowish white (4A2), pale yellow (4A3), Maize Yellow, or Cream Color. *Hyphal cords* up to 800 µm diam, light yellow (4A4) to yellowish brown (5D5), darkening to brown in KOH, abundant in substrate and soil.

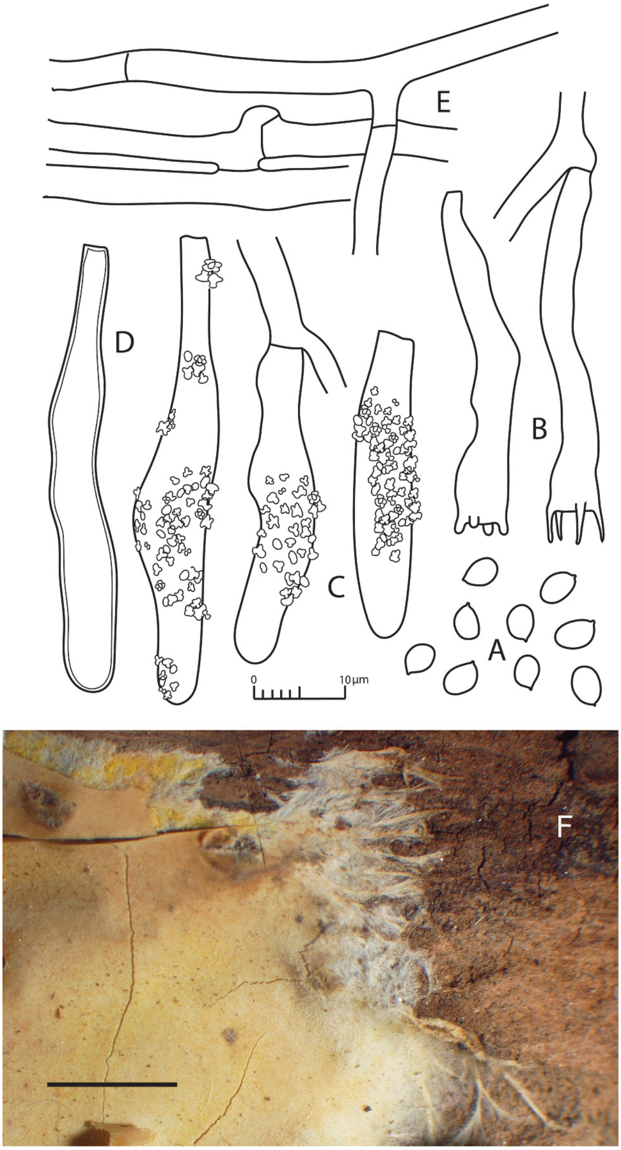

Fig. 5. *Rhizochaete rhizomorphosulphurea* (DAOM 02-01000675859). **A.** Basidiospores (from FRI7866, isolectotype). **B.** Basidia. **C.** Cystidia. **D.** Cystidium lacking encrustations with slightly thickened walls. **E.** Subicular hyphae. **F.** Basidiome with hyphal cords. Scale bar = 3 mm.

