FUNGAL BIOLOGY 119 (2015) 679–719

British Mycological Society promoting fungal science

journal homepage: www.elsevier.com/locate/funbio

Revisiting the taxonomy of *Phanerochaete* (*Polyporales*, *Basidiomycota*) using a four gene dataset and extensive ITS sampling

Dimitrios FLOUDAS[a,b,*], *David S. HIBBETT*[a]

[a]*Department of Biology, Clark University, 950 Main St, Worcester, 01610, MA, USA*
[b]*Department of Biology, Microbial Ecology Group, Lund University, Ecology Building, SE-223 62, Lund, Sweden*

ARTICLE INFO

Article history:
Received 9 December 2014
Received in revised form
2 April 2015
Accepted 13 April 2015
Available online 24 April 2015
Corresponding Editor:
Joseph Spatafora

Keywords:
Corticioid fungi
Multi-marker analyses
Phlebioid clade
Phylogeny
RPB1
RPB2

ABSTRACT

We amplified RPB1, RPB2, and the ITS and LSU ribosomal genes from species mostly in the phlebioid clade, focusing heavily in phanerochaetoid taxa. We performed Maximum Likelihood and Bayesian analyses for different combinations of datasets. Our results provide a strongly supported phylogenetic picture of the phlebioid clade, representing 89 species in the four genes analyses, of which 49 represent phanerochaetoid taxa. *Phanerochaete* sensu lato is polyphyletic and distributed across nine lineages in the phlebioid clade. Six of these lineages are associated to already described genera, while we describe the new genus *Phaeophlebiopsis* to accommodate *Phlebiopsis*-like species in one of the remaining lineages. We also propose three taxonomic transfers and describe nine new species, with four of those species currently placed in *Phanerochaete sanguinea* or *Phanerochaete velutina*. Finally, the placement of *Leptoporus mollis* along with other potential brown-rot species in the phlebioid clade suggests that, in addition to the *Antrodia* clade, brown-rot fungi may have evolved more than once in *Polyporales*.

Introduction

Phanerochaete is a diverse saprotrophic genus in *Polyporales* with global distribution. *Phanerochaete* species are associated with white-rotted wood and fruitbodies grow on fallen branches and logs, branches attached on trees, twigs, and even wood buried in soil. Fruitbodies are resupinate, membranaceous, crustaceous or detachable, smooth, tuberculate or hydnoid, of variable colour and may or may not have hyphal cords (Eriksson *et al.* 1978; Burdsall 1985).

Phanerochaete was introduced by Karsten (1889) and *Phanerochaete velutina* (syn. *Corticium decolorans*) is considered the generic type (Eriksson *et al.* 1978). The name *Phanerochaete* did not get used for a long time, until Donk reintroduced it and set its limits (Donk 1957 &1962). In the latter study, he used the membranaceous nature of the fruitbodies, the monomitic hyphal system, the lack of clamp connections or their rare presence in the well-developed subiculum (simple, double or multiple clamps per septum), and the presence of cystidia as characters for the delimitation of the genus.

The simplicity of the morphological characters that characterize *Phanerochaete* and the existence of species with fruitbodies that fulfill only some of these morphological criteria render the limits of the genus uncertain. Donk (1962) recognized this and suggested that acystidiate taxa, such as *Phanerochaete tuberculata* (syn. *Corticium tuberculatum*), or taxa with

* *Corresponding author*. Tel.: +46 725606512; fax: +46 (0)46 222 4720.
E-mail addresses: dimitrios.floudas@biol.lu.se, dfloudas@clarku.edu (D. Floudas), dhibbett@clarku.edu (D. S. Hibbett).
http://dx.doi.org/10.1016/j.funbio.2015.04.003
1878-6146/

agglutinated, compact subicula, such as *Phlebiopsis gigantea* (syn. *Peniophora gigantea*), but otherwise similar to *Phanerochaete*, should be included in the genus.

Other authors have also discussed and approached taxonomy of *Phanerochaete* in different ways (Parmasto 1968; Eriksson *et al.* 1978; Jülich & Stalpers 1980). Parmasto (1968) included acystidiate species in *Phanerochaete* and divided the genus in the subgenera *Phanerochaete* (cystidiate species) and *Phanericium* (acystidiate species). Eriksson *et al.* (1978) separated *Phanerochaete* into three groups instead of subgenera. Two of these groups coincided with the subgenera recognized by Parmasto, while they recognized a third group, which included only *Phanerochaete septocystidia*. Burdsall (1985) extended Parmasto's view, recognized 46 species in the genus and divided it into three subgenera (*Phanerochaete*, *Phanericium*, *Scopuloides*). This separation was based on combinations of subiculum's development and the presence or absence of cystidia. Subgenus *Phanerochaete* includes the more typical *Phanerochaete* forms, while the subgenera *Phanericium* and *Scopuloides* have been used to accommodate the non-typical forms.

Narrower views of *Phanerochaete* have led to the introduction of additional genera to accommodate phanerochaetoid taxa that do not fulfill the criteria of typical *Phanerochaete* (Table 1). Taxa in those genera usually share only some of the characters seen in *Phanerochaete*, while they share characteristics with other genera, such as *Phlebia*. Therefore, *Scopuloides*, *Phlebiopsis*, and *Efibula* were introduced to accommodate species that lack clamp connections and have compact subicula or no subiculum at all (Hjortstam & Ryvarden 1979; Jülich 1978; Wu 1990). *Hydnophlebia* was introduced based on the similarity of the subiculum of *Hydnophlebia chrysorhiza* with *Phanerochaete*, but the structural similarity of its teeth with *Phlebia* sensu lato (Parmasto 1967). Furthermore, the stereoid appearance of fruitbodies and the dimitic or pseudo-dimitic hyphal system have been used for the segregation of *Hjortstamia* from *Lopharia* (Boidin & Gilles 2002). *Rhizochaete* has been recently introduced to accommodate *Phanerochaete*-like species, including species traditionally placed in *Ceraceomyces*. *Rhizochaete* has been the only closely related to *Phanerochaete* genus to be described based on morphological and molecular characters (Greslebin *et al.* 2004).

Phanerochaete is a widespread genus that causes white-rot on both softwood and hardwood and has attracted the attention of researchers for a long time. There are currently 158 legitimate names under this name (MycoBank, August 2014), while it appears that even recently new species have being described (Hjortstam 2000; Gilbertson *et al.* 2001; Nakasone 2008) or new combinations have been proposed (Melo *et al.* 2012).

Phanerochaete is not only ecologically important, but it is also biotechnologically significant. *Phanerochaete chrysosporium* grows rapidly, has an optimum growth temperature at around 40 °C and produces numerous conidia (Burdsall & Eslyn 1974). These characteristics and the frequent isolation of *P. chrysosporium* from wood chips and stored wood have made the species a model organism for studies on wood decay and lignin degradation caused by white-rot species (Cullen & Kersten 2004; Kersten & Cullen 2007). Class II peroxidases and glyoxal oxidase, which are among the most important enzymes during lignin degradation, have been initially

Table 1 – Major genera related to phanerochaetoid fungi and their basic morphological characteristics.

Genus	Fruitbody	Hymenophore	Clamp connections	Hyphae	Cystidia	Subiculum
Phanerochaete	Effused to slightly reflexed	Smooth, tuberculate, odontioid	Rare or absent	Monomitic	Present, thin or thick-walled	Well-developed, loose
Hydnophlebia	Effused	Odontioid	Rare	Monomitic	Leptocystidia	Well-developed, loose
Scopuloides	Effused	Odontioid	Absent	Monomitic	Metuloids	Almost absent, compact
Phlebiopsis	Effused	Smooth to tuberculate	Absent	Monomitic	Metuloids	Compact
Efibula	Effused	Smooth	Absent	Monomitic	Absent	Compact
Hjortstamia	Effuse-reflexed to pileate	Smooth	Absent	Momitic to dimitic	Skeletocystidia	Well-developed
Rhizochaete	Effused	Smooth/slightly tuberculate	Absent, occasional, or present	Monomitic	Mostly present, thin or thick-walled	Well-developed, loose

discovered in cultures of *P. chrysosporium* (Tien & Kirk 1983; Tien & Kirk 1984; Kersten & Kirk 1987). More recently, the genomes of *P. chrysosporium* and *Phanerochaete carnosa* have been sequenced, shedding light into the wood degradation mechanisms of mushroom forming fungi (Martinez *et al.* 2004; Suzuki *et al.* 2012).

In spite of its importance, the limits of *Phanerochaete* and its relationships with other genera remain elusive. Few *Phanerochaete* species have been included in modern phylogenetic studies, aiming mainly to represent the genus (Hibbett & Binder 2002; Kim *et al.* 2003; Binder *et al.* 2005; Larsson 2007; Matheny *et al.* 2007). So far, only two major phylogenetic studies have focused on the genus *Phanerochaete* (de Koker *et al.* 2003; Wu *et al.* 2010). These studies have utilized only one genetic marker each, with the former study utilizing the internal transcribed spacer region (ITS) of the ribosomal genes and the latter study utilizing the nuclear ribosomal large subunit (nLSU). Both studies have suggested that *Phanerochaete* is polyphyletic with most species nested in *Polyporales* and a taxonomic revision of the genus is needed.

The aim of this study is to provide a better resolution of the limits of *Phanerochaete* and phanerochaetoid genera from a phylogenetic standpoint, based on a four gene phylogenetic analysis. We examine the relationships of the genus with other genera in *Polyporales* and evaluate the usefulness of morphological characters in the taxonomy of phanerochaetoid taxa. We also examine the species level relationships in *Phanerochaete* s.l. and propose taxonomic solutions at the generic and species level.

Material and methods

Specimens and cultures

We requested specimens and cultures from the Forest Products Laboratory of the Northern Research Station (CFMR, USDA, Madison, WI), the Finnish Museum of Natural History at University of Helsinki (Herbarium H), the New York State Museum (NYS) and the Farlow Reference Library and Herbarium of Cryptogamic Botany at Harvard University (FH). We also collected specimens and isolated cultures from areas of the eastern United States, Alaska, and the Virgin Islands, represented by the initials FD. Newly collected specimens and isolated cultures have been deposited at the herbarium of the Forest Products Laboratory (CFMR).

Culture conditions and DNA extraction

We isolated new cultures mostly from spore prints and occasionally from fruitbodies. We grew mycelia for DNA extraction in static liquid media (20 or 40 ml) containing per liter: 20 g malt extract, 0.5 g yeast extract and 1 ml of vitamin solution (cat. No. 1600449, MP Biomedicals). We incubated the cultures for 4–20 d at 25 °C. We harvested the mycelia by filtration and either directly extracted DNA or stored them at −20 °C.

We extracted DNA using two different methods. We pulverized the collected mycelia using liquid nitrogen and a small amount of sand. We transferred the resulting powder into a 1.5 ml Eppendorf tube, added 600 μl of 3 % SDS, vortexed thoroughly and incubated at 65 °C for 45–60 min with occasionally vortexing to cause cell lysis. We purified the sample using equal volumes of phenol: chloroform (1:1) and chloroform: isoamyl alcohol (24:1) repeating twice. We precipitated the DNA using 10 μl 3M sodium acetate and 0.54 Vol.% isopropyl alcohol. We washed the pellets twice with 1 ml 70 % ethanol, dried them at 65 °C for 10–15 min and resuspended the DNA in 100 or 200 μl of H_2O.

We extracted DNA from samples using approximately a 3 × 3 mm piece of the fruitbody. We used the E.Z.N.A forensic DNA kit (Omega Bio-Tek) and followed the standard protocol provided by the manufacturer, but instead of vortexing after adding the STL buffer, we added sand and used a micropestle to break down the sample. We made 1:100, 1:500, and 1:1000 dilutions of DNA extracted from mycelia and 1:10, 1:20, and 1:50 dilutions of DNA extracted from samples. The generated DNA extractions and aliquots have been stored at the Hibbett laboratory DNA collection at Clark University (http://web.clarku.edu/faculty/dhibbett/clarkfungaldb/).

PCR amplification, sequencing, and data assembly

We generated ITS (approx. 600–700 bp) and nLSU (approx. 1300 bp) sequences as described elsewhere (Justo & Hibbett 2011), using the ITS-1F/ITS4 (White *et al.* 1990; Gardes & Bruns 1993) and LR0R/LR7 (Vilgalys Lab, http://biology.duke.edu/fungi/mycolab/) primer pairs, respectively.

We also generated data for the protein coding genes RPB1 (RNA polymerase II largest subunit) and RPB2 (RNA polymerase II second largest subunit). We amplified the area between the conserved domains A and C of RPB1 (approx. 1400 bp) using the primer pair RPB1-Af/RPB1-Cr (Stiller & Hall 1997; Matheny *et al.* 2002). We used the additional primers: RPB1-2f, RPB1-2.1f, RPB1-2.2f, and RPB1-2.1r for sequencing (Froslev *et al.* 2005). We amplified the area between the domains five and seven of RPB2 (approx. 1100 bp) using the primers RPB2-f5F (Liu *et al.* 1999) and RPB2-b7.1R (Matheny 2005). For sequencing we used the additional primers: RPB2b6F/RPB26R2 (Matheny 2005; Matheny *et al.* 2007). Primer information can be found at: http://wordpress.clarku.edu/polypeet/.

We used the touchdown protocol for the PCR of both protein coding genes: 1) initial DNA denaturation at 94 °C for 2 min, 2) denaturation at 94 °C for 40 s, 3) annealing at 60 °C for 40 s (minus 1C per cycle), 4) extension at 72 °C for 2 min, 5) repeat for 9 cycles starting at step 2, 6) denaturation at 94 °C for 45 s, 7) annealing at 53 °C for 1 min 30 s, 8) extension at 72 °C for 2 min, 9) repeat for 36 cycles starting at step 6, 10) leave at 72 °C for 10 min.

We sequenced the amplification products for all four markers using BigDye 3.1 terminator sequencing chemistry (Applied Biosystems, Foster City, California, USA). Sequencing was performed either on an Applied Biosystems 3130 Genetic Analyzer or by Macrogen (http://www.macrogen.com/eng/). The resulting data were processed using Sequencer v.4.7 (GeneCodes, Ann Arbor, Michigan, USA).

We retrieved data deposited in GenBank (Benson *et al.* 2012) for all four genes. We also mined the sequenced genome sequences of *Phlebia brevispora* and *Dichomitus squalens* for their RPB1 and RPB2 genes (Floudas *et al.* 2012; Binder *et al.* 2013).

Sequence alignment and phylogenetics

We aligned each dataset using the online version of PRANK (http://www.ebi.ac.uk/goldman-srv/webprank/) with the default settings (Löytynoja & Goldman 2010). We used MacClade v.4.08 (Maddison & Maddison 2002) to examine each alignment and removed poorly aligned areas. We manually combined the datasets for concatenated analyses. We converted files to the Nexus and PHYLIP formats using ALTER (http://sing.ei.uvigo.es/ALTER/) (Glez-Peña *et al.* 2010) and calculated the percentage similarity of ITS sequences using Geneious Pro 5.5.5.

We performed Maximum likelihood (ML) analyses using RA × ML v. 7.6.6 (Stamatakis *et al.* 2008) under the GTR model with CAT distributed rate heterogeneity and 100 rapid bootstrap replicates (200 replicates for ITS datasets). We performed Bayesian analyses using MrBayes 3.2.2 (Ronquist *et al.* 2012) for eight million generations, with four chains and sampling every 1000 generations. We set the burn-in period to 0.25, which we found to be adequate after examining the likelihood scores using Tracer v1.5 (http://tree.bio.ed.ac.uk/software/tracer/). We performed phylogenetic analyses at Cipres (Miller *et al.* 2010; http://www.phylo.org/index.php/portal/) or at RA × ML BlackBox (http://embnet.vital-it.ch/raxml-bb/index.php) (Stamatakis *et al.* 2008). Alignments and phylogenetic trees have been deposited at TreeBase: http://purl.org/phylo/treebase/phylows/study/TB2:S17235.

Microscopy and species description

We examined sections of the samples using 1 % Phloxine-B or Congo Red stains. We examined amyloidity of spores and tissues using Melzer's reagent and cyanophily of spores using Cotton Blue. We used KOH (5 %) to soften the tissues and to examine staining reactions of the fruitbodies. KOH reactions were performed by placing drops of KOH on mature and younger areas of the fruitbody and observing the colour change over time. A KOH reaction is considered positive when the colour change is permanent after the KOH has dried out. Colour determination of the fruitbodies is based on the Munsell Soil Colour Charts (Munsell 2009). We observed the microscopic characters of fruitbodies with a Leica DFC2500 microscope. We captured images of spores, cystidia, and hyphae using a Leica DFC420 digital camera and we measured their dimensions (length and width) with the Leica Application Suite 3.5.0. using 100× or 60× objective lenses. Measurements were done from at least three specimens per species, when this was possible, and we measured at least 50 spores per species. Fewer spores were measured for the *Phaeophlebiopsis* species, which have rigid fruitbodies, making the preparation of thin sections and the observation of spores difficult.

Results

New sequences and datasets

We generated 345 ITS sequences from cultures and specimens mainly from taxa of the phlebioid clade, followed by taxa of the residual polyporoid clade (sensu Binder *et al.* 2005) and other clades in *Polyporales* (Table 2). We selected a subset of 107 isolates and generated 96 nLSU, 107 RPB1, and 86 RPB2 new sequences (Table 3). We selected targets for RPB2 sequencing after analyzing RPB1, targeting nodes that the RPB1 could not resolve. We retrieved 86 ITS, 30 LSU, 19 RPB2, and 19 RPB1, nucleotide sequences from GenBank and the AFTOL database (http://www.aftol.org/index.php; Hibbett *et al.* 2000; Binder & Hibbett 2002; Larsson *et al.* 2004; Lindner & Banik 2008; Wu *et al.* 2010; Justo & Hibbett 2011). All sequences have been deposited at GenBank under accession numbers: KP134783–KP135419 (Tables 2 and 3).

Comparison of the concatenated ribosomal markers dataset with the RPB1 and RPB2 datasets

We performed ML and Bayesian analyses for five combinations of the assembled nucleotide datasets (Table 4, Fig 1, Fig S1–S4). For the combined datasets, we kept only the 5.8s region of ITS, since the flanking regions were poorly aligned. The combined 5.8s and LSU dataset consists of 2038 bp (Table 4). Using this dataset, only 54.8 % of the nodes are statistically supported in both phylogenetic analyses (bootstrap support $\geq$ 75, posterior probability $\geq$ 0.95). Six major clades have been recognized in *Polyporales* (Binder *et al.* 2005; Justo & Hibbett 2011; Miettinen & Rajchenberg 2011). Five of these clades are supported in at least one analysis of the 5.8s-LSU dataset, except for the *Antrodia* clade (Fig S1).

The RPB1 dataset is 1398 bp long and includes parts of introns two and three (636 and 69 bp, respectively). In spite of its shorter length in comparison to the 5.8s-LSU dataset, RPB1 alone resulted in 60.5 % of the nodes being supported in both types of analyses (Table 4). All major clades in *Polyporales* were supported in at least one type of analysis, except for the residual polyporoid clade (Fig S2).

The RPB2 dataset is 1188 bp long after excluding all introns position from the analyses. In contrast to RPB1, only about half of the nodes are supported from both analyses of RPB2 (Table 4). The RPB2 dataset analyses resulted in no support for both the phlebioid and residual polyporoid clades (Fig S3).

Combination of RPB1 with the ribosomal markers resulted in a 3436 bp dataset and increased the supported nodes in *Polyporales* from both analyses to 70.6 % (Table 4, Fig S4). Addition of RPB2 to the RPB1-5.8s-LSU concatenated dataset increased its length by almost 1200 characters, but increased the supported nodes from both analyses only to 73 % of the total nodes (Table 4). However, the four genes analyses resulted in all six major clades in *Polyporales* receiving support from both types of analyses (Fig 1). The phylogenetic relationships between the six clades are supported only in some analyses (Fig 1, FigS1–S4), suggesting the even four genes datasets are unable to resolve the deep phylogenetic relationships in *Polyporales*.

For all datasets analyzed, we recovered three major clades in phlebioid clade termed here *Phanerochaete*, *Byssomerulius*, and *Phlebia* clades, which receive statistical support in at least one analysis from all five datasets except for the *Phlebia* clade in the RPB2 dataset analyses. These clades have been recovered in previous studies but frequently without support (Binder *et al.* 2005; Larsson 2007; Binder *et al.* 2013).

Grifola frondosa and *Candelabrochaete africana* are the only taxa that are not placed to any major clade in *Polyporales*. The placement of *G. frondosa* has been discussed previously

Table 2 – Specimens or strains used in the study. Extractions from samples are indicated with (S).

Taxon	ITS Accession no.	Culture strain or sample	Geographic region
Abortiporus biennis	KP135300	FD-319	USA (MA)
Antrodiella americana	KP135316	HHB-4100	USA (TN)
Antrodiella americana	KP135315	FD-199	USA (MA)
Antrodiella semisupina complex	KP135319	RLG-4021	USA (MA)
Antrodiella semisupina complex	KP135318	L-15719	USA (NY)
Antrodiella semisupina complex	KP135314	FD-136	USA (MA)
Antrodiella semisupina complex	KP135313	FD-3 (S)	USA (MA)
Antrodiella semisupina complex	KP135317	HHB-7663	USA (MI)
Bjerkandera adusta	KP134982	FP-101236	USA (WI)
Bjerkandera adusta	KP134983	HHB-12826	USA (AK)
Byssomerulius corium	KP135005	FD-376 (S)	USA (VI)
Byssomerulius corium	KP135006	MA-52	USA (AZ)
Byssomerulius corium	KP135004	FP-102092 (S)	USA (IL)
Byssomerulius corium	KP135007	FP-102382	USA (WI)
Byssomerulius corium	KP135008	FP-107055	USA (MI)
Candelabrochaete africana	KP135293	FP-102821	USA (PR)
Candelabrochaete africana	KP135292	FP-102901	USA (PR)
Candelabrochaete africana	KP135294	FP-102987	USA (PR)
Ceraceomyces serpens	KP135031	HHB-15692	USA (AK)
Ceraceomyces serpens	KP135032	L-11105	USA (NC)
Ceraceomyces serpens	KP135030	L-13818	Canada (ON)
Ceraceomyces sp.	KP135033	HHB-12679	USA (AK)
Ceraceomyces sp.	KP135034	FD-540 (S)	USA (MA)
Ceraceomyces sublaevis	KP135029	FP-101245	USA (WI)
Ceriporia alachuana	KP135341	FP-103881	USA (MD)
Ceriporia alachuana	KP135340	L-11510	USA (FL)
Ceriporia lacerata	KP135024	FP-55521-T	USA (LA)
Ceriporia purpurea	KP135044	KKN-223	USA (AZ)
Ceriporia purpurea	KP135042	HHB-3964	USA (TN)
Ceriporia reticulata	KP135041	RLG-11354	USA (AZ)
Ceriporia reticulata	KP135040	L-7837	USA (WA)
Ceriporia sp.	KP135043	HHB-478	USA (MD)
Ceriporia sp.	KP135047	HHB-4365	USA (NC)
Ceriporia sp.	KP135046	HHB-12714	USA (AK)
Ceriporia sp.	KP135045	RLG-11279	USA (AZ)
Ceriporia sp.	KP135048	FP-134993	USA (NY)
Ceriporia sp.	KP135049	FD-397 (S)	USA (VI)
Ceriporia sp.	KP135050	L-8020	USA (WA)
Ceriporia sp.	KP135053	HHB-4788	USA (FL)
Ceriporia sp.	KP135056	HHB-9594	USA (FL)
Ceriporiopsis aneirina	KP135023	HHB-15629	USA (AK)
Cerrena unicolor	KP135304	FD-299	USA (MA)
Cerrena unicolor	KP135305	AJ174 (S)	USA (FL)
Climacocystis borealis	KP135308	FD-31	USA (MA)
Climacodon septentrionalis	KP135344	RLG-6890	USA (NY)
Climacodon septentrionalis	KP135345	FP-72067	USA (MD)
Dichomitus squalens	KP135330	Ly-AD-421	–
Diplomitoporus crustulinus	KP135299	FD137	USA (MA)
Efibula americana	KP135011	FP-102156	USA (KY)
Efibula americana	KP135013	FP-102158 (S)	USA (IL)
Efibula americana	KP135016	FP-102165 (**TYPE**)	USA (KY)
Efibula americana	KP135009	FP-104126	USA (MD)
Efibula americana	KP135015	FP-110429 (S)	USA (MS)
Efibula americana	KP135012	HHB-8468	USA (AZ)
Efibula americana	KP135010	HHB-8508	USA (AZ)
Efibula americana	KP135014	HHB-10209	USA (WI)
Efibula clarkii	KP135019	FD-228 (**TYPE**) (S)	USA (MA)
Efibula gracilis	KP135027	FD-455	USA (CT)
Efibula gracilis	KP135028	FP-102052 (**TYPE**) (S)	USA (WI)
Efibula tuberculata	KP135017	H6028245 (OM-6707) (S)	Finland
Efibula tuberculata	KP135018	H6028243 (OM-11754) (S)	Finland
Gelatoporia subvermispora	KP135312	FD-354	USA (MA)
Gloeoporus dichrous	KP135059	FD-65 (S)	USA (MA)

(*continued on next page*)

Table 2 – (*continued*)

