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Bjerkandera carnegieae comb. nov. (*Phanerochaetaceae*, *Polyporales*), a wood-decay polypore of cactus

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Abstract. *Poria carnegieae* was described from Arizona growing on the woody ribs of the saguaro cactus, *Carnegiea gigantea*, and was transferred to *Ceriporiopsis* due to morphological evidence. Posterior phylogenetic studies showed a relationship of *Poria carnegieae* with *Bjerkandera*. New sequence data and morphologic evidence are presented to support the transfer of *Ceriporiopsis carnegieae* to *Bjerkandera*.

Key words: host specificity, phlebioid clade, phylogeny, taxonomy

Introduction

Poria carnegieae was described from Arizona growing on the woody ribs of the saguaro cactus, *Carnegiea gigantea* (Baxter 1941). Cultural characters, decay studies, and sexuality of the species were described and studied by Gilbertson and Canfield (1972) and Lindsey and Gilbertson (1977). Gilbertson and Canfield (1972: 1309) noted that the bipolar mating system and negative phenol oxidase reaction placed *P. carnegieae* with *Bjerkandera adusta* (syn. *Polyporus adustus*) based on Nobles' 1965 key pattern of wood-decay fungal cultures. Because of morphological features such as an effused basidiome, light-colored pores, monomitic hyphal system with thin-walled, clamped generative hyphae, lack of cystidia, and thin-walled basidiospores, *P. carnegieae* was transferred to *Ceriporiopsis* by Gilbertson and Ryvarden (1985). In a multigene phylogenetic study of the order *Polyporales* by Justo et al. (2017), *C. carnegieae* was recovered in a clade with two species of *Bjerkandera* in the *Phanerochaetaceae*. Subsequent phylogenetic studies confirmed and supported this relationship (Chen et al. 2018; Motato-Vásquez et al. 2020; Wang et al. 2021). Due to differences in morphological features of the basidiome, such as its resupinate and effused habit and uniform, light-colored context lacking a dark brown zone or black line between the tube layer and subiculum, researchers refrained from transferring *C. carnegieae* to *Bjerkandera* pending more data (Motato-Vásquez et al. 2020; Wang et al. 2021).

The purpose of this study is to provide additional phylogenetic and morphological evidence to support the transfer of *Poria carnegieae* to *Bjerkandera*. We also review additional biological information relating to this taxon.

Materials and methods

Morphological study

Specimens from the Center for Forest Mycology Research (CFMR) fungarium were studied. For microscopic analysis, free-hand sections of basidiomes were mounted in 2% (w/v) aqueous potassium hydroxide (KOH) and 1% (w/v) aqueous phloxine or Melzer's reagent. Cyanophily of hyphal and basidiospore walls was observed in 1% (weight/volume) cotton blue in 60% (w/v) lactic acid. Basidiospores were measured in KOH and phloxine mounts under oil immersion with at 100× magnification. Q values were calculated from average spore length divided by average spore width of at least 30 spores. Color codes and names follow Kornerup & Wanscher (1978). Micrographs of basidiomes were taken with an Olympus DP27 camera attached on an Olympus BX43 compound microscope.

DNA extraction, PCR amplification and sequencing

DNA extraction and amplification were performed from cultures at CFMR following a standard CTAB protocol (Mercado & Ortiz-Santana 2018). Sequencing was

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Table 1. Taxon sampling: voucher specimens/cultures and GenBank accession numbers. New sequences generated in this study are in boldface. (T) = type specimen.

