



Neotropical *Daedalea* (Basidiomycota, Fomitopsidaceae) revisited: *Daedalea rajchenbergiana* sp. nov. from Brazil

Revisión de *Daedalea* (Basidiomycota, Fomitopsidaceae) en el Neotrópico: *Daedalea rajchenbergiana* sp. nov. del Brasil

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ABSTRACT

Great progress has been made in recent years on taxonomy of brown rot polypores based on phylogenetic evidence, mainly *Daedalea* within Fomitopsidaceae. However, the relations within the Fomitopsidaceae family remain unresolved. Some neotropical species of *Daedalea* were never included in molecular phylogenetic analyses, such as *D. aethalodes*, *D. ryvarideniana*, and south American specimens of *D. modesta*. To clarify the relationships of those species within *Daedalea* there were carried out molecular phylogenetic analyses based on five molecular markers (ITS, nLSU, nSSU, RPB2, and TEF-1). *Daedalea* s.s. formed a strongly supported clade including most species, however, *Daedalea radiata* was grouped with *Rodofomitopsis*. A new neotropical species, *Daedalea rajchenbergiana* sp. nov., was described based on molecular phylogeny, morphology, and distribution evidence. The placement of *Daedalea aethalodes*, *D. ryvarideniana*, and *D. rajchenbergiana* sp. nov. within *Daedalea* s.s. was confirmed.

Keywords — Brown-rot; ‘antrodia’ clade; Taxonomy, Neotropical polypores.

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RESUMEN

Se han logrado grandes avances en los últimos años en la taxonomía de los políporos de la pudrición castaña basados en evidencia filogenética, especialmente *Daedalea* dentro de Fomitopsidaceae. Sin embargo, aún no se han resuelto las relaciones dentro de la familia Fomitopsidaceae. Pero algunas especies neotropicales de *Daedalea* no han sido incluidas aún en análisis filogenéticos moleculares, como son *D. aethalodes*, *D. ryvarideniana* y especímenes sudamericanos de *D. modesta*. Con el fin de aclarar las relaciones de dichas especies dentro de *Daedalea*, se llevaron a cabo análisis filogenéticos basados en cinco marcadores moleculares (ITS, nLSU, nSSU, RPB2 y TEF-1). *Daedalea* s.s. formó un clado de alto soporte incluyendo la mayoría de las especies, sin embargo, *D. radiata* se agrupó con *Rhodofomitopsis*. Una nueva especie neotropical, *Daedalea rajchenbergiana* sp. nov., se describió con base en filogenia molecular, morfología y distribución. Se confirmó la posición de *Daedalea aethalodes*, *D. ryvarideniana* y *D. rajchenbergiana* sp. nov. dentro de *Daedalea* s.s.

Palabras clave — Clado 'antrodia'; políporos neotropicales; pudrición castaña; taxonomía.

INTRODUCTION

Fomitopsidaceae Jülich 1981 belongs to Polyporales and it is characterized by a dimitic or trimitic hyphal system with clamped generative hyphae and skeletal hyphae projecting through the hymenium and thin-walled, smooth, and hyaline basidiospores (Justo *et al.*, 2017). The family is associated with a brown-rot, and currently includes the following genera: *Anthoporia* Karasinski & Niemelä, *Antrodia* P. Karst., *Buglossoporus* Kotl. & Pouzar, *Brunneoporus* Audet., *Cartilosoma* Kotl. & Pouzar, *Daedalea* Pers., *Fomitopsis* P. Karst., *Fragifomes* B.K. Cui, M.L. Han & Y.C. Dai, *Melanoporia* Murrill, *Neoantrodia* Audet, *Neolentiporus* Rajchenb., *Niveoporofomes* B.K. Cui, M.L. Han & Y.C. Dai, *Rhodofomes* Kotl. & Pouzar, *Rhodofomitopsis* B.K. Cui, M.L. Han & Y.C. Dai, *Rubellofomes* B.K. Cui, M.L. Han & Y.C. Dai and *Ungulidaedalea* B.K. Cui, M.L. Han & Y.C. Dai (Audet, 2017; Justo *et al.*, 2017; Decock *et al.*, 2022). Among these genera, *Daedalea* was originally proposed to include species with daedaloid, sinuous, and labyrinth-like hymenophore (Fries, 1821); later this concept was extended to include species with poroid hymenophore with the inclusion of the Neotropical *Daedalea aethalodes* (Mont.) Rajchenb. (Rajchenberg, 1986). Later, through morphological studies and molecular analyses of ITS and nLSU regions, *Daedalea* s.s. was shown as a monophyletic clade around the type species *Daedalea quercina* (L.) Pers. (Han *et al.*, 2015), including species distributed in different parts of the world (Li & Cui, 2013; Han *et al.*, 2015, 2016; Decock *et al.*, 2022).

In the Neotropics, six species of *Daedalea* have been recorded: *D. stereoides* Fr. and *D. hydroides* I. Lindblad & Ryvariden described for Costa Rica (Fries, 1851; Lindblad & Ryvariden, 1999); *D. modesta* (Kunze ex Fr.) Aoshima described for Suriname (Montagne, 1856); *D. neotropica* D.L. Lindner, Ryvariden & T.J. Baroni described for Belize (Lindner *et al.*, 2011); *D. ryvarideniana* Drechsler-Santos & Robledo described for Brazil (Drechsler-Santos *et al.*, 2012) and *D. aethalodes* described for

Brazil and found commonly in Paraguay and northern Argentina (Rajchenberg, 1986; Popoff & Wright, 1998; Gibertoni *et al.*, 2004; Robledo & Rajchenberg, 2007; Gugliotta *et al.*, 2010). Previous phylogenetic studies already positioned *Daedalea hydnoides*, *D. stereoides*, *D. modesta* and *D. neotropica* within *Daedalea* s. s. (Lindner *et al.*, 2011; Han *et al.*, 2015, 2016), however, some other Neotropical species lack phylogenetic information regarding their relationships within this clade, as is the case of *D. aethalodes* and *D. ryvarideniana*.