Taxon	ITS Accession no.	Culture strain or sample	Geographic region
Gloeoporus dichrous	KP135058	FP-151129	USA (MI)
Gloeoporus pannocinctus	KP135060	L-15726	USA (NY)
Hapalopilus rutilans	KP135419	FD-512	USA (NY)
Hydnophlebia cf. *chrysorhiza*	KP135339	PR-4154	USA (PR)
Hydnophlebia chrysorhiza	KP135048	FP-134985 (S)	USA (NY)
Hydnophlebia chrysorhiza	KP135337	HHB-18767 (S)	USA (IL)
Hydnophlebia chrysorhiza	KP135335	T-484	Canada (ON)
Hydnophlebia chrysorhiza	KP135338	FD-282	USA (FL)
Hydnophlebia omnivora 1	KP135334	KKN-112	USA (AZ)
Hydnophlebia omnivora 2	KP135332	ME-497	USA (FL)
Hydnophlebia omnivora 2	KP135333	HHB-6228	USA (AZ)
Hyphoderma litschaueri	KP135295	FP-101740	USA (WI)
Hyphoderma medioburiense	KP135298	FD-335	USA (MA)
Hyphoderma mutatum	KP135296	HHB-15479	USA (AK)
Hyphoderma setigerum	KP135297	FD-312	USA (MA)
Hyphodermella rosae	KP134978	FP-150552	USA (HI)
Irpex lacteus	KP135026	FD-9	USA (MA)
Irpex lacteus	KP135025	FD-93	USA (MA)
Ischnoderma resinosum	KP135303	FD-328	USA (NH)
Junghuhnia luteoalba	KP135321	FP-105992	USA (MD)
Junghuhnia luteoalba	KP135320	FP-105786	USA (MD)
Junghuhnia nitida	KP135323	FP-105195	USA (MD)
Junghuhnia nitida	KP135324	FP-133199	USA (WI)
Junghuhnia nitida	KP135325	FP-100622	USA (MN)
Meripilus giganteus	KP135307	FP-135344	United Kingdom
Meripilus giganteus	KP135306	FP-100460	Netherlands
Meruliopsis albostramineus	KP135051	HHB-10729	USA (VA)
Meruliopsis albostramineus	KP135052	L-9778	USA (AZ)
Meruliopsis sp.	KP135054	FD-497	USA (NY)
Meruliopsis sp.	KP135057	FD-278	USA (FL)
Meruliopsis sp.	KP135055	FP-102931	USA (PR)
Obba rivulosa	KP135309	FP-135416	USA (ID)
Panus lecomtei	KP135326	OKMCHD-30684	USA (GA)
Panus lecomtei	KP135327	HHB-6616	USA (FL)
Panus lecomtei	KP135328	HHB-11042	USA (AZ)
Panus lecomtei	KP135329	HHB-9614	USA (FL)
Phaeophlebiopsis caribbeana	KP135415	HHB-6990	USA (FL)
Phaeophlebiopsis caribbeana	KP135416	FD-442 (**TYPE**)	USA (VI)
Phaeophlebiopsis ignerii	KP135418	FD-425 (**TYPE**) (S)	USA (VI)
Phaeophlebiopsis peniophoroides	KP135417	FP-150577	USA (HI)
Phaeophlebiopsis sp.	KP135412	FP-100589	USA (GA)
Phaeophlebiopsis sp.	KP135413	HHB-6542	USA (FL)
Phaeophlebiopsis sp.	KP135414	HHB-9991 (S)	USA (FL)
Phanerochaete aff. *sanguinea*	KP135099	HHB-8519	USA (AZ)
Phanerochaete allantospora	KP135037	KKN-85 (S)	USA (AZ)
Phanerochaete allantospora	KP135038	KKN-111	USA (AZ)
Phanerochaete allantospora	KP135039	RLG-10478 (**TYPE**) (S)	USA (AZ)
Phanerochaete allantospora	KP135036	RLG-10542 (S)	USA (AZ)
Phanerochaete allantospora	KP135035	RLG-10949 (S)	USA (AZ)
Phanerochaete arizonica	KP135170	RLG-10248 (**TYPE**)	USA (AZ)
Phanerochaete australis	KP135075	Meijer-2422 (S)	Brazil
Phanerochaete australis	KP135076	HHB-7083	USA (FL)
Phanerochaete australis	KP135077	FP-102909	USA (PR)
Phanerochaete australis	KP135078	FP-102907	USA (PR)
Phanerochaete australis	KP135079	FP-102818	USA (PR)
Phanerochaete australis	KP135080	FP-102958	USA (PR)
Phanerochaete australis	KP135081	HHB-7105	USA (FL)
Phanerochaete burtii	KP135109	FD-35 (S)	USA (MA)
Phanerochaete burtii	KP135116	FD-171	USA (MA)
Phanerochaete burtii	KP135114	FD-187	USA (MA)
Phanerochaete burtii	KP135115	FD-243	USA (FL)
Phanerochaete burtii	KP135112	FD-248 (S)	USA (FL)
Phanerochaete burtii	KP135110	FD-292 (S)	USA (MA)
Phanerochaete burtii	KP135113	FD-333 (S)	USA (MA)

Table 2 – (*continued*)

Taxon	ITS Accession no.	Culture strain or sample	Geographic region
Phanerochaete burtii	KP135111	FD-355 (S)	USA (MA)
Phanerochaete burtii	KP135117	HHB-4618	USA (FL)
Phanerochaete calotricha	KP135107	H6028237 (Vanhanen 382) (S)	Finland
Phanerochaete carnosa	KP135126	FD-474 (S)	USA (NY)
Phanerochaete carnosa	KP135127	FD-478	USA (NY)
Phanerochaete carnosa	KP135129	HHB-9195	USA (MI)
Phanerochaete carnosa	KP135128	RLG-7412	USA (NM)
Phanerochaete chrysosporium	KP135093	HHB-11741	USA (IL)
Phanerochaete chrysosporium	KP135094	HHB-6251(**TYPE**)	USA (AZ)
Phanerochaete chrysosporium	KP135092	HHB-6612	USA (FL)
Phanerochaete citrinosanguinea	KP135095	FD-287 (**TYPE**) (S)	USA (MA)
Phanerochaete citrinosanguinea	KP135100	FP-105385	USA (MA)
Phanerochaete conifericola	KP135171	H6028235 (OM-8110) (S)	Finland
Phanerochaete conifericola	KP135172	H7017352 (Kotiranta 20 937) (S)	Russia
Phanerochaete conifericola	KP135174	H6028236 (Penttila 14 627) (S)	Finland
Phanerochaete conifericola	KP135173	H6012813 (OM-7749,7-**TYPE**) (S)	Finland
Phanerochaete conifericola	KP135177	FP-151125	USA (MI)
Phanerochaete conifericola	KP135175	HHB-15674	USA (AK)
Phanerochaete conifericola	KP135176	RLG-9919 (S)	USA (AZ)
Phanerochaete conifericola	KP135178	HHB-13753 (S)	USA (AK)
Phanerochaete ericina	KP135165	FP-101978	USA (IL)
Phanerochaete ericina	KP135166	FP-102181	USA (IL)
Phanerochaete ericina	KP135168	HHB-2295	USA (NC)
Phanerochaete ericina	KP135169	HHB-2714	USA (NC)
Phanerochaete ericina	KP135167	HHB-2288	USA (NC)
Phanerochaete exilis	KP135001	HHB-6988	USA (FL)
Phanerochaete krikophora nom. prov.	KP135164	HHB-5796	USA (MT)
Phanerochaete laevis	KP135147	DLC97-3 (S)	USA (WI)
Phanerochaete laevis	KP135148	HHB-1625 (S)	USA (MD)
Phanerochaete laevis	KP135149	HHB-15519	USA (AK)
Phanerochaete laevis	KP135150	HHB-17395	USA (AK)
Phanerochaete laevis	KP135151	FP-151101	USA (MI)
Phanerochaete laevis	KP135160	H6028230 (OM-10969,2) (S)	Finland
Phanerochaete laevis	KP135161	H7017353 (OM-11815) (S)	Sweden
Phanerochaete laevis	KP135159	H7016014 (Viner 70b) (S)	Russia
Phanerochaete laevis	KP135157	H6028239 (S)	Finland
Phanerochaete laevis	KP135158	H6012036 (OM-6890,2) (S)	Finland
Phanerochaete laevis	KP135152	FD-206 (S)	USA (MA)
Phanerochaete laevis	KP135153	FD-357 (S)	USA (NH)
Phanerochaete laevis	KP135156	FD-488	USA (NY)
Phanerochaete laevis	KP135155	FD-489	USA (NY)
Phanerochaete laevis	KP135154	FD-508	USA (NY)
Phanerochaete magnoliae	KP135082	RLG-6782	Canada (ON)
Phanerochaete magnoliae	KP135088	H6028242 (Penttila 14 222) (S)	Finland
Phanerochaete magnoliae	KP135084	OM-16852	USA (MA)
Phanerochaete magnoliae	KP135086	FD-341 (S)	USA (AK)
Phanerochaete magnoliae	KP135087	H6028241 (OM-7419) (S)	Finland
Phanerochaete magnoliae	KP135083	HHB-6253 (S)	USA (AZ)
Phanerochaete magnoliae	KP135085	H6033465 (Penttila 14 355) (S)	Finland
Phanerochaete magnoliae	KP135089	HHB-9829	USA (FL)
Phanerochaete magnoliae	KP135090	HHB-9701	USA (FL)
Phanerochaete pseudomagnoliae	KP135091	PP25 (**TYPE**)	South Africa
Phanerochaete pseudosanguinea	KP135096	FD-240 (S)	USA (FL)
Phanerochaete pseudosanguinea	KP135098	FD-244 (**TYPE**)	USA (FL)
Phanerochaete pseudosanguinea	KP135097	FP-100391	USA (MD)
Phanerochaete rhodella	KP135194	FP-150640 (S)	USA (WI)
Phanerochaete rhodella	KP135193	HHB-2879	USA (NC)
Phanerochaete rhodella	KP135187	FD-18	USA (MA)
Phanerochaete rhodella	KP135191	FD-286 (EPITYPE)	USA (MA)
Phanerochaete rhodella	KP135192	FD-329 (S)	USA (MA)
Phanerochaete rhodella	KP135188	FD-482	USA (NY)
Phanerochaete rhodella	KP135189	FD-486	USA (NY)
Phanerochaete rhodella	KP135190	FD-522 (S)	USA (MA)

(*continued on next page*)

Table 2 – (*continued*)

Taxon	ITS Accession no.	Culture strain or sample	Geographic region
Phanerochaete sanguinea	KP135101	HHB-7524	USA (MI)
Phanerochaete sanguinea	KP135102	HHB-9198	USA (MI)
Phanerochaete sanguinea	KP135104	H7017351 (OM-11838,2) (S)	Sweden
Phanerochaete sanguinea	KP135106	H7005110 (OM-13390,1) (S)	Norway
Phanerochaete sanguinea	KP135103	H6033480 (Kotiranta 22 978) (S)	Finland
Phanerochaete sanguinea	KP135105	H6028244 (Niemela 7993) (S)	Finland
Phanerochaete sanguineocarnosa	KP135122	FD-359	USA (MA)
Phanerochaete sanguineocarnosa	KP135123	FD-520 (S)	USA (MA)
Phanerochaete sanguineocarnosa	KP135118	FD-521 (S)	USA (MA)
Phanerochaete sanguineocarnosa	KP135119	FD-523 (S)	USA (MA)
Phanerochaete sanguineocarnosa	KP135120	FD-524 (S)	USA (MA)
Phanerochaete sanguineocarnosa	KP135121	FD-528 (**TYPE**) (S)	USA (MA)
Phanerochaete sanguineocarnosa	KP135125	DLC97-964 (S)	USA (MI)
Phanerochaete sanguineocarnosa	KP135124	HHB-2189 (S)	USA (NC)
Phanerochaete sordida I	KP135142	H6028229 (OM-10659) (S)	Finland
Phanerochaete sordida I	KP135143	H6028232 (Soderholm 3376) (S)	Finland
Phanerochaete sordida I	KP135141	H6028233 (OM-6698) (S)	Finland
Phanerochaete sordida I	KP135145	H6012677 (OM-14062) (S)	Finland
Phanerochaete sordida I	KP135144	H6026891 (Kunttu 3138) (S)	Finland
Phanerochaete sordida I	KP135139	HHB-7827	USA (MI)
Phanerochaete sordida I	KP135134	HHB-8122	USA (MI)
Phanerochaete sordida I	KP135135	HHB-9650	USA (FL)
Phanerochaete sordida I	KP135138	HHB-11458	USA (WI)
Phanerochaete sordida I	KP135137	FD-230	USA (FL)
Phanerochaete sordida I	KP135136	FD-241	USA (FL)
Phanerochaete sordida I	KP135140	FD-463	USA (NY)
Phanerochaete sordida I	KP135132	FD-491	USA (NY)
Phanerochaete sordida I	KP135133	FD-514	USA (NY)
Phanerochaete sordida II	KP135061	HHB-7423	USA (MT)
Phanerochaete sordida II	KP135062	FP-133262	USA (OR)
Phanerochaete sordida II	KP135063	HHB-15625	USA (AK)
Phanerochaete sordida II	KP135064	HHB-7201	USA (FL)
Phanerochaete sordida II	KP135065	DLC97-190 (S)	USA (MI)
Phanerochaete sordida II	KP135066	H6028228 (OM-10891) (S)	Finland
Phanerochaete sordida II	KP135067	HHB-9702	USA (FL)
Phanerochaete sordida II	KP135068	HHB-9899	USA (FL)
Phanerochaete sordida II	KP135074	HHB-9871	USA (FL)
Phanerochaete sordida II	KP135069	HHB-9999	USA (FL)
Phanerochaete sordida II	KP135071	FD-175	USA (MA)
Phanerochaete sordida II	KP135070	FD-106	USA (RI)
Phanerochaete sordida II	KP135073	FD-458	USA (NY)
Phanerochaete sordida II	KP135072	FD-483	USA (NY)
Phanerochaete sp.	KP135146	9614 (S)	USA (OH)
Phanerochaete sp.	KP135108	FD-214 (S)	USA (MA)
Phanerochaete sp.	KP135130	FD-245 (S)	USA (FL)
Phanerochaete sp.	KP135131	NM-586 (S)	Japan
Phanerochaete sp. s.l.	KP134987	FP-102023 (S)	USA (WI)
Phanerochaete sp. s.l.	KP134989	FP-102032 (S)	USA (WI)
Phanerochaete sp. s.l.	KP134988	FP-102036	USA (WI)
Phanerochaete sp. s.l.	KP134991	FP-102164	USA (IL)
Phanerochaete sp. s.l.	KP134995	FP-102166	USA (IL)
Phanerochaete sp. s.l.	KP134992	FP-102346 (S)	USA (WI)
Phanerochaete sp. s.l.	KP134990	HHB-3520	USA (MI)
Phanerochaete sp. s.l.	KP134994	HHB-11463	USA (WI)
Phanerochaete sp. s.l.	KP134993	HHB-12117 (S)	USA (WI)
Phanerochaete sp. s.l.	KP135000	FP-102936	USA (PR)
Phanerochaete sp. s.l.	KP135002	HHB-18100	New Zealand
Phanerochaete sp. s.l.	KP135003	HHB-18104	New Zealand
Phanerochaete sp. s.l.	KP135020	RLG-13408	USA (LA)
Phanerochaete sp. s.l.	KP135021	TJV-93-262-T	USA (LA)
Phanerochaete sp. s.l.	KP135022	FP-160003 (S)	USA (MP)
Phanerochaete subceracea	KP135162	FP-105974-R	USA (MD)
Phanerochaete subceracea	KP135163	HHB-9434 (S)	USA (OH)
Phanerochaete velutina	KP135179	H6028246 (Kotiranta 21 402) (S)	Finland

Table 2 – (*continued*)

Taxon	ITS Accession no.	Culture strain or sample	Geographic region
Phanerochaete velutina	KP135180	OM-15027 (S)	Finland
Phanerochaete velutina	KP135181	OM-14694,3 (S)	Finland
Phanerochaete velutina	KP135182	OM-14735 (S)	Finland
Phanerochaete velutina	KP135184	HHB-15343	USA (AK)
Phanerochaete velutina	KP135183	HHB-15074	USA (AK)
Phanerochaete velutina	KP135185	HHB-17428	USA (AK)
Phanerochaete velutina	KP135186	FD-346 (S)	USA (AK)
Phanerochaete xerophila	KP134996	HHB-8509	USA (AZ)
Phanerochaete xerophila	KP134998	KKN-63	USA (AZ)
Phanerochaete xerophila	KP134997	KKN-172	USA (AZ)
Phanerochaete xerophila	KP134999	KKN-203	USA (AZ)
Phlebia acerina complex	KP135378	FD-301	USA (MA)
Phlebia acerina complex	KP135372	HHB-11146	USA (WI)
Phlebia acerina complex	KP135373	MR-4280	USA (NC)
Phlebia acerina complex	KP135371	FP-135252	USA (NY)
Phlebia acerina complex	KP135375	DR-60	Dominican republic
Phlebia brevispora	KP135387	HHB-7030	USA (FL)
Phlebia centrifuga	KP135380	HHB-9239	USA (MI)
Phlebia centrifuga	KP135381	L-15541	USA (NY)
Phlebia centrifuga	KP135379	GB-1013	Romania
Phlebia chrysocreas	KP135358	HHB-6333	USA (WI)
Phlebia chrysocreas	KP135357	HHB-3946	USA (TN)
Phlebia floridensis	KP135385	HHB-6466	USA (FL)
Phlebia floridensis	KP135384	HHB-7175	USA (FL)
Phlebia floridensis	KP135383	HHB-9905	USA (FL)
Phlebia floridensis	KP135386	FP-102562-T	USA (MI)
Phlebia fuscoatra	KP135364	HHB-10782	USA (WI)
Phlebia fuscoatra	KP135367	HHB-15354-T	USA (AK)
Phlebia fuscoatra	KP135366	HHB-18642	USA (AK)
Phlebia fuscoatra	KP135364	FP-102173	USA (IL)
Phlebia nothofagi	KP135369	HHB-4273	USA (TN)
Phlebia nothofagi	KP135368	HHB-6906	USA (FL)
Phlebia nothofagi	KP135370	HHB-12067	USA (WI)
Phlebia radiata	KP135377	FD-85	USA (MA)
Phlebia radiata	KP135376	FD-121	USA (MA)
Phlebia rufa	KP135374	HHB-14924	USA (WA)
Phlebia setulosa	KP135382	HHB-6891	USA (FL)
Phlebia sp. s.l.	KP135405	HHB-18295	New Zealand
Phlebia sp. s.l.	KP135342	FD-427	USA (VI)
Phlebia sp. s.l.	KP135343	HHB-9768	USA (FL)
Phlebia sp. s.l.	KP135359	HHB-17984	New Zealand
Phlebia sp. s.l.	KP135360	HHB-18142	New Zealand
Phlebia uda	KP135361	FP-101544	USA (WI)
Phlebiopsis aff. *flavidoalba*	KP135396	OM-15205, 2 (S)	Indonesia
Phlebiopsis aff. *ravenelii*	KP135392	ECS-1971 (S)	USA (PR)
Phlebiopsis crassa	KP135393	HHB-8834	USA (MS)
Phlebiopsis crassa	KP135395	ME-516	USA (MS)
Phlebiopsis crassa	KP135394	KKN-86	USA (AZ)
Phlebiopsis flavidoalba	KP135398	OM-17897 (S)	USA (FL)
Phlebiopsis flavidoalba	KP135397	OM-17896 (S)	USA (FL)
Phlebiopsis flavidoalba	KP135399	ME-164	USA (GA)
Phlebiopsis flavidoalba	KP135400	MR-4252 (S)	USA (TN)
Phlebiopsis flavidoalba	KP135401	HHB-4617	USA (FL)
Phlebiopsis flavidoalba	KP135402	FD-263	USA (FL)
Phlebiopsis flavidoalba	KP135403	FD-374	USA (VI)
Phlebiopsis flavidoalba	KP135404	FD-407	USA (VI)
Phlebiopsis gigantea	KP135388	HHB-11416	USA (WI)
Phlebiopsis gigantea	KP135390	FP-70857	USA (GA)
Phlebiopsis gigantea	KP135389	FP-101815	USA (MS)
Phlebiopsis sp.	KP135391	FP-102937	USA (PR)
Phlebiopsis sp. s.l.	KP135363	RLG-13514	USA (LA)
Phlebiopsis sp. s.l.	KP135362	FP-110129	USA (MI)
Pirex concentricus	KP134984	OSC-41587	USA (OR)

(*continued on next page*)

Table 2 – (*continued*)

Taxon	ITS Accession no.	Culture strain or sample	Geographic region
Pirex concentricus	KP134985	Kropp160Bup6-R	USA (OR)
Pirex concentricus	KP134986	4YM6-R	USA (OR)
Rhizochaete americana	KP135409	FP-102188	USA (IL)
Rhizochaete filamentosa	KP135410	HHB-3169	USA (MD)
Rhizochaete filamentosa	KP135411	FP-105240	USA (IN)
Rhizochaete radicata	KP135407	FD-123	USA (MA)
Rhizochaete radicata	KP135406	FD-338	USA (MA)
Rhizochaete sp.	KP135408	FP-150712	Belize
Scopuloides rimosa complex	KP135346	FD-513	USA (NY)
Scopuloides rimosa complex	KP135349	HHB-4003	USA (NC)
Scopuloides rimosa complex	KP135352	HHB-15484	USA (AK)
Scopuloides rimosa complex	KP135348	HHB-11766	USA (IL)
Scopuloides rimosa complex	KP135351	RLG-5104	USA (NY)
Scopuloides rimosa complex	KP135347	FP-133363	USA (OR)
Scopuloides rimosa complex	KP135350	HHB-7042	USA (FL)
Scopuloides sp.	KP135353	FP-102935	USA (PR)
Scopuloides sp.	KP135354	FD-389 (S)	USA (VI)
Scopuloides sp.	KP135355	FP-150473	USA (HI)
Scopuloides sp.	KP135356	FP-150480	USA (HI)
Skeletocutis chrysella	KP135310	FD-305	USA (MA)
Skeletocutis nivea	KP135331	FD-5 (S)	USA (MA)
Spongipellis delectans	KP135301	HHB-10489	USA (MI)
Spongipellis pachyodon	KP135302	FD-314	USA (MA)
Steccherinum sp.	KP135322	FD-26	USA (MA)
Terana caerulea	KP134979	FP-106678	USA (MI)
Terana caerulea	KP134980	FP-104073	USA (MD)
Terana caerulea	KP134981	T-616	Belgium
Tyromyces chioneus	KP135311	FD-4	USA (MA)

(Justo & Hibbett 2011). *Candelabrochaete africana* is placed as the sister clade to the phlebioid clade in the three, four gene and RPB1 analyses, but this topology is strongly supported only in the Bayesian analyses.

ITS analyses of the Phanerochaete, Phlebiopsis, Byssomerulius, *and* Phlebia *clades*

We generated in total 344 ITS sequences in *Polyporales*. From those, we analyzed separately the ITS datasets of four smaller clades in the phlebioid clade, where most of *Phanerochaete* s.l. taxa are found (Fig 1). The largest dataset consists of 194 *Phanerochaete* s.s sequences (57 retrieved from GenBank, Fig 2). The other three datasets represent the *Phlebiopsis* clade (Fig 3), which is part of the *Phanerochaete* clade (Fig 1), the *Byssomerulius* clade (Fig 4), and the *Phlebia* clade (Fig 5) including 51, 39, and 30 *Phanerochaete* s.l. ITS sequences, respectively. We also analyzed two additional concatenated ITS and nLSU datasets, one including *Phanerochaete* taxa from Wu *et al.* (2010) and the other including *Ceriporia* and *Meruliopsis*, with inclusion of sequences from *Ceriporia viridans* and *Meruliopsis taxicola* (generic types), for which we did not have RPB1 and RPB2 (Fig S5).

Taxonomy

Phanerochaete sensu stricto

Phanerochaete sanguineocarnosa Floudas & Hibbett **sp. nov.** (Figs 1, 2 and 6)

MycoBank No.: 811925.

Etym.: a combination of the names *sanguinea* and *carnosa* indicating the intermediate characteristics of the species.

Holotype: **United States of America**: Massachusetts: Worcester Co., Uxbridge, Cormier Woods, on decorticated hardwood branch on the ground, 23 September 2012, FD-528 (CFMR!), nrITS KP135121.

Fruitbody resupinate, smooth, membranaceous, well-developed, 0.2–0.4 mm, detachable, extensively cracking, colour ranging from very pale yellow (2.5Y 9/2), yellow (2.5Y 8/6) to very pale brown (10 YR 7/4), in older parts reddish yellow (7.5 YR 6/8) to strong brown (7.5 YR 5/8). Margin white (2.5Y 9.5/1) to very pale yellow (2.5Y 9/2), fibrillose to extensively cordonic, and then hyphal cords slightly darker than fruitbody yellowish red (5 YR 5/8). KOH turns the fruitbody green, quickly changing to brown, upon drying the colour either fades to light brown or remains brown. Context almost white, lighter in colour than hymenophore in older samples.

Hyphal system monomitic, subhymenium and subiculum distinct. Subicular hyphae loosely arranged, sparsely branched, mainly in parallel orientation, thin-to thick-walled, up to 8 μm wide, covered with crystals, with abundant simple, double and multiple clamp connections seen in all samples, giving rise to new hyphae. Subhymenium consisting of thin-walled, short-celled, frequently branched hyphae, 4–6 μm. Basidia almost cylindrical, with four sterigmata, 24–30 × 4–5.5 μm, without basal clamp. Cystidia arising from the hymenium, thin-walled to slightly thick-walled, with occasional secondary septa, getting narrower towards the top, or cylindrical, fragile, sometimes covered with resinous material, when seen in water, but naked in KOH,

Table 3 – Taxa and sequences used in the multi-gene datasets analyses. Genbank sequences, genomic data or data absent are highlighted in grey.