Species voucher/cultures	GenBank accession numbers				
	ITS	LSU	*tef1-α*	*rpb1*	*rpb2*
Outgroup					
Candelabrochaete africana					
FP-102987-sp	KP135294	KP135199	–	KP134872	KP134975
Meruliaceae					
Ceriporiopsis gilvescens					
Niemela-5516	HQ659222	HQ659222	–	–	–
BRNM 710166	FJ496684	FJ496720	–	–	–
L3522sp	KY948760	–	–	KY948919	–
Climacodon septentrionalis					
AFTOL-767	AY854082	AY684165	AY885151	AY864872	AY780941
Hydnophlebia chrysorhiza					
FD-282	KP135338	KP135217	–	KP134848	KP134897
Mycoacia fuscoatra					
HHB-10782-Sp	KP135365	KP135265	–	KP134857	KP134910
Phlebia radiata					
AFTOL-484	AY854087	AF287885	AY885156	AY864881	AY218502
Irpicaceae					
Byssomerulius corium					
FP-102382	KP135007	KP135230	–	KP134802	KP134921
Ceriporia reticulata					
RLG-11354-Sp	KP135041	KP135204	–	KP134794	KP134922
Efibula americana					
FP-102165	KP135016	KP135256	–	KP134808	KP134916
Emmia lacerata					
FP-55521-T	KP135024	KP135202	–	KP134805	KP134915
Flavodon flavus					
WHC 1381	LC427029	LC427052	–	LC427064	–
Gloeoporus dichrous					
BRNU 631507	MG572751	MG572735	–	–	MG593280
FP-151129	KP135058	KP135213	–	KP134866	–
Gloeoporus pannocinctus					
L-15726-Sp	KP135060	KP135214	–	KP134867	KP134973
Gloeoporus thelephoroides					
BZ-289	MG572757	MG572741	–	–	MG593286
Hydnopolyporus fimbriatus					
Meijer3729 (O)	JN649346	JN649346	JX109904	–	JX109875
Irpex lacteus					
FD-9	KP135026	KP135224	–	KP134806	–
Meruliopsis cystidiata					
776308	MG572749	MG572733	–	–	MG593278
Meruliopsis taxicola					
SK 0075 (GB)	JX109847	JX109847	JX109901	–	JX109873
Trametopsis cervina					
TJV 93 216T	JN165020	JN164796	JN164882	JN164839	JN164877
Phanerochaetaceae					
Bjerkandera adusta					
Dai 14516	MW507097	MW520204	–	–	–
Dai 15665	MW507098	MW520205	–	–	–
Dai 15495	MW507099	–	–	–	–
Dai 13201	MW507100	MW520206	–	–	–
Dai 12640	MW507101	–	–	–	–
SFC20120409-08	KJ704814	KJ704829	–	–	–
SFC20111029-15	KJ704813	KJ704828	–	–	–
BRNM 771948	KT305935	KT305935	KT305938	–	–

Table 1. Continued.

Species voucher/cultures	GenBank accession numbers				
	ITS	LSU	*tef1-α*	*rpb1*	*rpb2*
HHB-12826-Sp	KP134983	KP135198	–	KP134784	KP134913
HMCC-23	MK051123	–	MK051163	MK051161	MK051162
Bjerkandera albocinerea					
MV 346 (T)	MH025421	MH025421	–	–	–
RP 317	MH025420	–	–	–	–
MW559	MH025419	MH025419	–	–	–
Dai 16411	MW507102	MW520207	–	–	–
Bjerkandera atroalba					
SP 446205, MW 425 (T)	KT305930	KT305930	–	–	–
SP 445629, MV 158	KT305932	KT305932	KT305940	–	–
SP 445672, MV 266	KT305931	KT305931	KT305939	–	–
Dai 17457	MW507103	MW520208	–	–	–
Bjerkandera carnegieae					
ERC-71-366	**OL376625**	**OL376623**	**OL405698**	–	**OL405701**
RLG 10553	**OL376626**	**OL376624**	–	–	–
RLG-7277-T	KY948792	KY948854	**OL405699**	KY948935	**OL405700**
JV1209/45	KX081134	–	–	–	–
JV0407/27-J	MW507122	–	–	–	–
Bjerkandera centroamericana					
JK0610/A13	KT305934	KT305934	KT305942	–	–
JK0610/A7 (T)	KT305933	KT305933	KT305941	–	–
JV1704/97	MW507104	–	–	–	–
Bjerkandera ecuadoriensis					
JV1906/C16-J (T)	MW507105	–	–	–	–
Bjerkandera fulgida					
Dai 16107 (T)	MW507106	MW520209	–	–	–
Dai 12284	MW507107	–	–	–	–
Dai 13597	MW507108	MW520210	–	–	–
Bjerkandera fumosa					
SFC20121009-04	KJ704824	KJ704839	–	–	–
BRNM771947	KT305937	KT305937	–	–	–
DAOM215869	DQ060097	AF287848	–	–	–
Dai 21100	MW507109	MW520211	–	–	–
Cui 10747	MW507111	MW520212	–	–	–
Dai 12674B	MW507112	MW520213	–	–	–
Homble 1900	KF698740	KF698751	–	–	–
Bjerkandera mikrofumosa					
MV 353	MH025416	MH025416	–	–	–
MV 363	MH023526	MH023526	–	–	–
MV 398	MH023527	MH023527	–	–	–
MV 420	MH023525	MH023525	–	–	–
MV 433	MH025418	–	–	–	–
MV 435	MH025417	MH025417	–	–	–
Catania 3269	MH025414	–	–	–	–
Robledo 1170	MH025415	–	–	–	–
JV1707/10J-1	MW507113	–	–	–	–
JV1707/10J-2	MW507114	–	–	–	–
Bjerkandera minispora					
Dai 15234 (T)	MW507115	MW520214	–	–	–
Cui 5376	MW507116	MW520215	–	–	–
Bjerkandera resupinata					
Dai 16642 (T)	MW507117	MW520216	–	–	–
Cui 8017	KU509526	–	–	–	–
Bjerkandera sp.					
JV1512/13-J	MW507118	–	–	–	–
L13104sp	KY948791	KY948855	–	KY948936	–

Table 1. Continued.

