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, monomitc 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
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 |
| **Merulaceae**          |     |     |        |      |      |
| *Cerioporia gilvescens* |     |     |        |      |      |
| Niemela-5516            |     |     |        |      |      |
| BRNM 710166             |     |     |        |      |      |
| L3522sp                 |     |     |        |      |      |
|                         | Hq659222 | Hq659222 | – | – | – |
| **Climacodon septentrionalis** |     |     |        |      |      |
| AFTOL-767               |     |     |        |      |      |
|                         | AY854082 | AY684165 | AY885151 | AY864872 | AY780941 |
| **Hydnophlebia chrysorhiza** |     |     |        |      |      |
| FD-282                  |     |     |        |      |      |
|                         | KP135338 | KP135217 | – | KP134848 | KP134897 |
| **Mycoacia fuscocatra** |     |     |        |      |      |
| HHB-10782-Sp            |     |     |        |      |      |
|                         | KP135365 | KP135265 | – | KP134857 | KP134910 |
| **Phlebia radiata**     |     |     |        |      |      |
| AFTOL-484               |     |     |        |      |      |
|                         | AY854087 | AF287885 | AY885156 | AY864881 | AY218502 |
| **Irpiceae**            |     |     |        |      |      |
| *Byssomerulius corium*  |     |     |        |      |      |
| FP-102382               |     |     |        |      |      |
|                         | KP135007 | KP135230 | – | KP134802 | KP134921 |
| **Cerioporia reticulata** |     |     |        |      |      |
| RLG-11354-Sp            |     |     |        |      |      |
|                         | KP135041 | KP135204 | – | KP134794 | KP134922 |
| **Ejfula americana**    |     |     |        |      |      |
| FP-102165               |     |     |        |      |      |
|                         | KP135016 | KP135256 | – | KP134808 | KP134916 |
| **Emmia lacera**        |     |     |        |      |      |
| FP-55521-T              |     |     |        |      |      |
|                         | KP135024 | KP135202 | – | KP134805 | KP134915 |
| **Flavodon flavus**     |     |     |        |      |      |
| WHC 1381                |     |     |        |      |      |
|                         | LC427029 | LC427052 | – | LC427064 | – |
| **Gloeoporus dichrous** |     |     |        |      |      |
| BRNU 631507             |     |     |        |      |      |
| FP-151129               |     |     |        |      |      |
|                         | MG572751 | MG572735 | – | – | MG593280 |
| **Gloeoporus pannocinctus** |     |     |        |      |      |
| L-15726-Sp              |     |     |        |      |      |
|                         | KP135060 | KP135214 | – | KP134867 | KP134973 |
| **Gloeoporus thelephoroides** |     |     |        |      |      |
| BZ-289                  |     |     |        |      |      |
|                         | MG572757 | MG572741 | – | – | MG593286 |
| **Hydnopolyopus fimbriatus** |     |     |        |      |      |
| Meijer3729 (O)          |     |     |        |      |      |
|                         | JN649346 | JN649346 | JX109904 | – | JX109875 |
| **Irpes lacteus**       |     |     |        |      |      |
| FD-9                    |     |     |        |      |      |
|                         | KP135026 | KP135224 | – | KP134806 | – |
| **Mersulopsis cystidiata** |     |     |        |      |      |
| 776308                  |     |     |        |      |      |
|                         | MG572749 | MG572733 | – | – | MG593278 |
| **Mersulopsis taxicola** |     |     |        |      |      |
| SK 0075 (GB)            |     |     |        |      |      |
|                         | JX109847 | JX109847 | JX109901 | – | JX109873 |
| **Trametopsis cervina** |     |     |        |      |      |
| TJV 93 216T             |     |     |        |      |      |
|                         | JN165020 | JN164796 | JN164882 | JN164839 | JN164877 |
| **Phanerochaetaceae**   |     |     |        |      |      |
| *Bjerkandera adusta*    |     |     |        |      |      |
| Dai 14516               |     |     |        |      |      |
| Dai 15665               |     |     |        |      |      |
| Dai 15495               |     |     |        |      |      |
| Dai 13201               |     |     |        |      |      |
| Dai 12640               |     |     |        |      |      |
| SFC20120409-08          |     |     |        |      |      |
|                         | KJ704814 | KJ704829 | – | – | – |
| SFC20111029-15          |     |     |        |      |      |
|                         | KJ704813 | KJ704828 | – | – | – |
| BRNM 771948             |     |     |        |      |      |
|                         | KT305935 | KT305935 | KT305938 | – | – |
| Species          | voucher/cultures | ITS            | LSU            | tef1-α          | rpb1          | rpb2          |
|------------------|------------------|----------------|----------------|-----------------|---------------|---------------|
| Bjerkandera albocinerea |                  |                |                |                 |               |               |
| MV 346 (T)       |                  | MHO25421       | MHO25421       |                 |               |               |
| RP 317           |                  | MHO25420       | –              | –               |               |               |
| MWW559           |                  | MHO25419       | MHO25419       |                 |               |               |
| Dai 16411        |                  | MWS07102       | MWS020207      | –               |               |               |
| BJerkandera atroalba |                |                |                |                 |               |               |
| SP 446205, MW 425 (T) |            | KT305930       | KT305930       |                 |               |               |
| SP 445629, MWW 158 |                | KT305932       | KT305932       | KT305940        | –             |               |
| SP 445672, MWW 266 |                | KT305931       | KT305931       | KT305939        | –             |               |
| Dai 17457        |                  | MWS07103       | MWS020208      | –               |               |               |
| Bjerkandera carnegiaeae |              |                |                |                 |               |               |