Taxon	Strain/Specimen	5.8s	28s(LSU)	RPB1	RPB2
Abortiporus biennis	**FD-319**	KP135300	KP135195	KP134783	KP134893
Amyloporia xantha	**AFTOL-1504**	DQ484059.1	DQ457649.1	KP134880	KP134912
Antrodiella americana	**HHB-4100-Sp**	KP135316	KP135196	KP134885	–
Antrodiella stipitata group	**FD-136**	KP135314	KP135197	KP134886	–
Bjerkandera adusta	**HHB-12826-Sp**	KP134983	KP135198	KP134784	KP134913
Bondarzewia montana	**AFTOL-452**	DQ200923.1	DQ234539.1	DQ256049.1	AY218474.2
Byssomerulius corium	**FP-102382**	KP135007	KP135230	KP134802	KP134921
Candelabrochaete africana	**FP-102987-Sp**	KP135294	KP135199	KP134872	KP134975 (fragment)
Ceraceomyces serpens	**HHB-15692-Sp**	KP135031	KP135200	KP134785	KP134914
Ceriporia alachuana	**FP-103881-Sp**	KP135341	KP135201	KP134845	KP134896
Ceriporia lacerata	**FP-55521-T**	KP135024	KP135202	KP134805	KP134915
Ceriporia purpurea	**KKN-223-Sp**	KP135044	KP135203	KP134788	KP134925
Ceriporia reticulata	**RLG-11354-Sp**	KP135041	KP135204	KP134794	KP134922
Ceriporia sp.	**L-8020**	KP135050	–	KP134789	–
Ceriporia sp.	**FP-134993**	KP135048	–	KP134792	–
Ceriporia sp.	**HHB-12714**	KP135046	–	KP134790	–
Ceriporia spissa	**FD-352**	–	KP135206	KP134793	KP134924
Ceriporiopsis aneirina	**HHB-15629-Sp**	KP135023	KP135207	KP134795	–
Cerrena unicolor	**FD-299**	KP135304	KP135209	KP134874	KP134968
Climacocystis borealis	**FD-31**	KP135308	KP135210	KP134882	KP134895
Climacodon septentrionalis	**AFTOL-767**	AY854082.1	AY684165.1	AY864873.1	AY780941.1
Coriolopsis galllica	**RLG-7630**	JN165013.1	JN164814.1	JN164821.1	JN164869.1
Datronia mollis	**RLG-6304**	JN165002.1	JN164791.1	JN164818.1	JN164872.1
Dentocorticium sulphurellum	**FP-11801/T-609**	JN165018.1	JN164875.1	JN164841.1	JN164876.1
Dichomitus squalens	**LYAD-421 SS1**	KP135330	–	e_gw1.35.248.1	gm1.454_g
Diplomitoporus crustulinus	**FD-137**	KP135299	KP135211	KP134883	–
Efibula americana	**FP-102165**	KP135016	KP135256	KP134808	KP134916
Efibula clarkii	**FD-228**	KP135019	–	KP134803	–
Efibula gracilis	**FD-455**	KP135027	–	KP134804	–
Efibula tuberculata	**OM-6707**	KP135017	–	KP134807	–
Fomitopsis pinicola	**AFTOL-770**	AY854083.1	AY684164.1	AY864874.1	AY786056.1
Ganoderma tsugae	**AFTOL-771**	DQ206985.1	AY684163.1	–	DQ408116.1
Gelatoporia subvermispora	**FD-354**	KP135312	KP135212	KP134879	KP134961
Gloeoporus dichrous	**FP-151129**	KP135058	KP135213	KP134866	–
Gloeoporus pannocinctus	**L-15726-Sp**	KP135060	KP135214	KP134867	KP134973
Grifola frondosa	**AFTOL-701**	AY854084.1	AY629318.1	AY864876.1	AY786057.1
Hapalopilus nidulans	**FD-512**	KP135419	–	KP134809	–
Heterobasidion annosum	**AFTOL-470**	DQ206988.1	–	DQ667160.1	AY544206.1
Hydnophlebia chrysorhiza	**FD-282**	KP135338	KP135217	KP134848	KP134897
Hydnophlebia omnivora 1	**KKN-112**	KP135334	KP135216	KP134846	–
Hydnophlebia omnivora 2	**ME-497**	KP135332	KP135218	KP134847	–
Hyphoderma litschaueri	**FP-101740-Sp**	KP135295	KP135219	KP134868	KP134965
Hyphoderma medioburiense	**FD-335**	KP135298	KP135220	KP134869 (fragment)	KP134966
Hyphoderma mutatum	**HHB-15479-Sp**	KP135296	KP135221	KP134870	KP134967
Hyphoderma setigerum	**FD-312**	KP135297	KP135222	KP134871	–

(*continued on next page*)

Table 3 – (*continued*)

Taxon	Strain/Specimen	5.8s	28s(LSU)	RPB1	RPB2
Hyphodermella rosae	**FP-150552**	KP134978	KP135223	KP134823	KP134939
Irpex lacteus	**FD-9**	KP135026	KP135224	KP134806	–
Ischnoderma resinosum	**FD-328**	KP135303	KP135225	KP134884	KP134972
Junghuhnia luteoalba	**FP-105786-Sp**	KP135320	KP135226	KP134887	KP134963
Junghuhnia nitida	**FP-105195-Sp**	KP135323	KP135227	KP134888	KP134964
Laetiporus sulphureus	**AFTOL-769**	DQ221108.1	AY684162.1	KP134881	DQ408118.1
Leptoporus mollis	**TJV93–174**	EU402584.1	EU402510.1	–	–
Lopharia cinarescens	**FP105043**	JN165019.1	JN164813.1	JN164840.1	JN164874.1
Meripilus giganteus	**FP-135344-Sp**	KP135307	KP135228	KP134873	KP134894
Meruliopsis alnbostramineus	**HHB-10729**	KP135051	KP135229	KP134787	KP134926
Meruliopsis sp.	**FD-497**	KP135054	–	KP134786	–
Meruliopsis sp.	**FD-278**	KP135057	KP135205	KP134796	KP134927
Obba rivulosa	**FP-135416-Sp**	KP135309	KP135208	KP134878	KP134962
Panus lecomtei	**HHB-11042-Sp**	KP135328	KP135233	KP134877	KP134970
Phaeophlebiopsis caribbeana	**HHB-6990**	KP135415	KP135243	KP134810	KP134931
Phaeophlebiopsis ignerii	**FD-425**	KP135418	–	KP134811	–
Phaeophlebiopsis peniophoroides	**FP-150577**	KP135417	KP135273	KP134813	KP134933
Phaeophlebiopsis sp.	**HHB-6542-Sp**	KP135413	KP135248	KP134812	KP134932
Phanerochaete sp.	**HHB-11463**	KP134994	KP135235	KP134797	KP134892
Phanerochaete sp.	**HHB-18104**	KP135003	KP135254	KP134798	KP134917
Phanerochaete sp.	**RLG-13408-Sp**	KP135020	KP135257 (fragment)	KP134801	KP134920
Phanerochaete allantospora	**KKN-111**	KP135038	KP135238	KP134791 (fragment)	KP134923 (fragment)
Phanerochaete arizonica	**RLG-10248-Sp**	KP135170	KP135239	KP134830	KP134949
Phanerochaete australis	**HHB-7105-Sp**	KP135081	KP135240	KP134840	KP134957 (fragment)
Phanerochaete burtii	**HHB-4618**	KP135117	KP135241	KP134829	KP134945
Phanerochaete calotricha	**Vanhanen-382**	KP135107	–	KP134826	–
Phanerochaete carnosa	**HHB-9195-Sp**	KP135129	KP135242	KP134831 (fragment)	KP134946
Phanerochaete chrysosporium	**HHB-6251-Sp**	KP135094	KP135246	KP134842	KP134954
Phanerochaete citrinosanguinea	**FP-105385**	KP135100	KP135234	KP134824	KP134941
Phanerochaete ericina	**HHB-2288**	KP135167	KP135247	KP134834	KP134950
Phanerochaete exilis	**HHB-6988**	KP135001	KP135236	KP134799	KP134918
Phanerochaete krikophora nom. prov.	**HHB-5796-Sp**	KP135164	KP135268	KP134837	KP134953
Phanerochaete laevis	**HHB-15519-Sp**	KP135149	KP135249	KP134836	KP134952
Phanerochaete magnoliae	**HHB-9829-Sp**	KP135089	KP135237	KP134838	KP134955
Phanerochaete pseudomagnoliae	**PP-25**	KP135091	KP135250	KP134839	KP134956
Phanerochaete pseudosanguinea	**FD-244**	KP135098	KP135251	KP134827	KP134942
Phanerochaete rhodella	**FD-18**	KP135187	KP135258	KP134832	KP134948
Phanerochaete sanguinea	**HHB-7524**	KP135101	KP135244	KP134825	KP134943
Phanerochaete sanguineocarnosa	**FD-359**	KP135122	KP135245	KP134828	KP134944
Phanerochaete sordida I	**FD-241**	KP135136	KP135252	KP134833	KP134947
Phanerochaete sordida II	**FD-106**	KP135070	KP135253	KP134841	KP134958
Phanerochaete subceracea	**FP-105974-R**	KP135162	KP135255	KP134835	KP134951
Phanerochaete xerophila	**HHB-8509-Sp**	KP134996	KP135259	KP134800 (fragment)	KP134919
Phebia acerina	**FD-301**	KP135378	KP135260	KP134862	–

Phlebia brevispora	**HHB-7030 SS6**	KP135387	–	fgenesh1_kg.11_#_110_#_isotig00485	fgenesh1_kg.4_#_90_#_isotig04043
Phlebia centrifuga	**HHB-9239-Sp**	KP135380	KP135262	KP134844	KP134974
Phlebia chrysocreas	**HHB-6333-Sp**	KP135358	KP135263	KP134861	KP134908
Phlebia floridensis	**HHB-9905**	KP135383	KP135264	KP134863	KP134899
Phlebia fuscoatra	**HHB-10782-Sp**	KP135365	KP135265	KP134857	KP134910 (fragment)
Phlebia nothofagi	**HHB-4273-Sp**	KP135369	KP135266	KP134858	KP134911 (fragment)
Phlebia radiata	**AFTOL-484**	AY854087.1	AF287885.2	AY864881.1	AY218502.2
Phlebia setulosa	**HHB-6891-Sp**	KP135382	KP135267	KP134864	KP134901
Phlebia sp.	**HHB-17984**	KP135359	KP135261	KP134860	KP134907
Phlebia sp.	**FD-427**	KP135342	–	KP134849	–
Phlebia sp.	**HHB-18295**	KP135405	KP135269	KP134814	KP134938
Phlebia tremellosa	**FD-323**	–	KP135231	KP134856	KP134900
Phlebia uda	**FP-101544-Sp**	KP135361	KP135232	KP134859	KP134909
Phlebiopsis 'ravenelii'	**FP-110129**	KP135362	KP135274	KP134850	KP134898
Phlebiopsis crassa	**KKN-86-Sp**	KP135394	KP135215	KP134820	KP134928
Phlebiopsis flavidoalba	**FD-263**	KP135402	KP135271	KP134819	KP134959
Phlebiopsis gigantea	**FP-70857-Sp**	KP135390	KP135272	KP134821	KP134930
Phlebiopsis sp.	**FP-102937**	KP135391	KP135270	KP134822	KP134929
Pirex concentricus	**OSC-41587**	KP134984	KP135275	KP134843	KP134940
Rhizochaete americana	**FP-102188**	KP135409	KP135277	KP134815	KP134934
Rhizochaete filamentosa	**HHB-3169-Sp**	KP135410	KP135278	KP134818	KP134935
Rhizochaete radicata	**FD-123**	KP135407	KP135279	KP134816	KP134937
Rhizochaete sp.	**FP-150712**	KP135408	KP135280	KP134817	KP134936
Scopuloides rimosa 1	**RLG-5104**	KP135351	KP135283	KP134852	KP134904
Scopuloides rimosa 2	**HHB-7042**	KP135350	KP135282	KP134853	KP134903
Scopuloides rimosa 3	**HHB-15484**	KP135352	KP135281	KP134851	KP134902
Scopuloides sp.	**FP-150473**	KP135355	KP135284	KP134854	KP134905
Scopuloides sp.	**FP-102935**	KP135353	KP135285	KP134855	KP134906 (fragment)
Skeletocutis chrysella	**FD-305**	KP135310	KP135286	KP134890	KP134976
Spongipellis delectans	**HHB-10489-Sp**	KP135301	KP135287	KP134876	KP134969
Spongipellis pachyodon	**FD-314**	KP135302	KP135288	KP134875	KP134971
Steccherinum sp.	**FD-26**	KP135322	KP135289	KP134889	–
Stereum hirsutum	**AFTOL-492**	AY854063.1	AF393078.1	AY864885.1	AY218520.2
Terana caerulea	**FP-104073**	KP134980	KP135276	KP134865	KP134960
Trametes betulina	**HHB-9942**	JN164983.1	JN164794.1	JN164822.1	JN164860.1
Trametes cinabarina	**AFTOL-772**	DQ411525.1	AY684160.1	JN164847.1	–
Trametes elegans	**FP-105679-sp**	JN164944.1	JN164799.1	JN164833.1	JN164861.1
Trametes versicolor	**FP-135156**	JN164919.1	JN164809.1	JN164825.1	JN164850.1
Trametopsis cervina	**AJ-185**	JN165020.1	JN164796.1	JN164839.1	JN164877.1
Tyromyces chioneus	**FD-4**	KP135311	KP135291	KP134891	KP134977
Xanthoporus higanensis	**AFTOL-774**	AY789078.1	AY684166.1	AY788846.1	AY780935.1

Table 4 – Support for phylogenetic clades recognized in *Polyporales* among different types of analyses and datasets. PHL = phlebioid clade, RPOL = residual polyporoid clade, CPOL = core polyporoid clade, ANTR = *Antrodia* clade, TYR = *Tyromyces* clade, CINER = *Cinereomyces* clade.

Dataset	Ingroup taxa	Characters	Number of nodes supported in at least one analysis	Number of nodes supported in both analyses	Clades					
					PHL	RPOL	CPOL	ANTR	TYR	CINER
5.8s + LSU	127	2038	87 (69 %)	69 (54.8 %)	–/1	78/0.96	–/1	–/–	100/1	100/1
RPB1	125	1398	90 (72.6 %)	75 (60.5 %)	–/1	–/–	96/1	–/0.97	100/1	100/1
RPB2	104	1188	64 (62.1)	51 (49.5 %)	–/–	–/–	90/1	–/0.97	100/1	100/1
5.8s + LSU + RPB1	127	3436	108 (85.7 %)	89 (70.6 %)	99/1	–/0.99	100/1	–/0.98	100/1	100/1
5.8s + LSU + RPB1 + RPB2	127	4624	104 (82.5 %)	92 (73 %)	93/1	87/1	100/1	79/1	100/1	100/1

36–62 × 3–7.7 μm. Basidiospores sub-ellipsoid to ellipsoid, occasionally slightly curved, smooth, thin-walled, Melzer (–), acyanophilous, (3) 4–5.5 (7) × 2.3–3.5 (3.8) μm (Q = 1.2–2.3, avQ = 1.8).

Habitat and distribution

Phanerochaete sanguineocarnosa has been collected on hardwood branches on the ground and is associated with white rot. The species range so far includes areas of the Northeast USA, reaching Michigan and North Carolina (Fig 2).

Remarks

Specimens of *Phanerochaete sanguineocarnosa* looks macroscopically similar to specimens of *Phanerochaete carnosa*, a close relative of the species. However, *P. sanguineocarnosa* has extensive hyphal cords (Fig 6N), and the KOH reaction turns the fruitbody brown to slightly olive-green, while in *P. carnosa* the green-brown colour is very distinct and hyphal cords are rare. Additionally, *P. sanguineocarnosa* stains the wood red-orange similar to *Phanerochaete sanguinea* and this was seen in several samples (Fig 6B), which has never been reported for *P. carnosa*. At the microscopic level, the cystidia of *P. sanguineocarnosa* look similar in size and shape to those of *P. carnosa* and they are smaller than those seen in *P. sanguinea*, but larger than the cystidia of *Phanerochaete pseudosanguinea* and *Phanerochaete citrinosanguinea*. Additionally, *P. sanguineocarnosa* has very frequent clamp connections at the subicular hyphae in comparison to *P. carnosa* or *P. sanguinea*. Furthermore, it grows on hardwood, while *P. sanguinea* and *P. carnosa* grow mostly on softwood.

Additional specimens examined

United States of America: Massachusetts: Worcester Co., Uxbridge, Cormier Woods, on the bark and decorticated parts of hardwood branch, 23 September 2012, FD-523; Worcester Co., Sturbridge, Wells State Park, on decorticated hardwood, 31 August 2011, FD-359; Worcester Co., Uxbridge, Cormier Woods, on hardwood bark, 23 September 2012, FD-520; Worcester Co., Uxbridge, Cormier Woods, on the bark of hardwood branch, 23 September 2012, FD-521; Worcester Co., Uxbridge, Cormier Woods, on decorticated hardwood branch on the ground, 23 September 2012, FD-524. Michigan: Gogebic Co. Black Oak Quadrangle, Ottawa National Forest, Sylvania Wilderness, hardwood branches, 22 August 1997, DLC97-964. North Carolina: Macon Co., Nantahala National Forest, Glen Falls-Blue Valley trail, on *Quercus* sp., 16 July 1969, HHB-2189.

Phanerochaete pseudosanguinea Floudas & Hibbett **sp. nov.** (Figs 1, 2, and 7)

MycoBank No.: 811926.

Etym.: from the Greek 'ψευδός' which means 'lying, false' and *sanguinea*, due to the resemblance of the species to *Phanerochaete sanguinea*.

Holotype: **United States of America**: Florida: Leon Co., Tallahassee, Lake Overstreet area, on fallen hardwood branch, 24 August 2009, FD-244 (CFMR!), nrITS KP135098.

Fruitbody resupinate, smooth, membranaceous, detachable, and extensively cracking, 0.2–0.3 mm. Colour ranging from reddish yellow (5 YR 6/8) in young part of the fruitbody to light red (2.5 YR 7/6) or dark red (2.5 YR 4/8) in mature areas. Margin fibrillose and yellow (10 YR 8/6) to cordonic and hyphal

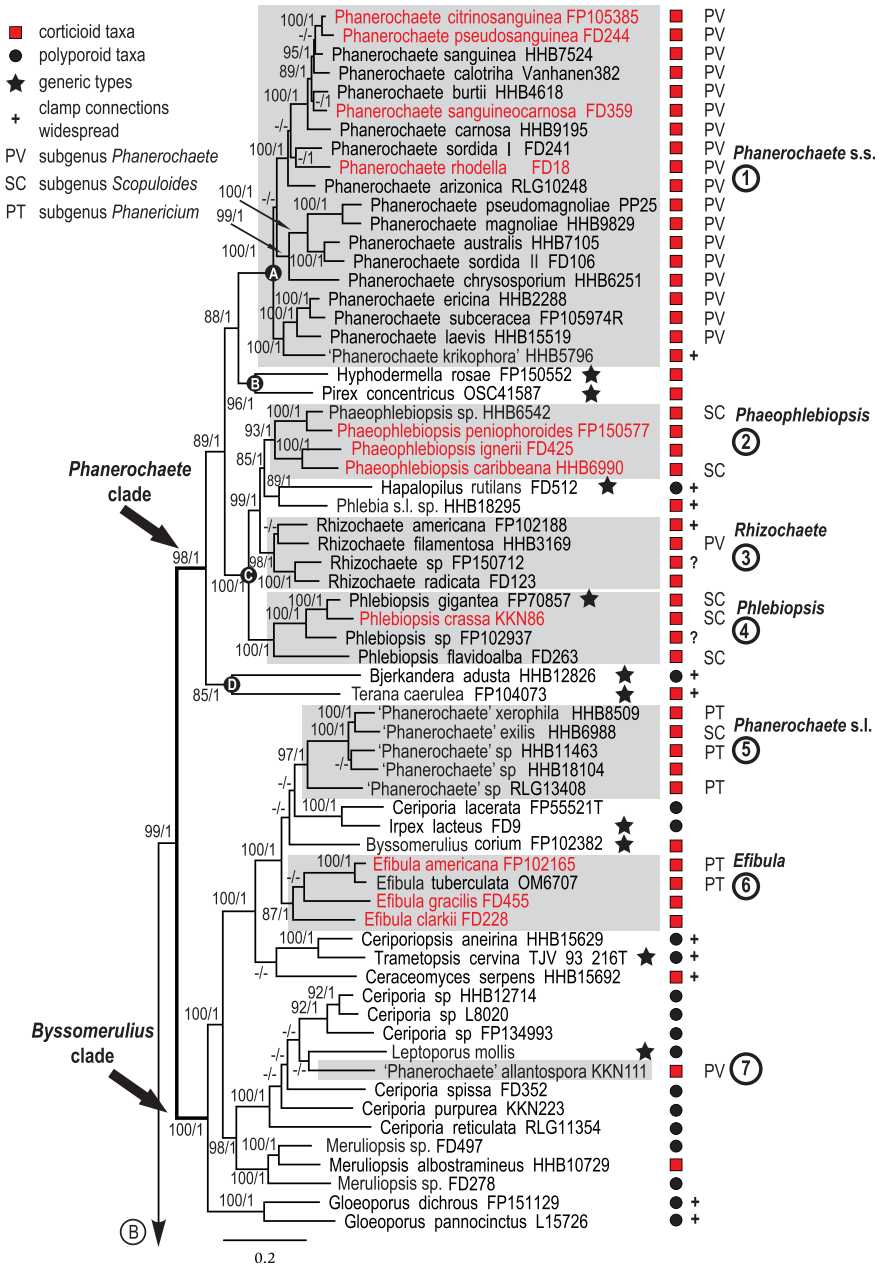

Fig 1 – Maximum likelihood phylogeny of the concatenated 5.8s, nLSU, RPB1, and RPB2 datasets. Bootstrap values ≥75 (left values) and posterior probabilities ≥ 0.95 from the Bayesian analysis (right values) are shown for each node. Areas shaded in grey (1–9) represent the nine lineages where phanerochaetoid fungi are found in the phlebioid clade. Clades labeled A–D represent the *Phanerochaete sensu stricto*, *Hyphodermella*, *Phlebiopsis*, and *Bjerkandera* clades, respectively. The area shaded in light green indicates *Phlebia sensu stricto*. Names in red font represent new combinations or newly described taxa. Names in quotation marks represent provisional names or uncertain identifications. Questionmarks indicate taxa with unknown clamp connections distribution. *Climacodon septentrionalis* has been labeled with (+) because of its variable clamp connections distribution. The placement of taxa in subgenera is sensu Burdsall (1985). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cords light red (2.5 YR 7/6). Context lighter in colour, but with pink or reddish tones. KOH turns the fruitbody olivaceous brown and partly translucent, the colour eventually fades to light brown.

Hyphal system monomitic, subiculum and subhymenium distinct, most hyphae covered by resinous yellow material that makes their observation in water difficult. Addition of 5 % KOH dissolves most of the resinous material, aiding observation of the sample. Subicular hyphae loosely arranged, sparsely branched, mainly in parallel orientation, wider that the rest of the fruitbody, 4–7 μm, thick-walled, with large crystals, double clamps occasionally present. Subhymenium

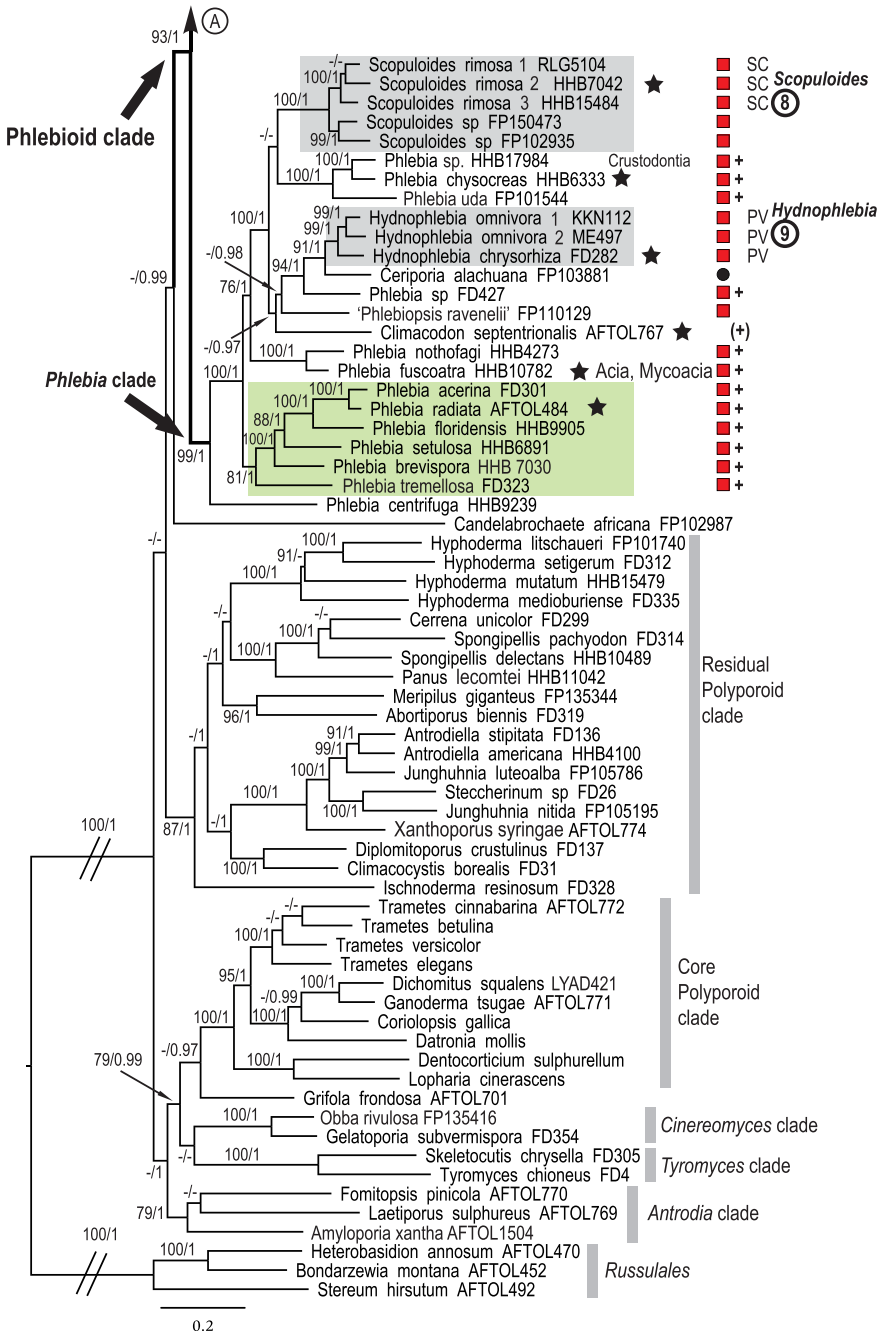

Fig 1 – (*continued*).

composed of frequently branched, thin-walled, short in length hyphae, 4–5 μm. Cystidia arising from the hymenium, occasionally projecting above the basidia, some almost hyphoid in appearance, thin-walled, getting narrower towards the top, but obtuse, with occasionally secondary septa, naked, but some covered with resinous material in water, 25–45 × 3.5–5 μm. Basidia almost cylindrical, with four sterigmata, 18–28 × 4–5 μm, without basal clamp. Basidiospores ellipsoid to subcylindrical and then occasionally curved, smooth, thin-walled, Melzer (–), acyanophilous, (3) 4–5.5 (6) × 2–2.5 (3) μm (Q = 1.5–2.8, avQ = 2).

Habitat and distribution

Known only from the three samples from Florida and Maryland. *Phanerochaete pseudosanguinea* grows on fallen hardwood branches and is associated with white rot.