Species voucher/cultures	GenBank accession numbers				
	ITS	LSU	*tef1-α*	*rpb1*	*rpb2*
Donkia pulcherrima					
GC 1707-11	LC378994	LC379152	LC387371	LC379157	LC387351
Geliporus exilisporus					
GC 1702-15	LC378995	LC379153	LC387372	LC379158	LC387352
Hyphodermella rosae					
FP-150552	KP134978	KP135223	–	KP134823	KP134939
Odontoefibula orientalis					
Wu 0805-59	LC363488	LC363493	LC387380	LC363499	LC387361
Wu 0910-57	LC363490	LC363495	LC387381	LC363501	LC387362
Phanerina mellea					
WEI 17-224	LC387333	LC387340	LC387382	LC387345	LC387363
Phanerochaete chrysosporium					
AFTOL-ID 776	AY854086	GQ470643	AY885155	AY864880	–
Phanerochaete sordida					
Wu 0711-81	LC387334	MF110289	LC270920	LC387346	LC387364
Phanerochaete taiwaniana					
Wu 0112-13	MF399412	MF399403	LC387383	LC314332	LC387365
Porostereum fulvum					
LY 18491	MG649452	MG649454	–	–	–
LY 18496	MG649453	MG649455	–	–	–
Porostereum spadiceum					
KUC 2013051	KJ668473	KJ668325	–	–	–
KUC20100728-24	JX463661	JX463655	–	–	–
KUC20080728-31	JX463660	JX463654	–	–	–
Rhizochaete radicata					
FD-123	KP135407	KP135279	–	KP134816	KP134937
Rhizochaete rubescens					
Wu 0910-45	LC387335	MF110294	LC270925	LC387348	LC387370
Terana caerulea					
FP 10473	KP134980	KP135276	–	KP134865	KP134960

conducted at the University of Wisconsin Biotechnology Center (UWBC) in Madison, WI. The internal transcribed spacer region (ITS), including ITS1, 5.8S and ITS2, was amplified with primer pair ITS1F/ITS4 (Gardes & Bruns 1993; White et al. 1990). The 5′ end of the 28S large subunit of the nuclear ribosomal RNA (LSU) was amplified with primers LR0R (Cubeta et al. 1991) and LR5 (Vilgalys & Hester 1990); *tef1-α* was amplified with primer pair EF1-983/EF1-1567R (Rehner & Buckley 2005) and *rpb2* with primers bRPB2-6F and bRPB2-7.1R (Matheny 2005). Thermocycler conditions followed Kuo and Ortiz-Santana (2020). Newly generated sequences were edited with Sequencher 4.8 (Gene Codes Corp., Ann Arbor, Michigan).

Phylogenetics analyses

New DNA sequences generated in the present work were combined with sequences retrieved from GenBank (NCBI) to construct two datasets. Scientific names and GenBank Accession Numbers of sequences are listed in Table 1. Dataset 1 was composed of ITS, LSU, *rpb1*, *rpb*2 and *tef1-α* sequences of four *Bjerkandera* species with at least one coding marker and 31 species of the 'phlebioid clade' with representatives from the *Phanerochaetaceae*, *Irpicaceae* and *Meruliaceae* (Binder et al. 2013; Justo et al. 2017; Chen et al. 2018, 2020). *Candelabrochaete africana* was selected as outgroup (Justo et al. 2017; Chen et al. 2018). Dataset 2 was composed of ITS and LSU sequences of 13 *Bjerkandera* species with *Porostereum* (*P. spadiceum* and *P. fulvum*) as outgroup taxa (Mota-to-Vásquez et al. 2020; Wang et al. 2021).

