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ORIGINAL ARTICLE

Molecular and morphological evidence reveal a new non-cystidiate species belonging to the core *Phanerochaete* (Polyporales)

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Abstract A new corticioid species is recognized in the genus *Phanerochaete* based on the material collected from the Changbaishan Nature Reserve in NE China. *Phanerochaete aurantiobadia* sp. nov. is characterized by an orange to reddish brown, resupinate basidiome turning coccine red upon contact with potassium hydroxide (KOH), lack of rhizomorphs and cystidia, and small ellipsoid spores. Phylogenetic analyses of internal transcribed spacer (ITS) and large subunit (LSU) sequences show that *Ph. aurantiobadia* is nested within the core *Phanerochaete* clade, where the type of the genus *Ph. velutina* is also nested. The new species is illustrated and compared with similar taxa, and some notes are given on *Phanerochaete* s.s.

Keywords Corticioid fungi · Fungal systematics · Phlebioid clade · Phylogeny · Resupinate basidiome · Wood-inhabiting basidiomycetes

Introduction

Phanerochaete P. Karst. is a large corticioid genus (Agaricomycetes, Basidiomycota) with about 100 described species (Kirk et al. 2008; MycoBank, www.mycobank.org). Species assigned to *Phanerochaete* usually have a more or less cream, red to whitish brown, membranaceous basidiome, lacking clamps on tramal and hymenial hyphae, and possess small ellipsoid spores. Several species also have prominent naked or encrusted cystidia. Recent studies have confirmed that the genus is highly polyphyletic and its species are distributed throughout the phlebioid clade belonging to the order Polyporales (Wu et al. 2010).

In 2011, a survey was conducted in the Changbaishan Nature Reserve, NE China, focusing on wood-inhabiting basidiomycetes (collectively polypores and corticioids). The reserve is located between 42° 35′ and 41° 15′ N, and between 127° 15′ and 129° 00′ E, and supports some of the most valuable natural forests in the country. The vegetation in the reserve is typically boreal and temperate. *Acer*, *Betula*, *Corylus*, *Fraxinus*, *Phellodendron*, *Populus*, *Quercus*, *Tilia*, *Ulmus* and several other deciduous tree genera are common in the lower part, while *Larix*, *Pinus*, *Abies* and *Picea* dominate the higher elevations. The coniferous, mixed and deciduous forests are distributed according to the altitude of the mountain range. The wood-inhabiting fungi are very rich in the reserve; more than 500 wood-decaying fungal species have been recorded in the area (Dai 2010), including 14 new species described from the reserve (Dai and Niemelä 1997, 2002).

Among the collected material was a new *Phanerochaete* species with an orange to reddish-brown basidiome, turning red upon contact with potassium hydroxide (KOH), and lacking cystidia and rhizomorphs. To establish its phylogenetic position, BLAST searches and analyses of the internal transcribed spacer (ITS) and large subunit (LSU) sequences were performed, and the results are presented here.

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Materials and methods

Morphology and taxon sampling for phylogenetic studies Morphological observations were made using a stereomicroscope and light microscope. Squash mounts were prepared in 5 % potassium hydroxide (KOH), cotton blue in lactic acid (CB), and Melzer's reagent (IKI). Thirty spores were measured per collection, and the given range of spore size was calculated from all spores measured. In the description, the following abbreviations were used: IKI− = non-amyloid and non-dextrinoid, CB− = non-cyanophilous, L_m = mean spore length, W_m = mean spore width, Q_m = mean variation in the length/width ratios, n = number of spores measured from given number of specimens. Color terms in the description followed Petersen (1996). Taxa sampled for phylogenetic analyses were selected from the phlebioid clade (Polyporales), based mainly on the study by Wu et al. (2010, see below), and also downloaded from GenBank.