Remarks

Macroscopically, the species resembles *Phanerochaete sanguinea* and the substrate was stained red-orange on both collected specimens. However, the cystidia of *Phanerochaete pseudosanguinea* are much smaller than those of *P. sanguinea* and the samples were collected on hardwood.

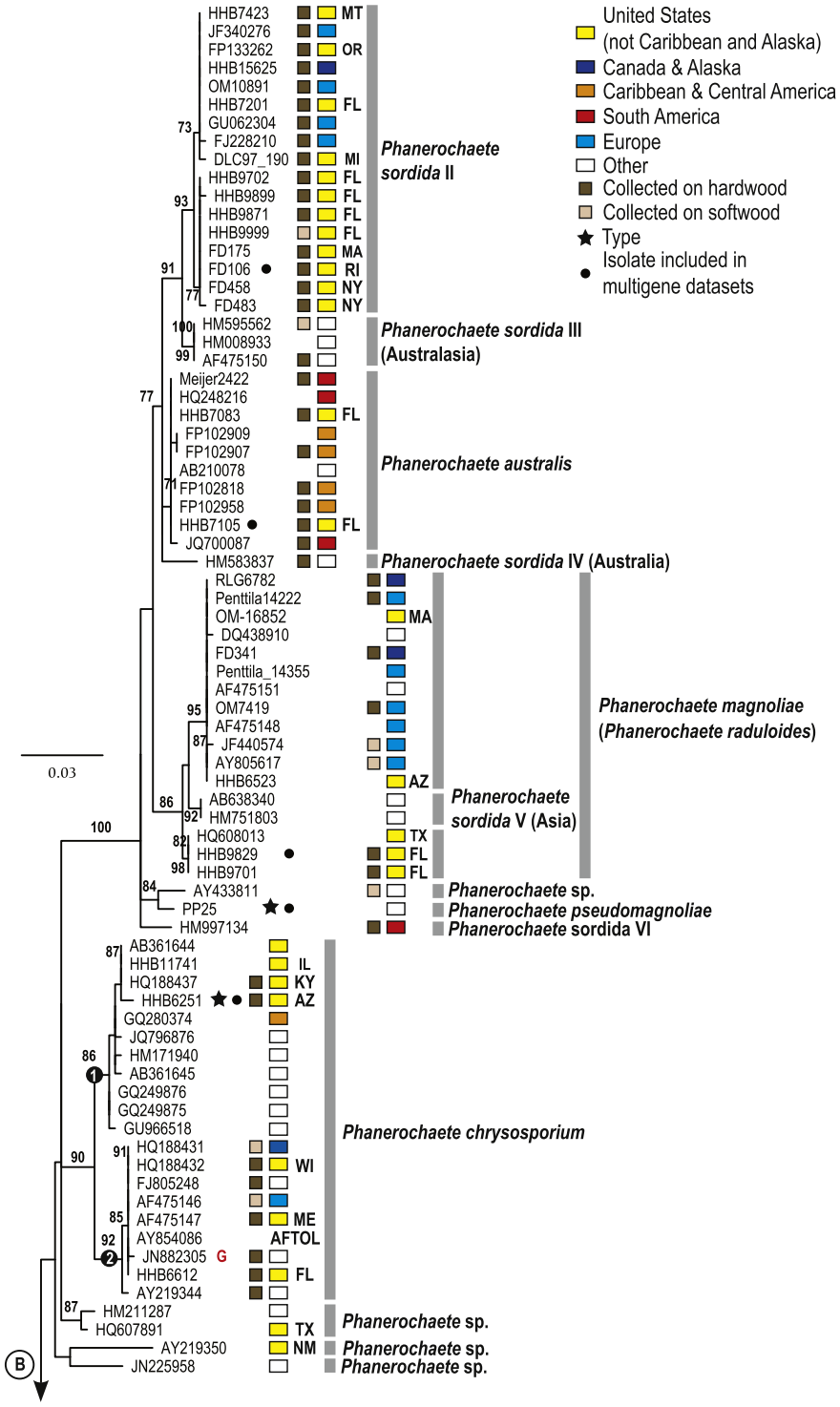

Fig 2 – Maximum likelihood analysis of ITS sequences of *Phanerochaete sensu stricto*. Bootstrap values ≥70 are shown. Names in red represent newly described taxa. An ITS sequence of *P. gigantea* was used as outgroup. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Microscopically, the species shares similarities with *Phanerochaete calotricha*, especially at the shape of cystidia and the size of spores. However, *P. pseudosanguinea* has fruitbodies with prominent pink-red colours and positive KOH reaction. Moreover, *P. calotricha* is closely related to *P. pseudosanguinea*, but has different ITS sequence (Fig 2).

Additional specimens examined

United States of America: Florida: Leon Co., Tallahassee, Lake Overstreet area, on fallen hardwood branch, 24 August 2009, FD-240.

Phanerochaete citrinosanguinea Floudas & Hibbett **sp. nov.** (Figs 1, 2, and 8)

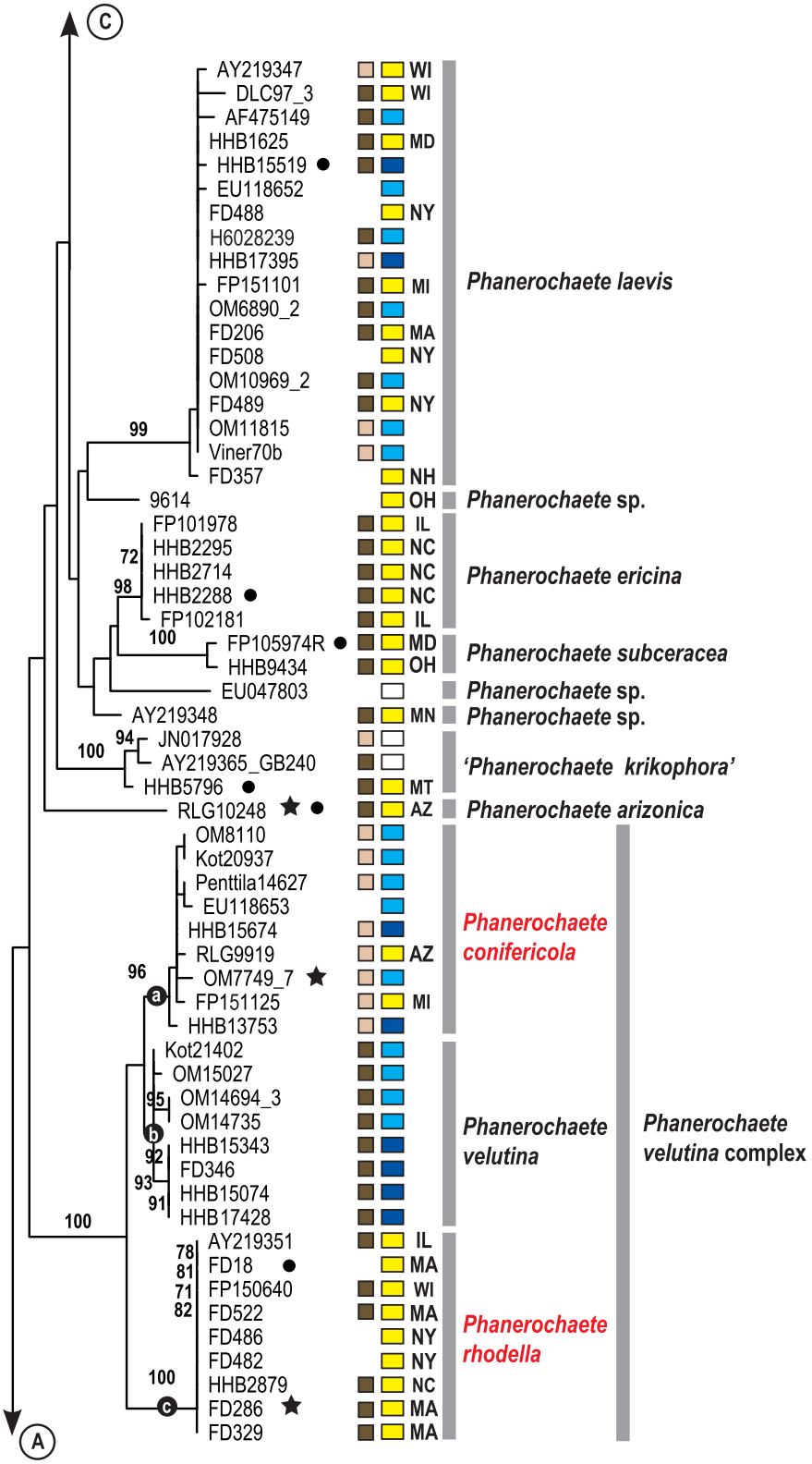

Fig 2 – (continued).

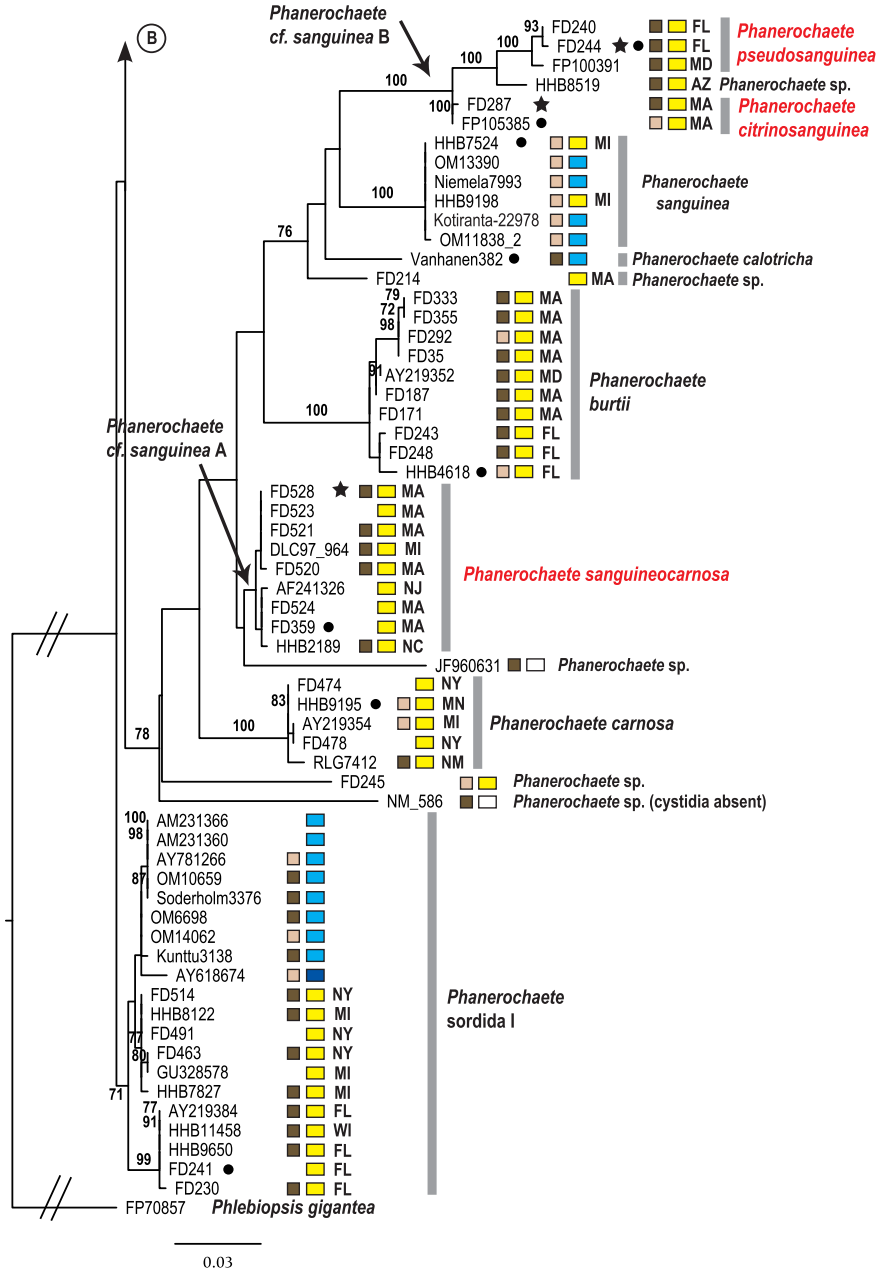

Fig 2 – (*continued*).

MycoBank No.: 811927.

Etym.: from the Greek 'κίτρινο;' (citrino) for yellow and *sanguinea*, due to the similarity of the species to *P. sanguinea*, but the distinct yellow shades.

Holotype: **United States of America**: Massachusetts: Worcester Co., Harvard Forest, hardwood branch on the ground, 13 September 2009, FD-287 (CFMR!), nrITS KP135095.

Fruitbody resupinate, smooth, slightly detachable and slightly cracking, 0.1–0.2 mm, developing from radial tufts of fibrils or cordons. Colour of fruitbodies in mature areas mostly yellow (2.5Y 8/6) to reddish yellow (5 YR 6/8). Margin extensively fibrillose, extending to small hyphal cords of reddish yellow (5 YR 6/8) colour. KOH stains the fruitbody permanently brown. Subiculum well-developed, concolorous with hymenophore.

Hyphal system monomitic, subiculum and subhymenium distinct. Subicular hyphae moderately branched, loosely arranged, in mostly parallel arrangement, with crystals that do not dissolve in KOH, 3–10 μm wide, thin to thick-walled. Simple clamp connections frequently seen, while double clamp connections were occasionally seen. Subicular hyphae thin-walled, frequently bending, but relatively loosely arranged, 2–3 μm wide. Basidia cylindrical, with four sterigmata, 26–30 × 4.5–4.8 μm, without basal clamp. Cystidia naked, arising from the hymenium and subhymenium, thin-walled and small in size, fragile, getting narrower towards the top or more or less cylindrical, occasionally with secondary septa, less than half of the cystidium projecting above the hymenium, 31–48 × 2.3–4.8. Basidiospores ellipsoid to

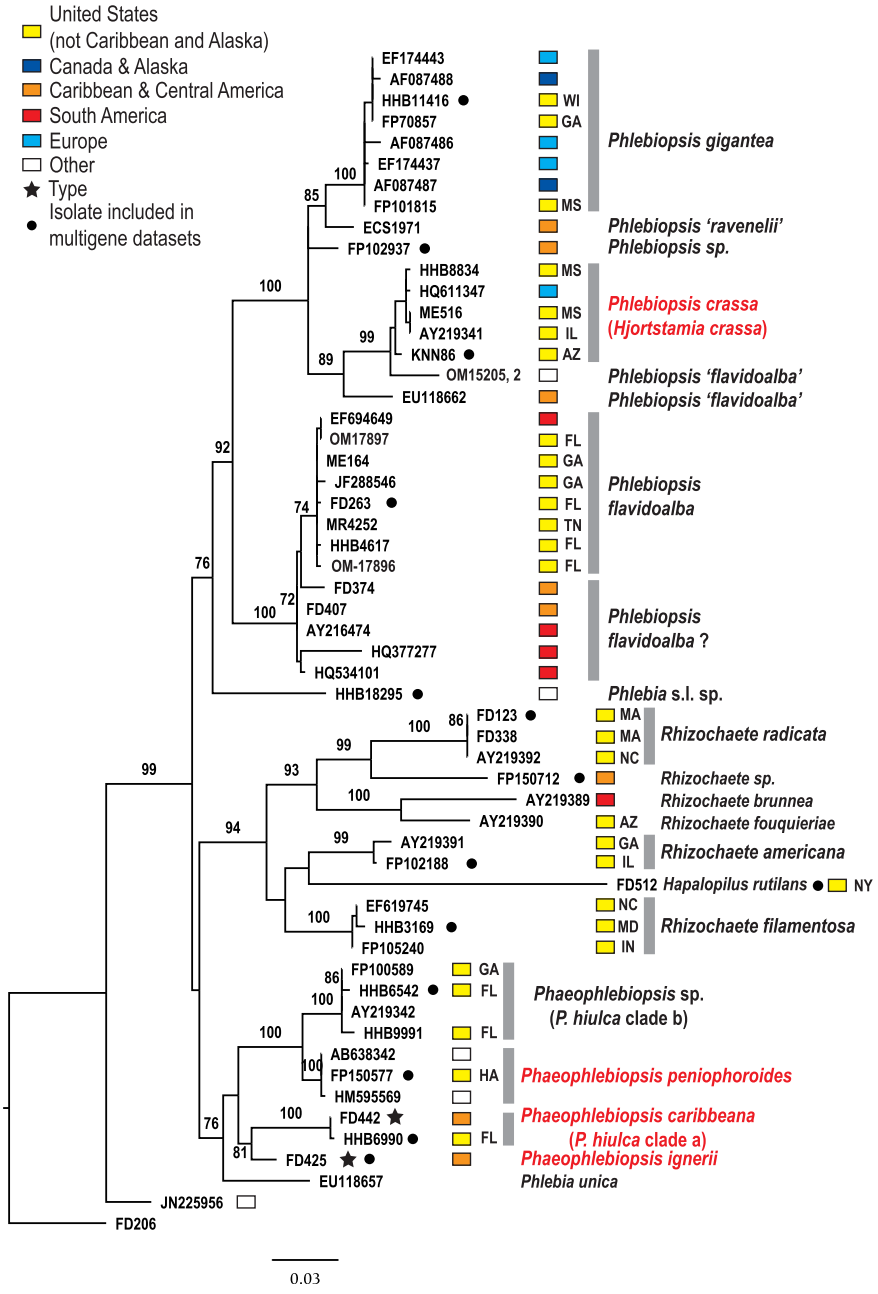

Fig 3 – Maximum likelihood analysis of ITS sequences from the *Phlebiopsis* clade. Bootstrap values ≥70 are shown. Names in red represent newly described taxa or new combinations. An ITS sequence of *P. laevis* (FD-206) was used as outgroup. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

subcylindrical, sometimes very slightly curved, smooth, thin-walled, Melzer (–), acyanophilous, 3.5–5.5 (6.5) × 2.3–3 μm (Q = 1.3–2.4, avQ = 1.9).

Habitat and distribution

Known only from Massachusetts (USA). It grows on hardwood and softwood and is associated with white rot.

Remarks

Even though we have seen only the type of the sample, the ITS sequences support that *Phanerochaete citrinosanguinea* is a separate species in the *Phanerochaete sanguinea* complex (Fig 1, ITS). The species shares with *P. sanguinea* the red-orange staining of colonized wood, associated with insect galleries (Fig 8A). However, the cystidia of *P. citrinosanguinea* are much smaller than those seen in *P. sanguinea*, the fruitbody has more yellow than red colours, and the samples were collected on hardwood and softwood. The species is more similar to *v pseudosanguinea*, but in *P. citrinosanguinea* spores are on average narrower than *P. pseudosanguinea*, the colour of the specimens is more yellow than red and the ITS similarity between the two species is 95.4–95.7 %. So far, *P. citrinosanguinea* has been found only in Massachusetts, but more sampling may extend the distribution range of the species.

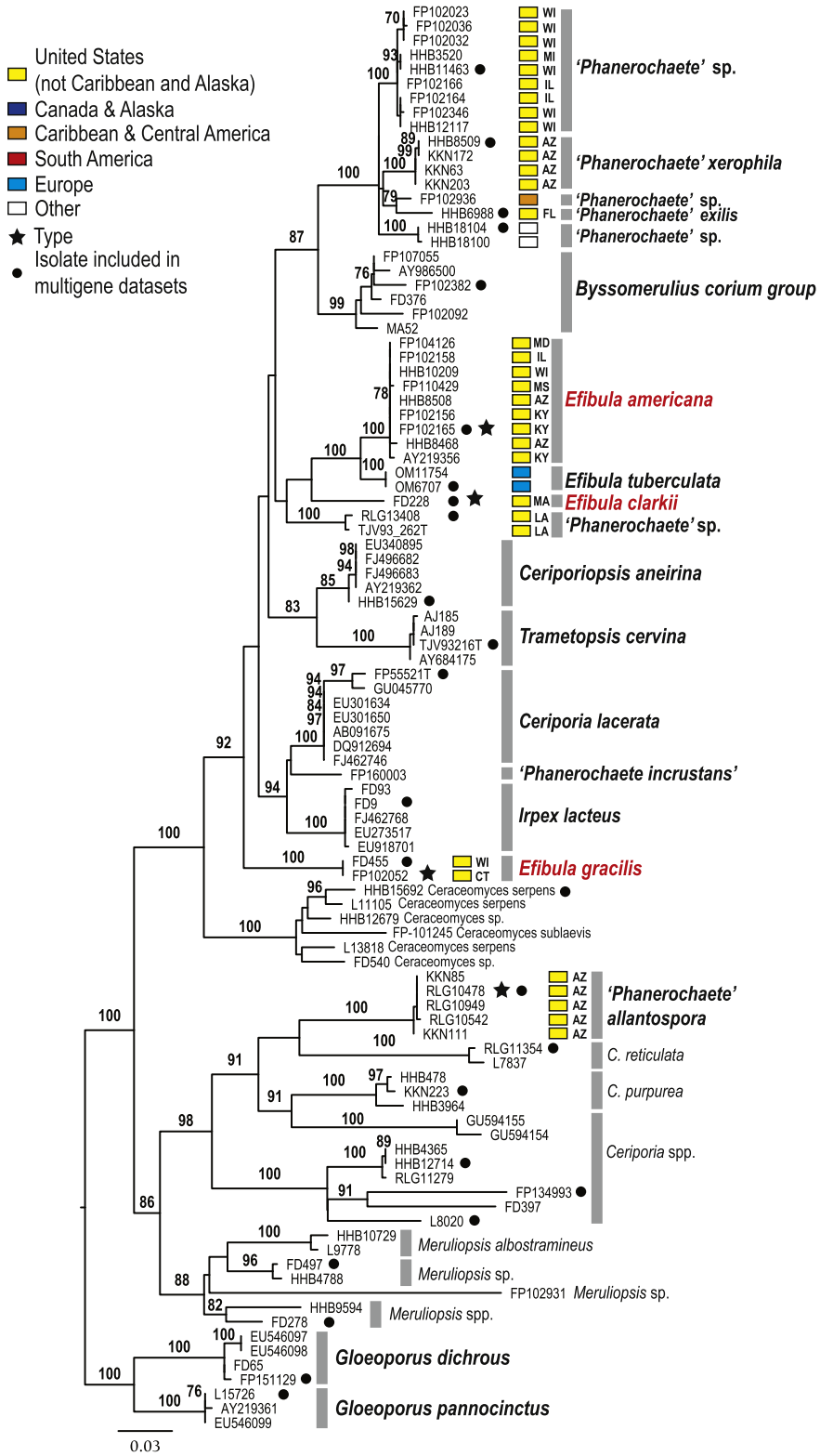

Fig 4 – Maximum likelihood analysis of ITS sequences from the *Byssomerulius* clade. Bootstrap values ≥70 are shown. Names in red represent newly described taxa or new combinations. *Gloeoporus* ITS sequences were used as outgroup. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

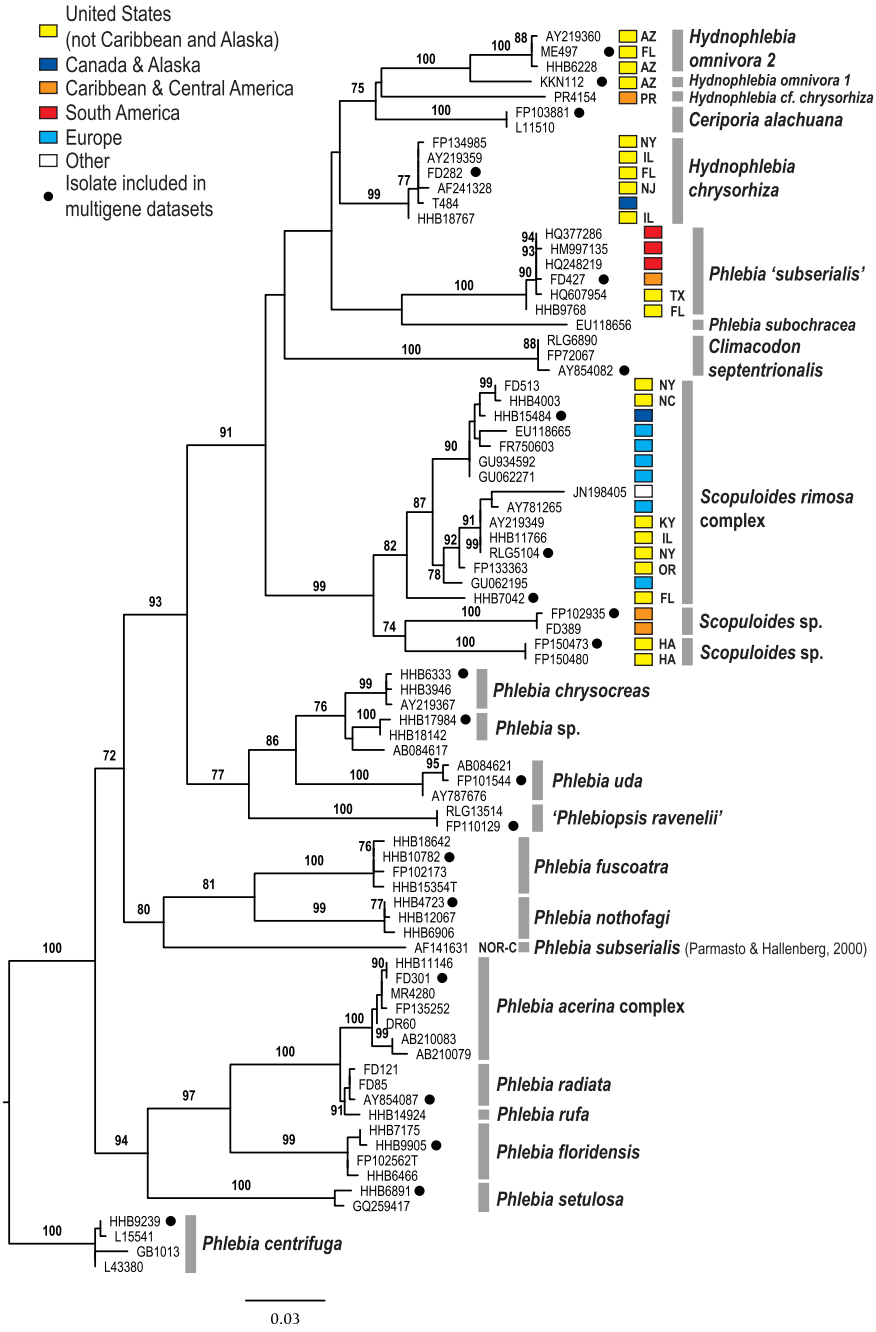

Fig 5 – Maximum likelihood analysis of ITS sequences from the *Phlebia* clade. Bootstrap values ≥75 are shown. The ITS sequences of *Phlebia centrifuga* were used as outgroup.