ITS region was aligned using ProbCons 1.12 (Do et al. 2005), whereas LSU, *rpb1*, *rpb*2 and *tef1-α* were individually aligned using MAFFT 7 (Katoh et al. 2017) using the G-INS-i alignment method. Alignments were manually inspected and adjusted using MEGA 6 (Tamura et al. 2013). ModelFinder (Kalyaanamoorthy et al. 2017) as implemented in the IQ-Tree software (Nguyen et al. 2015) was used to estimate the best-fit partitioning strategy and the best-fit model of nucleotide evolution for the dataset using 16 data blocks (ITS1; 5.8S; ITS2; LSU; *rpb1* codon positions, 1stpos, 2ndpos, and 3rdpos; *rpb1* introns; *rpb*2 codon positions, 1stpos, 2ndpos, and 3rdpos; *rpb*2 introns; *tef1-α* codon positions 1stpos, 2ndpos, and 3rdpos and *tef1-α* introns). Models were restricted for those implemented in MrBayes 3.2 (Ronquist et al. 2012). Bayesian inference (BI) and maximum likelihood (ML) phylogenetic analyses were applied to the concatenated datasets using the partition scheme and evolutionary models defined by ModelFinder. BI was performed following Robledo et al. (2020) in the CIPRES science gateway (Miller et al. 2010; http://www.phylo.org/). Maximum

likelihood searches were conducted with IQ-TREE. The analyses initially involved 100 ML searches, each one starting from one randomized stepwise addition parsimony tree. Branch supports were calculated using the UFBoot (ultrafast bootstrap approximation) (Hoang et al. 2018) implemented in IQ-TREE with 1000 replications. A node was considered strongly supported with BPP ≥ 0.95 or BS ≥95% (Hyde et al. 2013; Minh et al. 2020).

Results

Phylogenetic analyses

Dataset 1 included 50 terminals and 6143 characters, of which 1990 were parsimony informative, 2527 were variable and 3213 constants. The partitions and evolutionary models selected were: GTR+F+I+G4 (ITS1, ITS2, *rpb1* 3rdpos), JC+I+G4 (5.8S), K2P+I+G4 (LSU, *tef1-α* 1stpos, *tef1-α* 2ndpos and *rpb1* 2ndpos), GTR+F+G4 (*tef1-α* 3rdpos, *rpb1* 1stpos), HKY+F+I+G4 (*tef1-α* introns, *rpb2* introns, *rpb2* 1stpos), SYM+I+G4 (*rpb1* introns, *rpb2* 2ndpos and *rpb2* 3rdpos). Bayesian and ML analyses resulted in identical topologies. The ML tree is presented in Figure 1. The topology showed 3 main lineages at family level recovered with maximum support: *Phanerochaetaceae*, *Irpicaceae* and *Meruliaceae*. This is congruent with previous works (Justo et al. 2017; Chen et al. 2018). Within *Phanerochaetaceae*, *Bjerkandera* conform a lineage with maximum support including *B. adusta*, type species of the genus, and *C. carnegieae* like previous works (Justo et al. 2017; Chen et al. 2018). These multi-loci phylogenetic analyses support the taxonomic position of *C. carnegieae* within *Bjerkandera*.

Dataset 2 included 58 terminals and 1988 characters, of which 155 were parsimony informative, 197 variable and 1787 constants. The partitions and evolutionary models selected were: K2P+G4 (ITS1 and ITS2), K2P+I (5.8S and LSU). Bayesian and ML analyses resulted in similar topologies. The ML tree is presented in Figure 2. In this ITS-LSU tree, *C. carnegieae* is in a basal position within *Bjerkandera* and consistent with previous work (Motato-Vásquez et al. 2020; Wang et al. 2021).

Taxonomy

Based on strong phylogenetic evidence presented above and new morphological observations presented below, we propose the transfer of *Poria carnegieae* to *Bjerkandera*. This transfer implies a slight modification of *Bjerkandera* concept, now including species with resupinate effused and adnate basidiomes and with a uniform context without a dark line or dark zone separating the tube layer from the context.

Bjerkandera carnegieae (D. V. Baxter) Robledo, Nakasone & B. Ortiz, comb. nov. (Fig. 3A–F)

MycoBank MB 841466

Basionym: *Poria carnegieae* D. V. Baxter, Papers of the Michigan Academy of Sciences 26: 110. 1941.

≡ *Ceriporiopsis carnegieae* (D. V. Baxter) Gilb. & Ryvarden, Mycotaxon 22 (2): 364, 1985.

Descriptions and illustrations. Baxter (1941), Lowe (1966: 82), Gilbertson and Canfield (1972, basidiome and culture), Lindsey & Gilbertson (1977, culture), Gilbertson and Ryvarden (1986: 189–190). Photograph of the specimen JV1209/45 (GenBank accession number KX081134) included in the phylogeny (Fig. 2) is available at the Polypore Collection of Dr. Josef Vlasák, Hluboká nad Vltavou, Czech Republic, Edition 18.II. 2015, http://mykoweb.prf.jcu.cz/polypores/index.html accessed October 28, 2021.

