

1 Short title: Baltazar et al.: *Hydnum peroxydatum* belongs to *Hymenochaete*
2 Phylogenetic relationships of *Hydnum peroxydatum* support the synonymy of
3 *Hydnochaete* with *Hymenochaete* (Hymenochaetaceae, Agaricomycetes)

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17 **Abstract:** A combined dataset of rDNA ITS and LSU sequences was used to infer the
18 phylogenetic relationships of *Hydnochaete peroxydata* (\equiv *Hydnum peroxydatum*), the
19 type species of *Hydnochaete*. The species was retrieved nested within the
20 *Hymenochaete* s. str. clade; therefore, *Hydnochaete* is regarded as a synonym of
21 *Hymenochaete*, and the new combination *Hymenochaete peroxydata* is proposed.

22 **Keywords:** Basidiomycota, corticioid fungi, *Cyclomyces*, Hymenochaetales, ITS
23 and LSU rDNA, xanthochroic fungi

24 INTRODUCTION

1 Bresadola (1896) described *Hydnochaete* Bres. with the new species *Hydnochaete*
2 *badia* Bres. as type species, based on collections from southern Brazil, and
3 characterized by a hydroid hymenophore and presence of setae. Later, Dennis (1970)
4 regarded *Hyd. badia* as a synonym of *Hydnum peroxydatum* Berk. ex Cooke, a name
5 based on a collection from Venezuela, and proposed the binomial *Hydnochaete*
6 *peroxydata* (Berk. ex Cooke) Dennis.

7 *Hydnochaete* in its traditional sense now comprises ten species, mainly found in
8 warm temperate, subtropical and tropical areas (Ryvarden 1982, Parmasto and Wu
9 2005, Dai and Li 2010). It has commonly been classified with genera of
10 hymenochaetoid fungi with smooth (e.g., *Hymenochaete* Lév.), poroid (e.g., *Phellinus*
11 Quél. s. l.), and poroid to cyclolamellate (e.g., *Cyclomyces* Kunze ex Fr.)
12 hymenophores, mainly based on the xanthochroic reaction and presence of setae in
13 many species (Patouillard 1900, Corner 1948, 1991; Donk 1964, Jülich 1981, Ryvarden
14 2004).

15 Phylogenetic studies have shown that several *Hydnochaete* species belong to
16 *Hymenochaete* s. str., a monophyletic genus which also includes some *Cyclomyces* taxa,
17 including its type species *Cyclomyces fuscus* Kunze ex Fr. (Wagner and Fischer 2002,
18 He and Dai 2012, He and Li 2013, Parmasto et al. 2013). Several studies also show that
19 *Hymenochaete tabacina* (Sowerby : Fr.) Lév. and some other species of *Cyclomyces*,
20 *Hydnochaete*, and *Hymenochaete* s. l. form a clade independent from *Hymenochaete* s.
21 str. and are currently accepted in *Pseudochaete* T. Wagner & M. Fisch. (Wagner and
22 Fischer 2002, He and Dai 2012, He and Li 2013, Parmasto et al. 2013). Here
23 *Hymenochaete* s. str. refers to those species placed in the same clade of the type species
24 of *Hymenochaete*, i.e. *Hymenochaete rubiginosa* (Dicks. : Fr.) Lév., while
25 *Hymenochaete* s. l. also includes species of *Pseudochaete*.

1 The synonym of *Cyclomyces* with *Hymenochaete* would create an undesirable
2 nomenclatural situation because *Cyclomyces* is an older name but has considerable
3 fewer specific names than *Hymenochaete* (5 in *Cyclomyces* against ca. 110 in
4 *Hymenochaete*). Thus, Fischer and Wagner (2001) proposed the rejection of
5 *Cyclomyces* in favor of *Hymenochaete*, which later was approved by the 17th
6 International Botanical Congress (McNeill et al. 2006). Wagner & Fischer (2002) also
7 had to propose a new name for *C. fuscus* (type species of *Cyclomyces*) when combined
8 in *Hymenochaete*, viz. *Hymenochaete cyclolamellata* T. Wagner & M. Fisch., because
9 of the existence of the binomial *Hymenochaete fusca* P. Karst.

