Mycologia, 96(2), 2004, pp. 260-271.

Rhizochaete, a new genus of phanerochaetoid fungi

Alina Greslebin[1]

Centro de Investigación y Extensión Forestal Andino Patagónico (CIEFAP), C.C. 14, 9200 Esquel, Chubut, Argentina

Karen K. Nakasone[2]

Center for Forest Mycology Research, Forest Products Laboratory, 1 Gifford Pinchot Drive, Madison, Wisconsin 53726-2398

Mario Rajchenberg

Centro de y Investigación Extensión Forestal Andino Patagónico (CIEFAP), C.C. *14, 9200 Esquel, Chubut, Argentina*

Abstract: A new basidiomycete genus, *Rhizochaete* (Phanerochaetaceae, polyporales) is described. *Rhizochaete* is characterized by a smooth to tuberculate, pellicular hymenophre and hyphal cords that turn red or violet in potassium hydroxide, monomitic hyphal system of simple or nodose septate hyphae, cystidia, and small, cylindrical to subglobose basidiospores. It morphologically is most similar to *Phanerochaete.* Analyses of nuclear ribosomal and internal-transcribed spacer region sequence data support a close relationship between *Rhizochaete* and *Phanerochaete.* The new taxon *R. brunnea,* from southern Argentina, is described and illustrated. In addition, the new combinations *R. americana, R borneensis, R. filamentosa, R. fouquieriae* and *R. radicata* are proposed. A key to the species of *Rhizochaete* is provided.

Key words: Basidiomycetes, *Ceraceomyces americanus, Ceraceomyces fouquieriae,* internal transcribed spacer region, Phanerochaetaceae, *Phanerochaete borneensis, Phanerochaete filamentosa, Phanerochaete radicata,* Polyporales, *Rhizochaete brunnea,* ribsomal DNA, taxonomy

INTRODUCTION

During a survey of Corticiaceae sensu lato growing on *Nothofagus pumilio* (Poepp. & Endl.) Krass. (Greslebin and Rajchenberg 1997a, b, 1998, Greslebin 2001) in the southern forests of Argentina (Cabrera and Willink 1973), an undescribed taxon whose hymenial surface turned violet with drops of 2–5% KOH was found. The generic placement of this taxon could not be determined readily from its morphological features because it possessed characters assignable to several genera. The basidiocarp and the hyphal system had a phanerochaetoid appearance, but the hyphae were clamped regularly. In addition, the tubular cystidia with thickened walls were similar to those developed in some species of *Crustoderma* but differed in being encrusted with crystals and granular material. The taxon was associated with white rot, but the test for extracellular oxidases resulted in a negative or a very weakly positive reaction. The affiliation of this taxon to *Phanerochaete* P. Karst., *Phlebia* Fr., *Hyphoderma* Wallr.) *Crustoderma* Parmasto and *Ceraceomyces* Jülich was evaluated, but in all cases the new species did not conform to important features of these genera. Several species in the above-mentioned genera that had the hymenia1 surfaces turning red-violet with KOH solution showed similarities in hyphal morphology, type of encrustation and cystidia. Because morphological features were insufficient to establish a proper generic disposition, the large and small subunits of the nuclear ribosomal DNA and internal-transcribed spacer (ITS) region were sequenced and analyzed. The analyses showed a close relationship between the Argentinean taxon and *Ceraceomyces americanus* Nakasone, C.R. Bergman & Burds., *Ceraceomyces fouquieriae* (Nakasone & Gilb.) Nakasone, C.R. Bergman & Burds., *Phanerochaete filamentosa* (Berk. & M.A. Curtis) Burds. and *Phanerochaete radicata* (Henn.) Nakasone, C.R. Bergman & Burds. In this paper we describe the new genus *Rhizochaete* to accommodate these taxa, based on morphological and molecular studies.

MATERIALS AND METHODS

Morphological and cultural studies.–Freehand sections of fresh and dried basidiocarps were examined microscopically, mounted in 2–5% potassium hydroxide (KOH) and 1% aqueous phloxine, Melzer's reagent (reactions amyloid, dextrinoid or none [=IKI–]; Kirk et al 2001), 0.1% cotton blue in lactophenol and 1 % aqueous cresyl-blue (reaction metachromatic when walls turn purple). Color descriptions were taken from Munsell (1954) and herbarium designations from Holmgren et al (1990). Cultures were obtained

Accepted for publication August 27, 3003.

[1] E-mail: alina@ciefap.cyt.edu.ar

[2] Corresponding author. E-mail: knakasone@fs.fed.us

from context tissue of fresh basidiocarps or isolated from the associated wood rot and are kept at the culture collection at CIEFAP. Cultural features were studied and described according to Nobles (1965). The species code describing the cultures follows the system of Nobles (1965), with several modifications summarized by Nakasone (1990). Line drawings of microscopic features were made with a drawing tube on the microscope. Unless otherwise indicated, all specimens are at CIEFAP.

Phylogenetic analyses.–Taxa used in the phylogenetic analyses are listed in TABLE I. Three datasets, representing three different gene regions of the nuclear ribosomal gene, were analyzed. Based on previous phylogenetic studies of Homobasidiomycetes using the nuclear small-subunit ribosomal RNA gene (SSU rRNA) (Hibbett and Donoghue 2001, Lim 2001), 28 taxa were included in the first dataset, and *Gloeophyllum sepiarium* (Wulf. : Fr.) P. Karst. was chosen as outgroup taxon. The nuclear large-subunit ribosomal RNA (LSU rRNA) gene region includes 36 taxa of which 19 also were represented in the SSU rRNA dataset. Results from the SSU rRNA analysis and Parmasto's and Hallenberg's (2000) study of the phylogenetic relationships of phlebioid fungi based on the LSU rRNA. were used to determine the taxa included in the LSU rRNA dataset. *Gloeophyllum sepiarium* was designated outgroup taxon in the LSU rRNA dataset as well. The third dataset consists of sequences of the internal transcribed spacer region, including the 5.8S rRNA gene (ITS). Forty taxa were included in the ITS dataset. The taxa in this dataset were based on previous studies (Boidin et al 1998; de Koker et al 2003) and included a number of *Phanerochaete* species. Representative strains of five taxa of *Rhizochaete* were included in all three datasets.

Cultures and voucher specimens of strains sequenced in this study are deposited at CFMR (TABLE I). Cultures were grown in 50 ml of sterile 2% malt extract supplemented with 1% glucose and 0.1% yeast extract at 25 C for 1 wk. The cultures were harvested by filtration onto Miracloth (Chicopee Mills Inc., La Jolla, California), lyophilized and stored at −20 C. Total DNA was extracted following the protocol outline in Cenis (1992), with minor modifications, and further purified with a Geneclean kit (Qbiogene, Carlsbad, California). The ITS region was amplified with primers ITS5 and ITS4, the SSU RNA gene with primers NS1 and NS8, and the 5' end of the LSU RNA gene with primers LR0R and LR7 (White et al 1990) using a Taq PCR Core Kit (Qiagen, Hilden, Germany) in a PTC 200 DNA Engine thermal cycler (MJ Research, Watertown, Massachusetts). Primers were prepared by Operon Technologies Inc. (Alameda, California). Cycling parameters were: 1 cycle at 93 C for 2 min, followed by 35 cycles at 53 C for 2 min, 72 C for 2 min, and 93 C for 1 min. Amplified DNA products were cleaned with a QIAquick PCR Purification Kit (Qiagen, Hilden, Germany) then sequenced with an ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (PE Biosystems, Foster City, California), following the manufacturer's protocol. Primers used for sequencing were ITS1, ITS3 and ITS2 or ITS6 for the ITS region, NS1, NS2, NS3, NS5, NS7, NS6, NS8 and sometimes SR4 for the SSU rRNA gene, and LR0R, LR3R, LR17R, LR3, LR5 and LR7 for the LSU rRNA gene, (http://www.biology.duke.edu/fungi/mycolab/primers.htm). Sequences were obtained from an ABI Prism 377-18 DNA Sequencer (PE Biosystems, Foster City, California). This overlapping sequencing strategy resulted in the DNA regions being sequenced in both directions, except in a few areas. Sequences obtained from this study were submitted to GenBank (AY219389–AY219404).