Remarks. Descriptions and illustrations of the basidiome are readily available (see above), and our observations generally agree except as follows: (1) The subicular trama is composed primarily of slightly thick- to thick-walled subicular hyphae 3–5.5 µm diam with walls thin to 1.5 µm thick. (2) The tramal hyphae are 3–3.5 µm diam with walls thin to 0.5 µm thick. (3) Basidia are clavate, 15–21× 5–5.5 µm. (4) Basidiospores are slightly wider than previously reported, (4.5–)4.7–5.8 × (2.7–)2.8–3 µm, Q = 1.6–2, average of 33 spores = 5.3 ± 0.4 × 3 ± 0.2 µm, Q = 1.8.

Basidiomes of *B. carnegieae* are entirely effused and adnate with nearly white to ivory-white pores when fresh that darken slightly to light brown or buff, and a uniform, cream-colored context. The pore layer is very fragile and brittle when dried. These characters differ from most species of *Bjerkandera* which are pileate, effuse-reflexed, except the resupinate species *B. resupinata*. In addition, most species in the genus have dark gray to buff-colored pores that typically darken to black when bruised in contrast to the light-colored pores in *B. carnegieae* that darken to light brown. Furthermore, the context in *B. carnegieae* is uniformly light-colored, whereas other species of *Bjerkandera* have a tan, brown or black zone or line between the base of the tubes or pores and context. Motato-Vásquez et al. (2020) and Wang et al. (2021) have summarized some critical morphological characters of accepted species in *Bjerkandera* and included keys.

Despite these macromorphological differences with other species in the genus, *B. carnegieae* shares important characters such as a monomitic, clamped hyphal system of thin- to thick-walled generative hyphae with thick-walled hyphae dominating in the subiculum and trama (Fig. 3C–D), and basidia and basidiospores that are similar in shape and size. Furthermore, cultures of *B. carnegieae*, *B. adusta*, and *B. fumosa* share some important biological features, such as developing arthroconidia and a negative or weakly positive reaction on gallic acid agar with some mycelial growth and a negative or positive reaction on tannic acid agar, but no growth (Nobles 1948: 350; Gilbertson & Canfield 1972; Lombard et al. 1992). Finally, these three species have a heterocytic nuclear behavior and a bipolar mating system (Gilbertson & Canfield 1972; David 1988; Lombard et al. 1992). It is noteworthy that cultures of *B. mikrofumosa* and *B. atroalba* develop chlamydospores and not arthroconidia (Motato-Vásquez et. al. 2016, 2020).

Specimens examined. (All on saguaro, *Carnegiea gigantea* at CFMR): U.S.A., Arizona. Pinal County, Santa Rosa Valley, Papago Indian Reservation, Gu Komelik, 11 November 1971, E. R. Canfield, ERC 71-366 and ERC 71-367; Chiu Chiuschu, 11 November 1971, R. L. Gilbertson, RLG 10553. Pima County,