10 The phylogenetic analyses carried out by Wagner and Fischer (2002), He and
11 Dai (2012), He and Li (2013) and Parmasto et al. (2013) sampled many species,
12 including the type species of *Cyclomyces*, *Hymenochaete* and *Pseudochaete*. However,
13 the phylogenetic placement of *Hyd. peroxydata*, type species of *Hydnochaete*, remained
14 unknown. The assessment of its phylogenetic placement is required in order to verify
15 the current taxonomic status of *Hydnochaete*. The aims of this study were to address the
16 phylogenetic relationships of *Hyd. peroxydata* based on the analysis of a two-gene data
17 set containing nuc-LSU and ITS rDNA gene sequences, and to provide the necessary
18 taxonomic treatment.

19 MATERIALS AND METHODS

20 *Cultures and herbarium specimens.*—Cultures for DNA extraction were obtained from
21 fresh spore prints and kept at the authors' institutional culture collections (CIEFAPcc
22 and Laboratório de Micologia/BOT/UFRGS). They were grown on malt extract agar
23 (MEA) in the dark at 25 C and stored in sterile distilled water following Burdsall and
24 Dorworth (1994). Voucher specimens were deposited at Herbaria ICN and Centro de

1 Investigación y Extensión Forestal Andino Patagónico (CIEFAP, Esquel, Argentina).
2 Data about vouchers are given in the taxonomic treatment.
3 *DNA extraction and PCR conditions.*—For DNA extractions, strains were cultured in
4 malt peptone broth with 10% (v/v) of malt extract (Merck) and 0.1 % (w/v) Bacto
5 peptone (Difco), 2 mL medium in 15 mL tubes. The cultures were incubated at 25 C for
6 5 d in darkness. Total DNA was extracted with the UltraClean™ Microbial DNA
7 Isolation Kit (MO BIO laboratories Inc., USA), according to the manufacturer's
8 instructions. rDNA's ITS (including ITS1, 5.8S and ITS2) and nuLSU regions were
9 amplified using the universal primers ITS5-LR21 and LR0R-LR5, respectively (R.
10 Vilgalys lab webpage at <http://www.botany.duke.edu/fungi/mycolab>).

11 PCR reaction mixtures for amplification of both regions were modified from
12 Rajchenberg et al. (2011) in a final reaction volume of 50 µL with 100–500 ng DNA.
13 PCR reactions were performed in a thermal cycler (My Cycler™, BioRad) and the
14 thermal cycling program was the same described in Rajchenberg et al. (2011). The
15 amplified fragments were purified and sequenced on an ABI 3700 automated sequencer
16 (Perkin-Elmer, USA) at the DNA Synthesis and Sequencing Facility (Macrogen,
17 Korea). The same primers were used for amplification and sequencing. Sequences
18 generated in this study were submitted to GenBank and accession numbers are given in
19 TABLE I.

20 *Phylogenetic analyses.*—DNA sequences generated in this study were manually edited
21 with BioEdit 7.1.3.0 (Hall 1999), and additional sequences for the ingroup and
22 outgroup, based on studies of Wagner and Fischer (2002) and He and Dai (2012), were
23 retrieved from the GenBank nucleotide database. ITS sequences were not available for
24 *Hymenochaete acanthophysata* J.C. Léger. Sequence alignments were automatically
25 performed on MUSCLE v3.8.31 (Edgar 2004) and manually checked on MEGA v5.10

1 (Tamura et al. 2011). Alignments are available from TreeBASE
2 (<http://purl.org/phylo/treebase/phyloids/study/TB2:S14475>). The two DNA regions
3 were first analyzed independently (data not shown), and since there were no major
4 topological conflicts the data were combined into a single matrix for subsequent
5 analyses. Phylogenetic analyses were conducted for the two loci combined dataset under
6 maximum parsimony (MP) and Bayesian inference (BI) criteria. *Fomitopsis pinicola*
7 (Sw. : Fr.) P. Karst. and *Trametes villosa* (Sw. : Fr.) Kreisel were used as outgroup
8 species.