Hyphal system monomitic; generative hyphae simple-septate with scattered single clamp connections. *Subiculum* up to 400 µm thick, an open, non-agglutinated, loosely interwoven tissue; subicular hyphae 3.5-6 µm diam, simple-septate with scattered, single clamp connections, moderately branched, sometimes with H-connections, occasionally slightly ampullate, walls hyaline, thin, heavily coated with small, particulate, yellowish brown material that readily dissolves in 2% KOH and encrusted with small, discrete clusters of insoluble, hyaline crystals. *Subhymenium* up to 70 µm thick, a moderately dense, non-agglutinated tissue of upright hyphae; subhymenial hyphae, 3-4.5 µm diam, simple-septate, moderately branched, walls hyaline, thin, coated with small, particulate, yellowish brown material that readily dissolves in 2% KOH. *Hymenium* up to 45 µm thick, a dense palisade of cystidia and basidia. *Cystidia* clavate, subfusiform, or obclavate, with an obtuse apex, (25-)35-50(-65) × 5.5-9 µm, up to 12 µm diam including crystals, simple-septate at base, slightly protruding, enclosed, or embedded, walls hyaline, thin to slightly thickened, lightly to heavily coated with particulate, yellowish brown material that readily dissolves in 2% KOH and encrusted with clusters of insoluble, hyaline crystals. *Basidia* narrowly clavate to cylindrical, 30-40 × 5-6 µm, simple-septate at base, 4-sterigmate, walls hyaline, thin, coated with particulate, yellowish brown material that readily dissolves in 2% KOH. *Basidiospores* ellipsoid to broadly ellipsoid, (3.8-)4-4.5(-4.7) × 2.8-3.6 µm, $\bar{x}$ (isolectotype) = $4.2 \pm 0.2 \times 3 \pm 0.2$ µm, Q = 1.4 ± 0.1, walls hyaline, thin, smooth, acyanophilous, not reacting to Melzer's reagent.

Habitat and distribution: Reported on roots and stumps of teak in India, Uttarakhand State; saprobic, possibly causing a root rot.

Type specimen examined: India, Uttarakhand State, Dehr Dun (Dehradun), Forest Research Institute, New Forest, on *Tectona grandis* L., 31 May 1966, FRI-7866 (CFMR, lectotype designated here).

Additional specimen examined: India, Uttarakhand State, Dehr Dun (Dehradun), Forest Research Institute, on roots of *T. grandis*, 13 August 1965, B.K. Bakshi, DAOM95272-C (DAOM 02-01000675859).

Description and illustration: Bakshi *et al.* (1966).

Rhizochaete rhizomorphosulphurea is characterized by yellow to orange basidiomes and hyphal cords that turn darker orange or brown in KOH, long basidia, thin-walled cystidia, and ellipsoid basidiospores. Embedded cystidia are often heavily encrusted whereas those in the hymenium may be smooth or only lightly encrusted with clusters of insoluble hyaline crystals. It is not known if the color change in KOH is a typical reaction or the result of age, for the specimens tested are 50 years old. This species is most similar to *R. flava* which has shorter basidia on average and slightly longer and narrower basidiospores. Their geographic distributions are quite distinct — *R. rhizomorphosulphurea* is known only from India and *R. flava* from subtropical and tropical America.

Rhizochaete rhizomorphosulphurea is accepted as a distinct species although it is placed in synonymy under *R. sulphurina* in Index Fungorum and Mycobank. *Rhizochaete sulphurina* differs from *R. rhizomorphosulphurea* in having primarily clamped hyphae, larger cystidia, 40-90 × 10-12 µm, and slightly longer but narrower basidiospores, (4.5-)5-5.8 × 2.5-3 µm.

The description above is based on observations of the specimens cited and the original description by Bakshi *et al.* (1966). A holotype was not designated; thus, FRI-7866, one of the specimens cited in the protologue, is designated the lectotype of *P. rhizomorphosulphurea*. Vesicles reported by Bakshi *et al.* (1966) were not observed and may be cytoplasmic materials escaping from broken or punctured hyphal walls.

Phanerochaete mauiensis Gilb. & Adask., Mycotaxon 49: 384 (1993). **Fig. 6**

Basidiome resupinate, effused up to 20 cm, thin up to 180 µm thick, adherent, firm, membranous to subceraceous, readily breaking apart; hymenial surface smooth, pale yellow (4A3) to pale orange (5A3), not reacting to KOH; margin thinning out, white, fimbriate.