Phanerochaete rhodella (Peck) Floudas & Hibbett **comb. nov.** (Figs 1, 2, and 9)

MycoBank No.: 811934.

Basionym: *Corticium rhodellum* Peck Annual Report on the New York State Museum of Natural History 42: 124 (1889).

Holotype: **United States of America**: New York: Orleans Co., Lyndonville, C. E. Fairman, NYSf2591 (holotype of *C. rhodellum*, NYS!).

Epitypus hic designatus: **United States of America**: Massachusetts: Worcester Co., Harvard Forest, on bark and decorticated areas of hardwood, 13 September 2009, FD-286 (CFMR!), nrITS KP135191.

Fruitbody resupinate, smooth, with velutinous appearance, adnate, 0.1–0.2 mm, in older sampling extensively cracking and slightly decorticating at the margin. Colour of the fruitbodies variable, pink (5 YR 7/4, 5 YR 7/3, 5 YR 8/3), pinkish grey (5 YR 7/2, 5 YR 6/2), light grey (5 YR 7/1), light reddish brown (5 YR 6/3), reddish brown (5 YR 5/3), reddish grey (5 YR 5/2), yellowish red (5 YR 5/6), and reddish yellow (7.5 YR 7/8). Margin lighter in colour, mostly fading out, hyphal cords very rare, reddish yellow (5 YR 7/6). KOH (+) reaction of the fruitbody variable ranging from just a mark to a permanent brown-red staining. Context well-developed, separated in two zones, the subhymenium zone dark in colour, while the

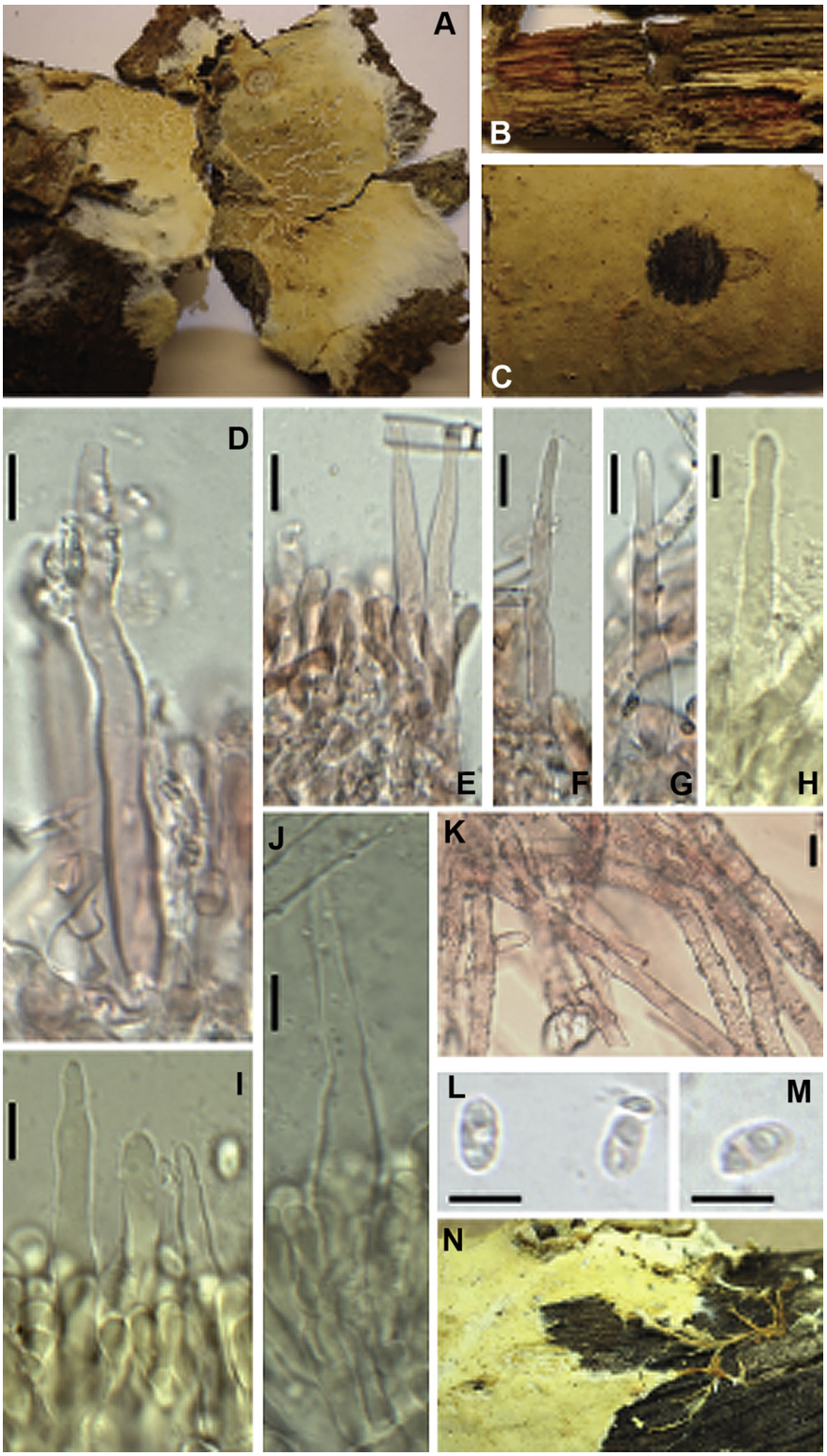

Fig 6 – *Phanerochaete sanguineocarnosa*. (A): young fruitbody (holotype), (B): substrate stained red, (C): reaction of mature fruitbody in 5 % KOH, (D–J): cystidia, (K): subicular hyphae with crystals, (L–M): basidiospores, n: hyphal cords ((A, H, I, J): FD-528, holotype; (B): FD521; (C), n: FD-523; (D–G), (L–M): FD-359, (K): HHB-2189). Scale bars: for cystidia and subicular hyphae = 10 μm, for basidiospores = 5 μm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

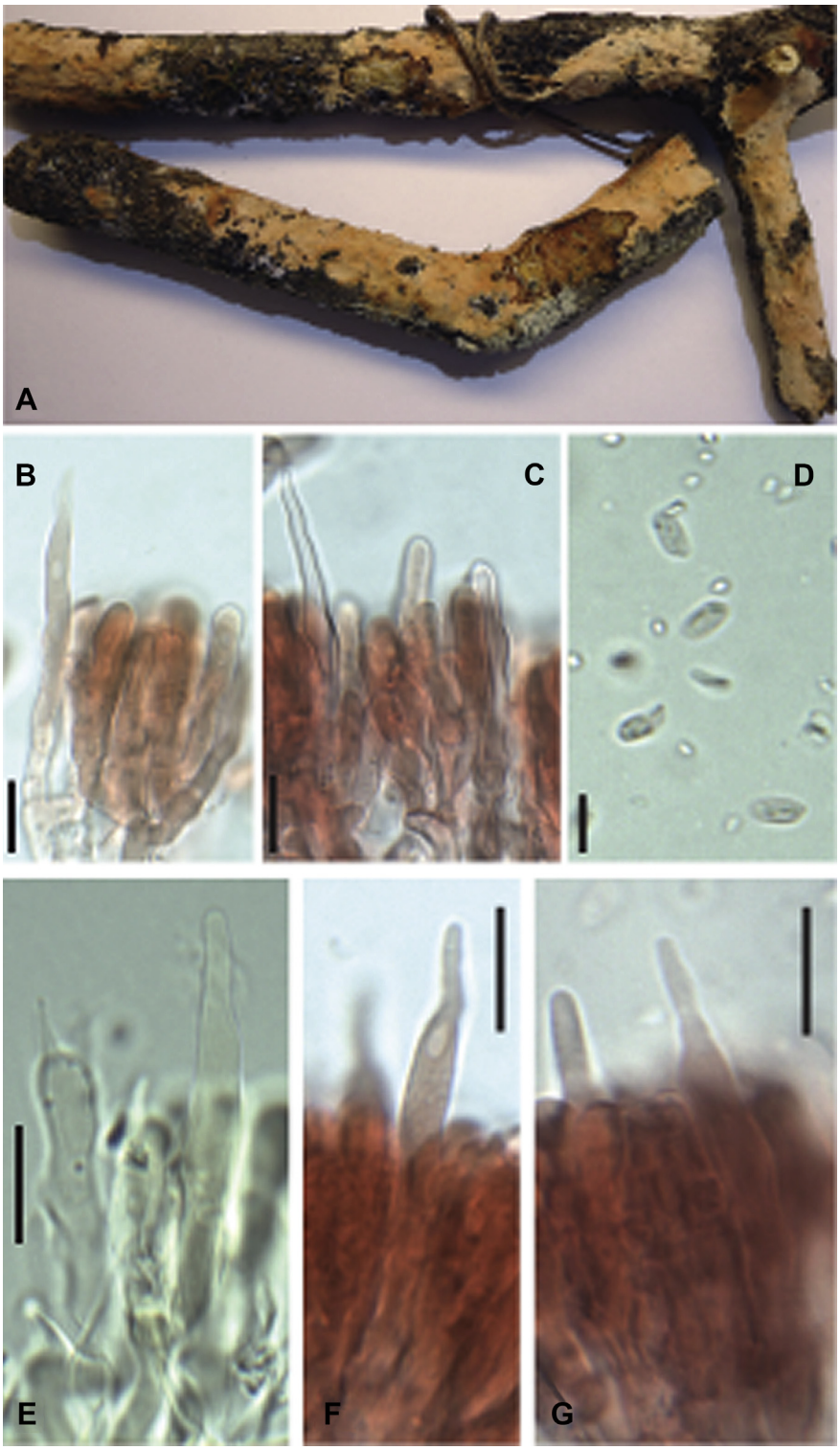

Fig 7 – *Phanerochaete pseudosanguinea*. (A): holotype (FD-244) with 5 % KOH reaction, (B-C) and (E–G): basidioles, basidia, and cystidia, (D): basidiospores. All microphotographs represent the holotype (FD-244). Scale bars: for cystidia = 10 μm, for basidiospores = 5 μm.

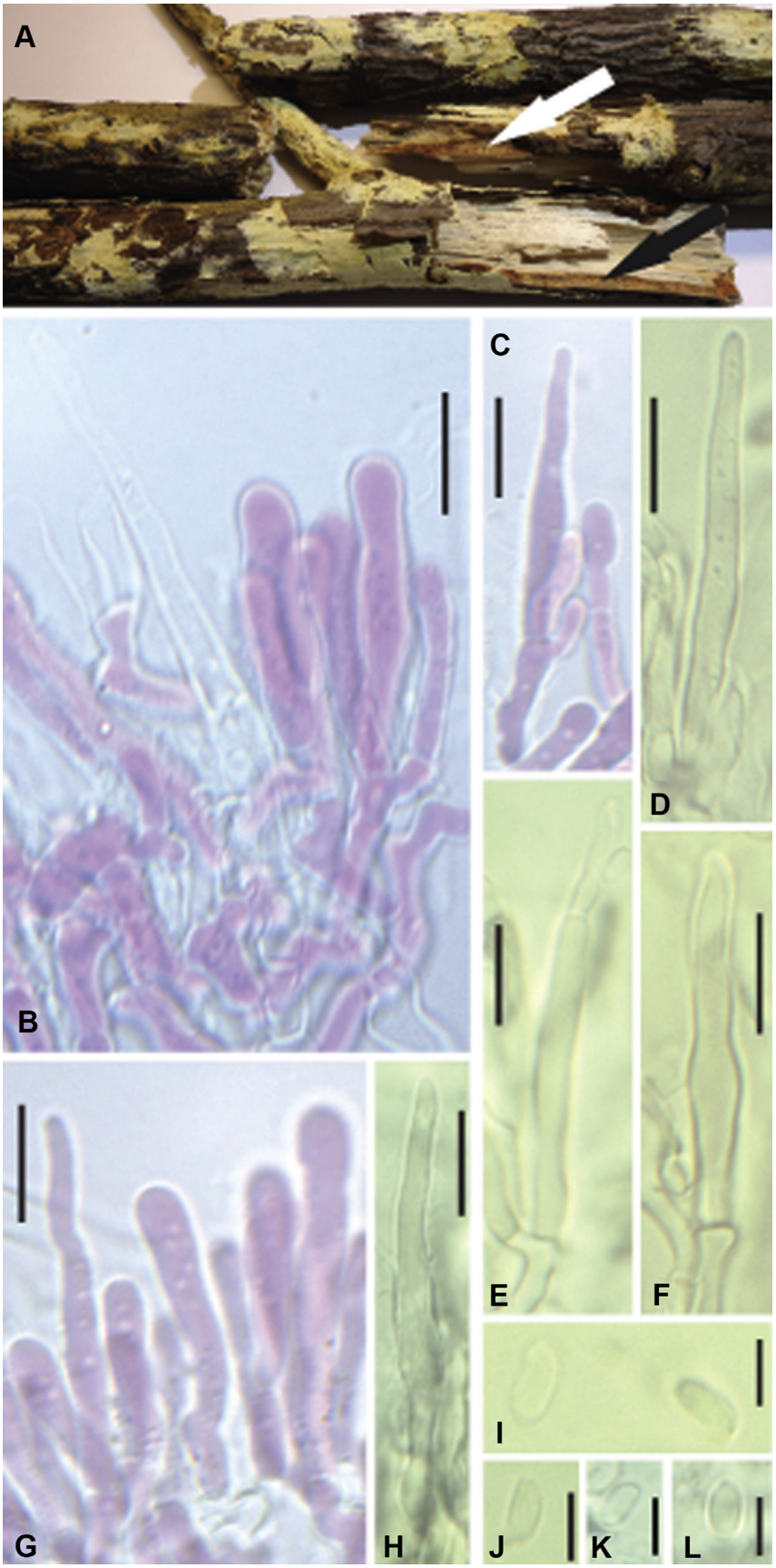

Fig 8 – *Phanerochaete citrinosanguinea*. (A): holotype (FD-287), arrows show the red-orange staining of the substrate, (B–H): cystidia and basidioles, (I–L): basidiospores. All microphotographs represent the holotype (FD-287). Scale bars: for cystidia = 10 μm, for basidiospores = 5 μm.

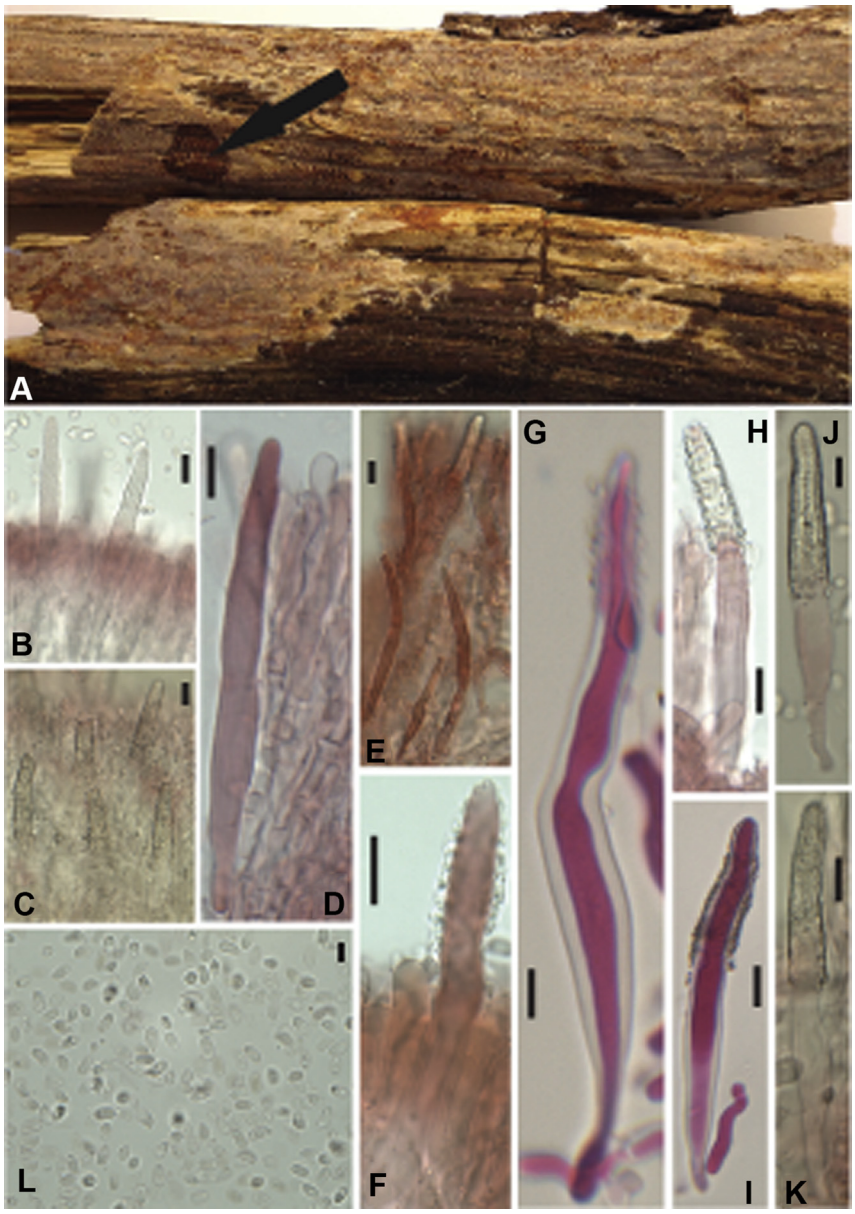

Fig 9 – *Phanerochaete rhodella*. (A): epitype (FD-286) and 5 % KOH reaction (arrow), (B–K): cystidia, (L): basidiospores. ((A-C, E, J, K, L): FD-286; (D, F, H): FD-18; (G, I): FD-482). Scale bars: for cystidia = 10 μm, for basidiospores = 5 μm.

subicular zone white. The zones are more distinct in well-developed samples.

Hyphal system monomitic, subhymenium and subiculum distinct. Subiculum well-developed and subicular hyphae slightly thick-walled to thick-walled, (5) 6–10 μm, sometimes anastomizing and not completely in loose arrangement, but mostly with parallel orientation, and occasional double clamp connections. Subhymenium well-developed, and in mature samples with multiple layers, moderately compact, consisting of frequently branched hyphae, 4–7 μm, thin-walled, with frequent anastomoses and without clamps. Basidia almost cylindrical with four sterigmata, 25–32 μm. Cystidia arising from the subhymenium, one third to half of their length projecting above the basidia, sword-like, or widening in the middle, with narrow base and obtuse or slightly narrower top. Cystidia naked in young specimens, others covered with yellowish crystalline material, thick-walled (60) 75–97 (117) × (5) 7–10 (14) μm. Basidiospores mostly ellipsoid, thin-walled, Melzer (–), acyanophilous, (4.5) 5–5.5 (7.5) × (2.0) 2.5–3.0 (3.8) μm (Q = 1.45–2.35, avQ = 1.88).

Habitat and distribution

Phanerochaete rhodella is currently found at the eastern part of North America, from North Carolina to Massachusetts and New York and west to Illinois and Wisconsin. When identified, the substrate of *P. rhodella* is hardwood.

Remarks

The east North American samples examined here have more frequently a pink-red (or vinaceous) tint, which we believe

was observed by Peck (1889), when he described *Corticium rhodellum*. Peck had seen specimens from New York and Pennsylvania, areas that this species is currently found. In his description he gave the metuloids smaller (40–51 × 10–11 μm), but our measurements of cystidia from the type agree with other samples from eastern North America. *Phanerochaete rhodella* is very similar to *Phanerochaete velutina* and *Phanerochaete conifericola* (Table 5). We believe that the only way to separate the species is the substrate (for comparison to *P. conifericola*), the size of cystidia (on average shorter for *P. rhodella*), the location of the samples and their ITS sequences. The designation of an epitype was made because of the age of the holotype. We had access to a very small piece of the holotype, which was very fragile and made observations difficult. Therefore, we think that an epitype will serve better for morphological observations of the species.

Additional specimens examined

United States of America: Massachusetts: Worcester Co., Rutland, Rutland State Park, White Hall Pond, on decayed piece of wood, 30 August 2008, FD-18; Worcester Co., Mt. Wachusett, on hardwood bark, 29 September 2010, FD-329; Worcester Co., Uxbridge, Cormier Woods, large hardwood branch on the ground, 23 September 2012, FD-522. New York: holotype of *Corticium rhodellum*, Orleans Co., Lyndonville, C.E. Fairman, NYSf2591; Essex Co., Adirondacks Ecological Center, north side of Wolf Lake, well-decayed pieces of wood, 15 August 2012, FD-482, FD-486. North Carolina: Macon Co., Nantahala National Forest, Cliffside Vista trail, on *Acer*, 12 August 1969, HHB-2879. Wisconsin: LaCrosse Co., West Salem, N6334 CTH C, Rhyme farm, on *Castanea dentata*, 21 September 2001, FP-150640.

Phanerochaete conifericola Floudas & Hibbett **sp. nov.** (Figs 1, 2, and 10)

MycoBank No.: 811928.

Etym.: *conifericola* comes from the word 'conifer' and the Greek 'κολλώ' meaning 'to stick on something', referring to the coniferous substrate of the species.

Holotype: **Finland**: Vilppula: on a fallen tree crown of *Picea abies*, 1–3 October 2003, H6012813 (OM-7749,7) (H!), nrITS KP135173.

Fruitbody resupinate, smooth, adnate, 0.1–0.3 mm. Colour of the fruitbody pale red (2.5 YR 7/2), reddish yellow (7.5 YR 7/6), pinkish white (7.5 YR 8/2), very pale brown (10 YR 8/4), strong brown (7.5 YR 5/6), only slightly cracking. Margin fibrillose, white. Hyphal cords, when present, large, easily observed, white. KOH reaction variable, mostly leaving a brown stain, but in some samples the colour fades (Fig 10A).

Hyphal system monomitic, subicular hyphae slightly thick-walled to thick-walled, with occasional double clamp connections, (6) 8–10 (12) μm, but subiculum relatively narrow. Subhymenium well-developed, compact, consisting of frequently branched hyphae without clamps, 3–5 μm. Basidia cylindrical to clavate, with four sterigmata, 24–50 × 4.4–7.5 μm. Cystidia arising from the subhymenium, one third to half of their length projecting above the basidia, sword-like, or widening in the middle, with a narrow base, naked in young specimens, but mature cystidia with yellowish crystalline material, thick-walled, with obtuse or more frequently slightly subulate top, (73) 83–115 (142) × (6) 7–11 (16) μm. Basidiospores mostly ellipsoid, thin-walled, Melzer (–), acyanophilous,

Table 5 – Summary of major characteristics among *Phanerochaete velutina*, *P. conifericola*, and *P. rhodella* in the *P. velutina* complex.

	Fruitbody colour	Rhizomorphs	KOH reaction	Substrate	Geographic region	Spores (μm)	Cystidia (μm)
P. velutina	Colour more beige to light yellow, pinkish tones less frequent	Frequent	Moderate, faints to a light brown scar	Hardwood, mostly bark	Boreal North America and Europe	(4.5) 5.0–5.5 (7.3) × (2.5) 2.8–3.3 (3.8)	(84) 94–122 (140) × (6.5) 7.5–10 (11.5)
P. rhodella	Pinkish tones frequently present to dark vinaceous	Rare	Strong, but variable, more persistent staining of red or brown shades	Hardwood, mostly decorticated	Eastern North America, temperate distribution	(4.5) 5.0–5.5 (7.5) × (2.0) 2.5–3.0 (3.8)	(60) 75–97 (117) × (5) 7–10 (14)
P. conifericola	Similar to *P. velutina*	Rare	Strong, brown persistent staining	Softwood, mostly decorticated	Mostly boreal North America and Europe	4.8–5.5 (6.5) × (2.5) 3.0–3.5 (4.0)	(73) 83–115 (142) × (6) 7–11 (16)

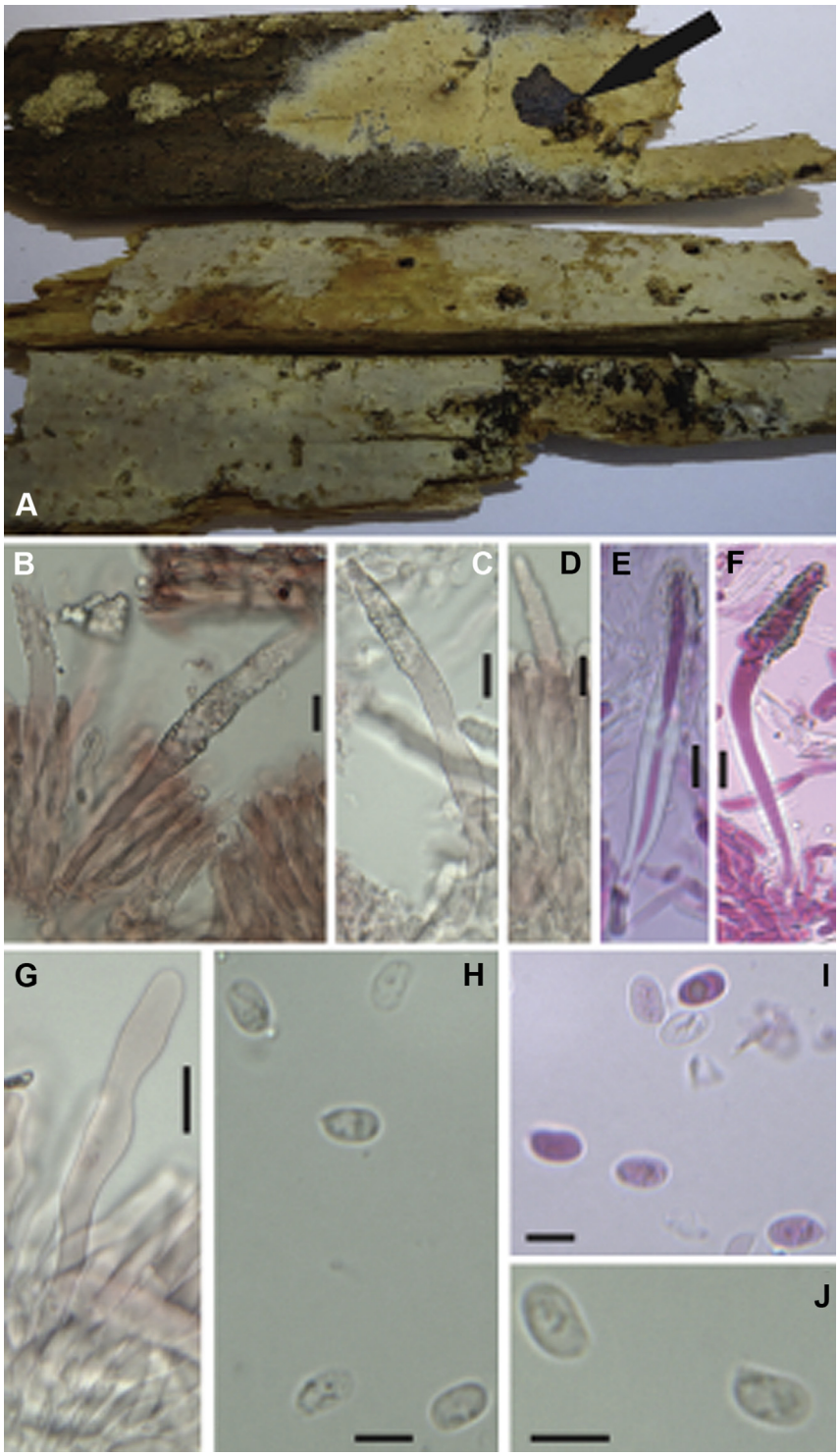

Fig 10 – *Phanerochaete conifericola*. (A): holotype (OM-7749,7) and 5 % KOH reaction (arrow), (B–G): cystidia, (H–J): basidiospores. ((F, I): OM-7749,7; (B, E, H, J): RLG-9919; (C, D, G): FP-151125). Scale bars: for cystidia = 10 μm, for basidiospores = 5 μm.