DNA extraction, amplification, and sequencing Samples for DNA extraction were chosen from dried herbarium material and were prepared as described by Ghobad-Nejhad (2011). Total DNA was extracted using the DNeasy Plant Mini Kit (QIAGEN AB, Sollentuna, Sweden). The ITS and LSU regions were amplified using ITS1F/ITS4B (or ITS1F/ITS4) and LR0R/LR7 primer sets, respectively (Gardes and Bruns 1993; White et al. 1990, Vilgalys lab, http://www.biology.duke.edu/fungi/mycolab/primers. htm). The PCR amplifications were carried out using Ready-To-Go® PCR Beads (Amersham Pharmacia Biotech, Uppsala, Sweden) following the manufacturer's recommendations, with thermal cycling parameters as described by Ghobad-Nejhad and Dai (2010). The purification and sequencing of PCR products were performed by Macrogen (Macrogen Inc., Seoul, Korea). The primers used for sequencing were the same as used for the PCR reactions. The newly obtained sequences were assembled in Sequencher® v. 4.1 (Gene Codes Corporation, Ann Arbor, MI, USA), and deposited in GenBank with accession numbers KP127068 (ITS) and KP127069 (LSU).

Alignment and phylogenetic analyses The new LSU sequence obtained in this study was appended to the alignment by Wu et al. (2010), with some modifications. The ITS dataset was made using the new and additional sequences downloaded from GenBank. The alignments were made in MUSCLE (multiple sequence alignment with high accuracy and high throughput; Edgar 2004), and adjusted in PhyDE® (Phylogenetic Data Editor) version 0.995 (Müller et al. 2005). The best-fit model for nucleotide evolution was determined (GTR+I+G for both ITS and LSU datasets) using MrModeltest 2.3 (Nylander 2004).

Bayesian analyses were conducted with MrBayes version 3.2.2 (Ronquist and Huelsenbeck 2003). Each of the ITS and LSU datasets was analyzed using two independent runs, with eight MC^3 chains running for 10 million generations, with tree and parameter sampling every 5000 generations. Burn-in was set to discard 50 % of samples and the majority-rule consensus tree was assembled from post-burn-in tree samples. For analysis of the LSU dataset, *Porpomyces mucidus* (Pers.) Jülich was used as an outgroup after Wu et al. (2010). The outgroup for analysis of the ITS alignment was chosen [*Hyphodermella corrugata* (Fr.) J. Erikss. & Ryvarden] with regard to the topology of the LSU tree obtained here.

Results

Based on a MegaBLAST search of the GenBank nucleotide database at NCBI (as of 26 Oct. 2014), the best hits using the new ITS sequence were (respectively): *Phanerochaete chrysosporium* Burds. (GenBank KJ995953, Ident. 89 %), *Ph. chrysosporium* (GenBank KJ995952, Ident. 89 %) and "Uncultured fungus" (GenBank KF800664, Ident. 89 %).

A MegaBLAST search of the GenBank nucleotide database at NCBI (as of 26 Oct. 2014) showed that the best hits using the new LSU sequence were (respectively): *Phanerochaete stereoides* Sheng H. Wu (GenBank GQ470661, Ident. 94 %), *Phanerochaete sanguinea* (Fr.) Pouzar (GenBank GQ470655, Ident. 94 %) and *Phanerochaete deflectens* (P. Karst.) Hjortstam (GenBank GQ470644, Ident. 94 %).

The LSU alignment covered 98 taxa and 889 characters, with 524 constant and 261 informative positions. The sequence belonging to the new species described below was nested in a well-supported clade (PP=100) containing *Ph. velutina* (DC.) P. Karst., which is the type species of *Phanerochaete*; this clade is the core *Phanerochaete* clade sensu Wu et al. (2010) (Fig. 1). Species belonging to this clade in the study by Wu et al. (2010) were also recovered here (we excluded insufficiently identified taxa from their study). Within this clade, our new species was found in a polytomy, with no specific sister taxon (Fig. 1). To construct the ITS dataset, we downloaded the available ITS sequences of the taxa in this clade from GenBank and supplemented them with additional GenBank sequences upon the results of the ITS BLAST search (conspecific ITS and LSU sequences were not sufficient to build a combined dataset).