Sequences obtained from this study were aligned manually in PAUP* 4.0b10 (Swofford 2002) and McClade (Maddison and Maddison 1992) with those obtained from GenBank (TABLE I). The SSU rRNA, LSU rRNA and ITS regions were analyzed separately. The aligned sequences are available from TreeBASE (S972). In each region, ambiguous sites were excluded before analyses. Phylogenetic analyses of the sequence data were performed with maximum-parsimony (MP) and maximum-likelihood (ML) methods, as implemented in PAUP, and with Bayesian inference, using MrBayes version 2.01 (Hulsenbeck and Ronquist 2000). For MP analyses, an initial heuristic search of 100 random taxon addition replicate searches was conducted with TBR branch-swapping, MAXTREES set to autoincrease, without constraints, unordered and equally weighted nucleotides, and retention of two shortest trees. The shortest trees were used as starting trees in a second heuristic search, with TBR branch swapping and MAXTREES set to 5000 to find the most-parsimonious trees. Bootstrap support for clades (Felsenstein 1985) was estimated from 1000 replicate heuristic searches with simple taxon addition sequence, retention of one tree per replicate, TBR branch swapping, and MAXTREES set to 5000. Consistency indices (CI, Kluge and Farris 1969) and retention indices (RI, Farris 1989) exclude uninformative characters. Decay indices (DI, Bremer 1988) were determined with AUTODECAY 4.0 (Eriksson 1998). The program MODELTEST 3.06 (Posada and Crandall 1998) performed nested likelihood ratio tests to determine the best model of sequence evolution for the three datasets. The values obtained from MODELTEST then were used in ML and Bayesian analysis. ML heuristic searches were performed in PAUP with TBR branch swapping. Bayesian analysis was implemented in MrBayes with four Markov chain Monte Carlo chains with no molecular clock enforced. One million or 1 500 000 generations were performed, with every 100 trees sampled. The first 1000 or 1500 trees were excluded from construction of the consensus tree. Bayesian analyses were performed three times to confirm the consistency of the consensus tree and posterior clade probabilities.

RESULTS

Rhizochaete Greslebin, Nakasone & Rajchenb., gen. nov.

Basidioma resupinatum, effusum, pelliculare vel membranaceum. Hymenophorum leve vel leviter tuberculatum, in solutionem KOH violaceum; rhizomorphis praesentes et perabundans. Systema hyphale monomiticum; hyphae fibulatae vel afibulatae, tenuitunicatae vel crassitunicatae, incrustatae, ochraceis materiis in KOH dissolventibus. Cystidia typice praesentes. Basidia anguste clavata, tetrasporis. Sporis

TABLE I. Taxa, strain numbers, and GenBank accession numbers

Taxa, strain number	SSU	LSU (strain no.[a])	ITS (strain no.[a])
Abortiporus biennis, KEW 210	AF334899	AF287842	—
Albatrellus syringae, CBS 728.85	AF026632	AF393045	—
Antrodia carbonica, DAOM 197828	—	AF287844	—
Antrodia xantha, K(M) 31145	—	—	AJ006681
Bjerkandera adusta, DAOM 215869	AF334904	AF287848	AJ006672 (K(M) 31061)
Bjerkandera fumosa, K(M) 32669	—	—	AJ006673
Byssomerulius albostranaineus, FP 100373[b]	AY219404	—	—
Ceraceomyces eludens, JS 20378	—	AF090881	—
Ceraceomyces microsporus, JS 22310	—	AF090876	—
Ceraceomyces serpens, KHL 8478	—	AF090882	—
Ceriporia purpurea, DAOM 213168	AF026594	AF287852	—
Ceriporiopsis gilvescens, JLL 3522[b]	AY219403	—	—
Ceriporiopsis subvermispora, FP 90031	AF334906	AF287853	—
Columnocystis abietina, HHB 12622	AF082848	—	—
Diplomitoporus lindbladii, K(M) 44271	—	—	AJ006682
Fomitopsis pinicola, DAOM 189134	—	AF287858	—
Gloeophyllum sepiarium, DAOM 137861	AF026608	AF393059	—
Gloeoporus taxicola (1), KEW 213	AF334913	AF287861	—
Gloeoporus taxicola (2), UL9508151	AF082682	—	—
Irpex lacteus, IFO 5367	AF082683	—	—
Leptoporus mollis, K(M) 39893	—	—	AJ006669
Lopharia spadicea, CBS 474.48	AF082853	—	—
Meripilus giganteus, DHS 93-193	AF026568	AF287874	—
Oxyporus latemarginatus, ATCC 9408	AF082670	—	—
Panus rudis, DHS 92-1 39	—	AF287878	—
Phanerochaete allantospora, KKN 111	—	—	AY219357
Phanerochaete arizonica, RLG 10816	—	—	AY19350
Phanerochaete australis, FP 102818	—	—	AY219373
Phanerochaete avellaneu, FP 104126	—	—	AY19355
Phanerochaete burtii, FP 104384	—	—	AY219352
Phanerochaete carnosa, HHB 10118	—	—	AY219354
Phanerochaete chrysorhiza, T484	—	AF139967	AY219359 (FP102002)
Phanerochaete chrysosporium, FPL 5175	AF026593	AF139966 (BKMF1767)	AY219344 (BKMF1767)
Phanerochaete crassa, FP 102496	—	—	AY219341
Phanerochaete ericina, FP 101978	—	—	AY219345
Phanerochaete hiulca, FP 100589	—	—	AY219342
Phanerochaete laevis (1), FP 101481	—	—	AY219347
Phanerochaete laevis (2), FP 101018	—	—	AY219348
Phanerochaete magnoliae, HHB 9829	—	—	AY219343
Phanerochaete omnivorum, HHB 5969	—	—	AY219360
Phanerochaete rimosa, FP 102099	—	—	AY219349
Phanerochaete sanguinea, F025062a	—	AJ406533	AY219353 (FP100391)
Phanerochaete sordida (1), HHB 7827	—	—	AY219377
Phanerochaete sordida (2), HHB 11458	—	—	AY219378
Phanerochaete sordida (3), HHB 9871	—	—	AY219385
Phanerochaete sordida (4), GEL 4160	—	AJ406532	—
Phanerochaete subceracea, FP 105974	—	—	AY219346
Phanerochaete tuberculata, FP 102168	—	—	AY219356
Phanerochaete velutina, FP 102157	—	—	AY219351
Phlebia albida, GB 1833	—	—	AY219368
Phlebia albomellea, FP 101843	—	—	AY219369
Phlebia centrifuga, FCUG 2396	—	AF141618	—
Phlebia chrysocreas, FP 102161	—	—	AY219367
Phlebia concentrica, OSC 41587	—	—	AY219364
Phlebia deflectens, FCUG 1568	—	AF141619	—

