Persoonia 39, 2017: 254–269
www.ingentaconnect.com/content/nhn/pimj

RESEARCH ARTICLE

ISSN (Online) 1878-9080
https://doi.org/10.3767/persoonia.2017.39.10

Morphological reassessment and molecular phylogenetic analyses of *Amauroderma* s.lat. raised new perspectives in the generic classification of the *Ganodermataceae* family

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Key words

Amauroderma
Ganoderma
polyporales
systematics
ultrastructure

Abstract *Ganodermataceae* is a remarkable group of polypore fungi, mainly characterized by particular double-walled basidiospores with a coloured endosporium ornamented with columns or crests, and a hyaline smooth exosporium. In order to establish an integrative morphological and molecular phylogenetic approach to clarify relationship of Neotropical *Amauroderma* s.lat. within the *Ganodermataceae* family, morphological analyses, including scanning electron microscopy, as well as a molecular phylogenetic approach based on one (ITS) and four loci (ITS-5.8S, LSU, TEF-1α and *RPB1*), were carried out. Ultrastructural analyses raised up a new character for *Ganodermataceae* systematics, i.e., the presence of perforation in the exosporium with holes that are connected with hollow columns of the endosporium. This character is considered as a synapomorphy in *Foraminispora*, a new genus proposed here to accommodate *Porothelium rugosum* (≡ *Amauroderma sprucei*). *Furtadoa* is proposed to accommodate species with monomitic context: *F. biseptata, F. brasiliensis* and *F. corneri*. Molecular phylogenetic analyses confirm that both genera grouped as strongly supported distinct lineages out of the *Amauroderma* s.str. clade.

Article info Received: 26 January 2017; Accepted: 29 June 2017; Published: 21 September 2017.

INTRODUCTION

Ganodermataceae is mainly characterized by pileate basidiomata, sessile to stipitate, hyphal system dimitic, with arboriform and skeleto-binding hyphae and double-walled basidiospores with a coloured endosporium ornamented with columns and crests, and a hyaline smooth exosporium. The family has a cosmopolitan distribution with about 220 species, as saprotrophs in dead wood, associated with roots of living and dead trees, and also as parasites/pathogens, causing white rot in woody tissues (Moncalvo & Ryvarden 1997, Ryvarden 2004).

Taxonomy of the family was almost exclusively based on morphological characteristics, such as appearance of pilear surface (i.e., dull or laccate), disposition of the hyphae in the pilear surface (i.e., anamixoderm, characoderm, cortex, hymeniderm, trichoderm) and basidiospore characters (shape and ornamentation pattern including some ultrastructural approaches). Despite extensive studies at generic and infrageneric levels (Furtado 1962, 1965, 1981, Steyaert 1972, 1980, Ryvarden & Johansen 1980, Corner 1983, Gottlieb & Wright 1999a, b, Ryvarden 2004, Torres-Torres & Guzmán-Dávalos 2012), only five genera are currently widely accepted, i.e., *Amauroderma*, *Ganoderma*, *Haddowia*, *Humphreya* and *Tomophagus* (Moncalvo et al. 1995, Moncalvo & Ryvarden 1997, Ryvarden 2004, Kirk et al. 2008, Tham et al. 2012). *Ganoderma* is characterized by ellipsoid to ovoid basidiospores, with a truncate apex and an endosporium with columnar ornamentations. *Tomophagus* also has basidiospores with a truncate apex; however, it is characterized by a pale and soft floccose context where chlamydospores are produced. *Humphreya* has basidiospores with truncate apex and the endosporium ornamented by typical longitudinal ridges. *Amauroderma* and *Haddowia* have basidiospores without truncate apex, differing mainly due to the ornamentation pattern of the endosporium, i.e., columnar to semi-reticulate in *Amauroderma* and with longitudinal ridges in *Haddowia* (Furtado 1981, Steyaert 1972, Ryvarden 2004, Tham et al. 2012).