(4.0) 4.8–5.5 (6.5) × (2.5) 3.0–3.5 (4.0) μm (Q = 1.2–2.17, avQ = 1.62).

Habitat and distribution

Phanerochaete conifericola has boreal distribution in the north hemisphere and is associated with white rot on softwood (Fig 2).

Remarks

Phanerochaete velutina, *Phanerochaete conifericola*, and *Phanerochaete rhodella* are three very similar species that are difficult to separate based on macromorphology. The three species share similar spore size, except for *P. conifericola* for which we measured slightly wider spores (Table 5). A more prominent difference relies on the smaller size cystidia of *P. rhodella*

in comparison to the other two species. The combination of ITS data (Fig 2, section 4.1), the substrate, and the geographic area can aid the identification of samples. The exact range of the three species is not known, but as more ITS sequences become available, we should be able to form a better idea about the species distribution.

Additional specimens examined

Finland: Somerniemi, on burned *Picea abies* log, 19–22 October 2003, H6028235 (OM-8110 & Emilia Pippola (G7)); Lieska, fallen and artificially charred *Pinus sylvestris*, 23–25 September 2003, H6028236 (Reijo Penttilä 14 627) **d Russia**: Sverdlovsk region, North Ural, Molebni Kamen, on corticated *Abies*, 12 August 2005, H7017352 (Kotiranta-20937) **d United States of America**: Alaska: Chicagoff island, Pavlov Harbor, on well-decayed *Picea sitchensis*, 25 July 1991, HHB-13753. Arizona: Pima Co., Coronado National Forest, Santa Catalina Mts., Mt Lemmon, on *Pinus ponderosa*, 18 September 1970, RLG-9919. Wisconsin: Emmet Co., Mackinaw city, Sturgeon Bay, on *Tsuga*, 15 September 2007, FP-151125.

Phlebiopsis clade

Phaeophlebiopsis Floudas & Hibbett **genus nov.**

MycoBank No.: 811929.

Etym.: From the Greek word 'φαιός' (phaeos), which means 'grey' and *Phlebiopsis*, due to the overall similarity to *Phlebiopsis*, but the grey-brown colour of the fruitbodies for some species.

Holotype: *Phaeophlebiopsis caribbeana* Floudas & Hibbett **sp. nov.**

Fruitbodies, resupinate, adnate, smooth, and hard, beige to pale brown to grey-brown and occasionally with purple tints, slightly or extensively cracking, periphery either concolorous or brown with very thin white margin, subiculum beige or brown, no hyphal cords.

Hyphal system monomitic, without or very rare clamp connections, thin or thick-walled, occasionally with crystals. Subhymenium and subiculum not easy to distinguish from each other, basal tissue relatively thin and then hyphae brown, thick-walled and brittle, or basal tissue well-developed and then hyphae agglutinated, hyaline and very difficult to separate, reminding *Phlebiopsis*. Cystidia of metuloid appearance, broad in the middle, subulate or more rarely obtuse or clavate, with narrow base, protruding above the hymenium or enclosed in the fruitbody, always thick-walled, very young cystidia can have scarce encrustation, but most cystidia have heavy encrustation of usually coarse crystals. Basidia clavate to subcylindrical, thin-walled, without clamp, forming a dense layer. Basidiospores 3.5–5.5 × 2–3.5 μm, subcylindrical, ellipsoid or ovoid, usually one side flattened and very slightly bent, thin-walled, inamyloid.

Remarks

Phaeophlebiopsis is very similar to *Phlebiopsis* and their separation is not easy. The decision for the introduction of the genus is based on the strongly supported phylogenetic separation of *Phaeophlebiopsis* and *Phlebiopsis* by the presence of *Hapalopilus rutilans*, *Rhizochaete*, and *Phlebia*-like species (Figs 1 and 3).

Phaeophlebiopsis ignerii Floudas & Hibbett **sp. nov.** (Figs 1, 3 and 11).

MycoBank No.: 811930.

Etym.: from 'Igneri', a group of native people who colonized the Lesser Antilles during the Pre-Colombian times.

Holotype: **Unites States of America**: St. John, USVI, Little Lameshur Bay, very close to the coast, underneath bark of dead hardwood, 8 February 2012, FD-425 (CFMR!), nrITS KP135418.

Fruitbody resupinate, very thin (less than 0.2 mm), adnate, mat, light gray (7.5 YR 7/1) to gray (7.5 YR 6/1), slightly cracking to reveal the brown subiculum. Margin abrupt, strong brown (7.5 YR 5/6), turning white at the very thin outer part.

Hyphal system monomitic, without clamps. Subhymenium and subiculum not easily distinguished. Hyphae below the hymenium agglutinated, perpendicular to the substrate, brown, and thick-walled. Tissue deeper in the fruitbody compact and hyphae anatomizing, frequently bending, difficult to separate and fragile, brown in colour or rarely hyaline, mostly thick-walled, 2–4.5 (6) μm. Large crystals widespread in the fruitbody. Cystidia metuloids, broad in the middle, thick-walled, with a slightly subulate top, but apparently few cystidia more clavate, projecting above the hymenium, or embedded in the fruitbody, the latter frequently with brown colour, 1/3 to ½ of the length of the cystidia covered with coarse crystals, 31–51 × 7–11.7 μm. Basidia forming a compact layer, with 4 sterigmata, around (12) 16–22 × 4–5 μm, without basal clamp. Basidiospores ovoid to ellipsoid, hyaline, thin-walled, Melzer (–), acyanophilous, 3.5–5.0 × 2.5–3.5 (4) μm (Q = 1.2–1.5, avQ = 1.33).

Habitat and distribution

Growing inside the bark of a dead hardwood tree. Type of rot unknown. Known only from St. John, USVI.

Remarks

The species looks macroscopically similar to *Phaeophlebiopsis caribbeana*, however, the cystidia of *Phaeophlebiopsis ignerii* are in general larger than those of *P. caribbeana*. The ITS sequences of the two species are an adequate way for their separation.

Phaeophlebiopsis caribbeana Floudas & Hibbett **sp. nov.** (Figs 1, 3, and 12).

MycoBank No.: 811931.

Etym.: From the Caribbean region, where the type was collected.

Holotype: **Unites States of America**: US VI: St. John, L'Esperance trail, on dead hardwood, 9 February 2012, FD-442 (CFMR!), nrITS KP135416.

Fruitbody resupinate, smooth, dull, less than one mm thick, adnate, very hard, extensively cracking, gray (10 YR 6/1), but in old samples the colour may fade to very pale brown (10 YR 8/2). Subiculum very thin, brown. Margin abrupt.

Hyphal system monomitic, hyphae thin-to thick-walled, subicular hyphae agglutinated, brown, very difficult to separate, almost perpendicular, clamps absent or rarely seen. Cystidia abundant, metuloids, some with brown walls, slightly projecting above the hymenium, or embedded in the fruitbody, about ½ of the cystidium covered with crystals, thickening in the middle, the top subulate or less frequently blunt,

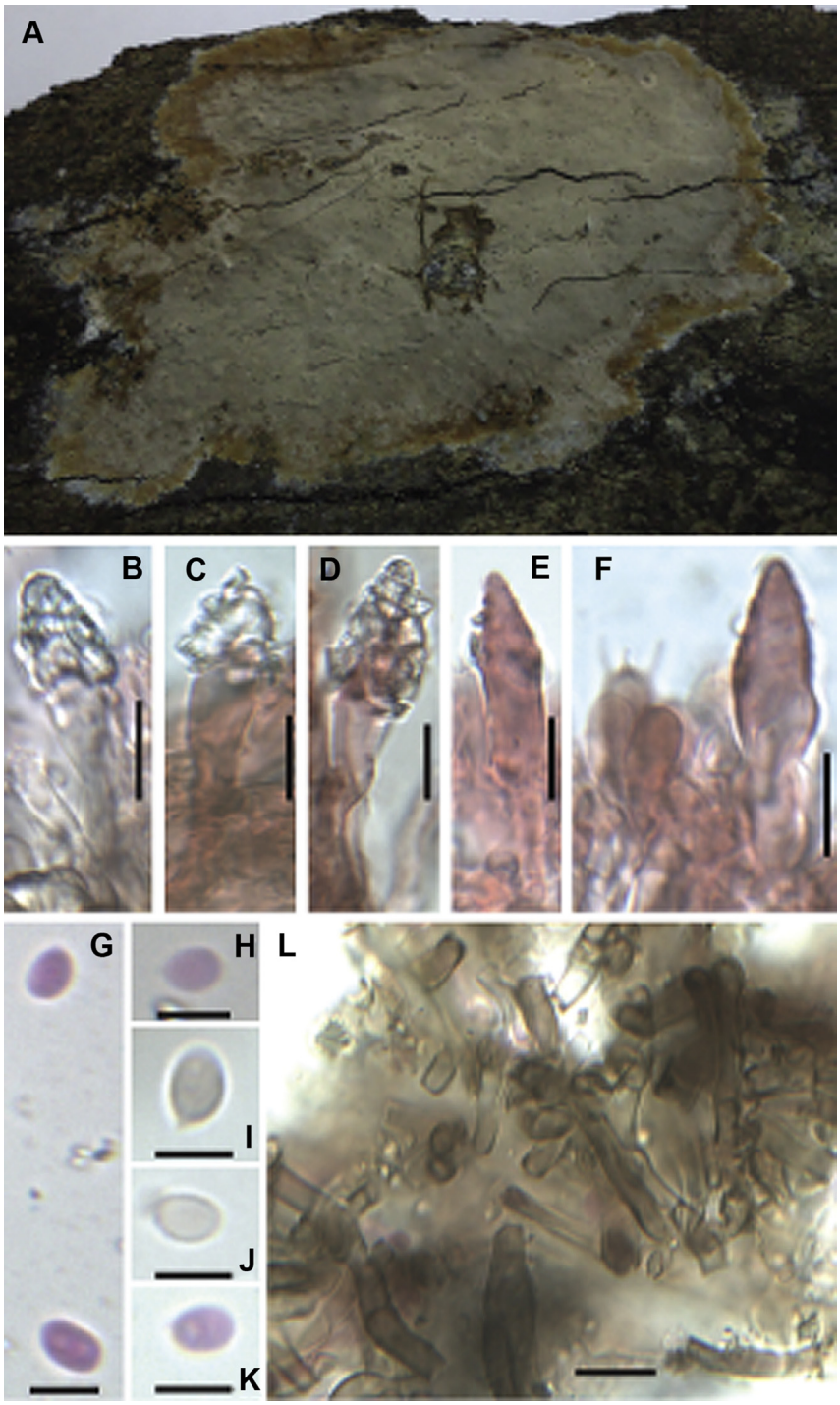

Fig 11 – *Phaeophlebiopsis ignerii*. (A): holotype (FD-425), (B–F): cystidia, (G–K): basidiospores, (L): subicular hyphae. All microphotographs represent the holotype (FD-425). Scale bars: for basidiospores = 5 μm, for other elements = 10 μm.

22–38 × 5–10 μm. Basidia with four sterigmata, 14–20 × 4 μm, without a basal clamp. Basidiospores difficult to find, ovoid to ellipsoid, hyaline, thin-walled, Melzer (–), 3.5–4.8 × 2–3 μm.

Habitat and distribution

Currently know only from St. John, VI, and the Everglades, FL. Both specimens were collected on bark of hardwood, associated with white-rot.

Remarks

We examined the type of *Peniophora hiulca* (W. A. Murrill & E. L. Murrill 71) in addition to our samples in order to decide which clade could represent *P. hiulca*. It seems that none of the specimens examined here agrees with the morphological characteristics of the type. Clade 'a' (Fig 3) does not represent *P. hiulca*, because the cystidia and spores are smaller, the subiculum and some cystidia of the fresh

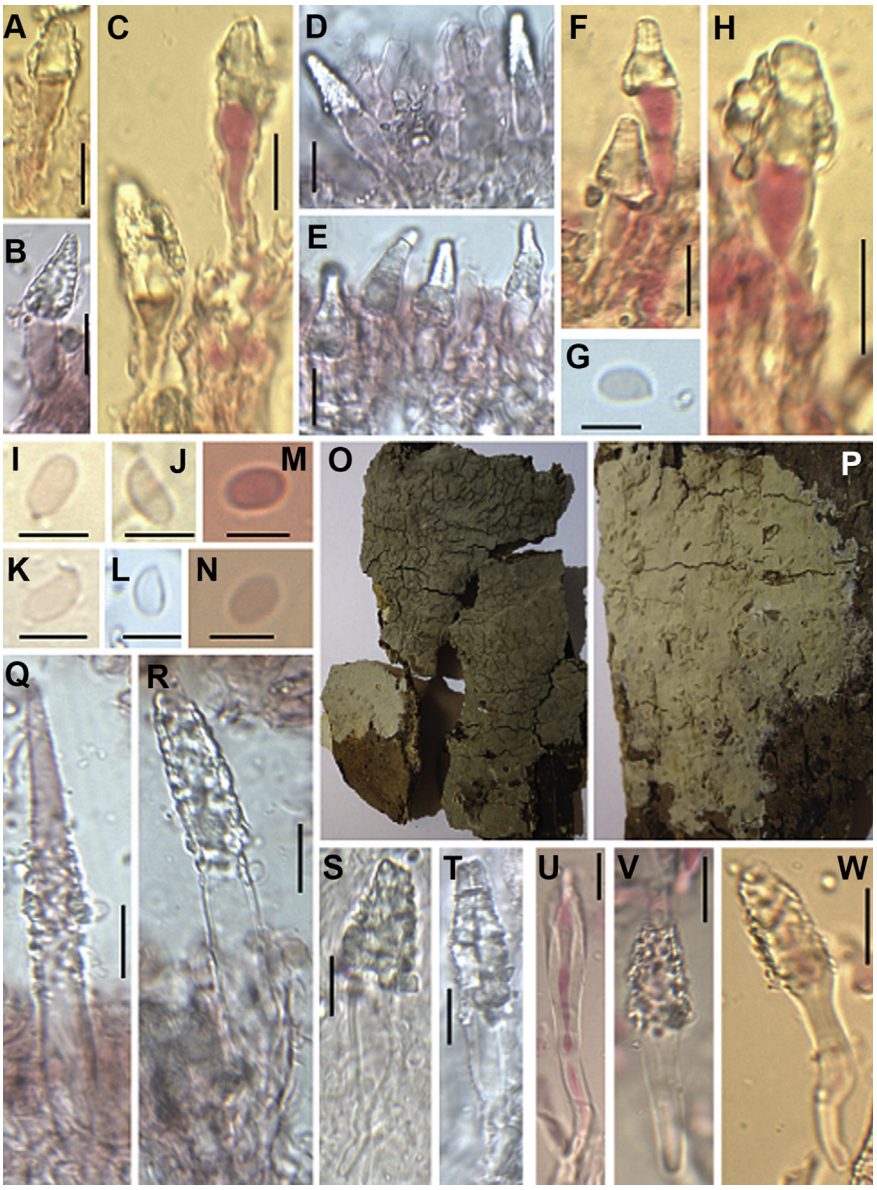

Fig 12 – Cystidia (A–H), basidiospore (G), and fruitbodies (O–P) of *Phaeophlebiopsis caribbeana*. Basidiospores (I–L) and cystidia (Q–T) of *Phaeophlebiopsis* sp. (*P. cf. hiulca* 2). Basidiospores (M–N) and cystidia (U–W) from the holotype of *Peniophora hiulca* (W. A. Murrill & E. L. Murrill, 71). ((A-C, F, H, O): holotype FD-442; (D, E, G, P): HHB-6990; (I-K, Q, R): FP-100589; (L, S, T): HHB-9991). Scale bars: for cystidia = 10 μm, for basidiospores = 5 μm.

sample were brown and the fruitbody much thinner in comparison to the type and the other samples under the name *P. hiulca* examined here. Clade 'b' (Fig 3) agrees in some aspects with the type. In our samples the cystidia are 42–62 (80) × 6.9–10.3 μm, and the spores have size around 4.6–5.4 × 2.4–3 μm. Both descriptions from Burt (1925) and Punugu *et al.* (1980) and also our measurements from the type agree with these measurements. However, while the samples we examined have thin, *Phlebiopsis*-like subiculum/subhymenium (agglutinated, difficult to open), the type of *P. hiulca* has a well-developed subiculum that it was not particularly difficult to open, the hyphae were not agglutinated, and we even saw unbranched thick-walled hyphae that remind skeletal hyphae.

We considered the possibility that the specimens of clade 'b' could represent *Phlebiopsis ravenelii*, because of their overall similarity and adjacent geographic area; *P. ravenelii* was described from South Carolina and the samples of clade b were collected in Georgia and Florida. However, it seems that there is confusion regarding the identity of that species. Burdsall (1985) described the metuloid cystidia larger (50) 70–100 × (8) 10–15 (20) μm than Punugu *et al.* (30–45 × 12–20 μm) (1980), but both authors had checked the isotype. Cooke himself (1879) provided only the size of the metuloids for the type (30–35 × 8–10 μm) to be closer to the measurements of Punugu *et al.* (1980) (but still those metuloids were narrower). ITS data generated in this study (Figs 3 and 5) suggests that the identity of *P. ravenelii* is unclear. The

confusion is greater given the synonymy of *P. ravenelii* and *Phlebiopsis roumeguerii* (the latter was described from European material, Burdsall 1985; Bernicchia & Gorjón 2010). The smaller size of metuloids described by Cooke (1879) and Punugu *et al.* (1980), we think that this species is not *P. ravenelii*. The confusion will be resolved when ITS sequences of specimens from the type localities of *P. hiulca* and *P. ravenelii* are generated.

Additional specimens examined

United States of America: Florida: Park-Dade Co., Everglades National Park, Gumbo Limbo trail, hardwood, 8 August 1972, HHB-6990.

Phaeophlebiopsis peniophoroides (Gilb. & Adask.) Floudas & Hibbett **comb. nov.**

MycoBank No.: 811936.

Basionym: *Phlebiopsis peniophoroides* Gilb. & Adask., Mycotaxon 49: 388, 1993.

Phlebiopsis crassa (Lév.) Floudas & Hibbett **comb. nov.**

MycoBank No.: 811935.

Basionym: *Thelephora crassa* Lév. Annales des Sciences Naturelles Botanique 2: 209, 1844.

Byssomerulius clade

Efibula clarkii Floudas & Hibbett **sp. nov.** (Figs 1, 4, and 13)

MycoBank No.: 811937.

Etym.: from Clark University, where the sample was collected.

Holotype: **Unites States of America**: Massachusetts: Worcester Co., Worcester, Clark University campus, on fallen *Quercus* sp. branch, 22 August 2009, FD-228 (CFMR!), nrITS KP135019.

Fruitbody resupinate, slightly tuberculate, very pale brown (10 YR 8/3, 10 YR 8/2) to brownish yellow (10 YR 6/6), the tuberculate areas have the darkest shades, extensively cracking to reveal the almost white subiculum. Margin almost abrupt, almost white, no hyphal cords seen.

Hyphal system monomitic, without clamps. Subiculum well-developed, hyphae loosely arranged in the upper part, but in a dense layer in the lower part composed of hyphal strands in parallel orientation, difficult to stain, mostly thin-walled, without clamps, but with frequent anastomoses, many hyphae have small tubercules, small crystals are scattered on the hyphae, 2.5–5.5 (7) μm. Subhymenium well-developed, composed of highly branched, anastomising, thin-walled hyphae, up to 4 μm wide. Cystidia none, occasionally hyphidia are observed. Basidia clavate, with four prominent, up to 4 μm in length, finger-like sterigmata, no basal clamp, 25 39 × 5–7.5 μm. Basidiospores oblong to ellipsoid, thin-walled, Melzer (–), acyanophilous, (5) 6.0–7.0 (7.8) × 3.0–3.5 (4.5) μm (Q = 1.32–2.4, avQ = 1.92).

Habitat and distribution

currently known only from the type locality at Worcester, Massachusetts. *Efibula clarkii* is associated with white rot.

Remarks

The compact basal layer close to the substrate results in the separation of the fruitbody in two parts when sections are attempted. The hymenium, subhymenium and upper subiculum are easily removed, while the dense layer usually remains on the substrate. *Efibula clarkii* is difficult to separate from other acystidiate phanerochaetoid taxa. Molecular characters are useful for its identification.

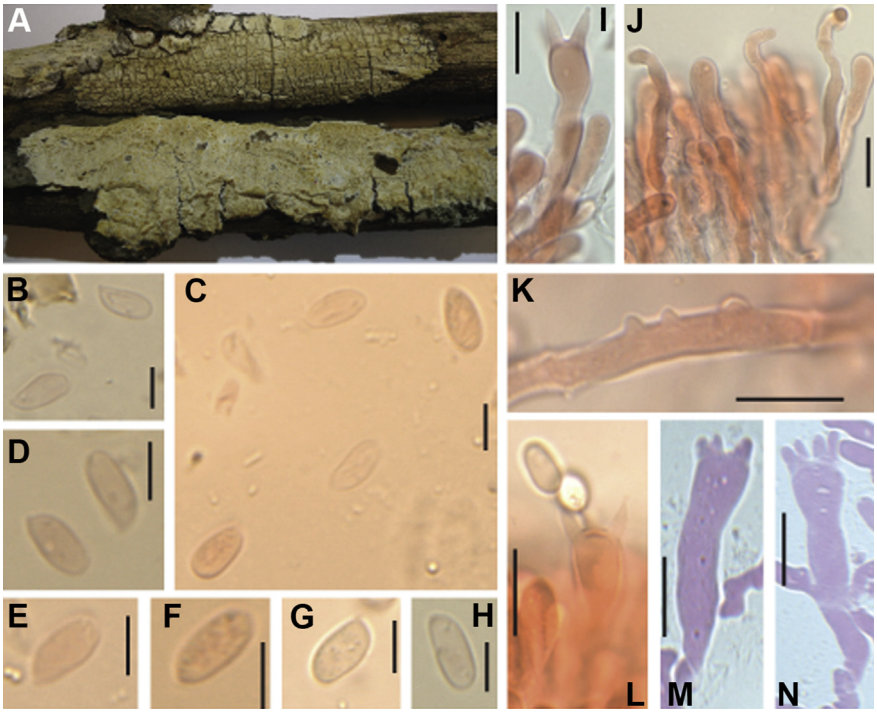

Fig 13 – *Efibula clarkii*. (A): holotype (FD-228), (B–H): basidiospores, (I, L–N): basidia, (J): hyphidia, (K): subicular hypha with tubercules. All microphotographs are from the holotype (FD-228). Scale bars: for basidiospores = 5 μm, for other elements = 10 μm.

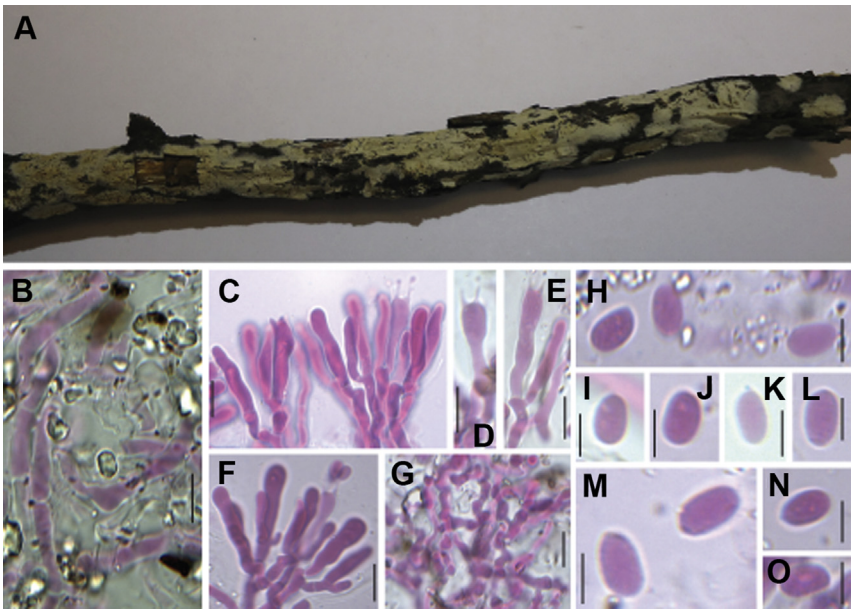

Fig 14 – *Efibula gracilis*. (A): holotype (FP-102052), (B): subicular hyphae close to the substrate, (C–F): basidia and basidioles, (G): twisted hyphae below the hymenium, (H–O): basidiospores ((A, B, K): FP-102052; (C-J, L–O): FD-455). Scale bars: for basidiospores = 5 μm, for other elements = 10 μm.