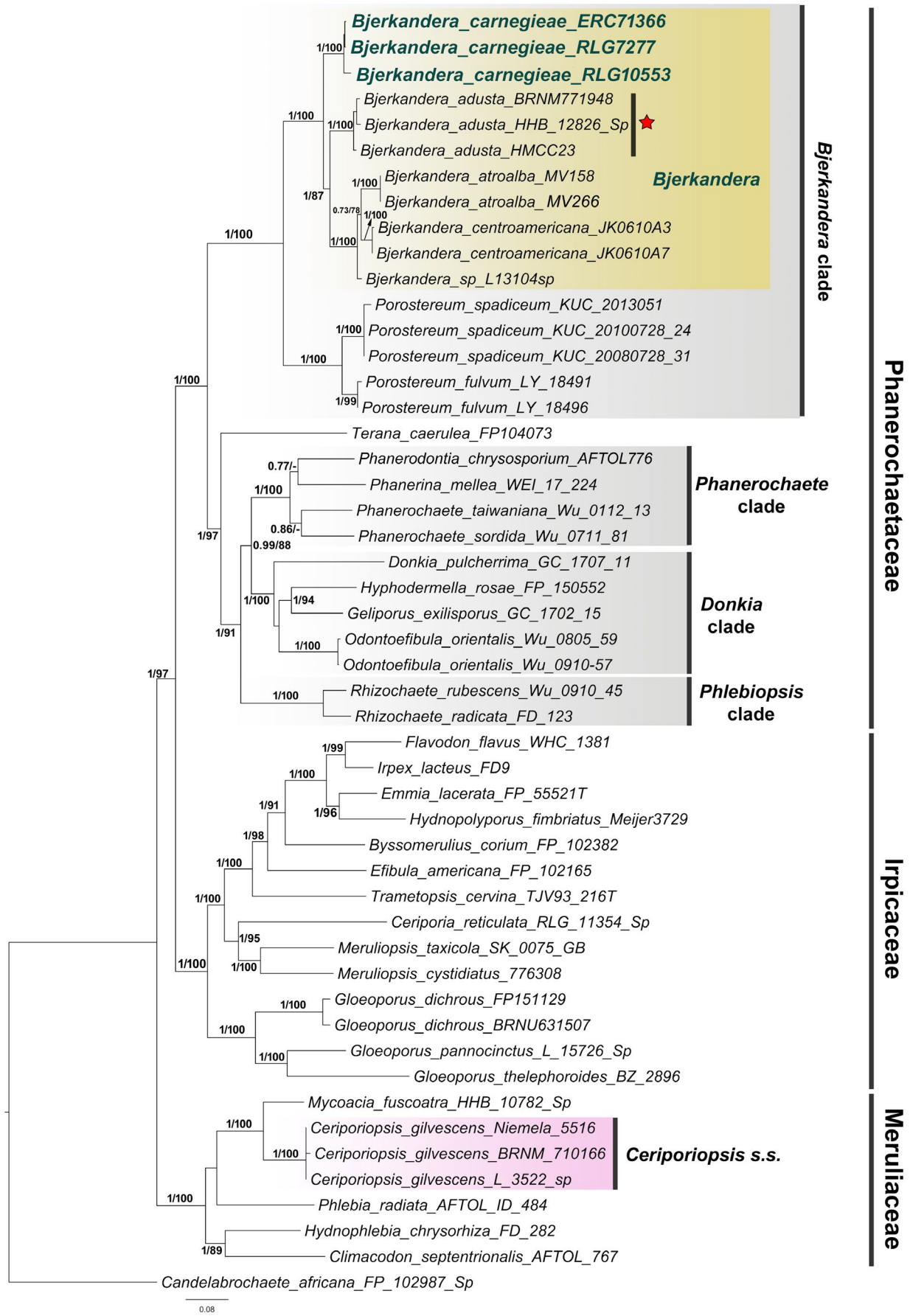

Figure 1. Maximum Likelihood (ML) tree of *Phanerochaetaceae* based on concatenated dataset of ITS + LSU + *rpb*1 + *rpb*2 + *tef1-α* sequence data. Branch support values are shown as BPP/BS, Bayesian posterior probability above 0.7 and Bootstrap values above 70%. ★= type species of *Bjerkandera*.

