NRC Research Press

ARTICLE

Acanthocorticium brueggemannii, a new corticioid genus and species related to cyphelloid fungi in the euagarics clade (Agaricales, Basidiomycota)

Juliano M. Baltazar, Sergio P. Gorjón, María Belén Pildain, Mario Rajchenberg, and Rosa Mara B. da Silveira

Abstract: ***Acanthocorticium brueggemannii*** gen. et sp. nov. is introduced based on specimens from Southern Brazil. This corticioid fungus is characterized by resupinate basidiomes with smooth to tuberculate hymenophore, a monomitic hyphal system with simple-septate hyphae, finely echinulate halocystidia, cylindrical to clavate, dextrinoid acanthophyses, and globose, hyaline, smooth, and thin-walled IKI– basidiospores. Phylogenetic analyses of a LSU data set and a combined data set of ITS and LSU were carried out and the new taxon was found to be related to cyphelloid fungi within the Agaricales. Descriptions and drawings of the microscopic features of *A. brueggemannii* are provided.

Key words: acanthophyses, Aphyllophorales, Corticiaceae s.l., Cyphellaceae, *Henningsomyces*, *Rectipilus*.

Résumé : ***Acanthocorticium brueggemannii*** gen. et sp. nov. est introduit à partir de spécimens du Brésil du Sud. Ce fongus est caracterisé par des basidiomes résupinés avec des hymenophores lisses à tuberculés, un système d'hyphes monomitique avec d'hyphes génératrices à cloisons simples, halocystides à parois finement échinulés, acantophyses dextrinoïdes cilindriques à clavées, et basidiospores globoses, hyalins, lisses et à paroi mince, IKI–. Les analyses phylogénétiques d'un ensemble de données de LSU et d'un ensemble de données combinée d'ITS et LSU ont été effectuées et le nouveau taxon fut récupéré et liée aux champignons cyphellés dans les Agaricales. On présent les descriptions du nouveau genre et la nouvelle espèce, ainsi que des dessins et caractéristiques microscopiques de *A. brueggemannii*.

Mots-clés : acanthophyses, Aphyllophorales, Corticiaceae s.l., Cyphellaceae, *Henningsomyces*, *Rectipilus*.

Introduction

Corticioid fungi, also called Corticiaceae s.l., are defined as non-poroid homobasidiomycetes that usually develop effused, resupinate basidiomes with smooth hymenophores on wood, but several variations of this concept are found in the literature (Hjortstam et al. 1988; Larsson 2007; Bernicchia and Gorjón 2010). They form an artificial assemblage, and this was already recognized by early authors such as Fries and Patouillard (Donk 1964).

Phylogenetic studies based on molecular data in the past two decades have confirmed that corticioid fungi are polyphyletic. One of the first studies to show this polyphyly was that by Hibbett and Donoghue (1995) in a phylogenetic study of Polyporaceae, although few corticioid species were included. Later, Hibbett and Thorn (2001) proposed the distribution of homobasidiomycetes in eight major clades, all of them containing corticioid genera. This hypothesis was confirmed by Binder and Hibbett (2002) and Yoon et al. (2003).

The first comprehensive phylogenetic study devoted to corticioid fungi was presented by Larsson et al. (2004). They found that corticioid species were distributed in 12 major clades within the homobasidiomycetes. A similar result was achieved by Binder et al. (2005) in a study of the phylogenetic distribution of resupinate fungi. Their study supported at least 12 major clades within the homobasidiomycetes, all of them including corticioid fungi.

The sampling of the study by Larsson et al. (2004) was later improved by Larsson (2007), who proposed the first phylogenetic-based classification at family level for these fungi. Larsson (2007) classified the corticioid genera in 43 families, distributed in 12 orders of Agaricomycetes

Received 7 March 2015. Accepted 16 June 2015.

J.M. Baltazar and R.M.B. da Silveira. Programa de Pós-Graduação em Botânica, Departamento de Botânica, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, Porto Alegre, CEP 91501-970, Rio Grande do Sul, Brazil.
S.P. Gorjón, M.B. Pildain, and M. Rajchenberg. Área de Protección Forestal, Centro de Investigación y Extensión Forestal Andino Patagónico, Ruta 259 km 16.4, C.C. 14, 9200 Esquel, Chubut, Argentina.
Corresponding author: Juliano M. Baltazar (e-mail: baltazarjmb@gmail.com).

Published at www.nrcresearchpress.com/cjb on 24 July 2015.

sensu Hibbett et al. (2007), plus three families and 57 genera that remained incertae sedis. In a recent work, Hibbett et al. (2014) presented a revised higher level phylogenetic-based classification of the Agaricomycetes and recognized corticioid fungi belonging to 16 of the 20 orders in this class.

During a survey of corticioid fungi in Southern Brazil, an undescribed taxon was found. Morphological studies showed that it could not be accommodated in any of the accepted genera according to their morphological circumscription. Furthermore, nuclear large subunit (nuc-LSU) and internal transcribed spacer (ITS) rDNA sequences were obtained and preliminary analyses showed that the new taxon belongs to Agaricales sensu Matheny et al. (2006).

Molecular evidence demonstrating that some corticioid fungi are phylogenetically related to members of Agaricales was first shown in the 1990s (Gargas et al. 1995; Bruns et al. 1998). Later, Bodensteiner et al. (2004) found that some corticioid species were phylogenetically related to cyphelloid and agaricoid fungi within the euagarics clade. In an extensive phylogenetic study of the Agaricales, Matheny et al. (2006) confirmed the placement of some corticioid fungi within three major clades of this order. Larsson (2007) classified 26 corticioid genera in nine families of Agaricales based on molecular data, plus one genus that remained as incertae sedis.

The aims of this paper are to describe a new genus and species, and to evaluate its phylogenetic relationships by the means of analyses of single-locus and two-loci data sets containing nuc-LSU and ITS rDNA sequences, respectively.

Materials and methods

Collecting and morphological analyses

Specimens of the new taxon were collected in Parque Estadual da Serra do Tabuleiro, State of Santa Catarina, Southern Brazil. This conservation unit has an area of ca. 85 000 ha and is in the Atlantic Forest biome (Ishiy et al. 2009).

Cultures for DNA extraction were obtained from fresh spore prints and were grown in Petri dishes and later in tubes with malt extract agar (MEA) in the dark at 25 °C until DNA extractions.

For light microscopic studies, basidiomes were cut by hand and sections were mounted in 3% potassium hydroxide with 1% aqueous phloxine solution, Melzer's reagent (iodine – potassium iodide (IKI)), and 0.1% cotton blue in 60% lactic acid. Line drawings were made with a camera lucida attachment. Specimens are deposited at ICN Herbarium (Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil) with duplicates at the phytopathological herbarium, Centro de Investigación y Extensión Forestal Andino Patagónico (CIEFAP, Esquel, Argentina). Color names follow Kornerup and Wanscher (1978).