9 MP analysis was performed in PAUP* v4.0b10 (Swofford 2002) with gaps
10 treated as missing characters, equal weighting of characters and transformations,
11 heuristic searches (TBR and MULTREES options on) with random addition of sequences
12 (1000 replicates), and MAXTREES set to auto-increase. Nodal support was tested with
13 bootstrap (BS) of 1000 replicates using the heuristic search option (TBR and MULTREES
14 options on) and 10 random addition sequences.

15 Bayesian analysis was conducted in MrBayes v3.2.1 (Ronquist et al. 2012).
16 Models of evolution were identified for each dataset using jModelTest v2.1.2 (Darriba
17 et al. 2012) under selection AIC, resulting in the model TPM2uf+I+G for ITS and
18 TIM3+I+G for LSU. BI posterior probabilities (PP) were estimated for 10^7 generations,
19 by running four chains and sampling a tree each 10^5 generations, and the first 5 % trees
20 from each run were discarded as burn in. The burn in was determined using Tracer v1.5
21 (<http://tree.bio.ed.ac.uk/software/tracer/>) to analyze MrBayes output files.

22 RESULTS

23 The combined dataset (ITS and LSU) included 21 taxa and a total of 1670 characters, of
24 which 1067 were constant, 161 were variable and parsimony uninformative, and 442
25 were parsimony informative. MP analysis resulted in three equally most parsimonious

1 trees (Tree length = 1229; CI = 0.6373; RI = 0.7785; RC = 0.5384), and one of them is
2 presented in FIG. 1. Six new sequences were generated for this study (see TABLE I).

3 The monophyly of the ingroup is fully supported with both MP and BI analyses
4 and only two topological incongruencies between the MP and BI analyses were
5 observed (FIG. 1, SUPP. FIG. 1). Those nodes are weakly supported with MP (BS < 80)
6 and not supported with BI analysis (PP < 0.85).

7 The ingroup taxa pertained to two major strongly supported clades:
8 *Hymenochaete* s. str. (13 species), and *Pseudochaete* (four species). From a total of 17
9 clades identified, ten were fully supported (BS 100/PP 1.0), five received moderate to
10 high support (BS > 80; PP > 0.94), and two terminal clades were not supported (FIG. 1).

11 The segregation of *Cyclomyces* and *Hydnochaete* as independent from
12 *Hymenochaete* was not supported by our analyses, since the type species of these three
13 genera were placed in the same clade (*Hymenochaete* s. str.) with full support (FIG. 1).
14 Furthermore, monophyletic groups of species with different hymenophoral types were
15 observed — e.g., *Hymenochaete rheicolor* (Mont.) Lév. (smooth) with *Hym.*
16 *cyclolamellata* (concentrically lamellate to poroid) and *Hym. xerantica* (Berk.) S.H. He
17 & Y.C. Dai (poroid); *Hym. rubiginosa* (smooth) with *Hym. paucisetigera* (Parmasto &
18 Sheng H. Wu) S.H. He & Y.C. Dai (hydroid). According to the results presented here
19 *Hymenochaete* s. str. and *Pseudochaete* each include at least three hymenophoral types.

20 The three *Hyd. peroxydata* specimens sampled clustered with full support with a
21 sister clade formed by *Hym. duportii* (Pat.) T. Wagner & M. Fisch. and *Hym. hydroides*
22 T. Wagner & M. Fisch. The whole group is nested in the *Hymenochaete* s. str. clade.

23 TAXONOMY

24 *Hymenochaete* Lév., Ann. Sci. Nat., Bot. Ser. III 5:150, 1846, nom. cons., non

25 *Hymenochaeta* P. Beauv. ex T. Lestib. 1819 (Cyperaceae).

1 = *Cyclomyces* Kunze ex Fr., *Linnaea* 5:512, 1830, nom. rej.