| ERC-71-366       |                  | OL376625       | OL376623       | OL405698        | –             | OL405701      |
| RLG 10553        |                  | OL376626       | OL376624       |                 |               |               |
| RLG-7277-T       |                  | KY948792       | KY948854       | OL405699        | KY948935      | OL405700      |
| JIV1209/45       |                  | KX081134       | –              | –               |               |               |
| JIV0407/27-J     |                  | MWS07122       | –              | –               |               |               |
| Bjerkandera centroamerican |           |                |                |                 |               |               |
| JK0610/A13       |                  | KT305934       | KT305934       | KT305942        | –             | –             |
| JK0610/A7 (T)    |                  | KT305933       | KT305933       | KT305941        | –             | –             |
| JIV1700/97       |                  | MWS07104       | –              | –               |               |               |
| Bjerkandera ecuadoriensis |             |                |                |                 |               |               |
| JIV1906/C16-J (T) |                  | MWS07105       | –              | –               |               |               |
| Bjerkandera fulgida |                |                |                |                 |               |               |
| Dai 16107 (T)    |                  | MWS07106       | MWS020209      | –               |               |               |
| Dai 12284        |                  | MWS07107       | –              | –               |               |               |
| Dai 13597        |                  | MWS07108       | MWS020210      | –               |               |               |
| Bjerkandera fumosa |                |                |                |                 |               |               |
| SFC20121009-04   |                  | KJ704824       | KJ704839       | –               |               | –             |
| BRNM771947       |                  | KT305937       | KT305937       | –               |               | –             |
| DAO M215869      |                  | DQ060097       | AF287848       | –               |               | –             |
| Dai 21100        |                  | MWS07109       | MWS020211      | –               |               | –             |
| Cui 10747        |                  | MWS07111       | MWS020212      | –               |               | –             |
| Dai 12674B       |                  | MWS07112       | MWS020213      | –               |               | –             |
| Homble 1900      |                  | KF698740       | KF698751       | –               |               | –             |
| Bjerkandera mikrofumosa |             |                |                |                 |               |               |
| MV 353           |                  | MHO25416       | MHO25416       | –               |               | –             |
| MV 363           |                  | MHO23526       | MHO23526       | –               |               | –             |
| MV 398           |                  | MHO23527       | MHO23527       | –               |               | –             |
| MV 420           |                  | MHO23525       | MHO23525       | –               |               | –             |
| MV 433           |                  | MHO25418       | –              | –               |               | –             |
| MV 435           |                  | MHO25417       | MHO25417       | –               |               | –             |
| Catania 3269     |                  | MHO25414       | –              | –               |               | –             |
| Robledo 1170     |                  | MHO25415       | –              | –               |               | –             |
| JIV1707/10J-1    |                  | MWS07113       | –              | –               |               | –             |
| JIV1707/10J-2    |                  | MWS07114       | –              | –               |               | –             |
| Bjerkandera minispora |              |                |                |                 |               |               |
| Dai 15234 (T)    |                  | MWS07115       | MWS02014       | –               |               | –             |
| Cui 5376         |                  | MWS07116       | MWS02015       | –               |               | –             |
| Bjerkandera resupinata |            |                |                |                 |               |               |
| Dai 16642 (T)    |                  | MWS07117       | MWS02016       | –               |               | –             |
| Cui 8017         |                  | KUS09526       | –              | –               |               | –             |
| Bjerkandera sp.  |                  |                |                |                 |               |               |
| JIV1512/13-J     |                  | KUS09714       | –              | –               |               | –             |
| L13104sp         |                  | KUS09526       | –              | –               |               | –             |
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, rpb2 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, rpb2 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; rpb2 codon positions, 1stpos, 2ndpos, and 3rdpos; rpb2 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+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+I+G4 (tef1-α 3rdpos, rpb1 1stpos), HKY+F+I+G4 (tefl-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. adjusta, 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 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) Robledolo, 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 Poly pore Collection of Dr. Josef Vlasák, Hluboká nad Vltavou, Czech Republic, Edition 18.11. 2015, http://mykoweb.prf.jcu.cz/polyposes/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 trama 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 subicum and trama (Fig. 3C–D), and basidia and basidiospores that are similar in shape and size. Furthermore, cultures of B. carnegieae, B. adjusta, 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 + rpb1 + rpb2 + 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%.
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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