DNA extraction and polymerase chain reaction (PCR) conditions

For DNA extractions, strains were cultured in malt peptone broth with 10% (*v*/*v*) of malt extract (Merck, Darmstadt, Germany) and 0.1% (*w*/*v*) Bacto peptone (Difco, Detroit, Michigan, USA), 2 mL medium in 15 mL tubes. The cultures were incubated at 25 °C for 5 days in darkness. Total DNA was extracted from the culture or from dried basidiomes with the UltraClean Microbial DNA Isolation Kit (MO BIO Laboratories Inc., Carlsbad, California, USA), according to the manufacturer's instructions.

rDNA's ITS (including ITS1, 5.8S, and ITS2) and nuc-LSU regions were amplified using the universal primers ITS5-LR21 and LR0R-LR5, respectively (Vilgalys and Hester 1990; White et al. 1990; Lapeyre et al. 1993). PCR reaction mixtures for amplification of both regions were modified from Rajchenberg et al. (2011) in a final reaction volume of 50 μL with 100–500 ng DNA. PCR reactions were performed in a thermal cycler (My Cycler; Bio Rad, Hercules, California, USA) and the thermal cycling program was the same as described in Rajchenberg et al. (2011). The amplified fragments were purified and sequenced on an ABI 3700 automated sequencer (Perkin-Elmer, Waltham, Massachusetts, USA) at the DNA Synthesis and Sequencing Facility (Macrogen, Seoul, Korea). The same primers were used for amplification and sequencing. Sequences generated in this study were submitted to GenBank and accession numbers are given in Table 1.

Phylogenetic analyses

DNA sequences generated in this study were manually edited with BioEdit 7.1.3.0 (Hall 1999), and additional sequences for the ingroup and outgroup, based on studies of Bodensteiner et al. (2004), Matheny et al. (2006) and Larsson (2007), were retrieved from the GenBank nucleotide database. Sequence alignments were automatically performed on MUSCLE version 3.8.31 (Edgar 2004) and manually checked on MEGA version 5.10 (Tamura et al. 2011). Alignments are available from TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S15052). Two data sets were used in this study: the first one was based on phylogenies by Bodensteiner et al. (2004), Matheny et al. (2006) and Larsson (2007), and comprises LSU sequences from representatives of major clades of Agaricales. The second data set is a combined matrix of ITS and LSU sequences of the *Henningsomyces–Rectipilus* clade A and the *Nia* clade sensu Bodensteiner et al. (2004), here treated as Niaceae. Phylogenetic analyses were conducted for both data sets under maximum parsimony (MP) and Bayesian inference (BI) criteria. The ingroup

Table 1. Specimens presented in this study with GenBank accession numbers for internal transcribed spacer (ITS) and large subunit (LSU) sequences.

Taxon	Voucher or strain	LSU	ITS
Ingroup			
*Acanthocorticium brueggemannii**	JMB2122	KT275195	KT275193
*Acanthocorticium brueggemannii**	JMB2621	KT275196	KT275194
Agaricus bisporus (J.E. Lange) Imbach	AFTOL-ID 448	AY635775	—
Alloclavaria purpurea (Fr. : Fr.) Dentinger & D.J. McLaughlin	AFTOL-ID 1736	DQ457657	—
Amanita brunnescens G.F. Atk.	AFTOL-ID 673	AY631902	—
Amanita muscaria (L. : Fr.) Lam.	ARs.n. 25 S	AF042643	—
Aphanobasidium pseudotsugae (Burt) Boidin & Gilles	—	AY586696	—
Armillaria mellea (Vahl : Fr.) P. Kumm.	AFTOL-ID 449	AY700194	—
Athelia rolfsii (Curzi) C.C. Tu & Kimbr.	AFTOL-ID 664	AY635773	—
Athelidium aurantiacum (M.P. Christ.) Oberw.	KHL 11068	EU118606	—
Calathella mangrovei E.B.G. Jones & Agerer	—	AF426954	—
Calathella mangrovei	1-31-01Jones	—	AY571029
Chondrostereum purpureum (Pers. : Fr.) Pouzar	HHB-13334	AF518607	—
Clavaria zollingeri Lév.	AFTOL-ID 563	AY639882	—
Clitocybula oculus (Peck) Singer	AFTOL-ID 1554	DQ151452	—
Coronicium alboglaucum (Bourdot & Galzin) Jülich	—	AY586650	—
Cristinia helvetica (Pers.) Parmasto	Kristiansen s.n.	EU118620	—
Cyphellopsis anomala (Pers. : Fr.) Donk	PB318	AY570998	AY571035
Cystidiodontia laminifera (Berk. & M.A. Curtis) Hjortstam	KHL 13057	EU118622	—
Cystostereum murrayi (Berk. & M.A. Curtis) Pouzar	KHL 12496	EU118623	—
Dendrothele acerina (Pers. : Fr.) P.A. Lemke	GEL5350	AJ406581	—
Dendrothele griseocana (Bres.) Bourdot & Galzin	—	AY293178	—
Fistulina antarctica Speg.	—	AY293181	—
Fistulina hepatica (Schaeff.) With.	—	AY293182	—
Flagelloscypha minutissima (Burt) Donk	CBS 823.88	AY571006	AY571040
Gloeostereum incarnatum S. Ito & S. Imai	Strain 3332	AF141637	—
Gymnopus dryophilus (Bull. : Fr.) Murrill	AFTOL-ID 559	AY640619	—
Halocyphina villosa Kohlm. & E. Kohlm.	—	AF426957	—
Halocyphina villosa	IFO32088	—	AY571042
Henningsomyces candidus (Pers. : Fr.) Kuntze	PB338	AY571008	AY571044
Henningsomyces candidus	RGT156	AF287864	AY571043
Henningsomyces puber (Romell ex W.B. Cooke) D.A. Reid	GUA-307	AY571009	AY571045
Henningsomyces sp.	C58569	AY571011	AY571046
Hydropus marginellus (Pers. : Fr.) Singer	AFTOL-ID 1720	DQ457674	—
Hygrocybe cantharellus (Schwein. : Fr.) Murrill	AFTOL-ID 1714	DQ457675	
Hygrocybe coccinea (Schaeff. : Fr.) P. Kumm.	AFTOL-ID 1715	DQ457676	—
Lachnella alboviolascens (Alb. & Schwein. : Fr.) Fr.	PB332	AY571012	AY571048
Lentinula edodes (Berk.) Pegler	TMI1941	AF261557	—
Lindtneria trachyspora (Bourdot & Galzin) Pilát	KGN 390/00	EU118646	—
Macrolepiota dolichaula (Berk. & Broome) Pegler & R.W. Rayner	AFTOL-ID 529	DQ411537	—
Marasmius oreades (Bolton : Fr.) Fr.	AFTOL-ID 1525	DQ156126	—
Merismodes fasciculata (Schwein.) Donk	PB342	AY571016	AY571052
Merulicium fusisporum (Romell) J. Erikss. & Ryvarden	Hjm s.n.	EU118647	—
Moniliophthora perniciosa (Stahel) Aime & Phillips-Mora	DIS71	AY916738	—
Nia vibrissa R.T. Moore & Meyers	—	AF334750	—
Nia vibrissa	REG M200	—	AY571053
Physalacria bambusae Höhn.	CBS712.83	DQ097349	—
Pleurotus ostreatus (Jacq. : Fr.) P. Kumm.	AFTOL-ID 564	AY645052	—
Pleurotus tuber-regium (Fr. : Fr.) Singer	—	AF135180	—
Pluteus atromarginatus (Konrad) Kühner	AFTOL-ID 1340	DQ094788	—
Podoserpula pusio (Berk.) D.A. Reid	AFTOL-ID 1522	DQ470821	—
Rectipilus idahoensis (W.B. Cooke) Agerer	PB313/RA	AY571020	AY571057
Tricholoma inamoenum (Fr. : Fr.) Gillet	—	AY293215	—
Tricholoma palustre A.H. Sm.	AFTOL-ID 497	AY700197	—
Typhula phacorrhiza (Reischard : Fr.) Fr.	—	AF393079	—
Volvariella gloiocephala (DC. : Fr.) Boekhout & Enderle	AFTOL-ID 890	AY745710	—

Table 1 (*concluded*).