2 = *Hydnochaete* Bres., *Hedwigia* 35(5):287, 1896, **syn. nov.**, non *Hydnochaete*

3 Peck 1897.

4 ***Hymenochaete peroxydata*** (Berk. ex Cooke) Baltazar, Gorjón & Rajchenb., comb.

5 nov.

6 MycoBank MB 804370

7 ≡ *Hydnum peroxydatum* Berk. ex Cooke, *Grevillea* 20(93):1, 1891 (basionym).

8 ≡ *Hydnochaete peroxydata* (Berk. ex Cooke) Dennis, *Kew Bull. Addit. Ser.*

9 3:105, 1970.

10 = *Hydnochaete badia* Bres., *Hedwigia* 35:287, 1896.

11 *Specimens examined.* BRAZIL. RIO GRANDE DO SUL: Riozinho. On dead

12 hardwood, 10 Apr 2010, *J.M. Baltazar 1819* (ICN, CIEFAP); São Francisco de Paula,

13 PROMATA-PUC. On dead hardwood, 26 Jun 2010, *J.M. Baltazar 2056* (ICN,

14 CIEFAP); SANTA CATARINA: Blumenau. 1894, *A. Möller n° 211* (S, lectotype of

15 *Hydnochaete badia*); Blumenau. *A. Möller n° 268* (S, paratype of *Hydnochaete badia*);

16 *A. Möller n° 801* (S, paratype of *Hydnochaete badia*); Blumenau, *A. Möller* (S);

17 Florianópolis, Unidade de Conservação Ambiental Desterro (UCAD). On dead

18 hardwood, 17 Sep 2010, *J.M. Baltazar 2102* (ICN, CIEFAP).

19 A monograph of *Hymenochaete* by Léger (1998) presented a morphological treatment

20 of species with smooth hymenophore. Ryvarden (1982) monographed *Hydnochaete*

21 with descriptions and drawings of all the accepted taxa.

22 DISCUSSION

23 Results of the present study are similar to those of Wagner and Fischer (2002), He and

24 Dai (2012), He and Li (2013) and Parmasto et al. (2013).

1 Sequences of two nuclear rDNA regions were used to infer the phylogenetic
2 placement of *Hyd. peroxydata*, the type species of *Hydnochaete*. Before the present
3 study, the phylogenetic relationships of *Hymenochaete* and allied genera using a
4 combined dataset of ITS and LSU sequences were only investigated by He and Li
5 (2013).

6 Specimens of *Hyd. peroxydata* are nested within the *Hymenochaete* s. str. clade
7 with full support, and two other hydroid species (*Hym. duportii* and *Hym. hydroides*)
8 form a sister group, but they are also closely related to species with a smooth
9 hymenophore such as *Hym. acanthophysata* and *Hym. murina* Bres.

10 *Hymenochaete* is accepted as monophyletic and includes species with
11 resupinate, pileate sessile or stipitate basidiomes, with smooth, fissured or verrucose,
12 hydroid, poroid or concentrically lamellate hymenophores, monomitic hyphal system,
13 simple septate hyphae, presence or absence of setae, and hyaline basidiospores.

14 *Pseudochaete* also includes species with smooth, hydroid and poroid to
15 concentrically lamellate hymenophores, and there is no evident morphological feature to
16 separate it from *Hymenochaete* s. str. *Pseudochaete tabacina* (Sowerby : Fr.) T. Wagner
17 & M. Fisch., type species of the genus, presents a holocenocytic nuclear behavior
18 (Wagner and Fischer 2002). However, data on the nuclear behavior of other species
19 currently accepted in *Pseudochaete* and of most species of *Hymenochaete* s. str. is
20 lacking, and the importance of this feature to segregate these genera remains unknown.
21 Since *Hymenochaete* s. str. and *Pseudochaete* can only be separated based on molecular
22 data, the generic placement of 70–80 species of *Hymenochaete* s. l. not yet included in
23 phylogenetic analyses remains unknown (Parmasto et al. 2013).