The aim of this work was to unveil the phylogenetic relationships of neotropical *Daedalea* species, including species never sequenced before: *D. aethalodes*, *D. ryvarideniana*, and neotropical specimens of *D. modesta* through multi-gene molecular analyses.

MATERIALS AND METHODS

Collections and morphological analysis

Morphological revisions were conducted on samples of different species of *Daedalea* hosted in fungaria FLOR and FACEN, following description format of Drechsler-Santos *et al.* (2012) and Robledo & Urcelay (2009), and comparing its morphological characteristics with specific literature (Rajchenberg, 1986; Drechsler-Santos *et al.*, 2012; Han *et al.*, 2015). Basidiomata colors were described according to Anonymous (2004). For microscopic analysis, free-hand sections of basidiome were mounted in 5% (w/v) aqueous potassium hydroxide (KOH) and 1% (w/v) aqueous phloxine or Melzer's reagent (Decock, *et al.*, 2013). 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.

DNA extraction, amplification, and sequencing

DNA was extracted from dried basidiomata, crushed with LyserMjøltnir 1.0 Franchi-Robledo™ 2012 for 2 – 3 min. Dust residue was transferred to an Eppendorf tube and mixed with lysis buffer (CTAB 2%) at 65 °C for at least 1 hour, followed by a chloroform extraction and final precipitation of DNA with isopropanol (Doyle, 1991).

ITS and LSU regions amplification was performed with ITS8/ITS6 and LR0R/LR5 primers (White *et al.*, 1990; Gardes & Bruns, 1993; Hopple & Vilgalys, 1999). PCR was executed following Gomez-Montoya *et al.* (2017) protocols, and its products were observed through electrophoresis in 1.5 % agarose gel. Amplicons were purified and sequenced in both directions using the same primers used in amplification. Cycle sequencing was realized in a DNA Analyzer Applied Biosystems 3730xl at MacroGen Ltd. (South Korea).

Phylogenetic analyses

New DNA sequences generated in the present work were combined with sequences retrieved from GenBank (NCBI) of ITS, nLSU, nSSU, RPB2 and TEF-1 markers. Scientific names and GenBank Accession Numbers of sequences are listed in Table 1. *Amyloporia xantha* and *A. carbonica* were selected as outgroup (Han *et al.*, 2016).

Each marker was individually aligned using MAFFT 7 (Kato *et al.*, 2019) 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 13 data blocks (ITS1; 5.8S; ITS2; nLSU; nSSU; RPB2 codon positions, 1stpos, 2ndpos, and 3rdpos; RPB2 introns; TEF-1 codon positions 1stpos, 2ndpos, and 3rdpos and TEF-1 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 dataset using the partition scheme and evolutionary models defined by ModelFinder. BI was performed following Robledo *et al.* (2021) in the CIPRES science gateway (Miller *et al.*, 2012; <http://www.phylo.org/>). Maximum likelihood searches were conducted with IQ-TREE. The analysis 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 $\geq 95\%$ (Hyde *et al.*, 2013; Minh *et al.*, 2020). Hereafter, support values are presented as BPP/BS in the text.

RESULTS

Phylogenetic analyses

The combined Dataset (ITS, nLSU, nSSU, RPB2, TEF-1) included 122 terminals and 4450 characters, of which 1222 were parsimony informative, 1490 were variable and 2875 constants. The partitions and evolutionary models selected were: GTR+F+I+G4 (ITS1, ITS2), HKY+F+I+G4 (5.8S, nSSU, TEF-1 1stpos), SYM+I+G4 (nLSU), GTR+F+I+G4: RPB2 1stpos, TEF-1 2ndpos, TEF-1 3rdpos), JC+I+G4 (RPB2 2ndpos), GTR+F+I+G4 (RPB2 3rdpos) and HKY+F+I+G4 (TEF-1 introns).

Bayesian and ML analyses resulted in identical topologies; the Bayesian consensus tree is presented in Figure 1. The topology recovered in our phylogenetic analyses is in general congruent with previous works regarding the ‘antrodia’ clade (Han *et al.*, 2015, 2016; Tibuhwa *et al.*, 2020; Decock *et al.*, 2022). Thirteen main strong supported lineages at genus level were recovered: *Fibroporia* (1/100), *Piptoporellus* (1/100), *Antrodia* s. s. (1/100), *Buglossoporus* (1/100), *Fragifomes* (1/100), *Rhodofomes* (1/100), *Niveoporofomes* (1/100) *Neoantrodia* (1/100), *Brunneoporus* (1/100), *Ungulidadaealea*, *Rhodofomitopsis* (1/100), *Fomitopsis* (1/100) and *Daedalea* (0.97/90). *Daedalea* s.

Table 1 (part 1 of 4). Vouchers specimens, geographic location and GenBank accession numbers of the samples included in the phylogenetic analyzes. T= type specimen. New sequences generated in this study are in boldface.

Tabla 1 (parte 1 de 4). Vouchers, origen geográfico y número de acceso de GenBank de las muestras incluidas en los análisis filogenéticos. T= especímenes tipo. Las nuevas secuencias generadas en este estudio se resaltan en negrita.