Taxon	Voucher or strain	LSU	ITS
Outgroup			
Calostoma lutescens (Schwabe) Burnap	Utley 750	JX184408	—
Strobilomyces floccopus (Vahl : Fr.) P. Karst.	AFTOL-ID 716	AY684155	AY854068

Note: *, newly sequenced voucher or strain; —, information not available.

sequences are all members of Agaricales, whereas two members of Boletales were used as outgroup species, viz. *Calostoma lutescens* and *Strobilomyces floccopus*, and selection of these taxa followed previous studies by Matheny et al. (2006) and Larsson (2007).

MP analyses were performed in **PAUP*** version 4.0b10 (Swofford 2002) with gaps treated as missing characters, equal weighting of characters and transformations, heuristic searches (TBR and MULTREES options on) with random addition of sequences (1000 replicates), and MaxTrees set to auto-increase. Nodal support was tested with bootstrap (BS) of 1000 replicates using the heuristic search option (TBR and MULTREES options on) and 10 random addition sequences.

Bayesian analyses were conducted in MrBayes version 3.2.1 (Ronquist et al. 2012). Models of evolution were identified for each data set using jModelTest version 2.1.4 (Darriba et al. 2012) under selection AIC, resulting in the model GTR+I+G for LSU in the first data set, and the model TVM+I+G for ITS and TIM3+I+G for LSU in the combined data set. BI posterior probabilities (PP) were estimated for 10^7 generations, by running four chains and sampling a tree each 10^5 generations, and the first 2% trees from each run were discarded as burn-in. The burn-in was determined using Tracer version 1.5 (http://tree.bio.ed.ac.uk/software/tracer/) to analyze MrBayes output files.

Results

Taxonomy

Acanthocorticium Baltazar, Gorjón & Rajchenb., gen. nov.

MYCOBANK NUMBER: MB 812888

DIAGNOSIS: *Acanthocorticium* is distinguished from other corticioid genera by the combination of dextrinoid acanthophyses, halocystidia that are finely echinulate at the apex, simple-septate generative hyphae, and globose, smooth, thin-walled and IKI– basidiospores.

TYPE SPECIES: *Acanthocorticium brueggemannii* Baltazar, Gorjón & Rajchenb.

ETYMOLOGY: The name is referred to the presence of abundant acanthophyses, which are very conspicuous in Melzer's reagent due to their dextrinoid reaction, besides the corticioid habit.

DESCRIPTION: Basidiome corticioid, resupinate, adnate, cartilaginous hard when dry. Hymenophore smooth to tuberculate, even to rimose.

Hyphal system monomitic, generative hyphae simple-septate. Halocystidia abundant in the subiculum and hymenium, hyaline, finely echinulate at the apex, IKI– to slightly dextrinoid, with a resinous cap. Acanthophyses present in the subiculum and dominating in the hymenium, cylindrical to clavate, hyaline, with short protuberances in the apical portion, dextrinoid. Basidiospores globose, hyaline, smooth and thin-walled, IKI–.

COMMENTS: *Acanthocorticium* is characterized by the resupinate, cartilaginous basidiome with smooth to tuberculate hymenophore, and microscopically by the presence of abundant, dextrinoid acanthophyses, apically echinulate halocystidia with a resinous cap, and globose, hyaline, IKI– basidiospores. It differs from other corticioid genera by the combination of its microscopic features, which is unknown from other corticioid fungi.

Halocystidia are known from several unrelated genera. They have been reported from members of *Dendrocorticium* M.J. Larsen & Gilb., which belongs to the Corticiales (Baltazar et al. 2013), *Gloeodontia* Boidin, Russulales (Gorjón and de Jesus 2012), and *Hyphodontia* J. Erikss. s.l. (Langer 1994) and *Resinicium* Parmasto (Nakasone 2007), both Hymenochaetales. In all these fungi, the apex of the halocystidium is smooth. It is noted, though, that the ornamentation is inconspicuous in the studied specimens of *Acanthocorticium*.

Acanthophyses of *Acanthocorticium* remind one of several species of *Aleurodiscus* Rabenh. ex J. Schröt. s.l. (Núñez and Ryvarden 1997), and in *Aleurodiscus dextrinoideocerussatus* Manjón et al. they are also dextrinoid (Moreno et al. 1990). *Acanthocorticium* is also similar to *Aleurodiscus cerussatus* (Bres.) Höhn. & Litsch. s.l. due to gross morphology, except by the basidiome color, which is whitish to cream in the latter. Notwithstanding these similarities, basidiospores of all members of *Aleurodiscus* s.l. are distinctly amyloid, while in *Acanthocorticium* they are IKI–.

Heteroacanthella Oberw., a genus in the Cantharellales, shares some micromorphological similarities with the new genus (Oberwinkler et al. 1990), but it is phylogenetically distant. *Heteroacanthella* has dominant subglobose to pyriform, acanthoid basidia that can be confused with the acanthophyses of *Acanthocorticium*, but these structures are easily differentiated when the dextrinoid reaction is considered.

Broom cells of some marasmioid mushrooms in Marasmiaceae – Marasmieae sensu Singer (1976) – are similar in shape to acanthophyses of *Acanthocorticium* (see Singer 1976, 1986; Kuo 2013; Oliveira et al. 2014), and in some species they are also dextrinoid. A more detailed morphological comparison is desirable to properly compare these structures.

Fig. 1. Microscopic features of *Acanthocorticium brueggemannii*, JMB 2621 (holotype): (A) basidiospores, (B) acanthophyses, (C) generative hyphae, and (D) halocystidia.