Fig. 1 LSU phylogram representing the placement of *Phanerochaete aurantiobadia* sp. nov. (bold) and the core *Phanerochaete* clade (box). Numbers beside nodes indicate Bayesian posterior probabilities≥50. Branches printed in bold refer to Bayesian posterior probabilities≥0.99. Species names are followed by GenBank accession numbers (green) and isolate numbers (lilac), respectively. The tree is rooted with *Porpomyces mucidus* ▶


Porpomyces mucidus AF347092 / KHL8620
Trechispora farinacea AF347089 / KHL8793
Rickenella mellea RMU66438 / Lamoure7420h19.91
Globulicium hiemale DQ873595 / Hjm19007
Ginnsia viticola GQ470670 / Wu001029clone1
Cyphellostereum laeve EU118621 / JJ020909
Candelabrochaete africana AF518670 / FP102987
Bjerkandera adusta GQ470629 / CWN00015
Porostereum spadiceum DQ679918 / Wu9708104
Terana caerulea GQ470677 / Wu8808031
Phlebia firma EU118654 / EdmanK268
Hyphodermella corrugata EU118630 / KHL3663
Phanerochaete aurantiobadia sp. nov. KP127069 / mg265
Phanerochaete stereoides GQ470661 / Wu9708118
Phanerochaete sacchari GQ470654 / Wu8803136
Phanerochaete carnosa GQ470642 / Wu93103
Phanerochaete deflectens GQ470644 / FCUG2777
Phanerochaete affinis EU118652 / KHL11839
Phanerochaete sanguinea GQ470655 / Wu030940
Phanerochaete aculeata GQ470636 / Wu8807012
Phanerochaete chrysosporium GQ470643 / BKMF1767
Phanerochaete chrysosporium AF139966 / T757(BKMF1767)
Phanerochaete sordida EU118653 / KHL12054
Phanerochaete velutina DQ679917 / FCUG1815
Phanerochaete canolutea GQ470641 / Wu9211105
Phanerochaete taiwaniana GQ470666 / Wu88082417
Phanerochaete taiwaniana GQ470665 / Wu011213
core Phanerochaete
Phanerochaete lutea GQ470651 / Wu880417-5
Phlebia unica EU118657 / KHL11786
Rhizochaete americana AY219391 / HHB-2004
Rhizochaete filamentosa AY219393 / FP-105240
Hapalopilus nidulans AY293184 / KEW211
Rhizochaete radicata AY219392 / HHB-1909
Rhizochaete brunnea AY219389 / MR-229
Rhizochaete fouquieriae AY219390 / KKN-121
Ceraceomyces violascens EU118612 / KHL11169
Phlebiopsis himalayensis GQ470673 / Wu880909-73
Phlebiopsis ravenelii GQ470674 / FCUG2216
Phlebiopsis flavidoalba EU118662 / KHL13055
Phlebiopsis gigantea AF141634 / FCUG1417
Phlebiopsis lamprocystidiata GQ470648 / Wu0109-14
Phlebiopsis lamprocystidiata GQ470647 / Chen1018
Hjortstamia crassa GQ470634 / Wu0504-22
Hjortstamia laxa GQ470649 / Wu9311-17
Hjortstamia brunneocystidiata GQ470639 / Chen1143
Hjortstamia brunneocystidiata GQ470640 / Chen666
Gelatoporia pannocincta AF141612 / FCUG2109
Gloeoporus dichrous EU118627 / KHL11173
Gloeoporus dichrous DQ679919 / FP-134973
Phlebia bresadolae AF141617 / FCUG1242
Panus rudis AF287878 / DSH-92-139
Phlebia queletii AF141626 / FCUG722
Hyphoderma definitum AJ406509 / GEL2898
Hyphoderma setigerum AJ406511 / GEL4001
Climacodon septentrionalis AF518610 / HHB-13438-sp
Phlebia tremellosa AY293200 / FPL-4294
Phlebia radiata EU522844 / TM03491
Phlebia acerina AF141615 / FCUG568
Phlebia rufa AF141628 / FCUG2397
Scopuloides rimosa EU118665 / KHL11916
Phanerochaete subglobosa GQ470662 / Wu870918
Phanerochaete chrysorhizon AF139967 / T-484
Phlebia subochracea AF141630 / FCUG1161
Phlebia subochracea EU118656 / KGN162/95
Phlebia aurea AJ406535 / GEL5339
Phlebia livida AF141624 / FCUG2189
Phlebia subserialis AF141631 / FCUG1434
Phlebia uda AF141614 / FCUG2452
Phlebia chrysocreas AY293199 / FPL-6080
Phanerochaete odontoidea GQ470653 / Wu9310-8
Phanerochaete subodontoidea GQ470663 / CWN00776
Phanerochaete subodontoidea GQ470664 / Wu0106-35
Phlebia centrifuga AF141618 / FCUG2396
Meruliopsis taxicola GQ470633 / FP105568
Phanerochaete ginnsii GQ470645 / Wu9210-22
Candelabrochaete septocystidia GQ470631 / RLG-9759-Sp
Leptoporus mollis AY293195 / KEW122
Ceriporia viridans AJ406518 / FO24398
Ceriporia reticulata EU118614 / KHL11981
Ceriporia purpurea AF287852 / DAOM213168
Ceriporia tarda GQ470632 / Wu9506-64
Ceraceomyces eludens AF090878 / JS27202
Ceraceomyces microsporus AF090875 / KHL8473
Ceraceomyces serpens AF090882 / KHL8478
Phlebia lilascens AF141621 / FCUG1801
Phanerochaete leptoderma GQ470650 / Chen479
Phanerochaete intertexta GQ470646 / Chen1362
Phanerochaete angustocystidiata GQ470638 / Wu9606-39
Phanerochaete angustocystidiata GQ470637 / Wu9310-18
Byssomerulius corium GQ470630 / FCUG2701
Phlebia albomellea AY293198 / CBS275.92
Phlebia nitidula AF141625 / FCUG2028
Cystidiodontia isabellina AJ406570 / GEL4978
Ceriporiopsis subvermispora AF287853 / FP90031
Irpex lacteus EU522839 / TM03480
Phanerochaete tropica GQ470672 / Wu8805151
Phanerochaete tuberculata GQ470669 / FCUG305
Phanerochaete tuberculata GQ470668 / FCUG368
0.83
0.54
0.54
0.52
0.86
0.84
0.55
0.61
0.57
0.71
0.68
0.90
0.84
0.57
0.52
0.98
0.90
0.66
0.57
0.64
0.52
0.97
0.51
0.92
0.96
0.89
0.95
0.57
0.82
0.1