TABLE I. Continued

Taxa, strain number	SSU	LSU (strain no:)	ITS (strain no.[a])
Phlebia lilascens (1), FCUG 1801	—	AF141621	—
Phlebia lilascens (2), FCUG 2005	—	AF141622	—
Phlebia nitidula, FCUG 2028	—	AF141625	—
Phlebia radiata, FPL 6140	AF026606	AJ406541 (GEL 5258)	AY219366 (JLL 15608)
Phlebia rufa, FCUG 2397	—	AF141628	—
Phlebia subserialis, FCUG 1434	—	AF141631	AY219365 (GB240)
Phlebia termellosa, JHG 344[b]	AY219402	AF141632 (FCUG 1813)	—
Phlebiopsis gigantea, HHB 5153[b]	AF219394	AF141634 (FCUG 1417)	AF087488 (C-P160)
Pulcherricium caeruleum, FPL 7658	AF334933	AF393073	—
Rhizochaete americana, HHB 2004[b]	AY219396	AY219391	AY219391
Rhizochaete brunnea, MR 229[b]	AY219395	AY219389	AY219389
Rhizochaete filamentosa, FP 105240[b]	AY19398	AY219393	AY219393
Rhizochaete fouquieriae, KKN 121[b]	AY19397	AY219390	AY219390
Rhizochaete radicata, HHB 1909[b]	AY19399	AY219392	AY219392
Scopuloides hydnoides, GEL 3859	—	AJ406573	—
Tyromyces chioneus, JEW 141	AF334938	AF393080	—
Tyromyces fumidiceps, FP 105742[b]	AY219400	—	—
Tyromyces subgiganteus, RLG 6893[b]	AY219401	—	—

[a] Strain number, if different from that in the first column, is given in parentheses.
[b] Voucher specimens and cultures are available from CFMR.

brevis cylindraceis, ellipsoideis vel subglogosis, tenuitunicatis, levibus, hyalinis, inamyloicleis.

Typus: *Rhizochaete brunnea* Greslebin, Nakasone & Rajchenb. sp. nov.

Etymology. Rhizo (Gr. Rhiza = root) referring to the rhizomorphs + chaete (Gr. Chaite = hair, setae, spine, bristle) referring to the presence of protruding cystidia.

Basidiocarp pellicular to membranaceous, subceraceous when fresh, coriaceous but friable to firm papyraceous upon drying; readily detachable from substrate and/or subiculum. *Hymenia1* surface continuous, smooth to slightly tuberculate, velutinous, yellowish, orange or brownish colored, turning red to violet with drops of KOH solution. *Context* packed-hypochnoid to densely wooly. *Margin* distinct, fimbriate to fibrillose; hyphal cords usually abundant, turning red to violet in KOH.

Hyphal system monomitic; generative hyphae with variable septation (some species simple septate, some species mostly simple sepltate but a few septa with clamps, and other species regularly clamped), thin to thick-walled, encrusted with dark yellow to yellowish brown, resinous-like granules that dissolve in KOH turning the solution pale violet; some hyphae also encrusted with hyaline crystals that do not dissolve In KOH. Crystalline encrustation usually restricted to subicular hyphae, and crystals aggregated in clusters or rosette-like structures larger and coarser than the colored granules. *Subhymenium* well developed, composed of tightly packed hyphae. Subiculum an open and loose *textura intricata;* a basal *textura porrecta* stratum usually present next to the substrate. Hyphal system and hymenial elements metachromatic. *Cystidia* present in all but one species, cylindrical to subfusiform, thin to thick-walled, always encrusted with dark yellow to yellowish-brown resinous-like granules that dissolve in KOH, hyaline crystals usually present. *Basidia* clavate to subcylindrical and sinuous, thin-walled or thickening towards the base. *Basidiospores* small, up to 6.5(–7) µm long, short cylindrical to ellipsoid, widely ellipsoid to subglobose in one species, thin-walled, sometimes appearing slightly thickened, smooth, inamyloid. Associated rot white, but extracellular oxidase test of cultures may produce a weak or negative reaction.

Comments. This genus is characterized by the combination of detachable, subpellicular to membranaceous basidiocarps, hymenial surface and hyphal cords that turn red or violet in KOH, hyphae and cystidia with two types of encrustation (dark yellow to yellowish-brown granules and hyaline crystals), and small, cylindrical to subglobose basidiospores with thin to slightly thickened walls. The color change of the hymenial surface and hyphal cords is produced by the dark yellow to yellowish-brown granules that coat the hyphae as they dissolve and turn violet in KOH. It is an acid-base reaction as the application of an acid solution recovers the original hymenial color.

Rhizochaete easily is distinguished from morphologically similar corticioid genera. For example, *Hyphoderma* has cystidia that are similar to those in *Rhizo-*

TABLE II. Comparison of some distinguishing basidiocarp features of *Rhizochaete* species and morphologically similar taxa

Taxa	Hymenium reaction to 2% KOH	Hyphal cord reaction to 2% KOH	Granules dissolving in 2% KOH	Multiple clamps
Ceraceomyces cerebrosus	none	none	yes	absent
Ceraceomyces sulphurinus	none	none	yes	absent
Phanerochaete burtii	none	red	no	present
Phanerochaete carnosa	green/black	none	yes	present
Phanerochaete crassa	none	NA[b]	NA[b]	absent
Phanerochaete flava	none	none	yes	absent
Phanerochaete hiulca	red	NA[h]	NA[b]	absent
Phanerochaete laevis	(red)[a]	NA[b]	yes	present
Phanerochaete salmoneolutea	red	none	yes	present
Phanerochaete sanguinea	olive-green	olive-green	NA[b]	present
Phanerochaete subceracea	reddish brown	none	NA[b]	present
Phanerochaete viticola	brown	NA[b]	yes	absent
Phlebiopsis gigantea	none	NA[h]	NA[b]	absent
Phlebiopsis himalayensis	purple	NA[h]	yes	absent
Rhizochaete americana	purplish red	purple	yes	absent
Rhizochaete borneensis	(red/violet) [a]	red/violet	yes	absent
Rhizochaete brunnea	violet	red	yes	absent
Rhizochaete filamentosa	purple/pink	red	yes	absent
Rhizochaete fouquieriae	red/violet	(red) [a]	yes	absent
Rhizochaete radicata	purple/red	red	yes	absent

[a] Parentheses indicate that the color change is present in most but not all specimens.
[b] Not applicable; hyphal cords or encrusting granules not produced.

chaete but its basidiospores are significantly larger. *Crustoderma* is associated with a brown rot, whereas *Rhizochaete* is associated with a white rot. *Phlebia sensu stricto* (Hjortstam 1997) and *Phlebiopsis* Jülich can be distinguished by their ceraceous to subgelatinous basidiocarps and tightly packed, agglutinated, subicular hyphae.