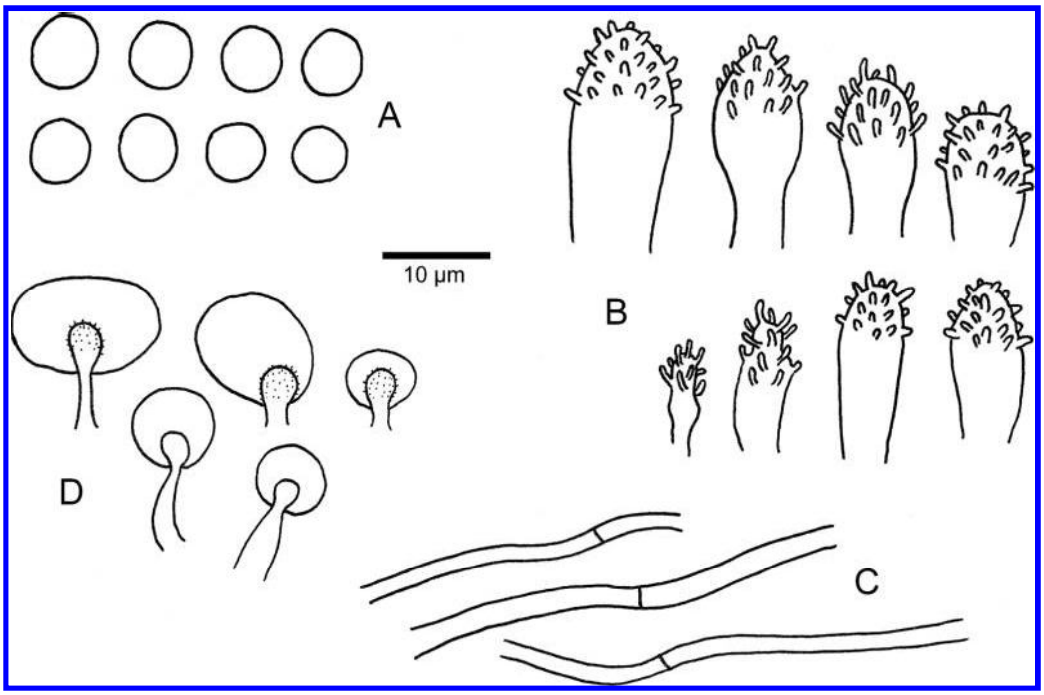
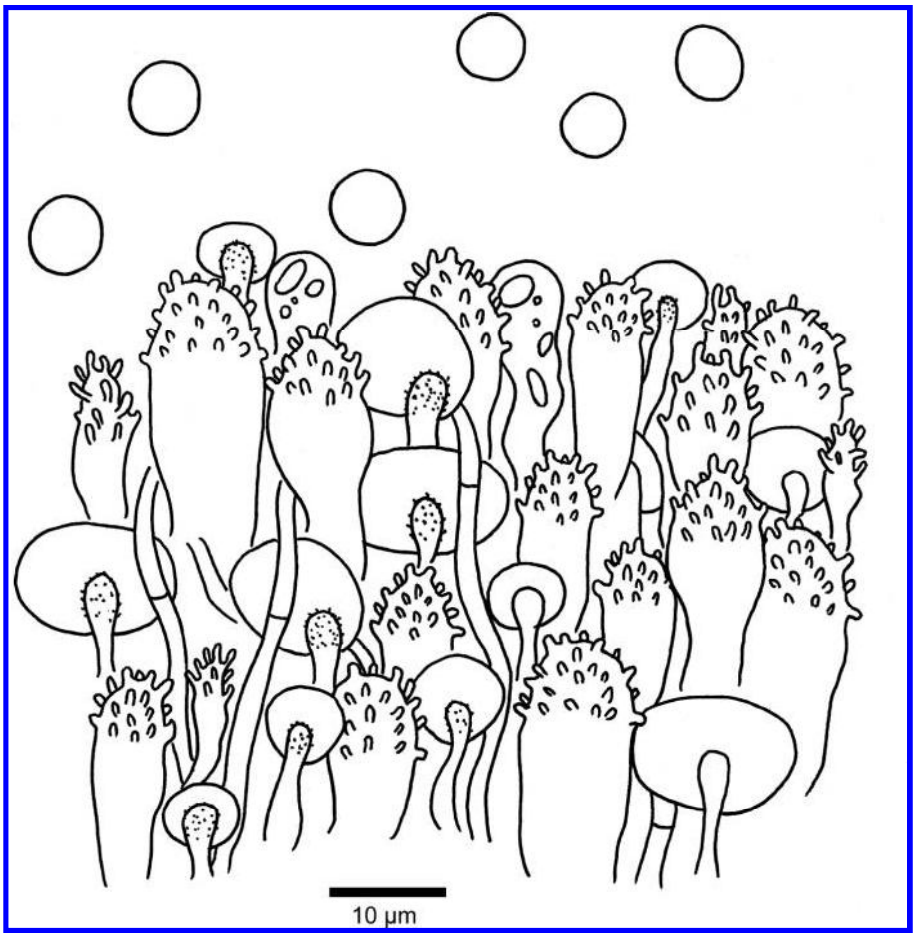


Fig. 2. Microscopic features of *Acanthocorticium brueggemannii*, JMB 2621 (holotype) in a section of the basidiome.



Acanthocorticium brueggemannii Baltazar, Gorjón & Rajchenb., sp. nov.

Figs. 1, 2

MYCOBANK NUMBER: MB 812889

DIAGNOSIS: *Acanthocorticium brueggemannii* differs from *Aleurodiscus dextrinoideocerussatus* Manjón et al. by wider acanthophyses with shorter apical projections, presence of halocystidia, lack of gloeocystidia, and globose, IKI– basidiospores.

HOLOTYPE: Brazil. State of Santa Catarina, Santo Amaro da Imperatriz, Hotel Caldas da Imperatriz, Trilha do Guamirim, on dead hardwood, 14 March 2012, J.M. Baltazar 2621 (ICN).

ETYMOLOGY: Named in honor of Fernando M. Brüggemann (Brazilian biologist), in recognition of his work for the research, conservation, and environmental education in the Parque Estadual da Serra do Tabuleiro, type locality of *A. brueggemannii*.

DESCRIPTION: Basidiome resupinate, adnate, cartilaginous hard when dry, up to 0.13 mm thick. Hymenophore smooth to tuberculate, even to rimose, pale gray (1C1, 1B1), gray (1D1) to grayish green (1D3), margin thinning out but defined, concolor with the hymenophore.

Hyphal system monomitic, generative hyphae simple-septate, pale yellowish, slightly thick-walled, 1.5–3.5 (–4) μm diameter. Halocystidia abundant in the subiculum and in the hymenium, rarely projecting, hyaline, finely echinulate at the capitate apex, IKI– to slightly dextrinoid, 3.4 (–4) μm diameter, with a resinous cap up to 12 μm diameter. Acanthophyses present in the subiculum and dominating the hymenium, cylindrical to clavate, hyaline, with short protuberances in the apical portion, (3–) 4.5–10 μm diameter, dextrinoid. Basidia not seen, basidioles few, cylindrical to clavate, hyaline, thin-walled. Basidiospores globose, hyaline, smooth, and thin-walled, with an inconspicuous apiculus, 5–6 μm diameter, IKI–, cyanophilous.

DISTRIBUTION: Known only from the type locality.

SUBSTRATE: Dead unidentified hardwood.

ADDITIONAL SPECIMEN EXAMINED (PARATYPE): Brazil. State of Santa Catarina, Santo Amaro da Imperatriz, Hotel Caldas da Imperatriz, Trilha do Guamirim, on dead hardwood, 18 September 2010, J.M. Baltazar 2122 (ICN).

COMMENTS: *Acanthocorticium brueggemannii* is characterized by the resupinate, cartilaginous hard basidiome, smooth to tuberculate hymenophore with grayish tints, abundant halocystidia with echinulate apex and a resinuous cap, variably dextrinoid acanthophyses with short protuberances in the apical portion, and globose, hyaline, smooth, thin-walled, cyanophilous and IKI– basidiospores. We could not find any basidia after persistent search, including the study of the specimens in fresh condition. The inner structure of the basidiomes suggests a catahymenium, but further studies with more specimens are desirable to confirm this. This is the only species of *Acanthocorticium* known at the time being.