Efibula gracilis Floudas & Hibbett **sp. nov.** (Figs 1, 4, and 14)

MycoBank No.: 811932.

Etym.: from the Latin word 'gracilis' for the simple fruitbody morphology.

Holotype: **Unites States of America**: Wisconsin: Dane Co., Madison, N. Entrance Picnic Point, on fallen branch, 10 September 1987, FP-102052-sp (CFMR!), nrITS KP135028.

Fruitbody resupinate, smooth, very thin, on decorticated smaller branches, cracking, colour very pale brown (10 YR 8/2, 10 YR 8.5/2), margin almost abrupt, no hyphal cords, context very thin, and more or less white.

Hyphal system monomitic, clamps absent. Subiculum and subhymenium reduced and difficult to discern. Hyphae in that layer frequently bending and branching, thin-walled, 3–5 μm. Close to the substrate hyphae wider (4–5.5 μm), not so frequently branching, arranged in parallel orientation and tightly packed. Basidia cylindrical to clavate, with four sterigmata, basal clamp absent, 17–30 × 5–6.5 μm. Basidiospores ellipsoid to oblong, thin-walled, Melzer (–), acyanophilous, (5) 5.5–7 × (3) 3.3–4 μm (Q = 1.25–2.03, avQ = 1.65).

Habitat and distribution

Efibula gracilis is currently known only from the type locality and the Yale University campus. The simple morphology of the fruitbodies make this species easily overlooked and additional sampling may increase its distribution range across eastern North America. Molecular characters are useful for the identification of the species.

Remarks

This species looks similar to *Phanerochaete avellanea*. However, the spores are consistently wider than those in *P. avellanea* and more ellipsoid than oblong (reminding *Efibula tuberculata*). Furthermore, the species has shorter and wider basidia than both *E. tuberculata* and *P. avellanea*.

Additional Specimens examined

Unites States of America: Connecticut: New Haven Co., New Haven, Yale University campus area, on fallen branch (diameter around 1 cm) of *Fagus* sp., 14 July 2012, FD-455.

Efibula americana Floudas & Hibbett **sp. nov.** (Figs 1, 4, and 15)

MycoBank No.: 811933.

Etym.: due to the distribution of the species in North America.

Holotype: **Unites States of America**: Maryland: Hancock Co., Hawesville, Wilamette Industries, on *Populus deltoides*, 22 May 1986, FP-102165 (CFMR!), nrITS FP-102165.

Fruitbody resupinate, smooth to reticulate, very pale to pale brown (10 YR 8/4, 2.5Y 8.5/2) to yellow (10 YR 8/6, 10 YR 7/8), in young samples margin fibrillose with small hyphal cords, in well-developed samples margin abrupt, when margin fibrillose then almost white. Context well-developed, almost white.

Hyphal system momonitic, hyphae thin-walled. Subhymenium distinct from subiculum. Subicular hyphae thin-walled, loosely arranged, with occasional large clamp connections, 4–6 μm, occasionally small tubercules seen and in some samples with abundant, thin crystals. Subhymenium relatively compact, but easy to open, with thin-walled up to 4 μm wide hyphae. Cystidia none, hyphidia rarely seen. Basidia cylindrical to clavate, with four prominent sterigmata, without basal clamp, 20–32 × 5–8 μm. Basidiospores ellipsoid to cylindrical, smooth, thin-walled, Melzer (–), acyanophilous, (4.5) 5.3–6.5 (7.3) × (2.3) 3–3.8 (4.5) μm (Q = 1.35–2.68, avQ = 1.71).

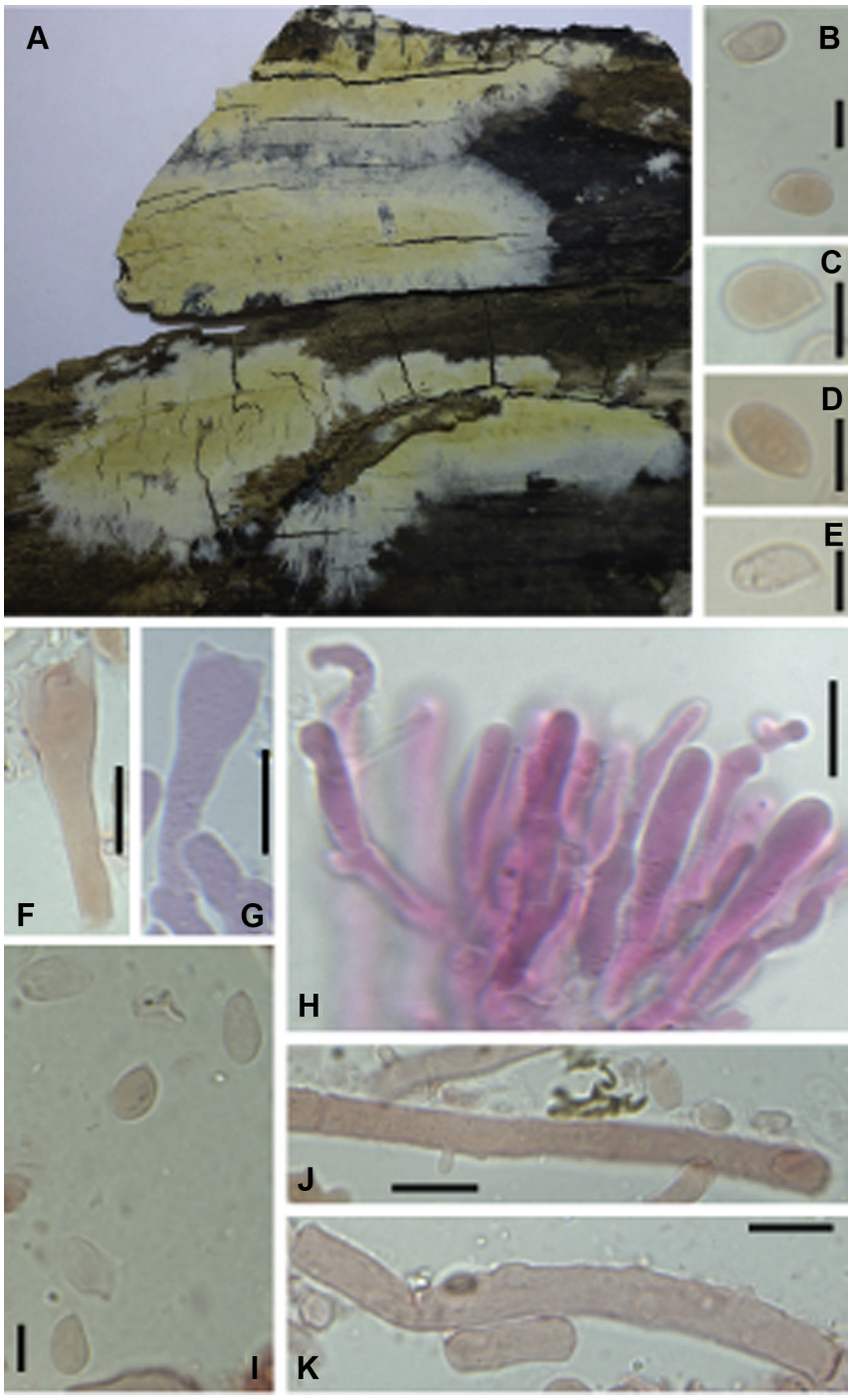

Fig 15 – *Efibula americana*. (A): holotype (FP-102165), (B–E, I): basidiospores, (F, G): basidia, (H): basidioles and hyphidia, (J, K): subicular hyphae with tubercules ((A-C, F, I): FP-102165; (D, E, J, K): FP-102158; (G): FP-102156; (H): FP-104126). Scale bars: for basidiospores = 5 μm, for other elements = 10 μm.

Habitat and distribution

Efibula americana has been collected so far from states east of the Mississippi river and is associated with white rot on hardwood.

Remarks

Efibula americana has mostly smooth hymenium, but the samples examined where only herbarium samples and we are not sure how fresh samples look like. The reason for mentioning this is that the hymenophore has faint reticulate appearance, which could be more prominent in fresh samples. The species can be easily get confused with *Efibula tuberculata* and we feel that there are no characters to easily separate them other than their geographic origin and the different ITS sequences.

Additional specimens examined

Unites States of America: Illinois: Jackson Co., Shawnee National Forest, Fountain bluff, on *Liriodendron tulipifera*, 2 June 1986, FP-102158. Kentucky: Hancock Co., Hawesville, Wilamette Industries, on *Populus deltoides*, 22 May 1986, FP-102156. Maryland: Calvert Co., Port republic, Scientists cliff, hardwood on the ground, 27 March 1956, FP-104126. Mississippi: Bolivar Co., Huntington Point, on branch, 1 August 1960, FP-110429-sp.

Discussion

Phanerochaete *sensu Burdsall is represented by nine phylogenetic lineages across the Phlebioid clade*

All three clades in the phlebioid clade, termed here *Phanerochaete*, *Byssomerulius,* and *Phlebia* clades, are represented by species with polyporoid or corticioid fruitbody morphology, traditionally placed in *Polyporales* or *Corticiaceae* s.l. In total, 14 corticioid and nine polyporoid genera are included here (Fig 1). Hymenophore morphology is not conserved within any of the three clades and numerous corticioid (including smooth, tuberculate and hydnoid hymenophores) species are phylogenetically related to polyporoid species. Such examples can be seen for *Hydnophlebia* and *Ceriporia alachuana*, for *Terana caerulea* and *Bjerkandera adusta*, for *Phlebiopsis*–*Rhizochaete* with *Hapalopilus rutilans*, for *Phanerochaete allantospora* with *Ceriporia* spp. and others (Fig 1). These results suggest that transitions between polyporoid and corticioid hymenophores have taken place multiple times in the phlebioid clade.

Within the phlebioid clade, we recognize nine phanerochaetoid lineages, eight of which receive strong support in the four gene phylogenetic analyses (Fig 1). De Koker *et al.* (2003) recovered only six phanerochaetoid clades, but due to the more limited sampling in that study the *Phaeophlebiopsis*, *Rhizochaete*, *Phlebiopsis* clades (2–4) and the *Scopuloides*, *Hydnophlebia* clades (8–9) (Fig1) appear as two clades only. Wu *et al.* (2010) recovered the *Phlebiopsis* (4), *Phanerochaete* s.s. (1), *Scopuloides* (8) and clade five (Fig 1 & S5B), in agreement to our results, but did not recover *Efibula* (6), *Rhizochaete* (3), *Phaeophlebiopsis* (2), and *Hydnophlebia* (9). However, the same study sampled two more clades for which we did not generate data (*Phanerochaete ginnsi* and the clade including *Phaeorchaete odontoidea* and *Phanerochaete subodontoidea*). These results suggest that *Phanerochaete* sensu Burdsall (1985) is polyphyletic, as has been previously suggested (de Koker *et al.* 2003; Wu *et al.* 2010). Four of the phanerochaetoid lineages, including *Phanerochaete sensu stricto* are found in the *Phanerochaete* clade. Three of the remaining lineages are found in the *Byssomerulius* clade and the last two lineages are found in the *Phlebia* clade (Fig 1). For lineages 1, 3, 4, 6, 8, 9 generic names are available, while we suggest here the genus *Phaeophlebiopsis* for lineage 2.

Evaluation of character distribution in Phanerochaete

Parmasto (1968), Eriksson *et al.* (1978), and Burdsall (1985) have tried to further separate *Phanerochaete* in different groups or subgenera. Burdsall (1985) used the presence/absence of cystidia and the degree of subiculum development as important characters for separation of *Phanerochaete* into subgenera *Phanerochaete*, *Phanericium*, and *Scopuloides*. Our results suggest that these characters have also polyphyletic origin and are not useful for further separation of *Phanerochaete* into smaller groups. Taxa of subgenus *Phanerochaete* are mainly found in the core *Phanerochaete* clade, but also in lineages 3,7, and 9 (Fig 1). Similarly, taxa of subgenus *Phanericium* are found in three lineages (including core *Phanerochaete*, Fig 1). Finally, members of subgenus *Scopuloides* are found in four lineages. Even if we consider the concept of *Phanerochaete* sensu Eriksson *et al.* (1978), and exclude *Scopuloides* from *Phanerochaete*, we will still end up with three phylogenetic lineages that contain *Phanerochaete* s.l. species (lineages 1, 3, and 6, Fig 1). *Phanerochaete septocystidia*, which represents the third group of *Phanerochaete* in the latter study (Eriksson *et al.* 1978), is distant from *Phanerochaete* s.s. (Wu *et al.* 2010).

Phanerochaete clade

We recovered the *Phanerochaete* clade with strong support in all types of analyses and combinations of genes, except for the ML of the RPB2 dataset. Clade *Phanerochaete* is separated into four smaller clades (*Phanerochaete sensu stricto*, *Hyphodermella*, *Phlebiopsis*, *Bjerkandera*), but only the *Phanerochaete* s.s. and *Phlebiopsis* clades are supported in at least one type of analyses of each dataset (nodes A-D, Fig 1).

Phanerochaete sensu stricto

Phanerochaete s.s. (clade 1, Figs 1 and 2) includes species mostly found in the subgenus *Phanerochaete* sensu Burdsall (1985). Most species in this clade have well-developed membranous fruitbodies, with or without hyphal cords and colours that range from almost white to brown, red or light orange. The subiculum is well developed, loose, consisting of broad hyphae without clamps or with rare single, double or multiple clamp connections. Cystidia are present ranging from thin-walled to cystidia of almost metuloid appearance and spores are hyaline and thin-walled. Two species in *Phanerochaete* s.s. do not share all of these characteristics. Sample NM-586 was originally identified as *Phanerochaete galactites*. However, this sample reacts with 5 % KOH solution and it cannot be the former species. The examination of the sample showed that there are no cystidia and therefore we believe it represents a *Phanericium*-like species (sensu Burdsall 1985) nested in *Phanerochaete* s.s (Fig 2). The second species is represented by sequences AY219365, JN017928 and sample HHB-5796 and does not fit in the traditional *Phanerochaete* concept. Both specimens GB-240 (AY219365) and HHB-5796 were labeled as *Phlebia subserialis*, but we doubt that this clade represents *P. subserialis*. Our results support three different areas where '*P. subserialis*' samples are found (Figs 2 and 5). We examined specimens HHB-5796 and FD-427 from two of the three clades and none of them fits the descriptions of *P. subserialis* (Eriksson *et al.* 1981; Bernicchia & Gorjón 2010), but we did not have access to the sample of the third clade (Parmasto & Hallenberg, 2000). Sample HHB-5796 has clamp connections at all septa and in this sense it resembles a *Phlebia* sp., even though the subiculum resembles *Phanerochaete*. It also shows similarities with the cystidia (32–54 × 3.3–5 μm) and spore shape of *P. subserialis*. However, the fruitbody reacts with 5 % KOH turning permanently red-brown, similar to

Phanerochaete laevis and *Phanerochaete subceracea*, which are closely related (Fig 1), the cystidia are not subulate, the spores are slightly smaller ((5.1) 5.5–6.3(6.8) × (2)2.1–2.7(3.4) μm) and the subiculum does not have the more compact consistency of *Phlebia*, but resembles *Phanerochaete*, with large and relatively thick-walled hyphae. Therefore, we believe that sample HHB-5796 and the accompanying sequences (Figs 1 and 2) represent the first clamped *Phanerochaete* species and shares similarities with *P. laevis* and *P. subceracea* at the shape of the cystidia and the KOH reaction. Since our observations are based only in one older sample, we prefer not to officially describe the species until more ITS sequences and samples are available. However, we choose to give the provisional name *Phanerochaete krikophora* (from the Greek word for κρίκος (krikos) = clamp and φέρω (phero) = to bear) to draw attention to this species and indicate that even within *Phanerochaete* s.s. species with deviating morphological characteristics may exist. The presence of clamped species in *Phanerochaete sensu stricto* should not sound peculiar. *Rhizochaete* was erected to included clamped and clampless species (Grezlebin *et al.* 2004), and our results also show that such cases frequently exist in the phlebioid clade.

Phanerochaete sordida *and* Phanerochaete chrysosporium. We recovered two major clades, where specimens under the name *Phanerochaete sordida* are found (clades I and II, Fig 2). Additional sampling of ITS GenBank sequences shows that because of the high ITS similarity between sequences in the vicinity of *P. sordida* clade I with *Phanerochaete australis*, *Phanerochaete magnoliae*, *Phanerochaete pseudomagnoliae,* and *Phanerochaete raduloides* the name *P. sordida* has been misapplied in what we believe could represent several species (similarity ≥ 95 %) and labeled here as '*P. sordida*' III-VI (Fig 2). Generated ITS from North American and Finnish samples or strains (*P. sordida* was described from Finnish material, Karsten 1882) suggest *P. sordida* represents either clade I or clade II (Fig 2). However, we did not have access to the type of *P. sordida* and we believe that the true identity of *P. sordida* is a complex issue that should be addressed in a separate study and after the type and other synonymized names (e.g. *Corticium eichlerianum*) have been reexamined.

Similarly, *Phanerochaete chrysosporium* sequences are separated to two sister clades (Fig 2, clades 1 and 2), which could represent separate species (95.7–97.5 % similarity between the two clades). We have sequenced the type, which is nested in clade 1 (HHB-6251, Fig 2). The possibility that two species exist under the name *P. chrysosporium* has been mentioned earlier (James *et al.* 2011), based on molecular data and differences on the anamorph produced by strains of the two clades. We have seen only three samples and we prefer to see more samples and add additional markers before we feel confident to propose the separation of *P. chrysosporium* in two species.

Phanerochaete velutina *complex*. ITS sampling for *Phanerochaete velutina* from Northern Europe and North America revealed three clades under that name (clades a-c, Fig 2). The three clades have very similar ITS sequences (97.3–98.5 % between clades 'a' and 'b', 97–97.6 % between clades 'a' and 'c', and 97.5–98 % between clades 'b' and 'c'), but they show geographic distribution and substrate differences. Specimens of clade 'c' are restricted to the eastern part of North America, but specimens of clades 'a' and 'b' are in found boreal parts of North America and Europe. Furthermore, clades 'b' and 'c' represent specimens from hardwood, while clade 'a' is restricted to softwood. Therefore, clades 'a' and 'b' are found in the same geographic regions, but they grow on softwood and hardwood respectively. We believe that the geographic and substrate distribution between the three clades support the presence of three species under the name *P. velutina*. We have not seen Karsten's type of *Corticium decolorans* (lectotype of *P. velutina*). However, the sample was collected on *Salix*, while the substrate of *Thelephora velutina* was not mentioned and *Corticium velutinum* was reported from fallen wood of *Quercus* and *Fagus* (de Candolle 1815; Fries 1838). Therefore, we suggest that *P. velutina* represents clade 'b', which is restricted on hardwood, while clade 'a' and clade 'c' represent separate species.

Peck described *Corticium rhodellum* from eastern North America (1889). Later, the species was synonymized with *P. velutina* (Burdsall 1985). We examined the type of *C. rhodellum* (NYSf2591). We found rare simple and double clamp connections and the subiculum has the construction of *Phanerochaete* s.s. Spores were frequently seen measuring around 5.2 × 3 μm (Fig 9). Metuloid-like cystidia were also frequent (thick-walled and heavily encrusted) measuring around 50–80 × 7–11 μm. Their size is on average smaller that those seen in typical *P. velutina* samples and agree with samples we have seen from eastern North America (clade c), even though slightly shorter. The type of *C. rhodellum* was collected at Lyndonville, NY and we have samples from the Adirondacks area (NY). Therefore, we believe that *C. rhodellum* represents this cryptic species from the east coast of North America (clade c) and we choose to use this name and re-describe it here. We also describe the species from clade 'a' (section 4.1). The separation of the three species is difficult. However, molecular characters and some morphological characters, even though not restricted in one clade or not found in all samples of a clade, can provide guidance to the identification of the three *P. velutina* species complex (Table 5).

Phanerochaete sanguinea *complex*. Three major lineages under the name *Phanerochaete sanguinea* were recovered from the ITS analysis, related to *Phanerochaete carnosa*, *Phanerochaete burtii*, *Phanerochaete calotricha,* and unidentified *Phanerochaete* species (Fig 2). *Phanerochaete sanguinea* is considered an easy species to identify at the field because it causes the characteristic red-orange staining of its substrate and to our knowledge this character has been restricted so far to *P. sanguinea* (Eriksson *et al.* 1978; Jülich & Stalpers 1980; Burdsall 1985). Our results suggest that this character is more widespread than previously thought and this has led to the expanded use of the name *P. sanguinea* in North America for more than one species. ITS sampling and examination of the samples suggest that *P. sanguinea* is a species restricted in boreal areas of North Europe and North America found on conifer wood (Fig 2).

The other two clades appear to contain samples similar to *P. sanguinea* from temperate and subtropical areas of North America (Fig 2). *Phanerochaete cf. sanguinea* clade A contains ITS sequences with 98.6–100 % similarity ITS, which we

believe is a separate species and we describe it here as *Phanerochaete sanguineocarnosa* (section 4.1). In contrast to the more uniform clade 1, *P. cf. sanguinea* clade B is more diverse at the ITS level. Specimens FD-240, FD-244, and FP-100391 have very similar ITS sequences (99.3–99.8 %) and represent an undescribed temperate/subtropical species in the *P. sanguinea* complex of North America, which we choose to describe here as *Phanerochaete pseudosanguinea* (section 4.1). Specimens FD-287 and FP-105385 have different ITS from the previous species (only 95.4–95.7 % similarity) and represent a third species under the *P. sanguinea* complex, described here as *Phanerochaete citrinosanguinea* (section 4.1). Specimen HHB-8519 has also different ITS from both species above (ITS similarity ranges between 96.3 and 97.6 % to both species), but since we have only one specimen sequenced we prefer not to discuss it further until more data is available.

Phanerochaete raduloides *and* Phanerochaete magnoliae. *Phanerochaete raduloides* and *Phanerochaete magnoliae* have been considered synonyms (Burdsall 1985). ITS sequences of *P. raduloides* and *P. magnoliae* form two small clades along with a third clade with GenBank sequences labeled as *Phanerochaete sordida* (Fig 2). Among these three clades, ITS sequence similarity is high (>98 %). The examination of the samples from two of the clades showed small differences in the length of the cystidia. The macromorphology of the samples is also different (Fig S6), but we feel that these differences are not strong enough to consider these clades separate species. We believe that more samples and additional molecular markers will be needed to clarify whether *P. raduloides* and *P. magnoliae* represent the same species or not.

Phlebiopsis clade

Our results support the monophyly of *Rhizochaete* (lineage 3, Fig 1), which has been previously described based on molecular and morphological data (Greslebin *et al.* 2004). The polypore *Hapalopilus rutilans* and a *Phlebia* s.l. are also found in the *Phlebiopsis* clade (Fig 1) as it has been shown before (Larsson 2007). Furthermore, we recovered two clades where *Phlebiopsis* species are nested. Clade four represents *Phlebiopsis* s.s., since *Phlebiopsis gigantea* is nested here (Figs 1 and 3). However, *Hjortstamia crassa* is also nested within clade four. *Hjortstamia* includes species with darker colours and stereoid fruitbodies, no clamp connections, monomitic to dimitic hyphal system and skeletocystidia (Boidin & Gilles 2002). Additionally, *Phlebiopsis* was described to accommodate *P. gigantea*, but as it has been discussed the exact limits of the genus are not clear (Eriksson *et al.* 1981) and for example the same study mentions that *Phlebiopsis roumegueri* looks similar to *P. gigantea*, but has almost no subiculum. The thinner subiculum is found in *Phlebiopsis flavidoalba* as well, which is related to *H. crassa* and *P. gigantea* (Figs 1 and 3). Burdsall (1985) questioned the dimitic nature of *H. crassa* and placed it under *Phanerochaete*, subgenus *Scopuloides*, related to species with compact and almost absent subiculum, such as *P. gigantea* or *Phanerochaete hiulca*. If we consider, the stereoid fruitbodies, the pseudodimitic hyphal system and the dark colours as important characters for the maintenance of *H. crassa* under that generic name, then *Phlebiopsis* s.s (clade 4) will have to be separated into multiple small genera without significant morphological characters to distinguish them. We feel that under these circumstances a better solution is to transfer *H. crassa* under the genus *Phlebiopsis* (see section 4.2), especially since *Phlebiopsis* has unclear morphological limits (Eriksson *et al.* 1981).

Clade two includes *Phlebiopsis*-like species, but it is separated from *Phlebiopsis* by *H. rutilans*, *Phlebia* s.l. (HHB-18295), and *Rhizochaete* (Fig 1). Species in this clade have been placed either in *Phanerochaete*, subgenus *Scopuloides* or in *Phlebiopsis* (Burdsall 1985; Gilbertson & Adaskaveg 1993). Therefore, we propose here the genus *Phaeophlebiopsis* to accommodate the four species. The choice is based on the grey coloured fruitbodies and the *Phlebiopsis*-like appearance we have seen for several fresh specimens of species in this clade.

Within this lineage, the ITS sampling for *P. hiulca* revealed two clades (Fig 3, clades a & b) with very different ITS sequences (87–89.9 % similarity), representing two species. *Phanerochaete hiulca* was described by Burt (as *Peniophora hiulca*) based on a Jamaican sample (Burt 1925). Later the species was transferred under *Phanerochaete* (Punugu *et al.* 1980). After examining the type of *P. hiulca* (W. A. Murrill & E. L. Murrill, 71) we believe that none of the two clades represent *P. hiulca*. Therefore, we describe clade 'a' as a new species (see remarks for *Phaeophlebiopsis caribbeana*, section 4.2). Specimen FD-425 was collected at St. John island (Virgin Islands, USA) and based on molecular and morphological data we believe that represents an undescribed species, which we describe here (see section 4.2). Finally, *Phlebiopsis peniophoroides* is transferred under *Phaeophlebiopsis* (section 4.2).