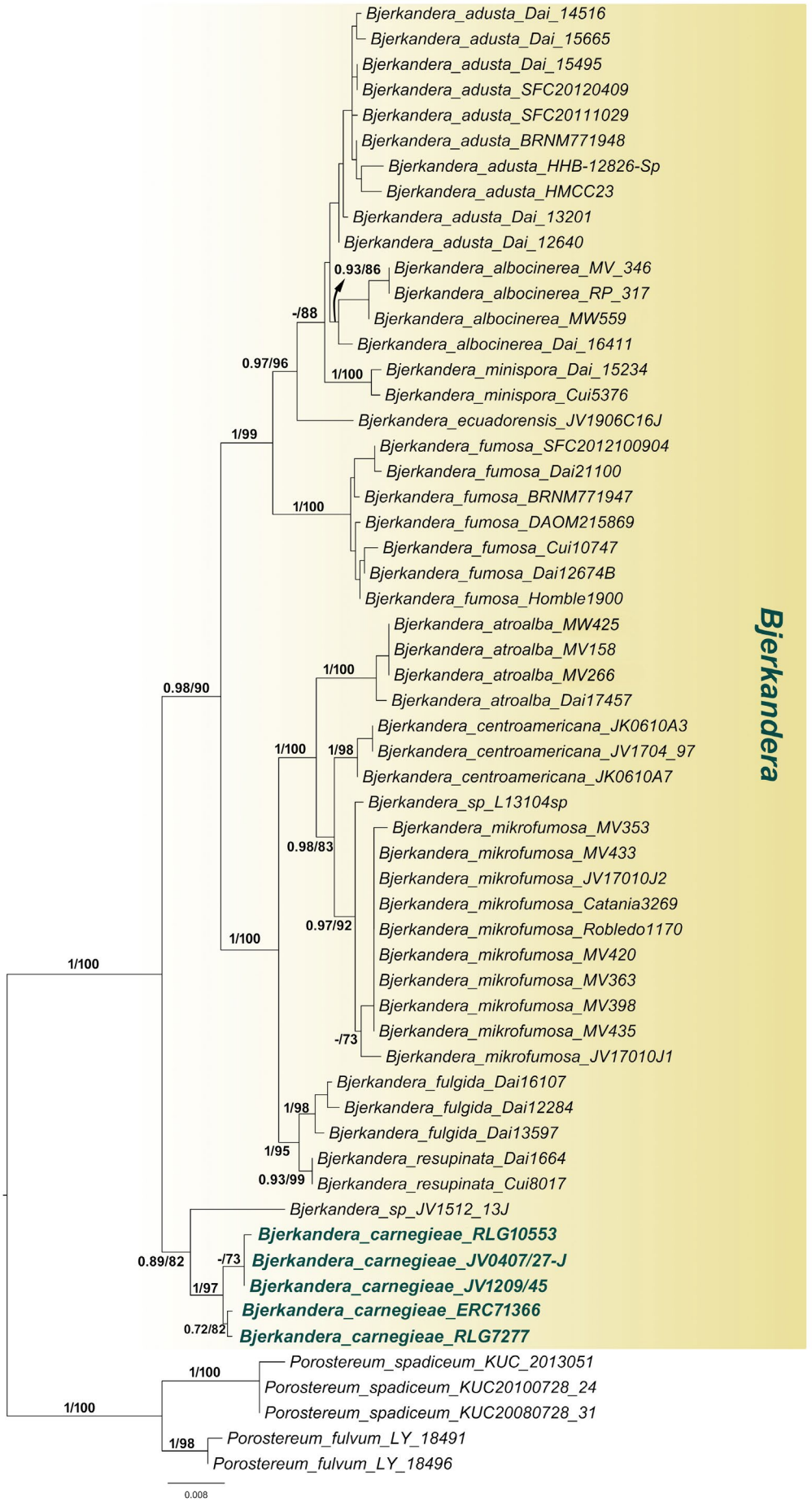

Figure 2. Maximum Likelihood (ML) tree of *Bjerkandera* based on concatenated dataset of ITS + LSU sequence data. Branch support values are shown as BPP/BS, Bayesian posterior probability above 0.7 and Bootstrap values above 70%.