At first glance, *A. brueggemannii* is similar to *Aleurodiscus dextrinoideocerussatus* due to the dextrinoid acanthophyses which dominate the whole basidiome. However, acanthophyses of *A. dextrinoideocerussatus* are narrower ((4–) 5–7 μm diameter) and have longer apical projections than those of *A. brueggemannii*. *Aleurodiscus dextrinoideocerussatus* is also different due to the presence of gloeocystidia and amyloid basidiospores, and the whitish to cream-colored hymenophore. Furthermore, *A. dextrinoideocerussatus* is a member of Russulales along with most other species of *Aleurodiscus* s.l. (Larsson 2007; Bernicchia and Gorjón 2010).

Phylogenetic analyses

Four new sequences from two specimens of *A. brueggemannii* were generated for this study, one from LSU and one from ITS for each specimen (Table 1).

The LSU data set included 55 taxa and a total of 967 characters, of which 546 were constant, 93 were variable and parsimony uninformative, and 328 were parsimony informative. MP analysis resulted in one most parsimonious tree (tree length = 1908; CI = 0.3412; RI = 0.5566; RC = 0.1899; Fig. 3).

The ingroup was recovered with full support (BS 100/PP 1.0) in both MP and BI analyses, and no major incongruities of topology between these two analyses were observed. Two major clades were recovered within the ingroup; one of them grouped the two members of Hygrophoraceae and had high support (BS 94/PP 1.0); another clade grouped all other sequences and was not supported (BS 78/PP 0.57). The latter clade consists of several clades including two or three species and mainly with high to full support; however, four larger clades were recovered. The first of them included *Acanthocorticium*, *Henningsomyces–Rectipilus* clade A and Niaceae, and it was supported only by BI (PP 0.99); the second included Amanitaceae and Clavariaceae; the third included Pterulaceae, Schizophyllaceae, and Stephanosporaceae, and the fourth included Cyphellaceae and Cystostereaceae. These clades were not supported, with the exception of the clade formed by Cyphellaceae and Cystostereaceae, which was supported only by BI (PP 0.96).

Most of terminal clades were highly (BS > 80; PP > 0.94) to fully (BS = 100; PP = 1.0) supported at least by one analysis, except Atheliaceae and inclusive clades within *Henningsomyces–Rectipilus* clade A and Niaceae.

Acanthocorticium was recovered as the sister group of *Henningsomyces–Rectipilus* clade A with full support, and also related to Niaceae, although this relationship was only supported by the BI analysis (PP 0.99).

The combined data set (ITS and LSU) included 16 taxa and a total of 1812 characters, of which 949 were constant, 295 were variable and parsimony uninformative, and 568 were parsimony informative. MP analysis resulted in

Fig. 3. Phylogenetic placement of *Acanthocorticium brueggemannii* inferred by maximum parsimony (MP) and Bayesian inference (BI) analyses of nuclear large subunit rDNA sequences data set. Tree topology is based on the consensus tree from the BI. Support values for internal nodes are given on the branches as bootstrap/posterior probability (BS/PP). Fully supported nodes (BS 100/PP 1.0) are indicated by black circles. Nodes without a BS value indicated incongruity between MP and BI analyses.

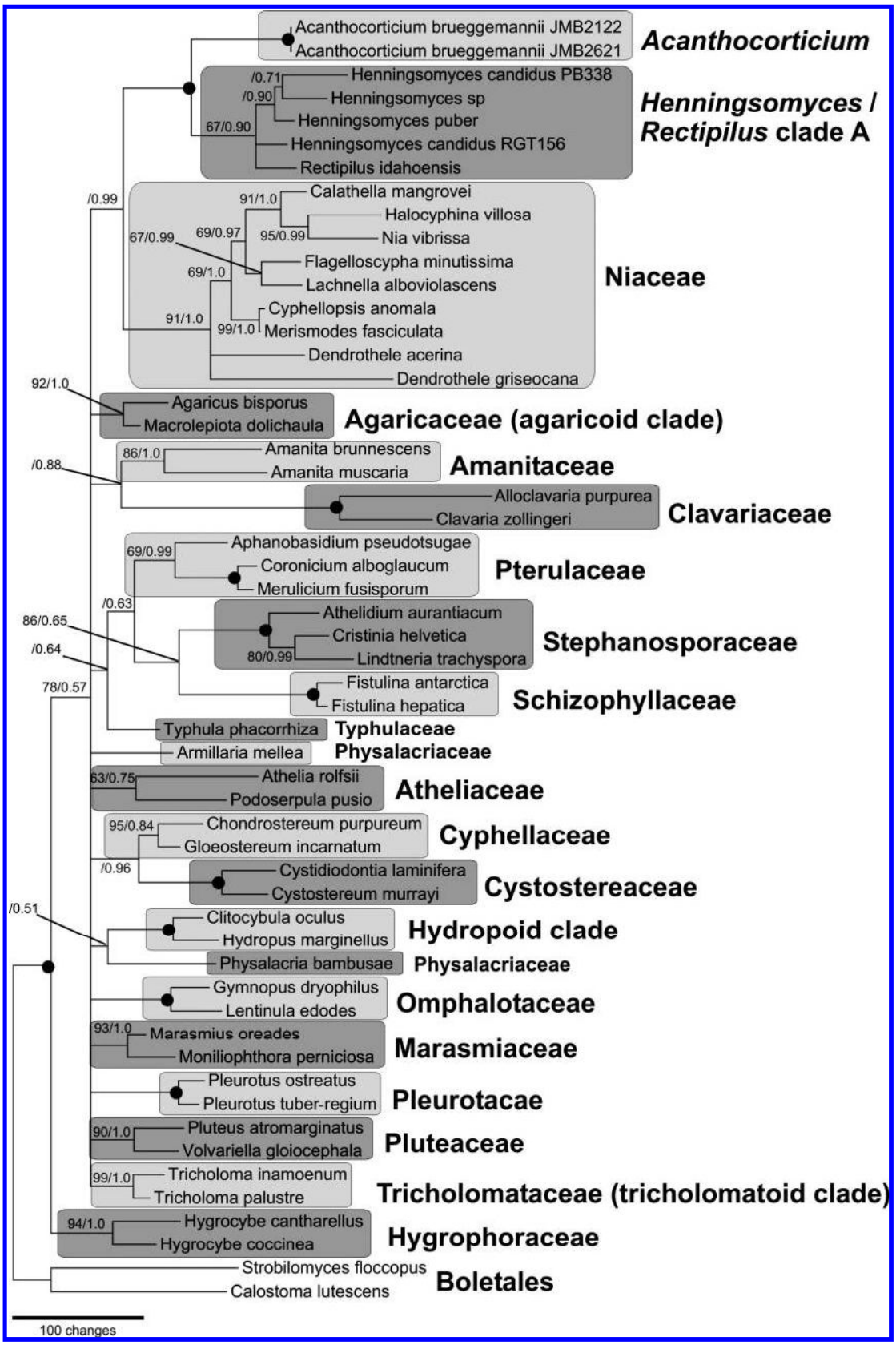
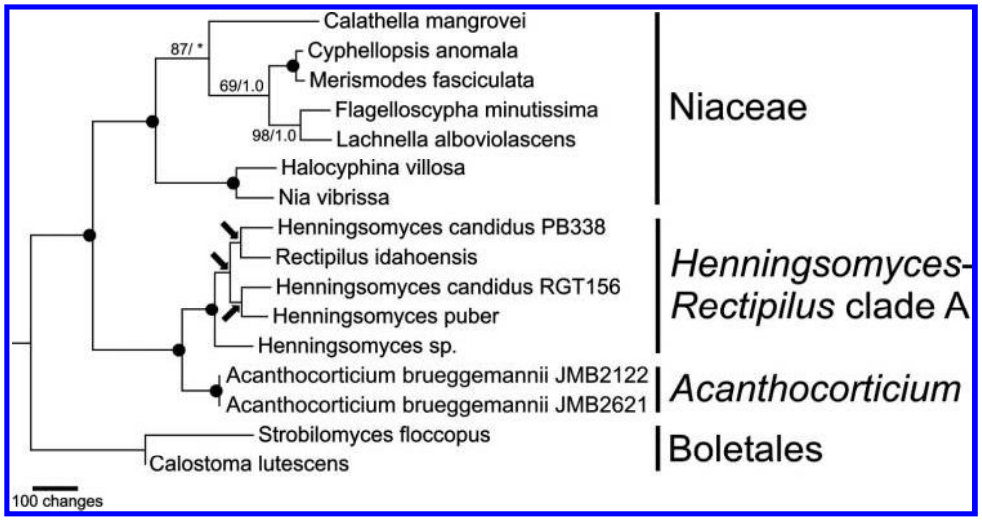