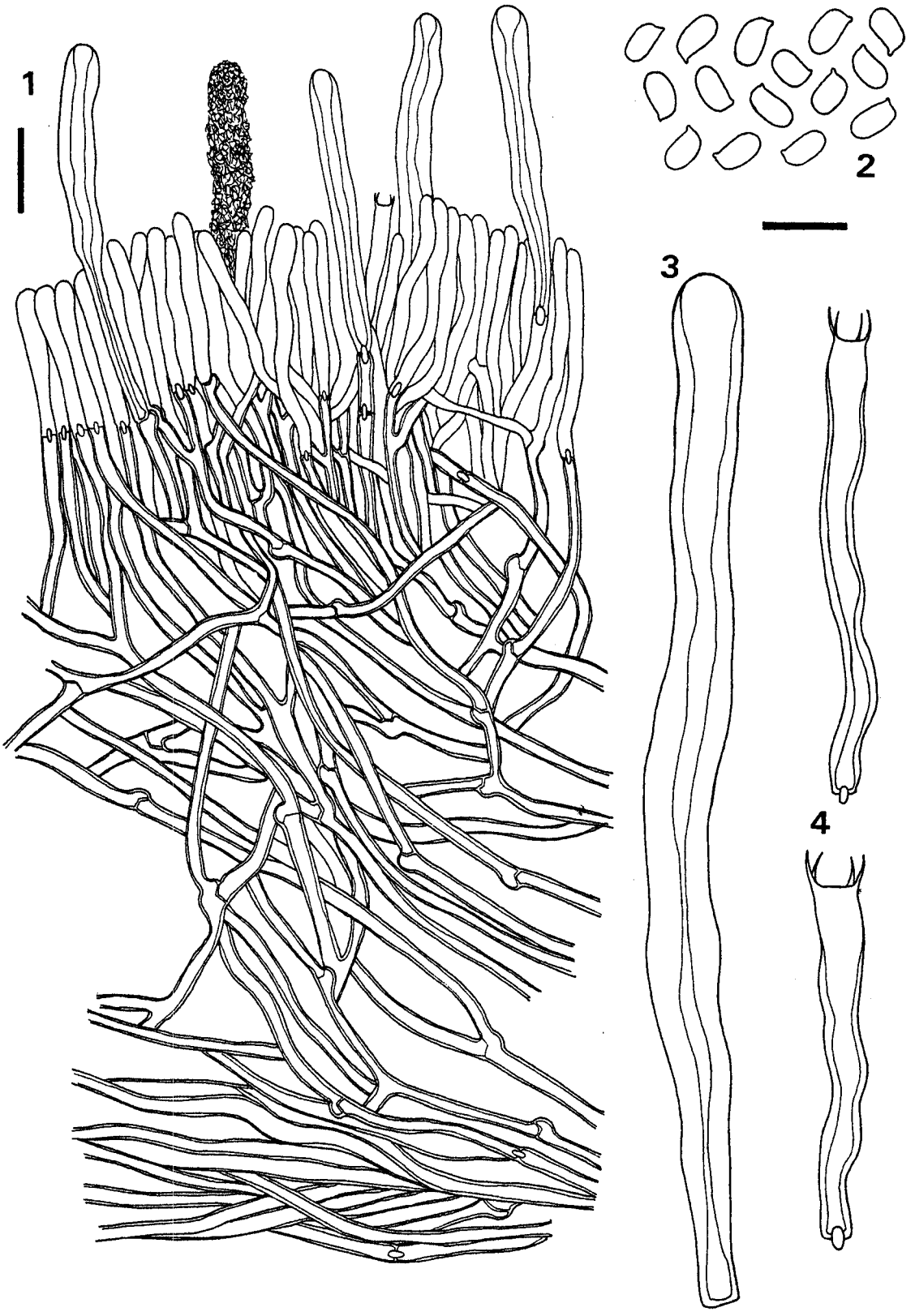
Rhizochaete is easily distinguished from the closely related genus *Phanerochaete* by the hyphal septation in the case of regularly clamped species. Simple-septate species of *Rhizochaete* develop rare single clamps but never multiple clamps that can be found in *Phanerochaete* species. Furthermore, all species of *Rhizochaete* develop a red or violet reaction of both the hymenium and hyphal cords to KOH. Although in some species of *Phanerochaete,* the hymenium turns red in KOH, the hyphal cords do not, e.g., *P. laevis, P. salmoneolutea* and *P. subceracea.* In other species such as *P. burtii,* the hyphal cords but not the hymenium turn red in KOH. The hymenia of *P. carnosa* and *P. sanguinea* produce a dark green or olive green reaction in KOH. A comparison of the distinguishing basidiocarp traits mentioned above for *Rhizochaete* and morphologically similar taxa in *Ceraceomyces, Phanerochaete* and *Phlebiopsis* is presented in TABLE II.

Rhizochaete can be confused with *Ceraceomyces,* and several species of *Rhizochaete* were transferred from *Ceraceomyces. Ceraceomyces,* as currently defined, is a collection of heterogeneous taxa, thus broad generalizations and comparisons to *Rhizochaete* are not possible. However, the type species of *Ceraceomyces, C. tessulatus* (Cooke) Jülich, has a pellicular hymenophore, hyphal cords that do not react with KOH, and lacks encrusting granules on the hyphae.

Rhizochaete brunnea Greslebin, Nakasone & Rajchenb., sp. nov. FIGS. 1–4

Basidiocarpum resupinatum, effusum, crassum, membranaceum; hymenophorum leve vel leviter tuberculatum, brunneum, in solutionem KOH violaceurn; rhizomorphis praesentes et perabundans. Systema hypharum monomiticum; hyphae fibulatae, leviter vel crassi tunicatae, metachromatisque, incrustatae; ochrdceis materiis in KOH dissolventibus. Cystidia cylindraceis, (80–)100–250 × 8–15 µm, crassitunicatis, metachromatisque, incrustatis. Basidia anguste clavata, 40–55(–60) × 5–6 µm, tetrasporis. Sporae ellipsoideae, 5–6.5(–7) × 3–3.5 µm, parietibus levibus, hyalinis, inamyloideis. Holotypus: BAFC 34527.

Basidiocarp resupinate, membranous, thick (0.3–2 mm) when fresh, with a coriaceous aspect but breaking readily upon drying, detachable from the substrate. Hymenia1 surface even to slightly tuberculate, velutinous to pilose under a 10× lens by the protruding cystidia, when fresh dark yellow, brownish-yellow or brown (10YR 6/8, 5/6; 7/5YR 5/6), slight



FIGS. 1–4. *Rhizochaete brunnea* micromorphology. 1. Vertical section through the basidiocarp. 2. Basidiospores. 3. Cystidium. 4. Basidia. Scale bars: 1 = 25 µm, 2–4 = 10 µm.

vinaceous when dried, turning violet in KOH solution (the original color being recovered upon the application of an acid solution), the coloration is due to the encrusted cystidia and its intensity varies according to cystidia abundance. *Context* up to 1.5 mm thick, with a compact hypochnoid texture, brownish yellow (10YR 6/8). *Margin* generally fibrillose, white or yellow, paler than the hymenia1 surface, with hyphal cords. *Hyphal cords* dark yellow, 100–1200 µm diam, firm, branched, abundant in the margin, developed under the basidiocarp and throughout the substrate.

Hyphal system monomitic; generative hyphae clamped, thick-walled, metachromatic, heavily encrusted with small, granular, dark melleous to chestnut-colored material that readily dissolves in KOH solution and turns the solution lilaceous; some hyphae, especially subicular ones, encrusted with polyhedral, hyaline crystals that do not dissolve in KOH. *Subhymenial hyphae* tightly intertwined and arranged perpendicular to the substrate, a compact *textura intricata* or *intricata-porrecta,* 5–6 µm diam, with walls thickened up to 1 µm. *Subiculum* a loose and open *textura intricata,* subicular hyphae up to 10 µm diam, with walls up to 2 µm thick, sometimes with secondary simple or ampullate septa, clamps sometimes difficult to discern; toward the base of subiculum hyphae arranged more or less parallel to the substrate; a basal stratum next to substrate usually present, a *textura porrecta* arranged parallel to the substrate. *Hyphal cords* composed of an inner core of parallel, tightly packed hyphae, 4–6 µm diam, clamped, with walls slightly thick to thickened, hyaline, and smooth, and wider hyphae 10–28 µm diam, sparsely septate, with walls thin to thick, containing refringent material that strongly stain with phloxine (appearing gloeopleurous-like) or, if lacking staining material then with walls up to 4 µm thick; outer layer composed of closely or loosely intertwined, yellowish hyphae 4–6 µm diam, with walls slightly thick to thick, heavily encrusted with granular, chestnut-colored granules and scattered, hyaline, polyhedral crystals. *Cystidia* cylindrical, (80–)100–250 × 8–15 µm, with thickened walls up to 4 µm except in the apex, metachromatic, some with adventitious septa, heavily encrusted with both chestnut-colored material and hyaline crystals. *Basidia* narrowly clavate, 40–55(–60) × 5–6 µm, with 4 sterigmata and a basal clamp, thick-walled toward the base, walls metachromatic. *Basidiospores* ellipsoid, 5–6.5(–7) × 3–3.5 µm, thin-walled, smooth, IKI–, guttulate.