Species Voucher/Isolate	Origin	GenBank Accession Numbers				
		ITS	nLSU	nSSU	TEF-1	RPB2
<i>Amyloporia carbonica</i> (Overh.) Vampola & Pouzar						
Cui 12212	China	KR605816	KR605755	KR605917	KR610745	—
<i>Amyloporia xantha</i> (Fr.) Bondartsev & Singer ex Bondartsev						
Cui 11544	China	KR605817	KR605756	KR605918	KR610746	KR610836
Dai 19011	China	OM039273	OM039173	OM039239	—	—
<i>Antrodia heteromorpha</i> (Fr.) Donk						
Dai 12755	USA	KP715306	KP715322	KR605908	KP715336	KR610828
CBS 200.91	Korea	DQ491415	AY515350	—	—	DQ491388
Dai 12742	China	KP715319	—	MG787728	MG787847	KT895887
<i>Antrodia serpens</i> (Fr.) P. Karst.						
Dai 7465	China	KR605813	KR605752	KR605913	KR610742	KR610832
Dai 14850	China	MG787582	MG787624	MG787731	MG787849	MG787798
B. Rivoire 3576	France	KC543169	—	—	KC543191	—
<i>Antrodia tanakae</i> (Murrill) Spirin & Miettinen						
Cui 9743	China	KR605814	KR605753	KR605914	KR610743	KR610833
Yuan 1106	China	KP715313	KP715329	KR605916	KP715343	KR610835
<i>Brunneoporus malicola</i> (Berk. & M.A. Curtis) Audet						
Harkonen K622	China	KU866261	—	—	KU866216	—
Cui 9491	China	KT968824	KT968828	—	—	KT988994
Ryvarden 31483	Zimbabwe	KU866245	—	—	KU866239	—
Miettinen 14798	USA	KU866244	—	—	KU866238	—
L-13022-Sp	Costa Rica	KC585288	KC585112	—	—	—
<i>Brunneoporus minutus</i> (Spirin) Audet						
Spirin 3477	Russia	KU866250	MG787633	MG787743	—	MG787808
<i>Brunneoporus cyclopis</i> (Miettinen & Spirin) Audet						
Miettinen 9166 (T)	Indonesia	NR154715	MG787627	MG787737	KU866242	MG787802
<i>Buglossoporus eucalypticola</i> M.L. Han, B.K. Cui & Y.C. Dai						
Dai 13660 (T)	China	KR605808	KR605747	KR605906	KR610736	KR610825
Dai 13660A	China	KR605809	KR605748	KR605907	KR610737	KR610826
<i>Buglossoporus quercinus</i> (Schräd.) Kotlába & Pouzar						
JV 0906/15-J	USA	KR605800	KR605739	KR605898	KR610729	KR610819
JV 1406/1	Czech Republic	KR605801	KR605740	KR605899	KR610730	KR610820
<i>Daedalea aethalodes</i> (Mont.) Rajchenb.						
M Campi 70	Paraguay	OP526843	OP526849	—	—	—
<i>Daedalea africana</i> Ryvarden & I. Johans.						
O 15372	Kenya	KP171196	KP171216	KR605871	KR610704	KR610795
<i>Daedalea allantoidea</i> M.L. Han, B.K. Cui & Y.C. Dai						
Dai 13612A	China	KR605795	KR605734	KR605892	KR610723	KR610813
<i>Daedalea americana</i> M.L. Han & B.K. Cui						
JV 0312/24.7-J	USA	KP171197	KP171217	KR605872	KR610705	KR610796
JV 0904/20	USA	KP171199	KP171219	—	—	—
JV 0904/19	USA	KP171198	KP171218	—	—	—
<i>Daedalea circularis</i> B.K. Cui & Hai J. Li						

s. included *D. ryvardeniana*, *D. aethalodes* and the neotropical specimen of *D. modesta*. However, it was not recovered as monophyletic as *D. radiata* did not group within *Daedalea* s. s., instead it grouped with *Rhodofomitopsis* without support. In addition, molecular phylogenetic analyses from the five-marker combined dataset of the ‘antrodia’ clade (Figure 1) confirmed the new taxon, *Daedalea rajchenbergiana* sp. nov. (described below) which grouped with *D. americana* (1/100) within *Daedalea* s. s.

Table 1 (part 2 of 4). Vouchers specimens, geographic location and GenBank accession numbers of the samples included in the phylogenetic analyzes. T= type specimen. New sequences generated in this study are in boldface.

Tabla 1 (parte 2 de 4). Vouchers, origen geográfico y número de acceso de GenBank de las muestras incluidas en los análisis filogenéticos. T= especímenes tipo. Las nuevas secuencias generadas en este estudio se resaltan en negrita.

<i>Daedalea circularis</i> B.K. Cui & Hai J. Li						
Cui 10125	China	JQ780411	KP171220	KR605875	KR610708	KR610799
Dai 13062	China	KP171200	KP171222	KR605877	KR610710	KR610801
Cui 10134	China	JQ314352	KP171221	KR605876	KR610709	KR610800
<i>Daedalea dickinsii</i> Yasuda						
Yuan 1090	China	KR605790	KR605729	KR605878	KR610711	KR610802
Yuan 2685	China	KP171201	KP171223	KR605879	KR610712	KR610803
Yuan 2707	China	KP171202	KP171224	KR605880	KR610713	KR610804
<i>Daedalea dochmia</i> (Berk. & Broome) T. Hatt.						
CBS 426.84	Thailand	DQ491401	AY515326	—	—	DQ491374
JZ36	India	MG719293	—	—	—	—
<i>Daedalea hydnoidea</i> I. Lindblad & Ryvarden						
Lindblad 3679	Costa Rica	KP171203	KP171225	—	—	—
<i>Daedalea modesta</i> (Kunze ex Fr.) Aoshima						
MCampi 6	Paraguay	OP526844	OP526850	—	—	—
Cui 10151	China	KP171205	KP171227	KR605883	KR610716	KR610806
Cui 10124	China	KR605791	KR605730	KR605882	KR610715	KR610805
Dai 10844	China	KP171206	KP171228	KR605884	KR610714	KR610807
<i>Daedalea neotropica</i> D.L. Lindner, Ryvarden & T.J. Baroni						
DLC04-100	Belize	FJ403218	—	—	—	—
DLC04-174	Belize	FJ403219	—	—	—	—
JV 1312/E18-J	Costa Rica	KT156688	—	—	—	—
<i>Daedalea pseudodochmia</i> (Corner) T. Hatt.						
Ryvarden 10533	China	FJ403210	—	—	—	—
<i>Daedalea quercina</i> (L.) Pers.						
Dai 2260	Suecia	KR605792	KR605731	KR605885	KR610718	KR610808
Dai 12659	Finlandia	KP171208	KP171230	KR605887	KR610719	KR610810
Miettinen 12662	Finlandia	JX109855	JX109855	—	JX109912	JX109883
<i>Daedalea radiata</i> B.K. Cui & Hai J. Li						
Yuan 3629 (T)	China	NR120047	—	—	—	—
ZGCVN774	India	MT378376	—	—	—	—
Cui 8487	China	JQ314349	KP171232	—	—	—
Cui 8575	China	KP171210	KP171233	KR605888	KR610720	KR610811
Cui 8624	China	KR605793	KR605732	KR605889	KR610721	—
<i>Daedalea ryvardeniana</i> Drechsler-Santos & Robledo						
FLOR41052 (T)	Brazil	OP526845	OP526851	—	—	—
URM80515	Brazil	OP526846	OP526852	—	—	—
<i>Daedalea sprucei</i> Berk.						
O 10546	Taiwan	KR605794	KR605733	KR605890	KR610722	KR610812
O 10547	Cuba	KP171211	KP171234	—	—	—
<i>Daedalea stereoides</i> Fr.						
10551	Ethiopia	FJ403215	—	—	—	—
<i>Daedalea stevensonii</i> Petr.						
O 10543	Borneo	KP171212	KP171235	KR605891	—	—
<i>Daedalea rajchenbergiana</i> Kossmann & Drechsler-Santos						
DS863 (T)	Brazil	OP526847	OP526853	—	—	—
DS866	Brazil	OP526848	OP526854	—	—	—
<i>Daedalea</i> sp.						
JV 1504/34	Costa Rica	MG787587	MG787634	MG787744	MG787854	MG787809
18198	Belize	FJ403211	—	—	—	—
Cui 16751	Australia	MW377279	MW377359	MW377437	—	—
Cui 16748	Australia	MW377280	MW377360	MW377438	—	—
Cui 16773	Australia	MW377281	MW377361	MW377439	—	—
Cui 16786	Australia	MW377282	MW377362	MW377440	—	—