Fig. 4. Phylogenetic placement of *Acanthocorticium brueggemannii* inferred by maximum parsimony (MP) and Bayesian inference (BI) analyses of a combined data set (nuclear large subunit and internal transcribed spacer sequences). Tree topology is based on the most parsimonious tree. Support values for internal nodes are given on the branches as bootstrap/posterior probability (BS/PP). Fully supported nodes (BS 100/PP 1.0) are indicated by black circles. Incongruity in topologies between MP and BI analyses is indicated with an asterisk instead of the PP value. Arrows indicate branches that collapsed in the strict consensus tree.



one most parsimonious tree (tree length = 2003; CI = 0.5880; RI = 0.6235; RC = 0.4143; Fig. 4).

The ingroup was recovered with full support in both MP and BI analyses, which resulted in trees with the same topology concerning major clades. Incongruities were observed in an internal node of Niaceae, which collapsed in the BI analysis (indicated by an asterisk in Fig. 4), and the internal nodes of *Henningsomyces–Rectipilus* clade A (see below). Two major, fully supported clades were recovered within the ingroup. One of them included members of Niaceae, grouped in three fully or highly supported clades. The position of *Calathella mangrovei* was not resolved in this analysis. Another major clade included two fully supported clades: one of them included two specimens of *Acanthocorticium*, and the other included *Henningsomyces* spp. and *Rectipilus idahoensis*. All nodes within *Henningsomyces–Rectipilus* clade A collapsed in the consensus tree, and the topology recovered by the BI analysis was different and had no support (data not shown).

Discussion

Results of the analyses presented above are similar to those of Bodensteiner et al. (2004), Matheny et al. (2006), and Larsson (2007), especially concerning the terminal clades. These results were expected because data sets used in the present work were based on those studies. However, relationships of some major clades are different in our analyses. For example, while Niaceae is closely related to Schizophyllaceae in Matheny et al. (2006); in Larsson (2007), it was recovered related to Cyphellaceae and Cystostereaceae; and in Bodensteiner et al. (2004), it appeared related to some marasmioid fungi; in the present study, Niaceae was recovered close to *Acanthocorticium* and *Henningsomyces–Rectipilus* clade A. In most cases, these discrepancies occurred in non-supported nodes. Another reason for these discrepancies can be differences among these studies regarding sampling: Bodensteiner et al. (2004) focused on cyphelloid taxa, Matheny et al. (2006) did not include members of *Henningsomyces–Rectipilus* clade A sensu Bodensteiner et al. (2004), and Larsson (2007) sampled mostly corticioid taxa. Finally, Matheny et al. (2006) used a five-loci data set, while other studies used LSU and ITS.

Acanthocorticium brueggemannii specimens formed a sister group of *Henningsomyces–Rectipilus* clade A (Figs. 3, 4). All members of the latter are cyphelloid fungi and are characterized by annual, tube-like, and soft basidiomes that grow sparsely or gregariously, being quite different from the corticioid *A. brueggemannii*. They also differ from *A. brueggemannii* by lacking cystidia and by having both simple septate and clamped generative hyphae in the same specimen. However, they share with *Acanthocorticium* a monomitic hyphal system with dextrinoid hyphae in some species (Agerer 1973; Wei and Qin 2009; Gorjón and Jesus 2014). Further analyses with a more comprehensive sampling of specimens and (or) molecular markers are needed to confirm the relationship of *Acanthocorticium* vis-à-vis *Henningsomyces/Rectipilus* p.p. Taxa from *Henningsomyces–Rectipilus* clade B were not included in our analyses because they are phylogenetically distant from *Henningsomyces–Rectipilus* clade A, and therefore from *A. brueggemannii*.

The second closest group related to *Acanthocorticium* is Niaceae (Figs. 2, 3). Here we accept the name Niaceae, and not Lachnellaceae, because the latter is invalid: it was originally published as "Lachnellacées" by Boudier (1907)

and is not valid according to Art. 32.1(b) and Art. 18.4 (McNeill et al. 2012). This family corresponds to a morphological and ecological diverse assemblage that includes *Nia vibrissa* (a gasteroid, marine fungus), two species of *Dendrothele* Höhn. & Litsch. (corticioid fungi that grow on the bark of living trees), *Halocyphina villosa* (a cyphelloid, marine fungus), plus other cyphelloid fungi. *Dendrothele acerina* and *Dendrothele griseocana* (generic type of *Dendrothele*) are the closest corticioid fungi related to *Acanthocorticium*. Species included in *Dendrothele* s.l. differ from *Acanthocorticium* by growing on bark of living trees, while *Acanthocorticium* is known from dead hardwood (Nakasone 2006; Bernicchia and Gorjón 2010; Gorjón et al. 2011). Furthermore, *Dendrothele* s.l. is characterized by discoid or crustose basidiomes, and microscopically by abundant dendrohyphidia and crystalline deposits, being quite distinct from *Acanthocorticium*.