In this current classification into five genera, several taxa are considered ‘deviating elements’ either by their microscopical characters (basidiospore shape and ornamentation or hyphal system), macroscopical characters (as stipe presence or context colour and consistence) or a combination of these features. In particular, regarding neotropical *Amauroderma* species there are taxa which not fit within the phylogenetic delimitation of *Amauroderma* s.str. senso Costa-Rezende et al. (2016), such as *Amauroderma sprucei* which distinguishes within the genus by its whitish context with hyaline dextrinoid skeletal hyphae and a vivid orange pore surface in most of the specimens (Decock & Herrera-Figueroa 2006). There are also monomitic or nearly so species within *Amauroderma*, as *A. trichodermatum* and *A. brasiliense* (Robledo et al. 2015), as well as species with basidiospores with reticulate endosporium (*A. deviatum*) (Ryvarden 2004).

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Based on phylogenetic evidence it has been shown that *Amauroderma* is polyphyletic, with *Amauroderma* s.str. forming a monophyletic clade and some *Amauroderma* species defined in its broad morphological sense grouped out of *Amauroderma* s.str. (Gomes-Silva et al. 2015, Costa-Rezende et al. 2016). Although several molecular phylogenetic studies have been published on *Ganoderma* and *Amauroderma*, no synthesis of molecular data has been presented with a phylogenetic overview in context of *Ganodermataceae*.

Regarding the 'deviating elements' in Neotropical *Amauroderma* and the scarce phylogenetic evidence around *Ganodermataceae*, the aim of our work was to develop an integrative morphological and molecular phylogenetic approach to clarify the relationship of Neotropical *Amauroderma* s.lat. within the *Ganodermataceae* family.

MATERIAL AND METHODS

Specimens and morphological studies

The studied specimens are deposited in FLOR, HUEFS and CORD herbaria. Herbarium acronyms follow Thiers (continuously updated, http://sweetgum.nybg.org/science/ih/). Microscopic examinations and measurements were done using Melzer's reagent, Cotton blue and/or 3–5 % KOH as mounting media. For the study of the hyphal system, sections of the basidiomata were incubated in hot (40 °C) 3 % NaOH solution, then dissected under a stereomicroscope and finally examined at 3 % NaOH solution at room temperature (Decock et al. 2013). Basidiospore-walls designations follow the concept of Furtado (1962). Melzer's reagent was used to check dextrinoid and amyloid reactions. In order to determine the size range of pores, hyphae and basidiospores, 5 % of the measurements at each end of the range are given in parentheses, when relevant, and forty basidiospores were measured.

For ultrastructural observations, both basidiospores with and without exospore were observed. In the first case, fragments of tubes were placed on stubs, then metalized with gold and observed at SEM. To observe the ornamentation in detail, we removed the outer layer of basidiospores according to Crespo & Robledo (2016). Fragments of tubes were placed on chromic acid (H_2CrO_4) crystal, covered by enough water drops to dissolve the crystals, and stored around 20 minutes. Then, this solution and dissepiment fragments were filtered (0.45 µm filter) by vacuum, adding water to remove acid. The filter was dried at room temperature and finally scraped with a blade in a stub with a drop of 70 % alcohol, metalized with gold and observed at SEM. The analyses were performed in Scanning Electronic Microscope (SEM) Zeiss LEO 1450VP of the Laboratorio de Microscopía Electrónica y Microanalisis (LABMEM) of the Universidad Nacional de San Luis, Argentina and JEOL JSM-6390LV.

DNA extraction and sequencing

DNA was extracted from dried basidiomata following the protocol of Doyle & Doyle (1987) modified by Góes-Neto et al. (2005). Primer pairs ITS8-F/ITS6-R (Dentinger et al. 2010) and LR0R/LR7 (Vilgalys & Hester 1990) were used to amplify the internal transcribed spacer (ITS) and large subunit (LSU) rDNA regions, respectively. Primer pairs *RPB1*-Af/*RPB1*-Cr (Matheny et al. 2002) and EF1-983F/EF1- 2212R (Rehner & Buckley 2005) were used to amplify the protein-coding genes RNA polymerase II largest subunit (*RPB1*) and translation elongation factor-1α (TEF-1α), respectively. Sanger Sequencing was performed with BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, California, USA) following manufacturer procedures. The same oligos were used as forward and reverse sequencing primers for the ITS, *RPB1* and TEF-1α. For LSU the primer LR7 was replaced by the LR5. The sequencing was performed at LAMOL (Universidade Estadual de Feira de Santana) and FIOCRUZ-MG (Brazil), as part of the FungiBrBol project.