The ITS alignment contained 19 taxa, with 614 characters, of which 396 were constant and 127 were parsimony-informative. *Phanerochaete aurantiobadia* described here found an isolated position within the core *Phanerochaete* clade (Fig. 2). The description and illustrations of the new species are presented below, and its similar taxa are also discussed.

Taxonomy

Phanerochaete aurantiobadia Ghobad-Nejhad, S.L. Liu & E. Langer, sp. nov. Figs. 3, 4 and 5

MycoBank no.: MB 810809

rDNA sequences ex holotype: GenBank KP127068 (ITS) and KP127069 (LSU).

Diagnosis: *Phanerochaete aurantiobadia* is characterized by an orange to reddish-brown resupinate basidiome, turning coccine red with KOH, lack of rhizomorphs and cystidia, lack of clamps, and small, cylindrical to ellipsoid spores.

Holotype: China, Jilin Province, Antu County, Erdaobaihe, Changbaishan Reserve, ca. 3–4 km south of Erdaocun town, Dayangdi; 42.385 Lat., 128.093 Long., ca. 730 m; natural forest mainly with *Quercus mongolica, Pinus koraiensis, Fraxinus mandshurica*, also some stands of *Acer* spp., *Tilia, Abies, Maackia amurensis*; on decorticated, standing angiosperm stump with a white rot; 7.IX.2011; Ghobad-Nejhad 2288, Dai, Wu, Sohrabi (holotype BJFC012122 in BJFC; isotype in Ghobad-Nejhad ref. collection).

Etymology: *aurantiobadia* (Lat.), referring to the color of the basidiome.