Table 1 (part 3 of 4). Vouchers specimens, geographic location and GenBank accession numbers of the samples included in the phylogenetic analyzes. T= type specimen. New sequences generated in this study are in boldface.

Tabla 1 (parte 3 de 4). Vouchers, origen geográfico y número de acceso de GenBank de las muestras incluidas en los análisis filogenéticos. T= especímenes tipo. Las nuevas secuencias generadas en este estudio se resaltan en negrita.

Dai 18551	Malaysia	MW377283	MW377363	MW377441	—	—
Dai 18562	Malaysia	MW377284	MW377364	MW377442	—	—
Dai 17823	Singapore	MW377285	—	MW377443	—	—
Fibroporia albicans B. K. Cui & Yuan Y. Chen						
Cui 9464	China	KC456250	KR605758	KR605920	KR610748	KR610838
Dai 10595	China	KC456249	KR605759	KR605921	KR610749	KR610839
Fibroporia citrina (Bernicchia & Ryvarden) Bernicchia & Ryvarden						
Cui 11604	China	KU550473	KU550492	KU550533	KU550568	KU550551
Fibroporia ceracea Yuan Y. Chen & B.K. Cui						
Dai 13013 (T)	China	KU550476	KU550490	KU550530	KU550563	KU550547
Fibroporia radiculosa (Peck) Parmasto						
Dai 13041	China	KP145010	KU550499	KU550538	KU550573	KU550554
Fibroporia gossypium (Speg.) Parmasto						
LY BR 3994	Argentina	KT895885	KU550496	KU550535	KU550570	KT895902
Fomitopsis betulina (Bulliard) B.K. Cui, M.L. Han & Y.C. Dai						
Dai 12665	China	KP171215	KP171238	KR605896	KR610724	KR610817
Miettinen 12388	Finland	JX109856	JX109856	—	JX109913	JX109884
Dai 11449	China	KR605798	KR605737	KR605895	KR610726	KR610816
Cui 10309	China	KR605796	KR605735	KR605893	KR610727	KR610814
Fomitopsis durescens (Overh. ex J. Lowe) Gilb. & Ryvarden						
Ryvarden 41410	Venezuela	KF937292	KF937294	KR605834	KR610669	KR610766
Overholts 4215 a	USA	KF937293	KF937295	KR605835	—	—
Fomitopsis hemitephra (Berkeley) G. Cunningham						
O 10808	Australia	KR605770	KR605709	KR605841	KR610675	—
Fomitopsis iberica Melo & Ryvarden						
O 10810	Portugal	KR605771	KR605710	KR605842	KR610676	KR610771
Fomitopsis nivosa (Berk.) Gilb. & Ryvarden						
JV 0509/52-X	China	KR605779	KR605718	KR605853	KR610686	KR610777
Fomitopsis palustris (Berkeley & M.A. Curtis) Gilbertson & Ryvarden						
Cui 7615	China	KR605780	KR605719	KR605855	KR610688	KR610779
KUC9219	Korea	JQ279692	JQ279693	JQ279696	—	JQ279695
Cui 7597	China	KP171213	KP171236	KR605854	KR610687	KR610778
Fomitopsis pinicola (Sw.) P. Karst.						
Cui 10312	China	KR605781	KR605720	KR605856	KR610689	KR610780
Cui 10405	China	KC844852	KC844857	KR605857	KR610690	KR610781
Cui 10532	China	KP171214	KP171237	KR605858	KR610691	KR610782
Fomitopsis subtropica B.K. Cui & Hai J. Li						
Cui 10578	China	KR605787	KR605726	KR605867	KR610698	KR610791
Fragifomes niveomarginatus (L.W. Zhou & Y.L. Wei) B.K. Cui, M.L. Han & Y.C. Dai						
Cui 10108	China	KR605778	KR605717	KR605851	KR610684	KR610776
Wei 5583	China	HQ693994	KC507175	KR605852	KR610685	—
Neoantrodia serialis (Fr.) Audet						
KHL 12010	Norway	NR154676	JX109844	—	—	—
Cui 10519	China	KP715307	KP715323	KR605911	KP715337	KR610830
Dai 7626	China	KR605812	KR605751	KR605912	KR610740	KR610831
Neoantrodia variiformis (Fr.) Audet						
CBS 309.82	USA	DQ491418	AY515344	—	—	DQ491391
JV0809_96	USA	KT995131	KT995154	MG787766	KU052736	MG787821
FP-104442-Sp	USA	KC585309	KC585134	—	—	—
Niveoporofomes globosporus (Ryvarden & Aime) Decock, Amalfi & Ryvarden						
M.C. Aime 3413	Belize	KC017760	KC017762	—	—	—
Niveoporofomes oboensis Decock, Amalfi & Ryvarden						
MUCL53518	Sao Tome	OM366266	OM366267	x*	OM329949	OM329950

Table 1 (part 3 of 4). Vouchers specimens, geographic location and GenBank accession numbers of the samples included in the phylogenetic analyzes. T= type specimen. New sequences generated in this study are in boldface.