Hyphal system monomitic; generative hyphae simple-septate. *Microbinding hyphae* absent or locally abundant in substrate, ≤ 0.7 µm diam, aseptate, frequently branched at right angles, walls hyaline, thin, smooth. *Subiculum* up to 75 µm thick, composed of a thin, dense layer of agglutinated hyphae arranged parallel to substrate

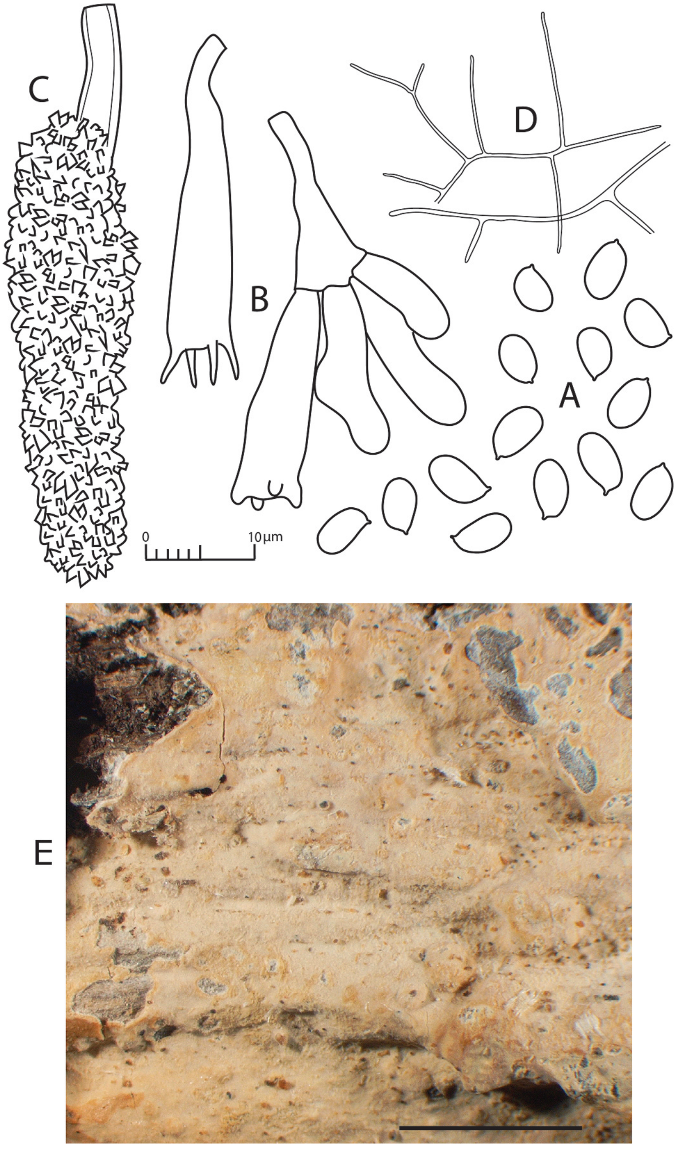

Fig. 6. *Phanerochaete mauiensis* (JEA 1462, isotype). **A.** Basidiospores (from RLG16784, paratype). **B.** Basidia. **C.** Encrusted cystidium. **D.** Microbinding hyphae. E. Basidiome (from RLG16784, paratype). Scale bar = 3 mm.

(sometimes absent) then becoming upright, forming an open tissue of non-agglutinated, loosely intertwined hyphae (sometimes absent); subicular hyphae 2.5-5 µm diam, simple-septate, moderately branched, walls hyaline, thin to slightly thickened, occasionally up to 1.5 µm thick, smooth to moderately encrusted with small, insoluble, hyaline crystals. *Subhymenium* thickening, up to 80 µm thick, composed of upright, closely packed, non-agglutinated, short-celled hyphae and embedded cystidia; subhymenial hyphae 2.3-3.2 µm diam, simple-septate, frequently branched, walls hyaline, thin, smooth. *Hymenium* a dense palisade of cystidia and basidia. *Cystidia* numerous, cylindrical to subfusiform, 40-60(-80) × 6.5-10(-15) µm, stalk 2.2-3.5 µm diam, embedded or protruding up to 35 µm, walls hyaline, slightly thick to 1 µm thick in stalk, up to 2.2 µm thick in main body, heavily encrusted with fused, insoluble, hyaline crystals. *Basidia* clavate, (20-)22-28 × (4.5-)5-5.5(-6.5) µm, simple-septate at base, walls hyaline, thin, smooth, 4-sterigmate. *Basidiospores* ellipsoid to broadly cylindrical, (4.4-)5-5.8(-6.4) × (2.8-)3-3.6 µm, $\bar{x}$ (2) = 5.2-5.4 × 3.1 µm, Q = 1.7, walls hyaline, thin, smooth, acyanophilous, not reacting in Melzer's reagent.