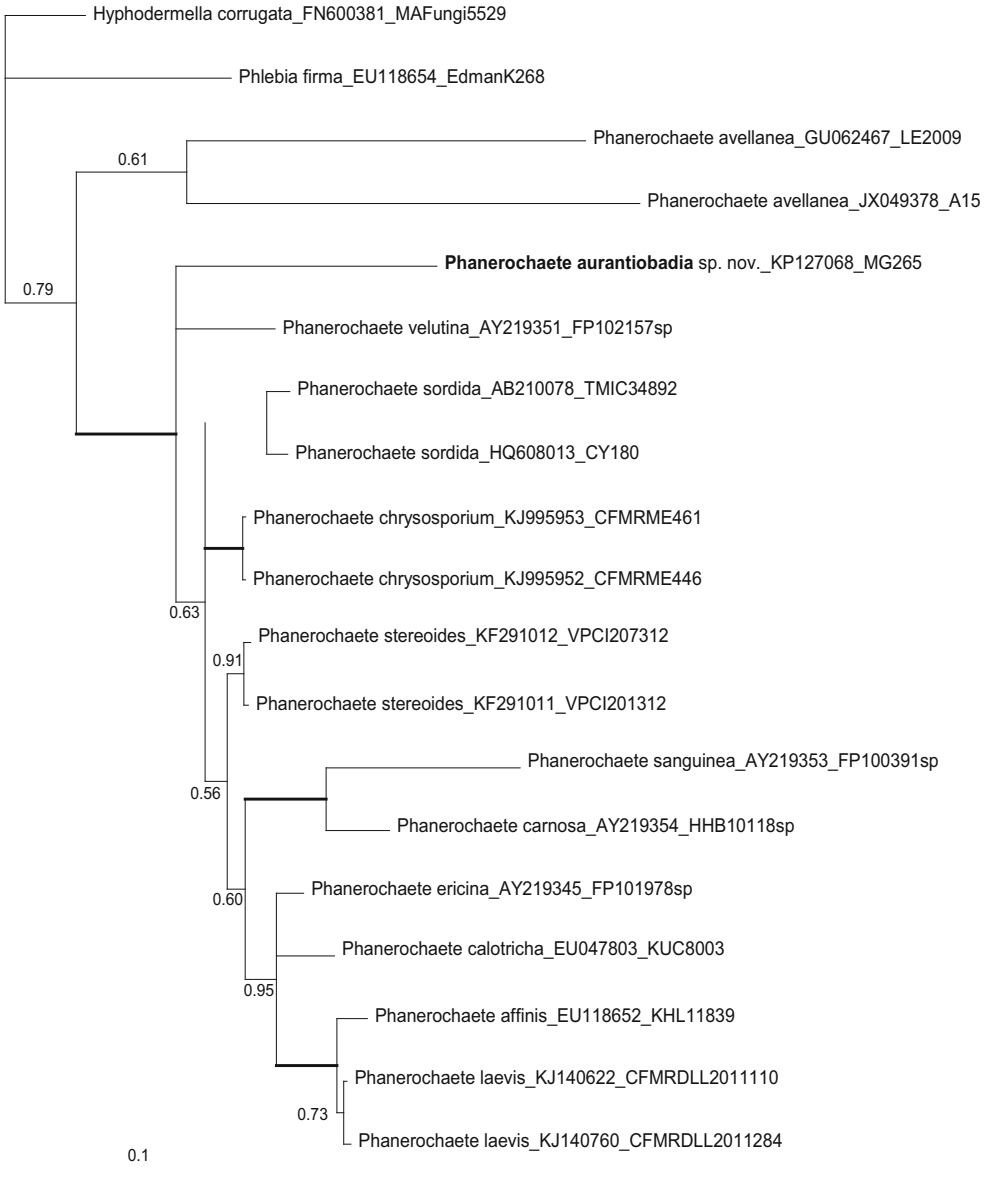

Fig. 2 ITS phylogram representing the placement of *Phanerochaete aurantiobadia* sp. nov. (bold) within the core *Phanerochaete* clade. Numbers beside nodes indicate Bayesian posterior probabilities≥50. Branches printed in bold refer to Bayesian posterior probabilities≥ 0.99. Species names are followed by GenBank accession numbers and isolate numbers, respectively. The tree is rooted with Hyphodermella corrugata

Fig. 3 Basidiome of *Phanerochaete aurantiobadia* sp. nov. in situ from the holotype

Basidiome annual, resupinate, adnate, less than 1 mm thick, orange-brown with a red tint, covered with pruina in the middle (older) parts. *Hymenial surface* smooth, immediately turning coccine red upon contact with KOH; *margin* buff to buff yellow, especially in younger parts, irregularly dentate at edges, slightly peeling out. *Rhizomorphs* absent.