Habitat. In pure stands of *Nothofagus pumilio* and mixed forests of *N. pumilio* and *N. betuloides* (Mirb.) Blume, fruiting on much-decayed logs in humid environments. HOLOTYPE. ARGENTINA. TIERRA DEL FUEGO: Ushuaia, Estancia el Valdéz, Río Valdez, on rotten trunk of *Nothofagus pumilio,* 5 Mar 1996, leg. *A. Greslebin 278, BAFC 34527* in BAFC.

Specimens examined. ARGENTINA. TIERRA DEL FUEGO: Ushuaia, Estancia el Valdéz, Río Valdéz, on fallen *N. pumilio,* 5 Mar 1996, leg. *A. Greslebin* 280, Ibid., 23 Mar 1998, leg. ipse *1449, 1450* and *1455;* Ibid., 23 Mar 1998, leg. *M. Rajchenberg 11455,* BAFC 34528. Montaña El Martial, on fallen log in mixed forest of *N. pumilio* and *N. betuloides,* 27 Mar 1998, leg. *M. Rajchenberg 11572* and *11578;* Ibid., 27 Mar 1998, leg. *A. Greslebin 1576 and 1577.* Lago Escondido, 10 Nov 1998, leg. *M. Rajchenberg 11844;* Ibid., 26 Apr 1999, leg. *A. Greslebin 1957.* Parque Nacional Tierra del Fuego, Río Pipo, 7 Nov 1998, leg. *M. Rajchenberg 11 782, 11 785 and 11 837.* Paseo del Turbal y Castorera, 25 Apr 1999, *leg. A. Greslebin 1921.* Río Negro, Parque Nacional Nahuel Huapi, Puerto Blest, 6 May 1999, leg. *M. Rajchenberg 11 873* and *11 890.*

Remarks. The brown, strongly velutinous hymenophore, the large cystidia, the thick-walled hyphal system and the relatively large basidia, with walls that thicken toward the base, distinguish this species from the others in the genus.

Cultural description.– FIGS. 5–10

Cultures studied. No. 229, from basidiocarp *M. Rajchenberg 11455; No. 230,* from associated decayed wood and mycelia of basidiocarp *A. Greslebin 1577.*

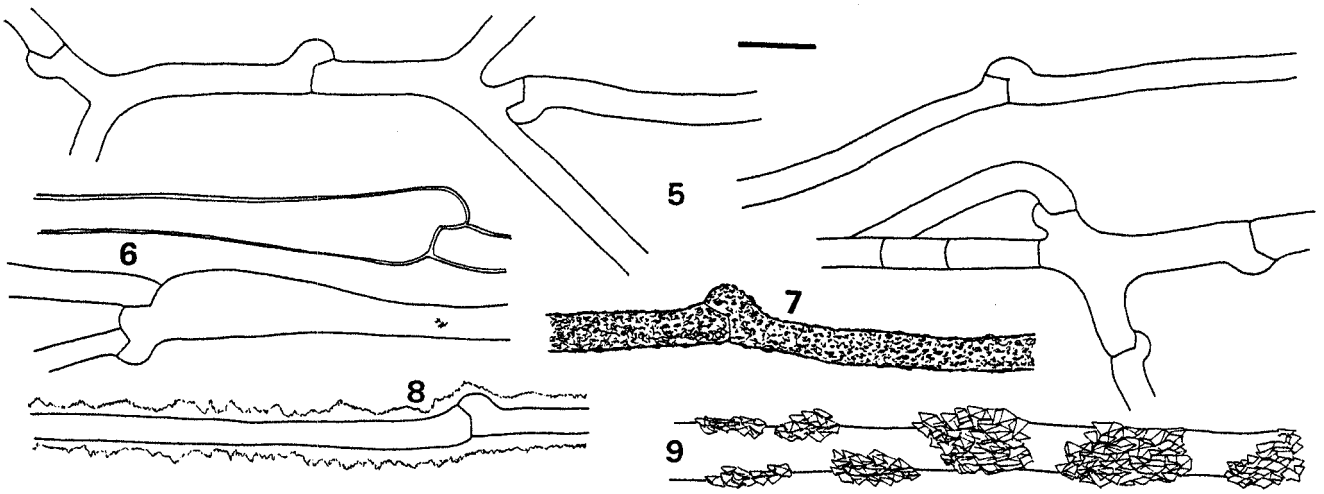
Macroscopic characters. Growth very slow, 6–6.5cm radius by 6 wk. Margin regular, hyaline, submerged in the agar. Behind the margin a woolly mat is formed, first as isolated punctual flakes that develop into a heterogeneous, felty to woolly, dark yellow to brownish yellow mat, with scattered denser areas, often with incipient hyphal cord formation. Drops of KOH solution turn the mat lilac or violet, but the color vanishes rapidly. Reverse bleached. Odor slightly sweet, fruity.

Oxidase reactions. GAA: ±, growth: trace; TAA: ±, growth: trace.

Microscopic characters. Marginal hyphae clamped, 3–5 µm diam, thin-walled, hyaline, branched, with long hyphal segments. Aerial mat with thin- and thick-walled generative hyphae covered with minute, dark yellow to brownish granules that readily dissolve in KOH solution. The size of these granules obscures their shape. At wk 6 some hyphae develop gelatinous, rough walls. Hyaline, polyhedral crystals formed on the hyphae and in the agar.

Species code. 1. (2) .3.27.31d.31e.32.37.40.47.50.54.

Remarks. Cultural features of *Rhizochaete brunnea* are similar to those of other *Rhizochaete* species (Nakasone et a1 1994), including its negative or weak oxidase reactions on GAA and TAA. However, the slow growth rate of *R. brunnea* is unusual in the genus.



FIGS. 5–9. *Rhizochaete brunnea* cultural characters. 5. Marginal hyphae. 6. Ampullate septa. 7. Hypha encrusted with granular material. 8. Hyphae with gelatinous, roughened walls. 9. Hyphae encrusted with hyaline crystals. Scale bar = 10 µm.

Rhizochaete americana (Nakasone, C.R. Bergman & Burds.) Greslebin, Nakasone & Rajchenb., comb. nov.

Basionym: *Ceraceomyces americanus* Nakasone, C.R. Bergman & Burds., Sydowia 46:56. 1994.

Remarks. Key characters of this species are clamped hyphae, fusiform, thin-walled cystidia, 33–44(–60) × 5–9(–12) µm, encrusted only with yellowish brown granules, and short cylindrical to ellipsoid basidiospores, 4–5(–5.5) × 2–2.5(–3) µm; reported from eastern North America. For a full description and illustrations, see Nakasone et a1 (1994).

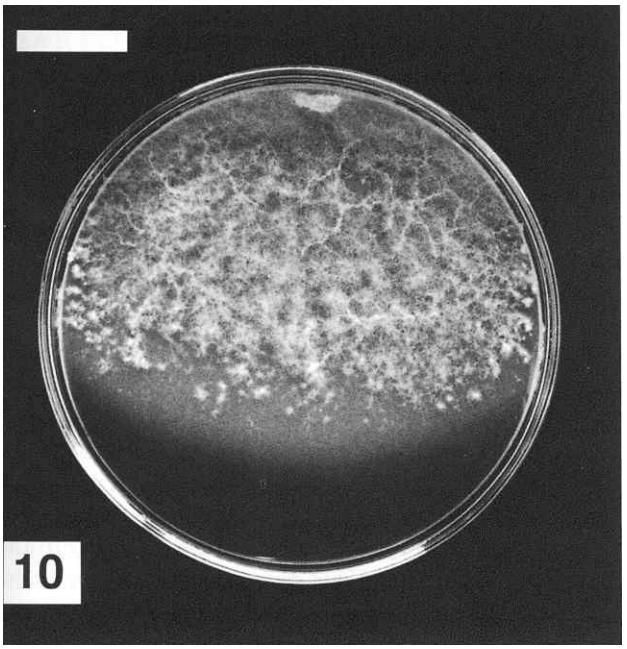


FIG. 10. *Rhizochaete brunnea.* Macroscopic aspect of culture at 6 wk. Scale bar = 20 mm.