The placement of *A. brueggemannii* within the Agaricales is not a surprise because some other corticioid fungi were found to belong to this group before (Gargas et al. 1995; Bruns et al. 1998; Hibbett and Thorn 2001; Bodensteiner et al. 2004; Larsson et al. 2004; Matheny et al. 2006; Larsson 2007; Hibbett et al. 2014). Agaricales is a highly diverse group and includes a large variety of types of basidiomes such as stipitate and pileate, gasteroid and secotioid, resupinate, coralloid, cyphelloid, pileate with poroid or tubular hymenophores (Hibbett et al. 2014). Some marasmioid mushrooms have dextrinoid broom cells in the hymenium or pileipellis that are similar to acanthophyses of *A. brueggemannii*. Marasmioid fungi were recovered phylogenetically close to *Henningsomyces–Rectipilus* clade A in the study by Bodensteiner et al. (2004), but this was not found by other studies. Other dextrinoid structures can be found in the group, e.g., hairs on pileus or stipe in *Crinipellis* Pat., and tramal hyphae in *Mycena* (Pers.) Roussel. The diversity of morphologies, ecological traits, etc., in the Agaricales is also found in most of the major clades within the Agaricomycetes (Hibbett et al. 2014), and finding synapomorphies other than nucleotide sequences is a challenge.

Additionally, *Acanthocorticium* is morphologically similar to some members of *Aleurodiscus* s.l., as discussed above in the taxonomic remarks. However, members of this group are well established within the Russulales as shown by Wu et al. (2001), and so they are not closely related to *Acanthocorticium*. Their similarities (e.g., the presence of dextrinoid acanthophyses) are probably the result of morphological convergence. However, basidiospores of these taxa are quite different: they are IKI– in *Acanthocorticium*, while in members of *Aleurodiscus* s.l., they are amyloid and often ornamented, which is a typical feature in members of Russulales.

Acknowledgements

The authors are grateful to Fernando M. Brüggemann (Hotel Plaza Caldas da Imperatriz, Brazil) for supporting field work and Larissa Trierveiler Pereira (Maringá, Brazil) for helping with phylogenetic analyses and preparation of the figures. André de Meijer (Guaraqueçaba, Brazil) is thanked for valuable observations in a first version of the manuscript. Two anonymous reviewers made valuable suggestions and are also thanked. J.M.B. had Ph.D. scholarships from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, GD 141495/2010-3) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, PDSE proceeding 9715/11-8). CAPES (Brazil) and Ministerio de Ciencia, Tecnología e Innovación Productiva (MINCyT, Argentina) are thanked for financial support (Bilateral cooperation CAPES/MINCyT Rede 003/11). Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul is also thanked for partially supporting this study (FAPERGS 11/2063-3). M.B.P. and M.R. are researchers of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina) and R.M.B.S. is researcher of CNPq.

References

Agerer, R. 1973. *Rectipilus*, eine neue Gattung cyphelloider Pilze. Persoonia, **7**(3): 389–436.

Baltazar, J.M., Silveira da, R.M.B., and Rajchenberg, M. 2013. *Asterostromella roseola* Bres. ex Rick is combined in *Dendrocorticium* (Corticiaceae, Agaricomycetes). Phytotaxa, **104**(1): 49–52. doi:10.11646/phytotaxa.104.1.7.

Bernicchia, A., and Gorjón, S.P. 2010. Corticiaceae s.l. Fungi Europaei n° 12. Candusso, Italy. pp. 1–1008.

Binder, M., and Hibbett, D.S. 2002. Higher-level phylogenetic relationships of homobasidiomycetes (mushroom-forming fungi) inferred from four rDNA regions. Mol. Phylogenet. Evol. **22**(1): 76–90. doi:10.1006/mpev.2001.1043. PMID:11796031.

Binder, M., Hibbett, D.S., Larsson, K.-H., Larsson, E., Langer, E., and Langer, G. 2005. The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). Syst. Biodivers. **3**(2): 113–157. doi:10.1017/S1477200005001623.

Bodensteiner, P., Binder, M., Moncalvo, J.-M., Agerer, R., and Hibbett, D.S. 2004. Phylogenetic relationships of cyphelloid homobasidiomycetes. Mol. Phylogenet. Evol. **33**(2): 501–515. doi:10.1016/j.ympev.2004.06.007. PMID:15336682.

Boudier, É. 1907. Histoire et classification des discomycètes d'Europe. Librairie des Sciences Naturelles, Paris. pp. 1–224.

Bruns, T.D., Szaro, T.M., Gardes, M., Cullings, K.W., Pan, J.J., Taylor, D.L., Horton, T.R., Kretzer, A., Garbelotto, M., and Li, Y. 1998. A sequence database for the identification of ectomycorrhizal basidiomycetes by phylogenetic analysis. Mol. Ecol. **7**(3): 257–272. doi:10.1046/j.1365-294X.1998.00337.x.

Darriba, D., Taboada, G.L., Doallo, R., and Posada, D. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nat. Methods, **9**(8): 772. doi:10.1038/nmeth.2109.

Donk, M.A. 1964. A conspectus of the families of Aphyllophorales. Persoonia, **3**(2): 199–324.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. **32**(5): 1792–1797. doi:10.1093/nar/gkh340. PMID:15034147.

Gargas, A., DePriest, P.T., Grube, M., and Tehler, A. 1995. Multiple origins of lichen symbioses in fungi suggested by SSU rDNA phylogeny. Science, **268**(5216): 1492–1495. doi:10.1126/science.7770775. PMID:7770775.

Gorjón, S.P., and de Jesus, M.A. 2012. Some new species and new records of corticioid fungi (Basidiomycota) from the Brazilian Amazon. Phytotaxa, **67**: 38–54.

Gorjón, S.P., and de Jesus, M.A. 2014. *Rectipilus stromatoides* sp. nov. (Agaricales, Basidiomycota), a new cyphelloid fungus from the Brazilian Amazon. Mycosphere, **5**(2): 393–396. doi:10.5943/mycosphere/5/2/12.

Gorjón, S.P., Greslebin, A.G., and Rajchenberg, M. 2011. *Dendrothele latenavicularis* sp. nov. (*Agaricales, Basidiomycota*) from the Patagonian Andes. Mycotaxon, **117**: 101–108. doi:10.5248/117.101.

Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp. Ser. **41**: 95–98.

Hibbett, D.S., and Donoghue, M.J. 1995. Progress toward a phylogenetic classification of the Polyporaceae through parsimony analysis of mitochondrial ribosomal DNA sequences. Can. J. Bot. **73**(S1): 853–861. doi:10.1139/b95-331.

Hibbett, D.S., and Thorn, R.G. 2001. Basidiomycota: Homobasidiomycetes. *In* The Mycota VII, Part B. Systematics and Evolution. *Edited by* D.J. McLaughlin, E.G. McLaughlin, and P.A. Lemke. Springer-Verlag, Berlin Heidelberg. pp. 121–168.

Hibbett, D.S., Binder, M., Bischoff, J.F., Blackwell, M., Cannon, P.F., Eriksson, O.E., Huhndorf, S., James, T., Kirk, P.M., Lücking, R., Thorsten Lumbsch, H., Lutzoni, F., Matheny, P.B., McLaughlin, D.J., Powell, M.J., Redhead, S., Schoch, C.L., Spatafora, J.W., Stalpers, J.A., Vilgalys, R., Aime, M.C., Aptroot, A., Bauer, R., Begerow, D., Benny, G.L., Castlebury, L.A., Crous, P.W., Dai, Y.-C., Gams, W., Geiser, D.M., Griffith, G.W., Gueidan, C., Hawksworth, D.L., Hestmark, G., Hosaka, K., Humber, R.A., Hyde, K.D., Ironside, J.E., Kõljalg, U., Kurtzman, C.P., Larsson, K.-H., Lichtwardt, R., Longcore, J., Miądlikowska, J., Miller, A., Moncalvo, J.-M., Mozley-Standridge, S., Oberwinkler, F., Parmasto, E., Reeb, V., Rogers, J.D., Roux, C., Ryvarden, L., Sampaio, J.P., Schüßler, A., Sugiyama, J., Thorn, R.G., Tibell, L., Untereiner, W.A., Walker, C., Wang, Z., Weir, A., Weiss, M., White, M.M., Winka, K., Yao, Y.-J., and Zhang, N. 2007. A higher-level phylogenetic classification of the Fungi. Mycol. Res. **111**(5): 509–547. doi:10.1016/j.mycres.2007.03.004. PMID:17572334.