Phylogenetic analyses

Chromatograms were manually edited using Geneious v. 6.1.8 (http://www.geneious.com). The sequences generated in this work were combined with ITS, LSU, *RPB1* and TEF-1α sequences of *Ganodermataceae* and outgroups (*Perenniporia medulla-panis*, *Perenniporiella chaquenia* and *P. pendula*) retrieved from GenBank (NCBI). Five datasets were constructed: one of them (ITS) is composed by the majority of the phylogenetic species of *Ganodermataceae*; the others (ITS, LSU, *RPB1* and TEF-1α) are composed of sequences from vouchers belonging to the main putative phylogenetic lineages of the *Ganodermataceae* family which have available sequences of at least two of the molecular markers mentioned above (except for *G. subresinosum* and *A. brasiliense* which were included even having only ITS sequences), in order to perform a multiloci phylogenetic analyses. The newly generated sequences and additional sequences downloaded from GenBank are listed in the Table 1.

The datasets were aligned using MAFFT v. 7 (Katoh & Standley 2013), under the G-INS-i criteria. Then, they were manually inspected using MEGA v. 6 (Tamura et al. 2013). Both ITS datasets were subdivided into three data partitions, ITS1, 5.8S and ITS2, while *RPB1* and TEF-1α were subdivided in introns, and 1st, 2nd and 3rd codon positions.

The best-fit model of nucleotide evolution to the datasets was selected by AIC (Akaike Information Criterion) using jModelTest2 v. 1.6 (Guindon & Gascuel 2003, Darriba et al. 2012). For the phylogenetic reconstruction two datasets were analyzed, the ITS dataset and the multiloci dataset (ITS+LSU+*RPB1*+TEF-1α). Bayesian Inference (BI) and Maximum Likelihood (ML) phylogenetic analyses were applied to the datasets. BI was performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) with two independent runs, each one beginning from random trees with four simultaneous independent chains, performing 1×10^7 replications, sampling one tree every 1×10^3th generation. The first 2.5×10^6 sampled trees were discarded as burn-in and checked by the convergence criterion (frequencies of average standard deviation of split < 0.01), while the remaining ones were used to reconstruct a 50 % majority-rule consensus tree and calculate Bayesian posterior probabilities (BPP) of the clades. ML searches were conducted with RAxML-HPC v. 8.2.3 (Stamatakis 2014), available in the CIPRES science gateway (Miller et al. 2010; http://www.phylo.org/). The analysis first involved 100 ML searches, each one starting from one randomized stepwise addition parsimony tree, under a GTRGAMMA model, with all other parameters estimated by the software. Only the best scored likelihood tree from all the searches was kept to access the reliability of the nodes. Multiparametric bootstrapping replicates under the same model are computed, allowing the program to halt bootstrapping automatically by the autoMRE option. An additional alignment partition file to force RAxML software to search for a separate evolution model for each partition was used.

A node was considered to be strongly supported if it showed a BPP ≥ 0.95 and/or BS ≥ 70 %. The final alignment and the retrieved topologies were deposited in TreeBASE (http://www.treebase.org), under accession ID: 20193 (http://purl.org/phylo/treebase/phylows/study/TB2:S20193).

Table 1 Species, vouchers and accession numbers of the specimens used in phylogenetic analyses.