Rhizochaete borneensis (Jülich) Greslebin, Nakasone & Rajchenb., comb. nov.

Basionym: *Phanerochaete borneensis* Jülich, J. Linn. Soc., Bot. 81:43. 1980.

Remarks. Key characters of this species are the bright yellow subiculum, simple septate hyphae with scattered single clamp connections, short, thin- to thick-walled cystidia, 20–33(–50) × 4.5–9 µm, encrusted with coarse, hyaline crystals, and broadly ellipsoid to subglobose basidiospores, 4–5 × 2.8–3.2 µm, with thin to slightly thick walls; reported from Borneo and Brunei (Hjortstam et a1 1998).

Rhizochaete filamentosa (Berk. & M.A. Curtis) Greslebin, Nakasone & Rajchenb., comb. nov.

Basionym: *Corticium filamentosum* Berk. & M.A. Curtis in Berk., Grevillea 1(12):178. 1873.

Remarks. Key characters of this species are simple septate hyphae with rare single clamp connections in the subiculum, cylindrical to narrowly obclavate cystidia, mostly thin-walled, with secondary septa, (30–)40–60 × 5–7 µm, usually encrusted with both hyaline crystals and colored granules, and short cylindrical basidiospores, 4–5 × 2–2.5 µm; reported from eastern North America. For a full description and illustrations, see Nakasone et al (1994).

Rhizochaete fouquieriae (Nakasone & Gilb.) Greslebin, Nakasone & Rajchenb., comb. nov.

TABLE III. Summary of likelihood models of evolution and parameters of three gene regions

Gene region	Model[a]	PINV[b]	a[c]	Base frequencies A	C	G	T
SSU	F81+G	0	1.629	0.4043	0.1639	0.1654	0.2664
LSU	TrNef+I+G	0.6114	0.6414	0.25	0.25	0.25	0.25
ITS	HKY+I+G	0.3960	0.6828	0.2693	0.2153	0.2001	0.3153

[a] F81, Felsenstein (1981); TrNef, Tamura-Nei equal base frequencies; HKY, Hasegawa-Kishino-Yano (Hasegawa et al 1985); I, proportion of invariant sites; G, shape parameter of the gamma distribution.

[b] Proportion of invariant sites.

[c] Gamma distribution shape parameter.

Basionym: *Hyphoderma fouquieriae* Nakasone & Gilb., Mycologia 70(2):272. 1978.

Remarks. Key characters of this species are clamped hyphae, cylindrical to clavate cystidia, thin- to slightly thick-walled, 35–55 × 5.5-8 µm, usually encrusted with both hyaline crystals and colored granules, and ellipsoid basidiospores, 5-6 × 3-4 µm; reported from Arizona. For a full description, see Nakasone and Gilbertson (1978).

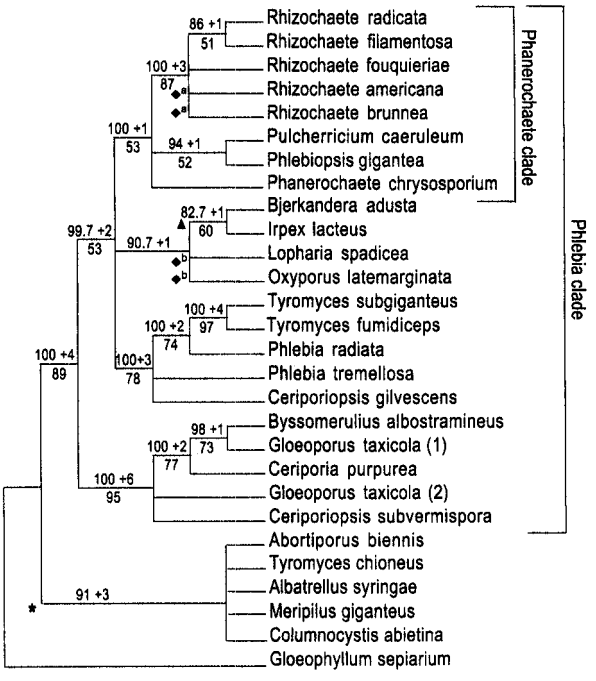


FIG. 11. Strict consensus of 385 most-parsimonious trees (tree length = 209 steps, CI = 0.496, RI = 0.712) of the small-subunit ribosomal RNA gene region. Numbers above the branches are average posterior clade probabilities from three Bayesian analyses. Decay indices are indicated above the branches preceded by a + sign. Bootstrap confidence levels are shown below the branches; values <50% are not shown. Asterisks (*) and triangles (p) indicate nodes that collapse in the Bayesian and maximum-likelihood trees, respectively. Diamonds (¨) with the same superscript letter indicate branches that are joined in maximum-likelihood and Bayesian trees.

Rhizochaete radicata (Henn.) Greslebin, Nakasone & Rajchenb., comb. nov.

Basionym: *Corticium radicatum* Henn., Pflanzenw. Ost-Afrikas, Lieferung 1, Theil C, p. 54. 1895.

Remarks. Key characters of this species are simple septate hyphae with rare single clamps connections in the subiculum, mostly thick-walled, clavate to fusiform cystidia, (40-)60-l00(-115) × 5-7 µm, usually encrusted with both hyaline crystals and colored granules, and short cylindrical to ellipsoid basidiospores, 4—5(—5.5)× (2.2-)2.5-3 µm; reported worldwide. For a full description, see Nakasone et al (1994).

Sequence alignments.–The SSU rDNA region sequence alignment totaled 1817 base pairs (bp), of which 119 characters (6.5%) were excluded because of ambiguity in alignment; 139 remaining characters were variable, of which only 56 (3%) were parsimony informative. In contrast, the ITS region was the shortest at 866 bp and was the most difficult to align. More than half of the ITS characters, 455 bp (53%), were excluded; 161 characters were variable, and of these 115 (29%) were parsimony informative. The LSU rDNA region was 932 bp long; 86 (9%) ambiguous characters were excluded, 222 characters were variable and 155 (17%) characters were parsimony informative. TABLE III lists the likelihood models used in the ML and Bayesian analyses of the three gene regions.

Sequence analyses.–The *Rhizochaete* taxa always formed a monophyletic clade in MP, ML, and Bayesian analyses of the SSU rDNA dataset. There were 385 MP trees of 209 steps, with CI = 0.499 and RI = 0.712. The strict MP consensus tree shown in FIG. 11 is congruent with, but slightly less resolved than, the ML and Bayesian trees. *Rhizochaete* is included in the unresolved *Phanerochaete* clade, nested within the larger *Phlebia* clade of Hibbett and Donoghue (2001).

Phylogenetic analyses of the LSU rDNA produced trees that generally are congruent with the trees of

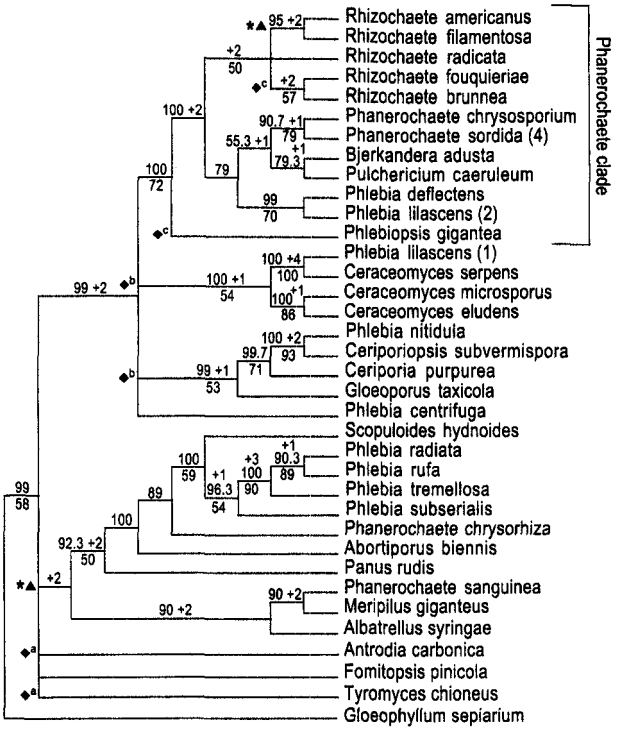


FIG. 12. Strict consensus of 14 most-parsimonious trees (tree length = 739 steps, CI = 0.323, RI = 0.519) of the large-subunit ribosomal RNA gene region. Symbols and numbers are described in FIG. 11.