Habitat and distribution: On bark and wood of angiosperms, especially branches, in Hawaii.

Type specimens examined: U.S.A., Hawaii, Maui County, Makawao District, Hana Highway, mile 6, on bark and wood of *Eugenia jambos* L. twigs, 13 June 1990, J.E. Adaskaveg 1462 (BPI-802945, holotype; ARIZ-AN028779, isotype).

Additional specimens examined: U.S.A., Hawaii, Hawaii Island, South Hilo District, Hilo, Hemmes residence, on bark of *Trema occidentalis* (L.) Blume, 18 June 1990, R.L. Gilbertson 16863 (ARIZ-AN030405). Maui, Makawao District, Hana Highway, mile 6, on decorticate *E. jambos*, 13 June 1990, R.L. Gilbertson 16784 (ARIZ-AN030377).

Description and illustration: Gilbertson & Adaskaveg (1993).

Phanerochaete mauiensis is characterized by an agglutinated subiculum with distinct, thin-walled hyphae, embedded, encrusted cystidia, and ellipsoid basidiospores. Because microbinding hyphae are not distributed evenly and found in one specimen only, it is best to consider this species monomitic. In the original description, Gilbertson & Adaskaveg (1993) described cylindrical spores, 5.5-6 × 2.5-3 µm, which are narrower than observed in the specimens cited above. This species is most similar to *Phanerochaete exigua* (Burt) Nakasone, Burds. & Lodge from Mexico which has cylindrical basidiospores, 5-7 × 2.5-3 µm. See Liberta (1968) for a description of *P. exigua*.

Phanerochaete mauiensis is included here because it may be mistaken for a species of *Rhizochaete* because of its pale orange-colored basidiome, fimbriate margins, and encrusted cystidia. However, it lacks critical features of the genus such hyphal cords and the tiny, resinous-like material embedded in the context that dissolves in KOH. Moreover, the agglutinated subicular tissue observed in some specimens of *P. mauiensis* is absent in *Rhizochaete*.

DISCUSSION

Rhizochaete is a well-defined genus, based on morphological and molecular characters, with a global distribution. It now contains 13 species including four taxa discussed in this paper. The pellicular, loosely adnate, fragile, often brightly colored basidiomes and hyphal cords are useful characters to distinguish *Rhizochaete* in the field. Most species of *Rhizochaete* have a limited geographic distribution except for *R. radicata*. Microscopically, species are characterized by a loose, open, non-agglutinated subiculum, cystidia, small ellipsoid basidiospores, and abundant, tiny particles of resinous-like material coating the hyphae and hymenial elements. These particles readily dissolve in KOH. Critical microscopic features for species identification include presence or absence of clamp connections, wall thickness and encrustation of cystidia, and shape and size of basidiospores. Basidiome and hyphal cord reaction to KOH solution are important characters also. With the addition *of R. flava, R. percitrina*, and *R. rhizomorphosulphurea*, the genus now includes species in which the basidiome and hyphal cords do not result in a red-violet color change in KOH. Furthermore, *R. percitrina* does not produce the tiny, particulate, resinous-like material, instead the resinous-like material aggregate into large, amorphous masses embedded in the subiculum.