Tabla 1 (parte 3 de 4). Vouchers, origen geográfico y número de acceso de GenBank de las muestras incluidas en los análisis filogenéticos. T= especímenes tipo. Las nuevas secuencias generadas en este estudio se resaltan en negrita.

<i>Niveoporofomes spraguei</i> (Berk. & M.A. Curtis) B.K. Cui, M.L. Han & Y.C. Dai						
4638	France	KR605784	KR605723	KR605862	KR610696	KR610786
Cui 8969	China	KR605785	KR605724	KR605863	KR610695	KR610787
JV 0509/62	USA	KR605786	KR605725	KR605864	KR610697	KR610788
<i>Piptoporellus baudonii</i> (Pat.) Tibuhwa, Ryvarden & S. Tibell						
Tibuhwa 09.2018		MT447067	MT447070	MT447064	MT452550	—
Ryvarden 25098		MT447068	MT447071	MT447065	MT452551	—
<i>Piptoporellus hainanensis</i> M.L. Han, B.K. Cui & Y.C. Dai						
Dai 13714	China	KR605806	KR605745	KR605904	KR610735	KR610824
<i>Piptoporellus soloniensis</i> (Dubois) B.K. Cui, M.L. Han & Y.C. Dai						
Cui 11386	China	KR605802	KR605741	KR605900	KR610732	KR610821
<i>Piptoporellus triquetus</i> M.L. Han, B.K. Cui, & Y.C. Dai						
Dai 13121	China	KR605807	KR605746	KR605905	KR610738	KR610827
<i>Rhodofomes cajanderi</i> (P. Karst.) B.K. Cui, M.L. Han & Y.C. Dai						
Cui 9888	China	KC507156	KC507166	KR605828	KR610662	KR610764
<i>Rhodofomes carneus</i> (Blume & T. Nees) B.K. Cui, M.L. Han & Y.C. Dai						
Ryvarden 10118	Tanzania	KF999921	KF999925	KR605831	KR610666	—
<i>Rhodofomes incarnatus</i> (K.M. Kim, J.S. Lee & H.S. Jung) B.K. Cui, M.L. Han & Y.C. Dai						
Cui 10348	China	KC844848	KC844853	KR605844	KR610679	KR610773
<i>Rhodofomes roseus</i> (Alb. & Schwein.) Kotl. & Pouzar						
JV 1110/9	Czech Republic	KR605783	KR605722	KR605861	KR610694	KR610785
<i>Rhodofomes subfeei</i> (B.K. Cui & M.L. Han) B.K. Cui, M.L. Han & Y.C. Dai						
Cui 9229	China	KR605789	KR605728	KR605869	KR610701	KR610793
<i>Rhodofomitopsis cupreorosea</i> (Berk.) B.K. Cui, M.L. Han & Y.C. Dai						
CBS 236.87	Costa Rica	DQ491400	AY515325	—	—	DQ491373
<i>Rhodofomitopsis feei</i> (Fr.) B.K. Cui, M.L. Han & Y.C. Dai						
Oinonen 60119006	Brazil	KC844851	KC844856	KR605837	KR610671	KR610767
Ryvarden 37603	Venezuela	KC844850	KC844855	KR605838	KR610670	KR610768
<i>Rhodofomitopsis lilacinogilva</i> (Berk.) B.K. Cui, M.L. Han & Y.C. Dai						
Schigel 5193	Australia	KR605773	KR605712	KR605846	KR610680	KR610774
<i>Rhodofomitopsis pseudofeei</i> B.K. Cui & Shun Liu						
Cui 16794 (T)	Australia	MK46195	MK461956	MK461964	MK463986	MK463984
Ryvarden 42928	Australia	KF999924	KF999928	KR605839	KR610672	KR610769
<i>Ungulidaedalea fragilis</i> (B.K. Cui & M.L. Han) B.K. Cui, M.L. Han & Y.C. Dai						
Cui 10919	China	KF937286	KF937290	KR605840	KR610674	KR610770