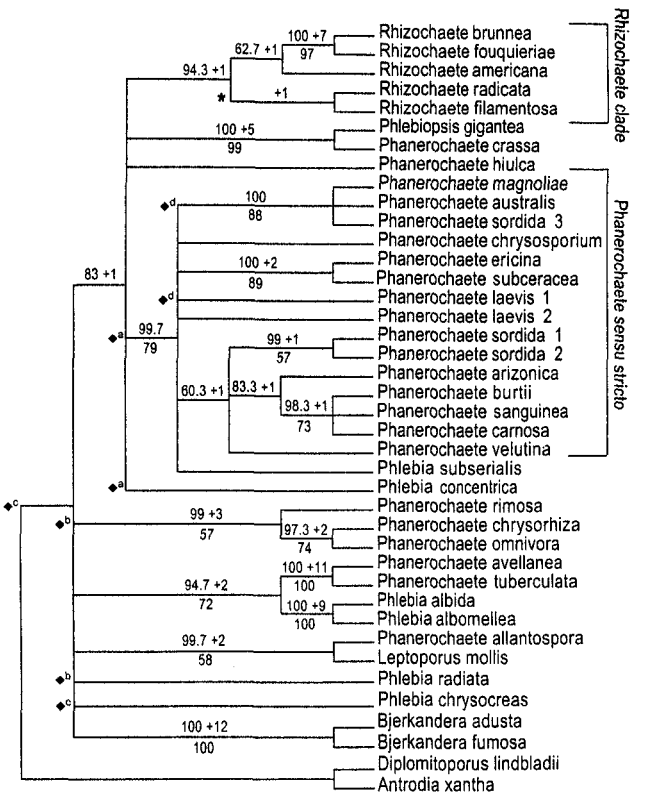


FIG. 13. Strict consensus of 2658 most-parsimonious trees (tree length = 435 steps, CI = 0.433, RI = 0.613) from maximum-parsimony analysis of the internal transcribed spacer region. Symbols and numbers are described for FIGS. 11 and 12.

the SSU region, although less than half of the taxa are shared between the two datasets. There were 14 MP trees of 739 steps with CI = 0.323 and RI = 0.519. The strict MP consensus tree of the LSU region is shown in FIG. 12. In this tree, the *Rhizochaete* species form a monophyletic clade that is sister to a heterogeneous clade containing *Phanerochaete chrysosporium, Phan. sordida, Bjerkandera adusta, Pulcherricium cueruleum, Phlebia deflectens* and *Phl. lilascens.* These two clades and *Phlebiopsis* constitute the *Phanerochaete* clade. The ML and Bayesian trees generally are congruent but more resolved than the MP consensus tree. Some branches paired in the ML and Bayesian trees but not in the MP trees are indicated on the figure. Note that in the ML and Bayesian trees *Phlebiopsis gigantea* is included in a clade with *R. fouquieriae* and *R. brunnea.* This *Rhizochaete/P. gigantea* clade had an average 98.7% credibility value by Bayesian analysis but only a 50% MP bootstrap confidence level. The other *Phanerochaete* species fall outside the *Phanerochaete* clade: *Phan. sanguineu* clusters with *Meripilus giganteus* and *Albatrellus syringae,* whereas *Phan. chrysorhiza* clusters with *Phlebia* spp. and *Scopuloides hydnoides.*

The ITS dataset includes a number of *Phanerochaete* species. There were 2658 most-parsimonious trees of 453 steps long with CI = 0.433 and RI = 0.613. In the strict MP consensus tree in FIG. 13, the *Rhizochaete* species form a monophyletic clade that is part of a five-way polytomy that includes *Phlebiopsis gigantea/Phan. crassa, Phan. hiulca,* a large, poorly resolved *Phanerochaete sensu stricto* clade that includes *Phlebia subserialis* and *Phlebia concentrica.* The ML and Bayesian tree topologies are similar but more resolved than the strict MP consensus tree; a few of the joined branches are indicated in the figure. In the ML and Bayesian trees, the *Rhizochaete, P. gigantea/Phan. crassa* and *Phan. hiulca* lineages are not included in the *Phanerochaete sensu stricto* clade that also includes *Phl. subserialis* and *Phl. concentrica.*

DISCUSSION

The most striking and consistent character of the new genus *Rhizochaete* is the red to violet reaction of the basidiocarp and hyphal cords to KOH that is related to the dark yellow to yellowish-brown granules that coat the hyphae and cystidia. This feature, though, is present in some species of *Phanerochaete, Ceraceomyces, Phlebia* and unrelated taxa such as *Hy-*

phodontia australis (Berk.) Hjortstam (Greslebin et al 2000). Other significant characters are the "phanerochaetoid" appearance of the hyphal system, the structure of the subiculum and subhymenium, the hyphal cords, and the shape and size of the basidiospores that are similar to some *Phanerochaete* species. The sum of these morphological characters indicates a close relationship of *Rhizochaete* to the genus *Phanerochaete,* and this relationship also is supported by molecular data.

Rhizochaete consists of species that have a monomitic hyphal system with either regularly nodose septate, regularly simple septate, or simple septate with scattered single clamps. In most genera in the Aphyllophorales, the species have one type of hyphal septation. It is not unusual, however, for one or more species to have simple septate hyphae in a genus of primarily nodose septate species. Examples of these genera include *Hyphoderma* Wallr., *Hyphodontia* J. Erikss., *Phlebia* Fr., *Radulodon* Ryvarden, *Resinicium* Parmasto and *Veluticeps* (Cooke) Pat. A few corticioid genera, namely *Botryobasidium* Donk and *Peniophora* Cooke, include a significant number of nodose septate and simple septate species.

Ribosomal DNA analyses support the formation of the new genus *Rhizochaete.* In general, analyses of the SSU, LSU and ITS-sequence data by MP, ML and Bayesian methods produced trees that support the monophyly of the *Rhizochaete* species. However, with ML and Bayesian analyses of the LSU, *Phkbiopsis gigantea* was included also in the *Rhizochaete* clade. *Rhizochaete* is closely related to the *Phanerochaete sensu stricto* clade. Of the taxa included in the datasets, *Phlebiopsis gigantea, Phan. crassa* and *Phan. hiulca,* appear to be the most closely related to *Rhizochaete.* These results are congruent with a phylogenetic study of the genus *Phanerochaete* that employed the ITS region (de Koker et a1 2003).

The *Rhizochaete* clade is relatively consistent in the analyses of the three datasets, although the positions of other taxa are not. Most of the conflicting results involve taxa in the LSU trees. For example, *Bjerkandera adusta* is embedded in the *Phanerochaete* clade in the LSU trees but not in the SSU and ITS trees. Boidin et al (1998) found that three species of *Bjerkandera* clustered together in a distinct clade basal to the *Phanerochaete* clade in an analysis of the ITS region. *Phlebia suberialis* similarly clusters with the *Phanerochaete sensu stricto* group in the ITS trees, also reported by Boidin et al (1998), but joins other *Phlebia* species in LSU (Parmasto and Hallenberg 2000) and SSU rDNA sequence analyses (Suhara et al 2002). In another example, *Phan. sunguinea* clusters with *Phan. burtii* and *Phan. carnosa* in the *Phanerochaete sensu stricto* clade in ITS trees. However, in the LSU trees, *Phan. sanguinea* is in a clade with *Meripilus giganteus* and *Albatrellus synngae,* basal representative taxa of the polyporoid clade (Hibbett and Donoghue 2001) and far removed from the *Phanerochaete* clade. Perhaps some of these inconsistencies and other minor ones not mentioned could be resolved with better taxon sampling and the inclusion of protein coding sequences. Sequences from all three DNA regions unfortunately were available only for eight taxa, so a combined sequence analysis was not attempted.