The tiny, resinous-like particles that dissolve in KOH are not unique to *Rhizochaete*. For example, *Ginnsia viticola* (Schwein.) Sheng H. Wu & Hallenb. has similar particles throughout its pellicular, reddish gray to greenish gray basidiome, but its large basidia and basidiospores, 8-12 × 4.5-5.5 µm, distinguish it from *Rhizochaete*. Species of *Phlebia* and *Mycoacia* also produce these particles but develop ceraceous basidiomes with dense, often agglutinated, subicular and subhymenial tissues.

By morphological criteria, *Rhizochaete* is a distinct, well-characterized genus but the molecular evidence is mixed. Phylogenetically, it is in the Phanerochaetaceae which includes four major groups – the Phanerochaete clade, the Donkia clade, the Phlebiopsis clade, and the Bjerkandera clade (Miettinen *et al.*, 2016). Floudas & Hibbett (2015) also recovered these four clades. *Rhizochaete* is in the Phlebiopsis clade that also includes the genera *Phlebiopsis*, *Phaeophlebiopsis*, and *Hapalopilus* P. Karst.

In our study, we analyzed the ITS and LSU datasets alone and together with maximum likelihood and Bayesian methods. Although the ITS sequence analyses always recovered *Rhizochaete* as a monophyletic genus with strong support, it was sister to a group of *Phanerochaete* species resulting in a paraphyletic Phlebiopsis clade. The LSU sequences, in contrast, recovered *Rhizochaete* as paraphyletic in clades with weak or no support but the Phlebiopsis clade remained intact. By combining ITS and LSU datasets, the Phlebiopsis clade was recovered with *Rhizochaete* paraphyletic with species divided between two sister clades. Nine species of *Rhizochaete* (with both ITS and LSU sequences), including the generic type, were in a moderately supported core *Rhizochaete* clade whereas *R. violascens* clustered with species of *Phaeophlebiopsis*, *Phlebiopsis*, and *P. unica* in a clade with weak or no support (Fig. 1). This was not unexpected since only LSU sequence was available for *R. violascens*, and in LSU-based phylogenetic analyses, *Rhizochaete* is usually resolved as a paraphyletic genus (Wu *et al.*, 2010; Chikowski *et al.,* 2016a; this study) except in one instance (Greslebin *et al.* 2004).

With ITS sequence data alone, *Rhizochaete* was paraphyletic with *H. rutilans* in a clade with *R. americana* (Floudas & Hibbett, 2015, Fig. 3). Other studies, however, recovered *Rhizochaete* as monophyletic based on ITS sequences (Greslebin *et al.*, 2004; Chikowski *et al.,* 2016a; this study). With the addition of *rbp*1 (Miettinen *et al.*, 2016, Fig. 3) or *rbp*1 and *rbp*2 (Floudas & Hibbett 2015, Fig. 1) to the ITS and LSU sequences, *Rhizochaete*, represented by three or four species, is resolved as a strongly supported genus.

In summary, depending on the taxa and genes included in the analyses, *Rhizochaete* is recovered either as a monophyletic clade (Greslebin *et al.*, 2004;

Chikowski *et al.,* 2016a) or as paraphyletic or polytomic together with *H. nidulans*, *Phanerochaete lutea*, *Phlebia unica*, and several species of *Phlebiopsis* (Wu *et al.,* 2010; Binder *et al.,* 2013; Floudas & Hibbett, 2015; Chikowski *et al.,* 2016a; Miettinen *et al.* 2016). It appears that the monophyly of *Rhizochaete* can only be resolved with the sequencing of additional *Rhizochaete* taxa and gene regions.

Despite the conflicting molecular phylogenetic studies, we believe that there is sufficient morphological and molecular evidence to accept *Rhizochaete* as a monophyletic genus. Additional morphological and molecular phylogenetic studies of species in the genus as well as related taxa are required to determine the scope and limits of *Rhizochaete*. Future studies should include sequences from *rbp*1 in addition to sequences of the ITS and LSU regions and include taxa such as *Phanerochaete galactites* and *Ceraceomyces cystidiatus* to determine if they are congeneric with *Rhizochaete*.

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