*sequence provided by Cony Decock from Decock *et al.*, 2022

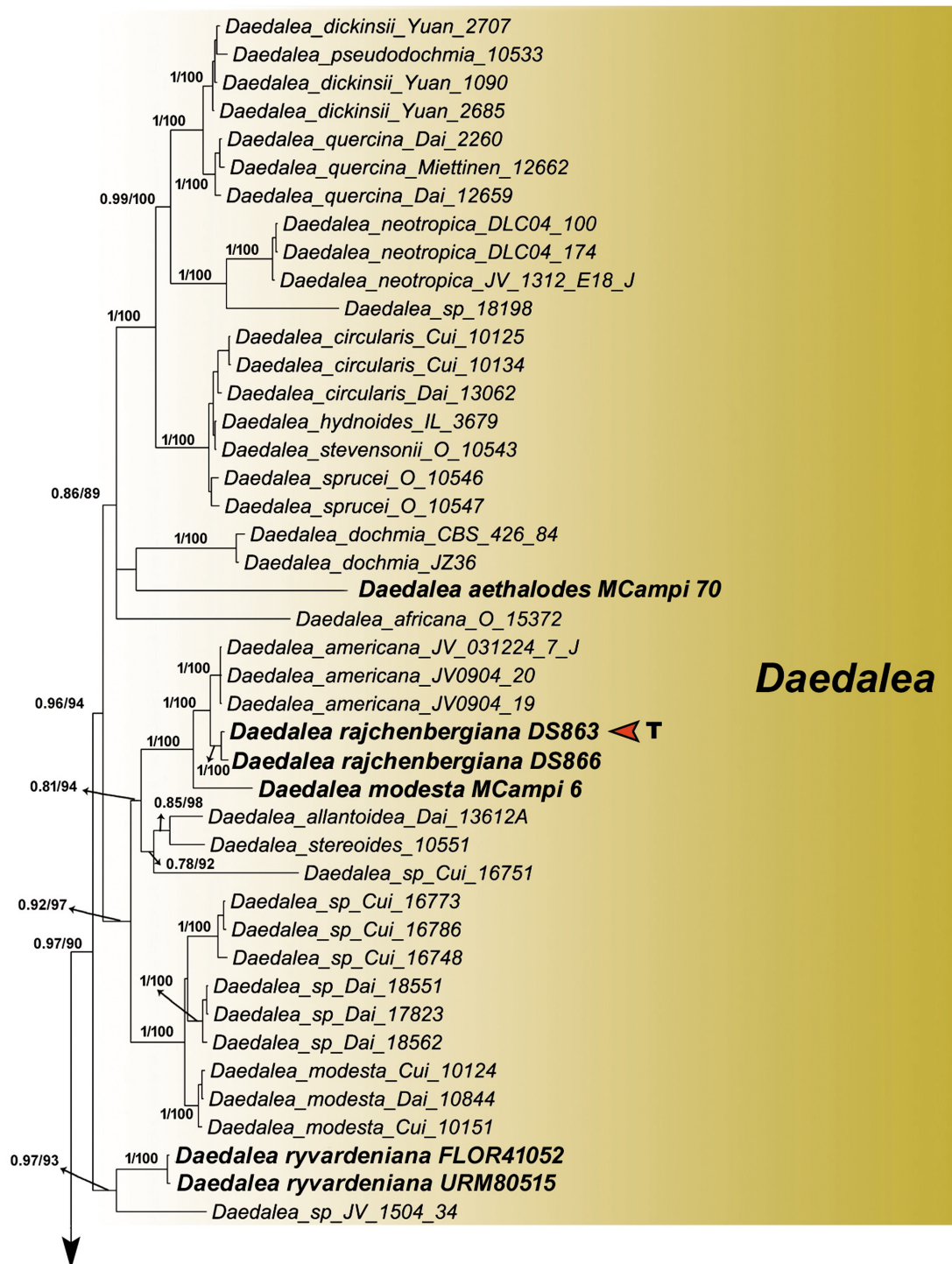
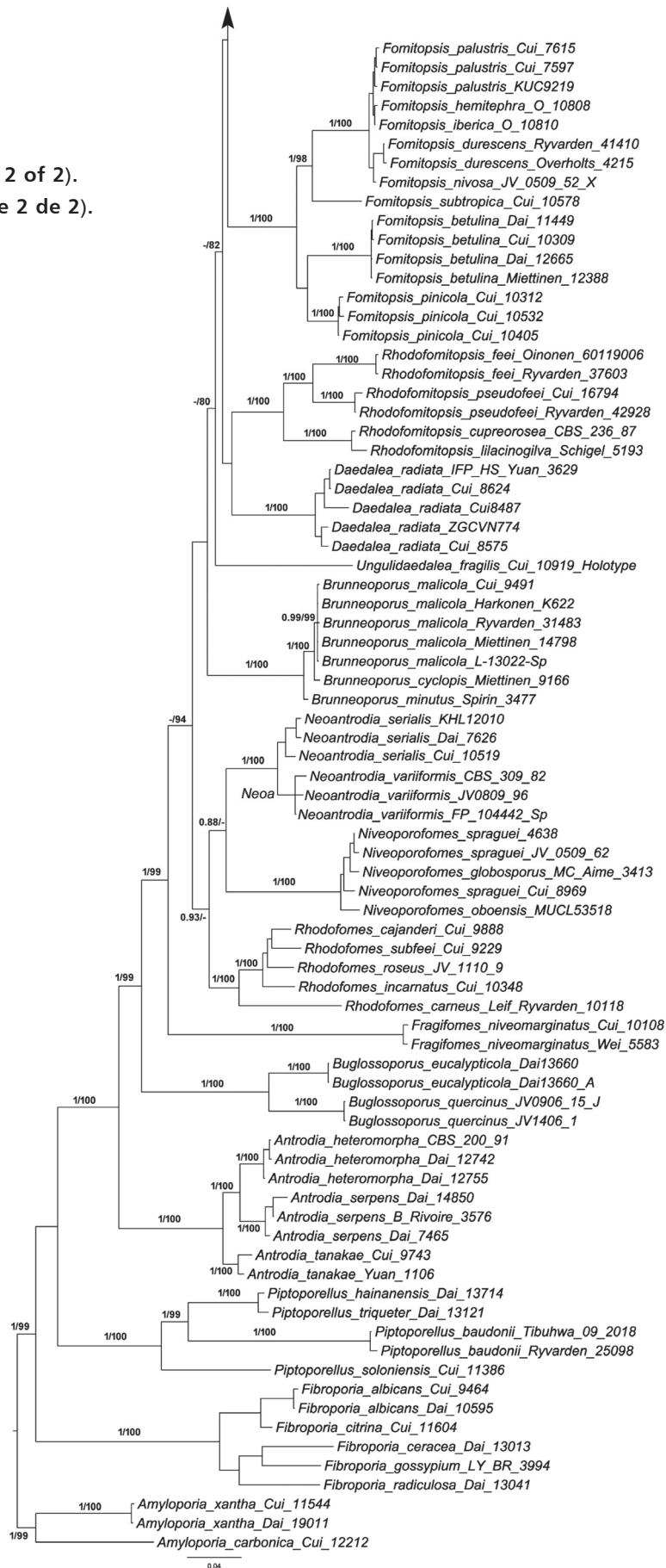


Fig. 1 (part 1 of 2). Bayesian consensus tree positioning *Daedalea* within the 'antrodia' clade based on concatenated sequence data ITS, nLSU, nSSU, TEF-1 and RPB2. Bayesian posterior probability above 0.75 and Bootstrap values above 75 % are shown. Red arrow and the letter T indicate type specimen.