Hyphal system monomitic, generative hyphae with simple septa, IKI−, CB−, frequently branched. Hyphae in subhymenium thin-walled, frequently branched, interwoven,

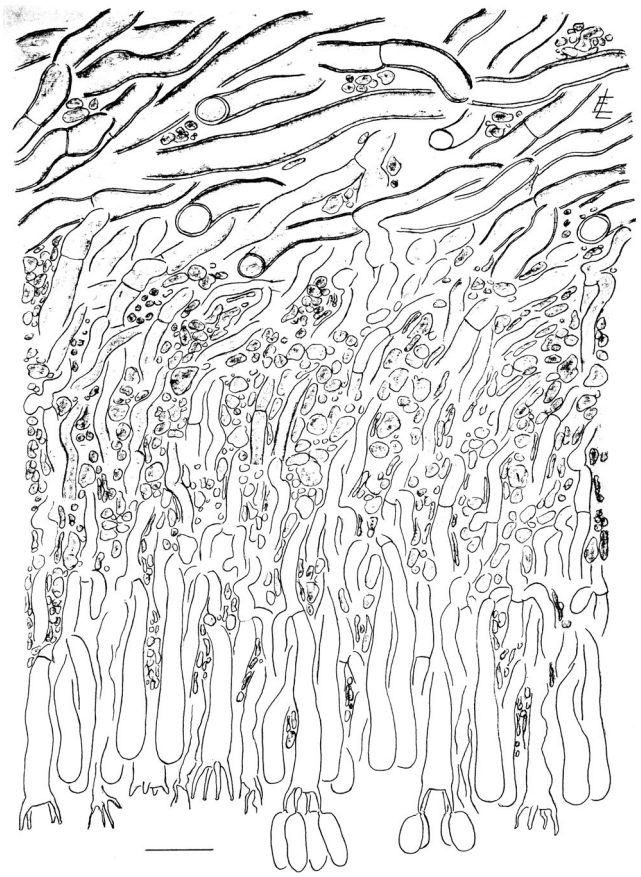

Fig. 4 Microscopic features of a section through the basidiome of *Phanerochaete aurantiobadia* sp. nov. drawn from the holotype. Bars=10 μm

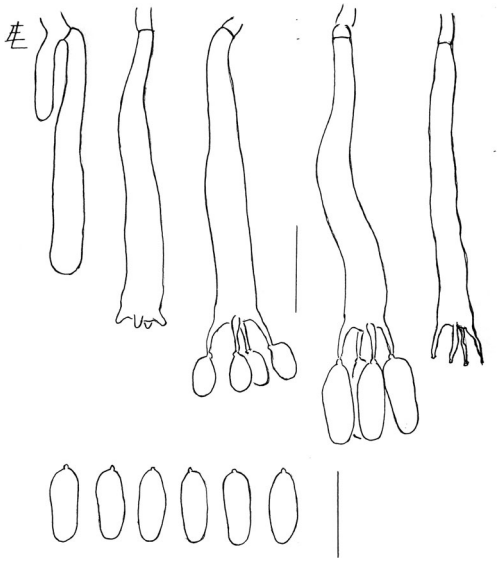

Fig. 5 Basidial ontogeny and basidiospores (typical mature spores of the upper spore size limit) of *Phanerochaete aurantiobadia* sp. nov. drawn from holotype. Bars=10 μm

2–3 μm in diam., and covered with coarse masses of orange-brown matter. *Subiculum* thin, subicular hyphae hyaline to pale brown, occasionally covered with masses of orange-brown matter, thick-walled (walls about 0.5 μm thick), 3–7 μm in diam., few occasional clamps might be present in subiculum.

Basidia long clavate, with a basal simple septum and four sterigmata, 24–36×4–5 μm. *Cystidia* absent (few subulate cystidioles may be rarely present). *Dendrohyphidia* none. *Basidiospores* ellipsoid to subcylindrical, with a slight abaxial depression, hyaline, thin-walled, smooth, IKI−, CB−, 5–8.3×2–3 μm, L_m=5.8 μm, W_m=2.34 μm, Q_m=2.46 (n=30/1).

Discussion (and notes on *Phanerochaete* s.s.)

As shown in the present (Fig. 1) and previous (Wu et al. 2010) studies, the genus *Phanerochaete* is highly polyphyletic. However, *Phanerochaete* s.s. is shown to comprise a number of *Phanerochaete* species assembled in a highly supported clade, referred to as the core *Phanerochaete* clade (Fig. 2), containing the generic type of *Phanerochaete*, i.e., *Ph. velutina.* Therefore, because of the settlement of our new species within this clade, we established its generic assignment in the genus *Phanerochaete*.