Hibbett, D.S., Bauer, R., Binder, M., Giachini, A.J., Hosaka, K., Justo, A., Larsson, E., Larsson, K.H., Lawrey, J.D., Miettinen, O., Nagy, L.G., Nilsson, R.H., Weiss, M., and Thorn, R.G. 2014. 14 Agaricomycetes. *In* Systematics and evolution. 2nd ed. The Mycota VII, Part A. *Edited by* D.J. McLaughlin and J.W. Spatafora. Springer Berlin Heidelberg. pp. 373–429.

Hjortstam, K., Larsson, K.-H., and Ryvarden, L. 1988. The Corticiaceae of North Europe, Vol. 1. Fungi Flora, Oslo.

Ishiy, S.T., Nunes, A., de Souza, A., Marterer, B.T.P., Brasil, D.M., and Mussatto, E. 2009. Parque Estadual da Serra do Tabuleiro — Retratos da fauna e da flora. criAG, Florianópolis. pp. 1–85.

Kornerup, A., and Wanscher, J.H. 1978. Methuen handbook of colours. 3rd ed. Eyre Methuen, London.

Kuo, M. 2013. Marasmioid mushrooms — Retrieved from the MushroomExpert.Com Web site. [Online.] Available from http://www.mushroomexpert.com/marasmioid.html [accessed 21 January 2015].

Langer, E. 1994. Die Gattung *Hyphodontia* John Eriksson. Bibl. Mycol. **154**: 1–298.

Lapeyre, B., Michot, B., Feliu, J., and Bachellerie, J.-P. 1993. Nucleotide sequence of the *Schizosaccharomyces pombe* 25S ribosomal RNA and its phylogenetic implications. Nucleic Acids Res. **21**(14): 3322–3322. doi:10.1093/nar/21.14.3322. PMID: 8341608.

Larsson, K.-H. 2007. Re-thinking the classification of corticioid fungi. Mycol. Res. **111**(9): 1040–1063. doi:10.1016/j.mycres.2007.08.001. PMID:17981020.

Larsson, K.-H., Larsson, E., and Kõljalg, U. 2004. High phylogenetic diversity among corticioid homobasidiomycetes. Mycol. Res. **108**(9): 983–1002. doi:10.1017/S0953756204000851. PMID:15506012.

Matheny, P.B., Curtis, J.M., Hofstetter, V., Aime, M.C., Moncalvo, J.-M., Ge, Z.-W., Yang, Z.-L., Slot, J.C., Ammirati, J.F., Baroni, T.J., Bougher, N.L., Hughes, K.W., Lodge, D.J., Kerrigan, R.W., Seidl, M.T., Aanen, D.K., DeNitis, M., Daniele, G.M., Desjardin, D.E., Kropp, B.R., Norvell, L.L., Parker, A., Vellinga, E.C., Vilgalys, R., and Hibbett, D.S. 2006. Major clades of Agaricales: a multilocus phylogenetic overview. Mycologia, **98**(6): 982–995. doi:10.3852/mycologia.98.6.982. PMID:17486974.

McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'Homme Van Reine, W.F., Smith, G.F., Wiersema, J.H., and Turland, N.J. 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code): adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, Königstein.

Moreno, G., Blanco, M.N., and Manjón, J.L. 1990. Mycological studies from the Natural Park of Monfragüe (Extremadura, Spain). VI. Aphyllophorales. Mycotaxon, **39**: 351–360.

Nakasone, K.K. 2006. *Dendrothele griseocana* (Corticiaceae) and related taxa with hyphal pegs. Nova Hedwig. **83**(1–2): 99–108. doi:10.1127/0029-5035/2006/0083-0099.

Nakasone, K.K. 2007. Morphological and molecular studies on *Resinicium* s. str. Can. J. Bot. **85**(4): 420–436. doi:10.1139/B07-035.

Núñez, M., and Ryvarden, L. 1997. The genus *Aleurodiscus* (Basidiomycotina). Synop. Fungorum, **12**: 1–164.

Oberwinkler, F., Langer, E., Burdsall, H.H., Jr., and Tschen, J. 1990. *Heteroacanthella*: a new genus in the Tulasnellales. Trans. Mycol. Soc. Jpn. **31**: 207–213.

Oliveira, J.J.S., Sanchez-Ramirez, S., and Capelari, M. 2014. Some new species and new varieties of *Marasmius* (*Marasmiaceae*, Basidiomycota) from Atlantic Rainforest areas of São Paulo State, Brazil. Mycol. Progr. **13**(3): 923–949. doi:10.1007/s11557-014-0978-y.

Rajchenberg, M., Gorjón, S.P., and Pildain, M.B. 2011. The phylogenetic disposition of *Antrodia* s.l. (Polyporales, Basidiomycota) from Patagonia, Argentina. Austral. Syst. Bot. **24**(2): 111–120. doi:10.1071/SB11003.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., and Huelsenbeck, J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. **61**(3): 539–542. doi:10.1093/sysbio/sys029. PMID:22357727.

Singer, R. 1976. Marasmieae (Basidiomycetes - Tricholomataceae). Flora Neotrop. **17**: 1–347.

Singer, R. 1986. The agaricales in modern taxonomy. 4th ed. Koeltz Scientific Books, Koenigstein.

Swofford, D.L. 2002. **PAUP***. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Mass. pp. 1–142.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., and Kumar, S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol. Biol. Evol. **28**(10): 2731–2739. doi:10.1093/molbev/msr121. PMID:21546353.

Vilgalys, R., and Hester, M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J. Bacteriol. **172**(8): 4238–4246. PMID:2376561.

Wei, Y.-L., and Qin, W.-M. 2009. Two new species of cyphelloid fungi (*Basidiomycota*) from China. Mycotaxon, **110**: 225–232. doi:10.5248/110.225.

White, T.J., Bruns, T., Lee, S., and Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In* PCR protocols: a guide to methods and applications. *Edited by* M.A. Innis, D.H. Gelfand, J.J. Shinsky, and T.J. White. Academic Press, San Diego, Calif. pp. 315–322.

Wu, S.-H., Hibbett, D.S., and Binder, M. 2001. Phylogenetic analyses of *Aleurodiscus* s.l. and allied genera. Mycologia, **93**(4): 720–731. doi:10.2307/3761826.

Yoon, S.-I., Kim, S.-Y., Lim, Y.-W., and Jung, H.-S. 2003. Phylogenetic evaluation of stereoid fungi. J. Microbiol. Biotechnol. **13**(3): 406–414.