Fig. 1 (parte 1 de 2). Árbol Bayesiano de consenso posicionando a *Daedalea* dentro del clado 'antrodia' basado en secuencias concatenadas de ITS, nLSU, nSSU, TEF-1 y RPB2. Se muestran la probabilidad posterior por encima de 0.75 y valores de Bootstrap por encima del 75%. La flecha roja y T indican especímenes tipo.

Fig. 1 (part 2 of 2).
Fig. 1 (parte 2 de 2).



Taxonomy

Daedalea rajchenbergiana Kossmann & Drechsler-Santos **sp. nov.**

Fig. 2

MycoBank # 844612

Daedalea rajchenbergiana is characterized by its effused-reflexed to pileate basidiomata with concentric zonations with reddish to buff colors, small, regular pores (5–8/mm) and small basidiospores $3.2\text{--}4.4 \times 1.6\text{--}2.6 \mu\text{m}$.

Type specimen.— BRAZIL. Bahia, Urucuca, Parque Estadual da Serra do Condurú, 28 November 2012, *Drechsler-Santos E.R.* 863 (FLOR 70928).

Etymology.— In honor of Prof. Mario Rajchenberg for his contributions to fungal taxonomy in the Neotropics.

Basidiomata annual, effused-reflexed to pileate, dimidiate to flabelliform, gregarious to imbricate, flexible and coriaceous, individual pilei up to 80 mm wide and 70 mm long, 1–2 mm thick near the margin, and up to 10 mm thick at the base, often concrescent up to 150 mm; upper surface glabrous, pale brownish-orange (oac726) to reddish-brown (oac684) at the center, peach (oac762) to cream-buff (oac765) closer to the margin, drying brownish-buff (oac734) to dark-buff (oac777), concentrically zonate, zonations marked by darker colored lines, slightly radially scrupose; margin thinning out, entire, regular to wavy, white (oac909); context smooth, homogenous, pale peach (oac793) to brownish-cream (oac717), up to 10 mm thick.

Hymenophore poroid, regular, pores round to angular, 5–8/mm; hymenial surface white (oac909) to pale-peach (oac793), with brown patches at older parts (oac637) when fresh, drying cream (oac794) to buff (oac798); tubes up to 1.5 mm deep, concolorous with pore surface.

Hyphal system dimitic. Generative hyphae with clamps, hyaline, thin-walled, straight to sinuous, sparsely branched, $2\text{--}3 \mu\text{m}$ wide; skeletal hyphae dominating, thick-walled to solid, but at parts with thinner-walls and several secondary simple-septa, hyaline to yellowish, straight to sinuous, unbranched or with short sword-like to tortuous branches at the base, sometimes with a very tortuous outline from irregularities of the wall, $2.5\text{--}6.5 \mu\text{m}$ wide.

Cystidia absent, but skeletal hyphae often protruding in the hymenium. Cystidioles clavate, fusoid to irregularly shaped, resembling primordial dendrohyphidia. Basidia clavate, $15\text{--}22 \times 4.5\text{--}7 \mu\text{m}$.

Basidiospores ellipsoid to cylindrical, $3.3\text{--}4.3 \times 1.7\text{--}2.2\text{--}(2.6) \mu\text{m}$, $L_{\text{avg}} = 3.7$, $W_{\text{avg}} = 2.0$, $Q = (1.4\text{--})1.6\text{--}2.3$, $Q_{\text{avg}} = 1.9$, hyaline, thin-walled, smooth, IKI-.

Specimens examined.— BRAZIL. Amazonas, Novo Airão, Parque Nacional Anavilhanas, Ponto de Coleta 13 – Igarapé Santo Antônio ($2^{\circ}23'23''$ S, $60^{\circ}58'22''$ W), 06 December 2013, *Drechsler-Santos E.R.* 1274 (FLOR 70934); Bahia, Urucuca, Parque Estadual da Serra do Condurú, 28 November 2012, *Drechsler-Santos E.R.*, 863 (FLOR 70928 holotype); *ibid.*, *idem*, *Drechsler-Santos E.R.*, 866 (FLOR 70929); *ibid.*, *idem*, *Drechsler-Santos E.R.* 876 (FLOR 70930); *ibid.*, *idem*, *Drechsler-Santos E.R.* 883 (FLOR 70931); *ibid.*, 29 November 2012, *Drechsler-Santos E.R.* 890 (FLOR 70932); Mato Grosso, Chapada dos Guimarães, Parque Nacional da Chapada dos Guimarães, Trilha das Cachoeiras, 23 March 2013, *Drechsler-Santos E.R.*



Fig. 2. *Daedalea rajchenbergiana*. A-B) General view in situ, DS863 (FLOR 70928, holotype). C) General view in situ, DS1951 (FLOR 70938). D) General view in situ, DS1962 (FLOR 70940). E) Pilear surface details, DS1969 (FLOR 70941). F) Pore surface detail, DS1954 (FLOR 70939). (Photos by E.R. Drechsler-Santos).

Fig. 2. *Daedalea rajchenbergiana*, A-B) Vista general in situ, DS863 (FLOR 70928 holotipo). C) Vista general in situ, DS1951, (FLOR 70938). D) Vista general in situ, DS1962 (FLOR 70940). E) Detalles de la superficie del píleo, DS1969 (FLOR 70941). F) Detalles de los poros, DS1954 (FLOR 70939). (Fotos por E.R. Drechsler-Santos).