Besides *Ph. aurantiobadia* described here, there is another species in the core *Phanerochaete* clade whose basidiomes turn red with KOH: *Phanerochaete affinis* (Burt) Parmasto has light orange to tan basidiomes, turning red with KOH, but unlike *Ph. aurantiobadia*, its basidiome is separable and its hyphae have single or multiple clamps; it also has thick-

walled, encrusted cystidia and encrusted subicular hyphae (Punugu et al. 1980).

Most of *Phanerochaete* s.l. species showing a red color change with KOH have been assigned to the genus *Rhizochaete* Gresl., Nakasone & Rajchenb. *Rhizochaete* is a small genus introduced by Greslebin et al. (2004) as a segregate of *Phanerochaete*, differing mainly in the characteristic reaction of basidiome and rhizomorphs (hyphal cords) to KOH, which turns them red or violet. This character, however, is apparently plesiomorphic, shown in distantly related species in the *Phanerochaete* phylogeny. As demonstrated by Wu et al. (2010) and as shown in the LSU analysis presented here (Fig. 1), *Rhizochaete* is not monophyletic, and all species assigned to it stand out of the core *Phanerochaete* clade. *Phanerochaete aurantiobadia* differs from *Rhizochaete* species by the lack of encrusted cystidia and rhizomorphs.

The core *Phanerochaete* clade (Fig. 2), which corresponds to clade III in the study by Wu et al. (2010), contains four species lacking cystidia (see Figs. 1 and 2): *Ph. canolutea* Sheng H. Wu, *Ph. stereoides*, *Ph. avellanea* (Bres.) J. Erikss. & Ryvarden, and *Ph. aurantiobadia*. In *Ph. canolutea*, the basidiome is greyish yellow, and the basal hyphae are thick-walled (Wu 2000). *Phanerochaete stereoides* has brown subicular hyphae, a bit wider spores than *Ph. aurantiobadia*, and no reaction with KOH (Wu 1995). Spores in *Ph. avellanea* are more or less similar in size to *Ph. aurantiobadia*, but the hymenial surface in the former is cream to ochraceous, and has no red reaction with KOH (Bernicchia and Gorjón 2010).

Larsson (2007) assigned the non-cystidiate *Phanerochaete* species to the *Byssomerulius* family. However, it seems that the species lacking cystidia do not belong to a single family, and find different positions in several clades in the *Phanerochaete* phylogeny.

From a morphological viewpoint, it seems that there is no obvious synapomorphy to delimit taxa in the core *Phanerochaete* clade. Taxa in this clade show a range of basidiome coloration, with different hymenophoral configurations, and may have or lack cystidia and cystidioles. Still, it is noteworthy that this clade receives high statistical support, consists of merely *Phanerochaete* spp. (at least up until now), and contains the generic type. Within this clade, *Ph. ericina* (Bourdot) J. Erikss. & Ryvarden has a basidiome similar in color to that of *Ph. aurantiobadia*, but has no reaction with KOH, and has cystidia agglutinated with encrusting orange granules (Eriksson et al. 1978).

Microscopically, *Ph. aurantiobadia* somewhat resembles *Ph. calotricha* (P. Karst.) J. Erikss. & Ryvarden, which has, however, a white to ochraceous basidiome, and numerous cystidioles (though cystidioles in the latter species have also been called cystidia in some descriptions; in this study we use the term 'cystidioles' to describe short hymenial cystidia in order to distinguish them from the large, prominent cystidia in many *Phanerochaete* species). *Phanerochaete sanguinea* also has a red-coloured basidiome, more or less similar to *Ph. aurantiobadia*, but it has cylindrical cystidia (Bernicchia and Gorjón 2010). *Phanerochaete infuscata* Hjortstam & Ryvarden has subulate cystidioles that may be rarely present in *Ph. aurantiobadia*, but its basidiome is ash-grey to greyish brown and somewhat grandinioid (Hjortstam and Ryvarden 2004). In *Phanerochaete tropica* (Sheng H. Wu) Hjortstam, the hymenial surface is white to amber, and it also has fusiform cystidioles (Wu 1990). *Phanerochaete tuberculata* (P. Karst.) Parmasto lacks cystidia and has a cinnamon-buff to clay-colored basidiome, but differs from *Ph. aurantiobadia* in its deeply cracked basidiome, white arachnoid margin, and lack of red reaction with KOH (Eriksson et al. 1978).

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