In a study of the mitochondrial SSU rRNA gene, Ko and others (2001) reported that *Phan. filamentosa* clustered with *Antrodia carbonica* and *Oligoporus fragilis* instead of *B. adusta* and *Phan. chrysosporium.* This is not consistent with results presented here and might reflect a misidentified specimen or a different mode of evolution of the mitochondrial SSU rRNA gene from that of the nuclear rRNA genes.

In conclusion, *Rhizochaete* is a polythetic genus that is defined by the combination of basidiocarp macromorphology, including hyphal cords, and its reaction with KOH, hyphal septation, hyphal arrangement, two types of encrustation, cystidia, and basidiospore shape and size. The recognition of this new genus also is supported by molecular data.

KEY OF THE SPECIES OF RHIZOCHAETE

1. Generative hyphae simple-septate, with scattered single clamp connections 2
1. Generative hyphae regularly clamped (nodose-septate) 4
2. Cystidia with thin walls, reported from eastern North America . . . . . *R. filamentosa*
2. Cystidia with thickened walls 3
3. Cystidia generally <50 µm long, reported from Borneo and Brunei . . . . . *R. borneensis*
3. Cystidia generally >50 µm long, widely distributed . . . . . *R. radicata*
4. Cystidia thin-walled, encrusted with yellowish brown granules only, reported from eastern North America . . . . . *R. americana*
4. Cystidia encrusted with both yellowish brown granules and hyaline crystals 5
5. Cystidia thick-walled, >80 µm long, basidiospores ellipsoid, 5–6.5(–7) × 3–3.5 µm, reported from Argentina . . . . . *R. brunnea*
5. Cystidia thin- to slightly thick-walled, <80 µm long, basidiospores ellipsoid to broadly ellipsoid, 5–6 × 3–4 µm, reported from southwestern U.S.A. . . . . *R. fouquieriae*

ACKNOWLEDGMENTS

We thank Agencia Nacional de Promoción Científica y Técnica, Argentina (PMT-PICT 4062/96 and 4044/98), for sup porting AG and MR, researchers for the National Research

Council of Argentina (CONICET). Dr. N. Hallenberg (Gothenburg, Sweden) provided several herbarium specimens used in this study.

LITERATURE CITED

Boidin J, Mugnier J, Canales R. 1998. Taxonomie moleculaire des Aphyllophorales. Mycotaxon 66:445–491.

Bremer K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42(4):795–803.

Cabrera AL, Willink A. 1973. Biogeografía de América Latina. Washington, D.C.: Porgrama Regional de Desarrollo Científico y Tecnológico. 122 p.

Cenis JL. 1992. Rapid extraction of fungal DNA for PCR amplification. Nuc Acids Res 20(9):2380.

de Koker TH, Nakasone K, Haarhof J, Burdsall Jr HH, Janse BJH. 2003. Phlyogenetic relationships of the genus *Phanerochaete* inferred from the internal transcribed spacer region. Mycol Res 107(9):1032–1040.

Eriksson T. 1998. AutoDecay. Version 4.0. Department of Botany, Stockholm University, Stockholm: distributed by the author.

Farris JS. 1989. The retention index and homoplasy excess. Syst Zool 38(4):406–407.

Felsenstein J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. J Mol Evol 17: 368–376.

———. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39(4):783–791.

Greslebin AG. 2001. Sistotremataceae (Corticiaceae, Aphyllophorales) of the Patagonian Andes forests of Argentina. Mycol Res 105(11):1392–1396.

———, Rajchenberg M. 1997a. Corticioid Aphyllophorales (Basidiomycota) from the Patagonian Andes forests of Argentina. 1. Lachnocladiaceae on *Nothofagus pumilio.* Mycotaxon 65:197–203.

———, ———. 1997b. Corticioid Aphyllophorales (Basidiomycota) from the Patagonian Andes forests of Argentina. 2. *Hyphodontia decorticans sp. nov.* Mycotaxon 65: 205–209.

———, ———. 1998. Corticioid Aphyllophorales (Basidiomycotina) from the Patagonian Andes forests of Argentina. 3. The genus *Dendrothele.* Mycotaxon 67:469–486.

———, ———, Bianchinotti MV. 2000. On *Hyphodontia australis* (Corticiaceae, Basidiomycota). Mycotaxon 74(1):37–43.

Hasegawa M, Kishino H, Yano T. 1985. Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. J Mol Evol 22:160–174.

Hibbett DS, Donoghue MJ. 2001. Analysis of character correlations among wood decay mechanisms, mating systems, and substrate ranges in Homobasidiomycetes. Syst Biol 50(2):215–242.

Hjortstam K. 1997 (1998). Checklist to genera and species of corticioid fungi (Basidiomycotina, Aphyllophorales). Windahlia 23:1–54.

———, Roberts PJ, Spooner BM. 1998. Corticioid fungi from Brunei Darussalam. Kew Bull 53(4):805–827.

Holmgren PK, Holmgren NH, Barnett LC. 1990. Index herbariorum. Part I: The herbaria of the world. 8th ed. Reg Veg 120:1–693.

Hulsenbeck JP, Ronquist FR. 2000. MrBayes: a program for the Bayesian inference of phylogeny. Biometrics 17: 754–755.

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. Ainsworth & Bisby's Dictionary of the Fungi. Wallingford, United Kingdom: CAB International. 655 p.

Kluge AG, Farris JS. 1969. Quantitative phyletics and the evolution of anurans. Syst Zool 18:1–32.

Ko KS, Jung HS, Ryvarden L. 2001. Phylogenetic relationships of *Hapalopilus* and related genera inferred from mitochondrial small subunit ribosomal DNA sequences. Mycologia 93(2):270–276.

Lim YW. 2001. Systematic study of corticioid fungi based on molecular sequence analyses [Doctoral dissertation]. Seoul, South Korea: Seoul National University. 228 p.

Maddison WP, Maddison DR. 1992. MacClade version 3. Sunderland, Massachusetts: Sinauer Associates.

Munsell Company. 1954. Munsell soil color charts. Baltimore.

Nakasone KK. 1990. Cultural studies and identification of wood-inhabiting Corticiaceae and selected Hymenomycetes from North America. Mycol Mem 15:1–412.

———, Bergman CR, Burdsall Jr HH. 1994. *Phanerochaete filamentosa-Corticium radicatum* species complex in North America. Sydowia 46(1):44–62.

———, Gilbertson RL. 1978. Cultural and other studies of fungi that decay ocotillo in Arizona. Mycologia 70(2): 266–299.

Nobles MK. 1965. Identification of cultures of wood-inhabiting Hymenomycetes. Can J Bot 43:1097–1139.

Parmasto E, Hallenberg N. 2000. A taxonomic study of phlebioid fungi (Basidiomycota). Nord J Bot 20:105–118.

Posada D, Crandall KA. 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14(9):817–818.

Suhara H, Maekawa N, Kubayashi T, Sakai K, Kondo R. 2002. Identification of the basidiomycetous fungus isolated from butt rot of the Japanese cypress. Mycoscience 43:477–481.

Swofford DL. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods). Version 4. Sunderland, Massachusetts: Sinauer Associates.

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