1012 (FLOR 70933); Nova Ubiratã, ESEC do Rio Ronuro, Entrada Sudoeste (12°34'20.28"S 54°21'57.24"W), 23 February 2017, *Drechsler-Santos E.R.* 1951 (FLOR 70938); *ibid.*, *idem*, *Drechsler-Santos E.R.* 1954 (FLOR 70939); *ibid.*, Rio Ronuro left bank (13°3'44.28"S 54°15'13.68"W), 24 February 2017, *Drechsler-Santos E.R.* 1962 (FLOR 70940); *ibid.*, *idem*, *Drechsler-Santos E.R.* 1969 (FLOR 70941); Primavera do Leste, Alminhas (15°31'13.1"S, 54°12'29.3"W) 22 December 2013, *Alves-Silva, G.* 562 (FLOR 70942). Pará, Belterra, Floresta Nacional de Tapajós, BR163 – KM67 – Trilha 67 (Seringal na entrada da trilha), 27 January 2015, *Drechsler-Santos E.R.*

1632 (FLOR 70935); *ibid.*, *idem*, Drechsler-Santos E.R. 1635 (FLOR 70936); *ibid.*, 28 January 2015, Drechsler-Santos E.R. 1649 (FLOR 70937).

Ecology and distribution.— Saprobe, found on dead angiosperm branches and trunks, causing a brown-rot. So far, the species is known in tropical areas of Brazil, in the Amazon Rainforest, Atlantic Rainforest and Cerrado ecosystems.

Additional *Daedalea* specimens studied:

***Daedalea aethalodes*:** PARAGUAY, Central, Campus Universitario UNA, San Lorenzo, 25°19'40.79"S 57°31' 14.41" W, 27-IV-2016, Michelle Campi MCampi 70 (FACEN 004306); ***Daedalea ryvarideniana*:** BRAZIL, Mato Grosso, Chapa dos Guimarães, Vêu da Noiva, 15°24'25"S, 55°50'17"W, 12-VI-2011, Ferreira-Lopes VFL001 (FLOR 41053, holotype).; Paraíba: Sumé, Fazenda Almas, 7°28'16"S, 36°53'53"W, 10-VIII-2008, Nogueira-Melo *et al.* 033PB (URM80515). ***Daedalea modesta*:** PARAGUAY, Alto Paraná, Refugio Biológico Tati Yupi, 25°21'51.9"S 54°34'47.8"W, 26/IX/2015, Michelle Campi MCampi 6 (FACEN 3445).

DISCUSSION

The multi-gene phylogenetic analyses recovered *Daedalea* as a moderately high supported clade (0.97/90). All the Neotropical species included in the analyses grouped within *Daedalea*. *Daedalea aethalodes* and *D. ryvarideniana* were previously placed in *Daedalea* based on their micromorphological characters, i.e. presence of a catathymenium; generative hyphae with irregularly thickened walls, the shape of the basidiospores, and by producing a brown-rot, regardless of the poroid hymenophore in the case of *D. aethalodes* (Rajchenberg, 1986; Drechsler-Santos *et al.*, 2012). *Daedalea ryvarideniana* clustered with an unidentified Costa Rican specimen (JV 1504/34) in a basal position with moderately high support (0.97/93). *Daedalea aethalodes* formed a low supported clade with *D. dochmia*. Both of these species present a poroid hymenophore (Carranza-Morse & Gilbertson, 1986; Rajchenberg, 1986; Hattori, 2005), however, *D. dochmia* has a trimitic hyphal system while *D. aethalodes* a dimitic hyphal system with binding processes (Carranza-Morse & Gilbertson, 1986; Drechsler-Santos *et al.*, 2012). Further sampling and molecular markers of *D. aethalodes* are necessary to resolve its phylogenetic relationships within *Daedalea*.

The new Neotropical species, *D. rajchenbergiana*, formed a group of maximum support with *D. americana*. Morphologically, both species are similar, but *D. americana* differs by having larger pores (4–5/mm, vs 5–8/mm in *D. rajchenbergiana*) and larger basidiospores ($4.0\text{--}5.1 \times 2.1\text{--}3.0 \mu\text{m}$ vs $3.3\text{--}4.3 \times 1.7\text{--}2.2$ in *D. rajchenbergiana*) (Han *et al.*, 2015). Additionally, *D. americana* is only known from North and Central America (Han *et al.*, 2015) while *D. rajchenbergiana* was found in tropical areas of Brazil. Another species with a strikingly similar upper surface and which co-occurs with *D. rajchenbergiana* is *D. ryvarideniana*, which is easily distinguishable by its large (1–3/mm) and irregular, daedaloid pores, and much larger basidiospores ($7.0\text{--}11.0 \times 2.5\text{--}3.5 \mu\text{m}$) (Drechsler-Santos *et al.*, 2012). Finally, *D. rajchenbergiana* presents remarkably small pores which distinguishes it from all other species in the genus.

Regarding *D. modesta*, two different clades were recovered: one with a Paraguayan specimen (M Campi 6) and another with Chinese specimens (Cui 10151; Cui 10124 and Dai 10844). Based on our results the Paraguayan specimen would represent *D. modesta*, since the type locality is Suriname (Montagne, 1856), whereas the Asian specimens would represent an undescribed species of *Daedalea*. Further analyses are needed to confirm its taxonomic status. On a final note, *Daedalea* sp. 18198 from Belize (as *D. quercina* in Lindner et al., 2011) clustered with *Daedalea neotropica* originally described for Belize (Lindner et al., 2011).

It has been shown that changes in the number of molecular markers and the species and specimen sampling modify the topology of the tree, the phylogenetic relationships between *Daedalea* species and their support values (Han et al., 2015, 2016). Previous multigene phylogenetical analyses showed *D. radiata* in different unsupported or questionable positions, either within or as a sister group of *Daedalea* (Li & Cui, 2013; Han et al., 2015, 2016; Decock et al., 2022). Our result showed *D. radiata* outside of *Daedalea* s. s. clustered with *Rhodofomitopsis*, however without support, indicating that the number of sequences and genes are not yet sufficient to determine the genus of the species. Further samplings of members of the ‘antrodia’ clade are needed to determine the taxonomical status of this species.

Additional molecular markers and more samples of poorly represented Neotropical species might help resolve phylogenetical relationships within *Daedalea*.

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