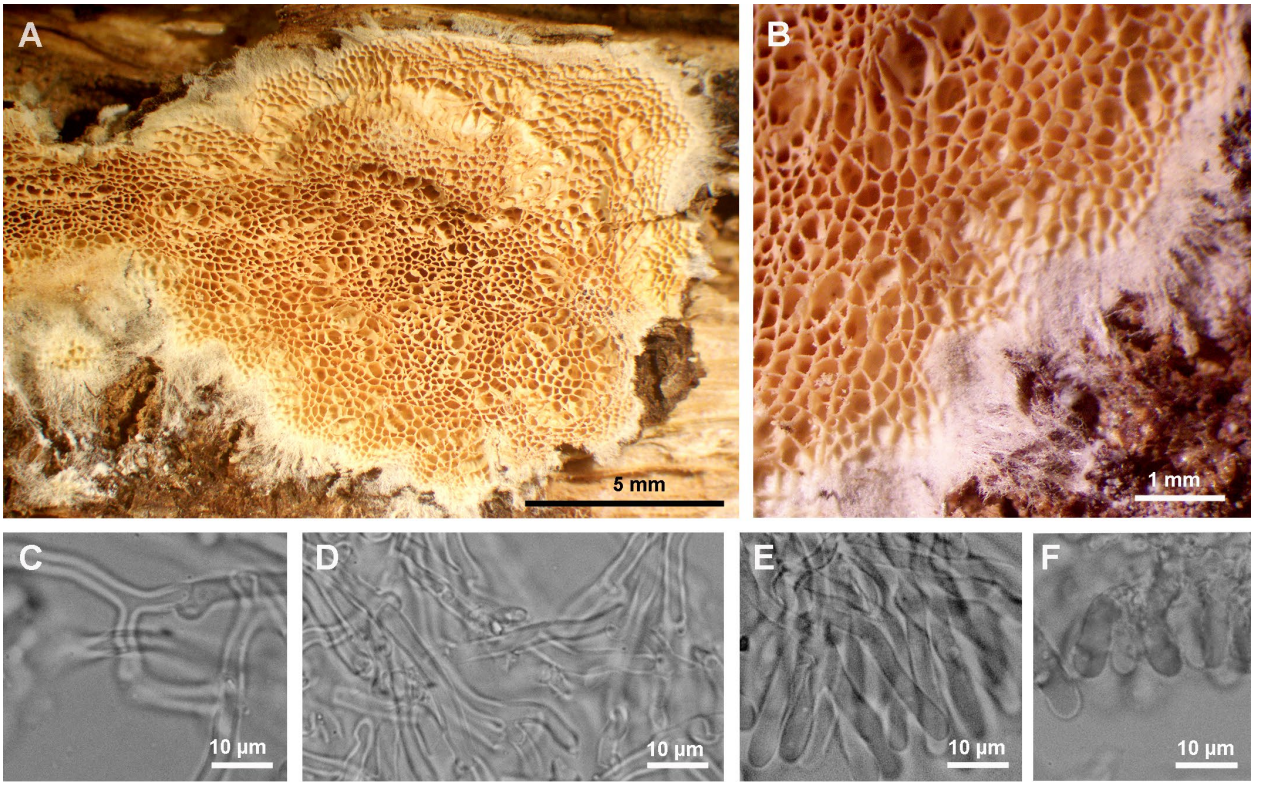

Figure 3. Morphological features *Bjerkandera carnegieae* (specimen ERC71366) A-B, macromorphological features: A – general view of basidioma; B – detail of pores and margin. C–E – microscopic features: C – contex; D – trama of the tubes; E – dissepiment edge; F – hymenium. Pictures by K. Nakasone.

Saguaro National Monument, 30 August 1967, R. L. Gilbertson, RLG-7277; near San Pedro Valley, Redington Road, 26 February 1971, R. L. Gilbertson, RLG 10081; Tucson Mountains, Picture Rocks Pass, 24 October 1972, J. P. Lindsey, JPL 93.

Discussion

Our multi-gene phylogenetic tree of the phlebioid clade shown in Figure 1 is consistent with previous studies (Justo et al. 2017; Chen et al. 2018). Similarly, the ITS-LSU analysis of the genus *Bjerkandera* recovered a tree shown in Figure 2 that is congruent with that in Motato-Vásquez et al. (2020) and Wang et al. (2021). Phylogenetic studies showed that the current concept of *Ceriporiopsis* is polyphyletic with species recovered in several different phylogenetic clades (Tomšovský et al. 2010; Zhao & Cui 2014; Gómez-Montoya et al. 2017). The type of *Ceriporiopsis*, *C. gilvescens*, clusters in a lineage with *Phlebia* and *Mycoacia* (Binder et al. 2013; Zhao & Cui 2014; Zhao & Wu 2016; Justo et al. 2017).

The transfer of *P. carnegieae* to *Bjerkandera* requires a slight modification to the genus description to include species with effused basidiomes and uniform context without a dark line or dark zone separating the tube layer from the context. We believe that this is a better solution than the creation of a new genus for *B. carnegieae* that lacks strong phylogenetic, morphological, or biological characters. More studies of *Bjerkandera* sp. JV1512/13J (as *Ceriporiopsis* sp. in Wang et al. 2021) and *Bjerkandera* sp. L13104sp, both from Costa Rica, are required to see if sequence data are also supported by morphological and biological characters to describe it as a new taxon.

Bjerkandera carnegieae was originally described by Baxter (1941) from southern Arizona as an important agent of decay in the saguaro cactus, *Carnegiea gigantea*. Most specimens of this species are from saguaro, but a few specimens are also known on other woody *Cactaceae*, such as *Pachycereus* sp and *Lemaireocereus* sp, from desert areas of Mexico (Lindsey & Gilbertson 1977; and data retrieved from MycoPortal, October 15, 2021). ITS BLAST searches in GenBank have recovered some environmental samples with 100% sequence identity with *B. carnegieae*, mostly from Arizona, but also from Puerto Rico and Brazil (Fröhlich-Nowoisky et al. 2012). Although the fungal diversity growing in saguaro has been recorded (Gilbertson et al. 1974; Lindsey & Gilbertson 1975), tree-like cacti are 'under sampled' in other parts of America. The biographical connection of desert areas from USA and Central Argentina has been previously reported, not only in similar physiognomic structure, spiny bush and trees and tree-like cacti, but in plant taxa, i.e. *Prosopis* spp., and polypores are not the exception. See for instance *Inocutis texana*, originally described from North America that has been registered in xerophitic areas of central Argentina (Robledo & Urcelay 2009; Rajchenberg & Robledo 2013). The only polypore so far registered in a tree-like cactus in Central Argentina has been *Ceriporia xylostromatoides*, growing inside a dead falling *Stetsonia coryne* (Robledo & Urcelay 2009).

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