Hydnophlebia *and* Scopuloides *are part of the* Phlebia *clade (lineages 8 and 9)*

Several genera are represented in *Phlebia* clade including poroid, hydnoid, merulioid, and smooth hymenophore morphologies. The complexity of the clade is increased by the presence of species with or without clamp connections. A major problem in the taxonomy of species in this clade resides in the delimitation of *Phlebia*. Eriksson *et al.* (1981) has discussed the difficulty of *Phlebia* based on the simplicity of the morphological characters used, such as the waxy-gelatinous consistency of the hymenophore and the narrow, densely arranged basidia. This in turn has led to the expansion of *Phlebia* over time to include species with hydnoid hymenophore e.g. *Phlebia uda* (former *Mycoacia*), *Phlebia fuscoatra* (former *Acia*, *Mycoacia*) (Nakasone 1997) or even clampless species e.g. *Phlebia deflectens* (Eriksson *et al.* 1981). Phylogenetic studies have shown that *Phlebia* as traditionally viewed is polyphyletic (Binder *et al.* 2005; Larsson 2007; Wu *et al.* 2010; Binder *et al.* 2013). Our results are in agreement with previous studies even with the inclusion of few *Phlebia* species. *Phlebia* s.l. species seen in the *Phlebia* clade here (Fig 1) are intermixed with species from genera without clamp connections such as *Scopuloides* and *Hydnophlebia*, but also polypores such as *Climacodon septentrionalis*,*Ceriporia alachuana*, and *Ceriporiopsis gilvescens*. The latter species is placed in the *Phlebia* clade according to other studies (Tomsovsky *et al.* 2010; Miettinen & Rajchenberg 2011). This suggests that the broader concept of *Phlebia* cannot be followed. We have identified here *Phlebia sensu stricto*, which includes six species (Fig 1) including *Merulius tremellosus* in

Phlebia (Nakasone & Burdsall 1984). *Phlebia rufa* seems also to be a member of this clade (Fig 5). Even within *Phlebia* s.s. morphological characters are variable. The hymenophore can be tuberculate (*Phlebia brevispora*, Nakasone *et al.* 1981), hydnoid, phlebioid, or merulioid, while the cystidia can be embedded or projecting and naked or encrusted or even completely absent, suggesting that the use of morphological characters to delimitate genera in the phlebioid clade may be difficult even within small, phylogeny-based genera. The narrower *Phlebia* proposed here suggests that a large number of *Phlebia* species will need to be transferred under new generic names in the future, but it seems that such options exist at least in the *Phlebia* clade, e.g. *Mycoacia*, *Crustodontia*, *Mycoaciella* (Donk 1931; Eriksson *et al.* 1978; Hjortstam & Ryvarden 2005). A solution is also needed for *C. alachuana*, since *Ceriporia viridans* (the generic type of *Ceriporia*) appears to be nested in the *Ceriporia* clade (Fig S5).

We suggest that the phanerochaetoid genera *Scopuloides* and *Hydnophlebia* form well-supported clades and they should be preserved to accommodate hydnoid species without or only rare clamp connections and with well-developed (*Hydnophlebia*) or reduced subiculum (*Scopuloides*) in the *Phlebia* clade. Within both genera it seems that cryptic species exist (Fig 5) and in the future they should be described. We prefer not to address the species taxonomy of both genera before better sampling is done for both clades.

Phanerochaetoid lineages in the Byssomerulius clade (lineages 5, 6, and 7)

The *Byssomerulius* clade includes here taxa from ten genera. A similar problem of intermixed traditionally polyporoid genera (in particular *Ceriporia*, *Ceriporiopsis*) with corticioid genera e.g. *Byssomerulius* exists in this clade as well. We recovered two major subclades. The first subclade includes taxa from *Ceriporia* and *Meruliopsis*, and also *Leptoporus mollis* and *Phanerochaete allantospora*. The four genes phylogeny strongly supports the separation of the two genera in two clades (Fig 1) and it seems that the generic types of *Ceriporia* and *Meruliopsis* are nested in these clades (Fig S5A). Nevertheless, *Ceriporia* appears to be paraphyletic, since *L. mollis,* and *P. allantospora* are nested within *Ceriporia*. The four-gene phylogeny cannot resolve the internal phylogenetic relationships of *Ceriporia*, *L. mollis,* and *P. allantospora*. *Leptoporus mollis* could be transferred under *Ceriporia*, since it shows similarities to the latter genus except that it is associated with brown rot, while *Ceriporia* species are associated with white rot (Gilbertson & Ryvarden 1986). Even if we accept this solution, *P. allantospora* will still be nested in *Ceriporia*. Since the internal topology of *Ceriporia*, *P. allantospora,* and *L. mollis* does not receive support in the four gene phylogeny, we prefer not to make any nomenclatural changes until better sampling of the clade is being done.

Along with *L. mollis*, *Meruliopsis albostramineus,* and *Ceriporia reticulata* have been reported to cause brown-rot (Fig 5A), even though for both species the type of rot they cause has been questioned (Lombard & Gilbertson 1965; Lowe 1966; Niemela 1985; Ryvarden & Gilbertson 1993). Nevertheless, the placement of *L. mollis* in the phlebioid clade, along with other potential brown-rot species, suggests that brown rot has appeared more than once in *Polyporales* in addition to the *Antrodia* clade.

The second clade includes the phanerochaetoid lineages five and six, *Byssomerulius corium*, *Irpex lacteus,* and *Ceriporia lacerata* (Fig 1). Lineages five and six are well-supported, but the internal relationships of the whole clade are not resolved. *Byssomerulius corium* has similarities with *Phanerochaete* s.l. However, the placement of the polyporoid species *C. lacerata*, and the dimitic *I. lacteus* among *Byssomerulius,* and *Phanerochaete* s. l. taxa complicates this picture. Furthermore, the morphological diversity in the clade seems to be more complex that it appears here, since *Phlebia nitidula*, *Phlebia mellea,* and *Cystidiodontia isabellina* appear to be part of the clade (Larsson 2007; Wu *et al.* 2010).

A solution could be to use two generic names to accommodate lineages five and six (Fig 1). The lack of support however in the broader clade makes such a choice premature in the current study. Nevertheless, we suggest here that lineage six represents *Efibula*. Wu (1990) described *Efibula* to accommodate *Phanerochaete*-like species without cystidia, and without or with rare clamps connections, but subiculum more similar to *Phlebia*. Zmitrovich *et al.* (2006) expanded *Efibula* by transferring many acystidiate *Phanerochaete* species under this generic name. As it has been shown later (Wu *et al.* 2010) *Efibula* as seen by Zmitrovich *et al.* (2006) is polyphyletic. Our results show that *Efibula tropica* (syn. *Phanerochaete tropica*), which is the generic type of *Efibula* in closely related to taxa from clade six (Figs S5B, 1) and probably belongs in this clade. This clade, in addition to *E. tropica*, includes four more species (Fig 1). *Phanerochaete tuberculata* is nested here and the name *Efibula* is the correct generic name as it has been suggested (Zmitrovich *et al.* 2006). The other three lineages include specimens that were placed under various names such as *Phanerochaete avellanea*, *P. tuberculata*, and *Phanerochaete arizonica*, but none of them represents those species and they are described as new (see section 4.3). The differences of the ITS sequences between the *Efibula tuberculata*, *Efibula americana*, *Efibula clarkii,* and *Efibula gracilis* (86–92 % similarity only), but also the unique LSU and RPB1 sequences for each of the last three species, suggest that these four lineages represent separate species in spite of their small morphological differences.

Lineage five includes five species in the four genes phylogeny (Fig 1). Additionally, several Asian species appear to be present in the clade based on the ITS-nLSU analysis (Fig S5B). The species in the clade include species with or without cystidia, but all without clamp connections and more or less smooth hymenophore. We prefer not to propose a new genus until better resolution is provided for the broader clade. A number of species here represent rather confusing entities due to their simple morphology that were placed under various names including *P. tuberculata*, *P. avellanea*, *Phanerochaete jose-ferreira*. *E. tuberculata* is nested in clade four as discussed above, but we don't have reliable sequences for the other two species and we are hesitant to use these names for the species, since they were described from Europe (Bourdot & Galzin 1911; Reid 1975). We prefer not to make any taxonomic rearrangements until a better solution is available.

Future directions in modern taxonomy of phanerochaetoid fungi

Our results suggest that phanerochaetoid fungi are widely distributed in the phlebioid clade, frequently in close proximity to morphologically diverse species from corticioid or polyporoid genera such as *Phlebia* and *Ceriporia*. That makes the use of morphology in the taxonomy of phanerochaetoid fungi challenging. We suggest that future taxonomic treatments at the generic level should rely heavily on molecular data, followed by the use of morphological data, when this is possible.

The species level taxonomy of phanerochaetoid fungi is in need of a more extensive sampling. As our ITS results suggest here, more than one species under one name might be frequent in this type of fungi (e.g. *Scopuloides rimosa*, *Phanerochaete chrysosporium*). In order to address this we will need to include additional molecular data from types and designated epitypes. Finally, species delimitation in phanerochaetoid fungi might require additional genetic markers in combination to ITS data.

Conclusions

The first four gene analyses of *Phanerochaete* and related genera in the phlebioid clade suggest that *Phanerochaete* s.l. is polyphyletic and provide an improved phylogenetic picture of *Phanerochaete* s.s. and related genera. We recognize nine well-supported lineages distributed across the phlebioid clade. For six of these lineages, the generic names *Phanerochaete* (1), *Rhizochaete* (3), *Phlebiopsis* (4), *Efibula* (6), *Hydnophlebia* (8), and *Scopuloides* (9) are able to accommodate phanerochaetoid fungi with additional nomenclatural changes. We propose the genus *Phaeophlebiopsis* (2) to accommodate *Phlebiopsis*-like species that cannot be placed in the latter genus. For lineages five and seven, we choose not to propose taxonomic changes until more sampling and the use of additional genetic markers provide a better phylogenetic picture for the clades. We describe in total nine new species, four of which are found in *Phanerochaete* s.s and represent cryptic species in *Phanerochaete sanguinea* and *Phanerochaete velutina*. In addition to the nomenclatural consequences for *Phanerochaete* s.l., our results suggest one or more previously overlooked brown-rot lineages in the phlebioid clade represented by *Leptoporus mollis* and potentially other species.

Acknowledgements

The project was supported by the PolyPEET project of an NSF grant (DEB 0933081) and the NAMA Memorial Fellowship. We would like to thank Karen Nakasone for helpful comments on the manuscript, Alfredo Justo for advice throughout the project, collection of samples and generation of molecular data, and Otto Miettinen for kindly providing some of the sequences and specimens. We would also like to acknowledge Beatriz Ortiz Santana, Daniel Lindner, and the personnel at the Forest Products Lab (Madison, Wisconsin) for allowing us to use cultures and herbarium material during this project. We kindly thank the editor and an anonymous reviewer for their critical comments on the manuscript. Finally, we would like to acknowledge the Finnish Museum of Natural History at University of Helsinki (Herbarium H), the New York State Museum (NYS) and the Farlow Reference Library and Herbarium of Cryptogamic Botany at Harvard University (FH) for providing herbarium material during this study.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.funbio.2015.04.003.

REFERENCES

Benson DA, Cavanaugh M, Clark K, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayers EW, 2012. GenBank. *Nucleic Acids Research* 1–7. http://dx.doi.org/10.1093/nar/gks119.

Bernicchia A, Gorjón SP, 2010. In: *Corticiaceae s.l. Fungi Europaei* n°12. Candusso, Italia.

Binder M, Hibbett DS, 2002. Higher-level phylogenetic relationships of Homobasidiomycetes (mushroom-forming fungi) inferred from four rDNA regions. *Molecular Phylogenetics and Evolution* **22**: 76–90.

Binder M, Hibbett DS, Larsson KH, Larsson E, Langer E, Langer G, 2005. The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi. *Systematics and Biodiversity* **3**: 113–157.

Binder M, Justo A, Riley R, Salamov A, Lopez-Giraldez F, Sjokvist E, Copeland A, Foster B, Sun H, Larsson E, Larsson KH, Townsend J, Grigoriev IV, Hibbett DS, 2013. Phylogenetic and phylogenomic overview of the Polyporales. *Mycologia* **105**: 1350–1373.

Boidin J, Gilles G, 2002. À propos du genre *Lopharia* sensu lato (Basidiomycetes, Aphyllophorales). *Bulletin trimestriel de la Société mycologique de France* **118**: 91–115.

Bourdot H, Galzin A, 1911. Hyménomycètes de France: III. Corticiées: Corticium, Epithele, Asterostromella. *Bulletin trimestriel de la Société mycologique de France* **27**: 223–266.

Burdsall Jr HH, Eslyn EW, 1974. A new *Phanerochaete* with a *Chrysosporium* imperfect state. *Mycotaxon* **1**: 123–133.

Burdsall Jr HH, 1985. A contribution to the taxonomy of the genus *Phanerochaete* (Corticiaceae, Aphyllophorales). *Mycologia Memoir* **10**: 1–165.

Burt EA, 1925. The Thelephoraceae of North America. XIV. *Annals of the Missouri Botanical Garden* **12**: 213–357.

Cooke MC, 1879. On Peniophora. *Grevillea* **8**: 21.

Cullen D, Kersten PJ, 2004. Enzymology and molecular biology of lignin degradation. In: Brambl R, Marzluf GA (eds), *The Mycota III; Biochemistry and Molecular Biology*, 2nd edn. Springer-Verlag, Berlin-Heidelberg, pp. 249–273.

De Candolle AP, 1815. *Flore Française* **6**: 33.

De Koker TH, Nakasone KK, Haarhof J, Burdsall Jr HH, Janse BJH, 2003. Phylogenetic relationships of the genus *Phanerochaete* inferred from the internal transcribed spacer region. *Mycological Research* **107**: 1032–1040.

Donk MA, 1931. Revisie van de Nederlandse Heterobasidiomycetae en Homobasidiomycetae – Aphyllophoraceae I. *Mededelingen van de Nederlandse Mycologische Vereeniging* **18–20**: 67–200.

Donk MA, 1957. The proposed names for Hymenomycetes. VII: "Thelephoraceae" (Conclusion). *Taxon* **6**: 106–123.

Donk MA, 1962. Notes on resupinate Hymenomycetes-VI. *Persoonia* **2**: 217–238.

Eriksson J, Hjortstam K, Ryvarden L, 1978. The Corticiaceae of North Europe. *Mycoaciella-Phanerochaete* **5**: 889–1047 Fungiflora. Oslo, Norway.

Eriksson J, Hjortstam K, Ryvarden L, 1981. The Corticiaceae of North Europe. *Phlebia-Sarcodontia* **6**: 1051–1275 Fungiflora. Oslo, Norway.

Floudas D, Binder M, Riley R, Barry K, Blanchette RA, Henrissat B, Martínez AT, Otillar R, Spatafora JW, Yadav JS, Aerts A, Benoit I, Boyd A, Carlson A, Copeland A, Coutinho PM, de Vries RP, Ferreira P, Findley K, Foster B, Gaskell J, Glotzer D, Górecki P, Heitman J, Hesse C, Hori C, Igarashi K, Jurgens JA, Kallen N, Kersten P, Kohler A, Kües U, Kumar TKA, Kuo A, LaButti K, Larrondo LF, Lindquist E, Ling A, Lombard V, Lucas S, Lundell T, Martin R, McLaughlin DJ, Morgenstern I, Morin E, Murat C, Nagy LG, Nolan M, Ohm RA, Patyshakuliyeva A, Rokas A, Ruiz-Dueñas FJ, Sabat G, Salamov A, Samejima M, Schmutz J, Slot JC, St John F, Stenlid J, Sun H, Sun S, Syed K, Tsang A, Wiebenga A, Young D, Pisabarro A, Eastwood DC, Martin F, Cullen D, Grigoriev IV, Hibbett DS, 2012. The paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* **336**: 1715–1719.

Fries E, 1838. *Epicrisis Systematis Mycologici* 561.

Frøslev TG, Matheny PB, Hibbett DS, 2005. Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): a comparison of RPB1, RPB2 and ITS phylogenies. *Molecular Phylogenetics and Evolution* **37**: 602–618.

Gardes M, Bruns TD, 1993. ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.

Gilbertson RL, Ryvarden L, 1986. *North American polypores*. . In: *Synopsis Fungorum Special Volume*, vol. 1. Fungiflora, Oslo.

Gilbertson RL, Adaskaveg JE, 1993. Studies on wood-rotting basidiomycetes of Hawaii. *Mycotaxon* **49**: 369–397.

Gilbertson RL, Desjardin DE, Rogers JD, Hemmes DE, 2001. Fungi from the Mamane-Naio vegetation zone of Hawaii. *Fungal Diversity* **6**: 35–69.

Glez-Peña D, Gómez-Blanco D, Reboiro-Jato M, Fdez-Riverola F, Posada D, 2010. ALTER: program-oriented format conversion of DNA and protein alignments. *Nucleic Acids Research* Web Server issue. ISSN: 0305–1048.

Greslebin A, Nakasone KK, Rajchenberg M, 2004. *Rhizochaete*, a new genus of Phanerochaetoid fungi. *Mycologia* **96**: 260–271.

Hibbett DS, Gilbert LB, Donoghue MJ, 2000. Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. *Nature* **407**: 506–508. http://dx.doi.org/10.1038/35035065.

Hibbett DS, Binder M, 2002. Evolution of complex fruiting-body morphologies in homobasidiomycetes. *Proceedings of the Royal Society of London B* **269**: 1963–1969.

Hjortstam K, Ryvarden L, 1979. Notes on Corticiaceae (Basidiomycetes) IV. *Mycotaxon* **9**: 505–519.

Hjortstam K, 2000. Two new species of *Phanerochaete* (Basidiomycotina, Aphyllophorales), and a key to species from subtropical and tropical areas. *Karstenia* **40**: 53–62.

Hjortstam K, Ryvarden L, 2005. New taxa and new combinations in tropical corticioid fungi (Basidiomycotina, Aphyllophorales). *Synopsis Fungorum* **20**: 33–41.

James TY, Lee M, van Diepen LTA, 2011. A single mating-type locus composed of homeodomain genes promotes nuclear migration and heterokaryosis in the white-rot fungus Phanerochaete chrysosporium. *Eukaryotic Cell* **10**: 249–261.

Jülich W, 1978. Studies in resupinate Basidiomycetes – V. *Persoonia* **10**: 137–140.

Jülich W, Stalpers JA, 1980. *The resupinate non-poroid Aphyllophorales of the northern temperate hemisphere*, vol. 74, Verh. Koninkl. Nederlanse Akad. Wetens., Naturerk. Tweede Reeks1–335.

Justo A, Hibbett DS, 2011. Phylogenetic classification of *Trametes* (Basidiomycota, Polyporales) based on a five-marker dataset. *Taxon* **60**: 1567–1583.

Karsten PA, 1882. Symbolae ad mycologiam Fennicam. X. *Meddelanden af Societas pro Fauna et Flora Fennica* **9**: 57–67.

Karsten P, 1889. Kritisk öfversigt af Finland's Basidsvamper (Basidiomycetes; Gaster- and Hymenomycetes). *Bidrag till Kännedom of Finlands Natur Folk* **48**: 1–470.

Kersten PJ, Kirk TK, 1987. Involvement of a new enzyme, glyoxal oxidase, in extracellular H_2O_2 production by Phanerochaete chrysosporium. *Journal of Bacteriology* **169**: 2195–2201.

Kersten P, Cullen D, 2007. Extracellular oxidative systems of the lignin-degrading basidiomycete Phanerochaete chrysosporium. *Fungal Genetics and Biology* **44**: 77–87.

Kim SY, Park SY, Ko KS, Jung HS, 2003. Phylogenetic analysis of *Antrodia* and related taxa based on partial mitochondrial SSU rDNA sequences. *Antonie van Leeuwenhoek* **83**: 81–88.

Larsson KH, Larsson E, Koljalg U, 2004. High phylogenetic diversity among corticioid homobasidiomycetes. *Mycological Research* **108**: 983–1002.

Larsson KH, 2007. Re-thinking the classification of corticioid fungi. *Mycological Research* **3**: 1040–1063.

Lindner DL, Banik MT, 2008. Molecular phylogeny of *Laetiporus* and other brown rot polypore genera in North America. *Mycologia* **100**: 417–430. http://dx.doi.org/10.3852/07-124R2.

Liu YL, Whelen S, Hall BD, 1999. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* **16**: 1799–1808.

Lombard FF, Gilbertson RL, 1965. Studies on some western Porias with negative or weak oxidase reactions. *Mycologia* **57**: 43–76.

Lowe JL, 1966. Polyporaceae of North America. The genus *Poria*. *Technical Publication of the State University College of Forestry at Syracuse University* **90**: 1–183.

Löytynoja A, Goldman N, 2010. webPRANK: a phylogeny-aware multiple sequence aligner with interactive alignment browser. *BMC Bioinformatics* **11**: 579.

Maddison DR, Maddison WP, 2002. *MacClade4: Analysis of phylogeny and character evolution*. Sinauer Associates, Sunderland, MA.

Martinez D, Larrondo LF, Putnam N, Gelpke MDS, Huang K, Chapman J, Helfenbein KG, Ramaiya P, Detter JC, Larimer F, Coutinho PM, Henrissat B, Berka R, Cullen D, Rokhsar D, 2004. Genome sequence of the lignocellulose degrading fungus *Phanerochaete chrysosporium* RP78. *Nature Biotechnology* **22**: 695–700.

Matheny PB, Liu YJ, Ammirati JF, Hall BD, 2002. Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). *American Journal of Botany* **89**: 688–698.

Matheny PB, 2005. Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (Inocybe; Agaricales). *Molecular Phylogenetics and Evolution* **35**: 1–20.

Matheny PB, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson RH, Hughes KW, Hofstetter V, Ammirati JF, Schoch CL, Langer E, Langer G, McLaughlin DJ, Wilson AW, Frøslev T, Ge ZW, Kerrigan RW, Slot JC, Yang ZL, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vauras J, Hibbett DS, 2007. Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Molecular Phylogenetics and Evolution* **43**: 430–451.

Melo I, Cardoso H, Duenas M, Salcedo I, Telleria MT, 2012. *Peniophora aluticolor* (Fungi, Basidiomycota), an orphan species re-studied. *Nova Hedwigia* **94**: 437–440.

Miettinen O, Rajchenberg M, 2011. *Obba* and *Sebipora*, new polypore genera related to *Cinereomyces* and *Gelatoporia* (Polyporales, Basidiomycota). *Mycological Progress*. http://dx.doi.org/10.1007/s11557-010-0736-8.

Miller MA, Pfeiffer W, Schwartz T, 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceeding of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010*. New Orleans, LA, pp. 1–8.

Munsell C (ed.), 2009. *Munsell Soil Color Charts*. Grand Rapids, Michigan (USA).

Nakasone KK, Eslyn WE, 1981. A new species, *Phlebia brevispora*, a cause of internal decay in utility poles. *Mycologia* **73**: 803–810.
Nakasone KK, Burdsall, 1984. Merulius, a synonym of Phlebia. *Mycotaxon* **21**: 241–246.
Nakasone KK, 1997. Studies in *Phlebia*. Six species with teeth. *Sydowia* **49**: 49–79.
Nakasone KK, 2008. Type studies of corticioid Hymenomycetes described by Bresadola. *Cryptogamie Mycologie* **29**: 231–257.
Niemelä T, 1985. Mycoflora of Poste-de-la-Baleine, Northern Quebec. Polypores and the Hymenochaetales. *Naturaliste Canadien* **112**: 445–472.
Parmasto E, 1967. Corticiaceae U.R.S.S. IV. Descriptiones taxorum novarum. Combinationes novae. *Eesti NSV Teaduste Akadeemia Toimetised* **16**: 377–394.
Parmasto E, 1968. *Conspectus systematis Corticiacearum*. Inst. Zool. Bot. Acad. Sci. R. P. S. S, Estonicae. Tartu 261.
Parmasto E, Hallenberg N, 2000. A taxonomic study of phlebioid fungi (Basidiomycota). *Nordic Journal of Botany* **20**: 105–118.
Peck CH, 1889. *Annual Report on the New York State Museum of Natural History*, vol. 42124.
Punugu A, Dunn MT, Welden AL, 1980. The peniophoroid fungi of West Indies. *Mycotaxon* **10**: 428–454.
Reid DA, 1975. Notes on some Yugoslav fungi. *Acta Botanica Croatica* **34**: 133–137.
Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP, 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.
Ryvarden L, Gilbertson RL, 1993. European polypores. Part 1. *Synopsis Fungorum* **6**: 1–387.
Stamatakis A, Hoover P, Rougemont J, 2008. A rapid bootstrap algorithm for the RAxML web-servers. *Systematic Biology* **75**: 758–771.
Stiller JW, Hall BD, 1997. The origin of red algae: implications for plastid evolution. *Proceedings of the National Academy of sciences of the United States of America* **94**: 4520–4525.
Suzuki H, MacDonald J, Syed K, Salamov A, Hori C, Aerts A, Henrissat B, Wiebenga A, vanKuyk PA, Barry K, Lindquist E, LaButti K, Lapidus A, Lucas S, Coutinho P, Gong Y, Samejima M, Mahadevan R, Abou-Zaid M, de Vries RP, Igarashi K, Yadav JS, Grigoriev IV, Master ER, 2012. Comparative genomics of the white-rot fungi, *Phanerochaete carnosa* and *P. chrysosporium*, to elucidate the genetic basis of the distinct wood types they colonize. *BMC Genomics* **13**: 444–461.
Tien M, Kirk TK, 1983. Lignin-degrading enzymes from the Hymenomycete *Phanerochaete chrysosporium* Burds. *Science* **221**: 661–663.
Tien M, Kirk TK, 1984. Lignin-degrading enzyme from *Phanerochaete chrysosporium*: Purification, characterization, and catalytic properties of a unique H_2O_2-requiring oxygenase. *Proceedings of the National Academy of Sciences of the United States of America* **81**: 2280–2284.
Tomsovsky M, Menkis A, Vasaitis R, 2010. Phylogenetic relationships in European *Ceriporiopsis* species inferred from nuclear and mitochondrial ribosomal DNA sequences. *Fungal Biology* **114**: 350–358.
White TJ, Bruns T, 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*. Academic Press, Inc., New York, pp. 315–322.
Wu SH, 1990. The Corticiaceae (Basidiomycetes) subfamilies Phlebioideae, Phanerochaetoideae and Hyphodermoideae in Taiwan. *Acta Botanica Fennica* **142**: 1–123.
Wu SH, Nilsson HR, Chen CT, Yu SY, Hallenberg N, 2010. The white-rotting genus *Phanerochaete* is polyphyletic and distributed throughout the phlebioid clade of the Polyporales (Basidiomycota). *Fungal Diversity* **42**: 107–118. http://dx.doi.org/10.1007/s13225-010-0031-7.
Zmitrovich IV, Malysheva VF, Spirin WA, 2006. A new morphological arrangement of the Polyporales. I. Phanerochaetineae. *Mycena* **6**: 4–56.