24 ACKNOWLEDGEMENTS

1 The authors are grateful to Olivier Chauveau and Larissa Trierveiler Pereira for
2 contributions on a preliminary draft of the manuscript and suggestions on the
3 phylogenetic analyses. Loreta Brandão de Freitas and Patrícia Valente da Silva also
4 made suggestions for these analyses. JMB has Ph.D. scholarships from CNPq (GD
5 141495/2010-3) and CAPES (PDSE—proceeding 9715/11-8). CAPES (Brazil) and
6 MINCyT (Argentina) are thanked by financial support (Bilateral cooperation
7 CAPES/MINCyT Rede 003/11). MBP and MR are researchers of CONICET
8 (Argentina).

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5 FIG. 1. Phylogenetic relationships of *Hymenochaete* s. l. inferred with a combined
6 dataset (rDNA ITS and LSU) under maximum parsimony (MP) and Bayesian inference
7 (BI) analyses. Tree topology is based on one of the three equally most parsimonious
8 trees. Support values for internal nodes are given on the branches as bootstrap/posterior
9 probability (BS/PP). Fully supported nodes (BS 100/PP 1.0) are indicated by black
10 circles. Incongruous topologies between MP and BI analyses are indicated with an
11 asterisk instead of the PP value. Species names in boldface indicate the type species of
12 *Cyclomyces* (*Hym. cyclolamellata*), *Hydnochaete* (*Hym. peroxydata*), *Hymenochaete*
13 (*Hym. rubiginosa*) and *Pseudochaete* (*P. tabacina*). Species names are followed by
14 symbols indicating hymenophore types: ♣ = smooth, ♦ = hydroid, ♥ = poroid to
15 cyclolamellate.

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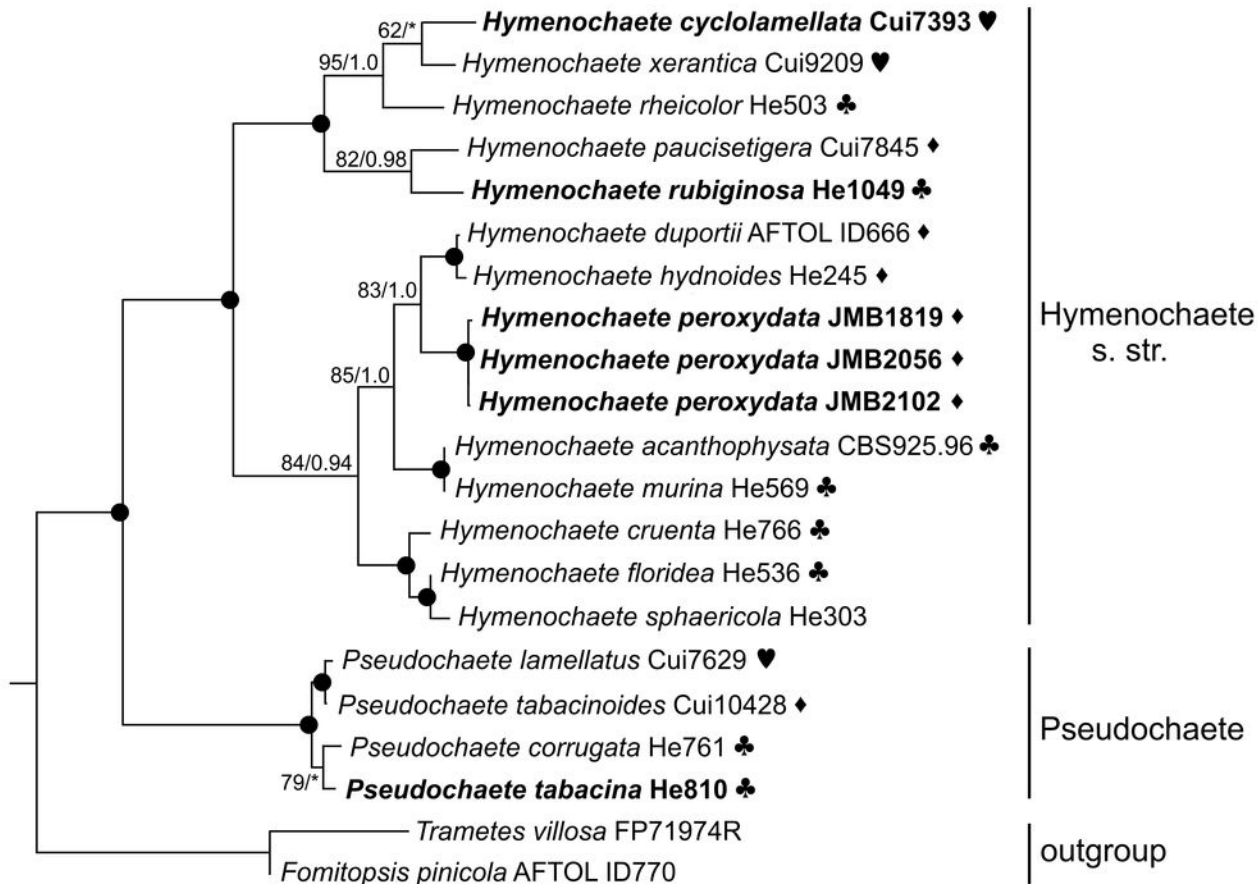


TABLE I. Specimens presented in this study with GenBank accession numbers for the ITS and LSU sequences (newly sequenced strains are indicated in boldface; – information not available)

Species	voucher/strain #	GenBank accession		Reference
		numbers		
		LSU	ITS	
<i>Hymenochaete acanthophysata</i>	CBS 925.26	AF385144	–	Wagner and Fischer (2002)
<i>Hymenochaete cruenta</i>	He766	JQ279681	JQ279595	He and Dai (2012)
<i>Hymenochaete cyclolamellata</i>	Cui7393	JQ279629	JQ279513	He and Dai (2012)
<i>Hymenochaete duportii</i>	AFTOL-ID 666	AY635770	DQ404386	–
<i>Hymenochaete floridea</i>	He536	JQ279683	JQ279597	He and Dai (2012)
<i>Hymenochaete hydroides</i>	He245	JQ279680	JQ279590	He and Dai (2012)
<i>Hymenochaete murina</i>	He569	JQ716412	JQ716406	He and Li (2013)
<i>Hymenochaete paucisetigera</i>	Cui7845	JQ279644	JQ279560	He and Dai (2012)
<i>Hymenochaete peroxydata</i>	J.M. Baltazar 1819	KF371647	KF371644	this study
<i>Hymenochaete peroxydata</i>	J.M. Baltazar 2056, CIEFAPcc 409	KF371648	KF371645	this study
<i>Hymenochaete peroxydata</i>	J.M. Baltazar 2102, CIEFAPcc 411	KF371649	KF371646	this study
<i>Hymenochaete rheicolor</i>	He503	JQ279632	JQ279530	He and Dai (2012)
<i>Hymenochaete rubiginosa</i>	He1049	JQ279667	JQ716407	He and Li (2013)
<i>Hymenochaete sphaericola</i>	He303	JQ279684	JQ279599	He and Dai (2012)
<i>Hymenochaete xerantica</i>	Cui9209	JQ279635	JQ279519	He and Dai (2012)
<i>Pseudochaete corrugata</i>	He761	JQ279621	JQ279606	He and Dai (2012)
<i>Pseudochaete lamellata</i>	Cui7629	JQ279617	JQ279603	He and Dai (2012)

<i>Pseudochaete tabacina</i>	He810	JQ279626	JQ279611	He and Dai (2012)
<i>Pseudochaete tabacinoidea</i>	Cui10428	JQ279618	JQ279604	He and Dai (2012)
Outgroups				
<i>Fomitopsis pinicola</i>	AFTOL-ID 770	AY684164	AY854083	–
<i>Trametes villosa</i>	FP71974R	JN164810	JN164969	Justo and Hibbett (2011)