		Genbank acession numbers			
Species name	Voucher	ITS	LSU	*RPB1*	TEF-1α
Amauroderma aurantiacum	FLOR52205	KR816510	KU315205	–	–
	DHCR540 (HUEFS)	MF409961	MF409953	MF436687	–
	URM78847	JX310840	–	–	–
A. calcigenum	FLOR52315	KR816514	–	–	–
A. calcitum	FLOR50931/DHCR538 (HUEFS)	KR816528	KU315207	MF436690	–
	FLOR52230	KR816529	–	–	–
A. elegantissimum	URM82789	JX310844	KT006617	–	–
	URM82787	JX310843	KT006616	–	–
A. exile	URM82794	JX310845	–	–	–
A. floriformum	URM83250	JX310846	–	–	–
A. intermedium	GAS910 (HUEFS)	MF409959	–	MF436685	–
	FLOR52248	KR816527	KU315209	–	–
A. omphalodes	DHCR499/501 (HUEFS)	MF409956	MF409951	MF436682	MF421238
	DHCR500 (HUEFS)	MF409957	MF409952	MF436683	MF421239
A. partitum	URM83039	JX310853	–	–	–
	URM82882	JX310852	–	–	–
A. perplexum	CUI6496	KJ531650	KU220001	–	–
	WEI5562	KJ531652	–	–	–
	DAI10811	KJ531651	KU220002	–	–
A. aff. *praetervisum*	FLOR52249	KR816511	–	–	–
A. praetervisum	REC18707	JX310855	–	–	–
	URM84230	KC348461	–	–	–
	GOMES SILVA 909	JX310856	–	–	–
A. pseudoboletum	FLOR52318	KR816516	–	–	–
A. rude	CANB643174	KU315197	–	–	–
	CANB795782	KU315198	–	–	–
	CANB359451	KU315199	–	–	–
A. rugosum	CUI9012	KJ531665	KU220011	–	KU572503
	ZHOU547	KJ531675	–	–	–
	CUI9011	KJ531664	KU220010	–	KU572504
A. schomburgkii	DHCR504 (HUEFS)	MF409958	–	MF436684	–
	FLOR52177	KR816522	KU315215	–	–
	URM83228	JX310848	–	–	–
A. sp.	INPA249751	KR816525	–	–	–
A. subresinosum	WEI5569	KJ531649	–	–	–
	THP48	FJ154784	–	–	–
	THP16	FJ154782	–	–	–
A. yunnanense	CUI7974	KJ531653	KU220013	–	–
	DAI13021	KJ531654	–	–	–
	YUAN2253	KJ531655	–	–	–
Furtadoa brasiliensis	URM83578	JX310841	–	–	–
	TBG58	JX982569	–	–	–
F. biseptata	FLOR50932	KU315196	KU315206	–	–
Foraminisporus sprucei	FLOR52191	KU315200	KU315216	–	–
	FLOR52184	KU315201	–	–	–
	FLOR52195	KU315202	–	–	–
	DHCR512 (HUEFS)	MF409960	–	MF436686	MF421240
	DHCR554 (HUEFS)	MF409962	MF409954	MF436688	–
	DHCR560 (HUEFS)	MF409963	MF409955	MF436689	MF421241
Ganoderma adspersum	R1212	AJ006685	–	–	–
	GATO00	AM906057	–	–	–
	GAD3	JN222418	–	–	–
G. annulare	KCTC16803	JQ520160	–	–	–
G. applanatum	KM120830	AY884178	–	–	–
	GA165	DQ425009	–	–	–
	GA117	DQ424996	–	–	–
	ATCC44053	JQ520161	–	–	–
	WEI5787	KF495001	KF495011	KF494978	–
	Dai 12483	KF494999	KF495009	–	KF494977
G. aridicola	DAI 12588	KU572491	–	–	KU572502
G. cf. *australe*	K621	JN596327	–	–	–
	G561	JN596326	–	–	–
G. australe	DHCR411 (HUEFS)	MF436675	MF436672	MF436680	MF436677
	DHCR417 (HUEFS)	MF436676	MF436673	MF436681	MF436678
	GDGM25745	JX195205	–	–	–
	HMAS86596	AY884180	–	–	–
G. australe cplx	FLOR52289	KU315203	KU315217	–	–
G. austroafricanum	CMW41454	KM507324	–	–	–
G. boninense	WD2085	KJ143906	–	KJ143945	KJ143925
	WD2028	KJ143905	–	KJ143944	KJ143924
G. carnosum	KM109415	AY884175	–	–	–
	GCR1	JN222419	–	–	–
G. chalceum	URM80457	JX310812	–	–	–
G. coffeatum	FLOR50933	KU315204	–	–	–
G. cupreum	GANOTK7	JN105702	–	–	–
	GANOTK4	JN105701	–	–	–
	KR61	FJ655470	–	–	–
	KL161	FJ655466	–	–	–

Table 1 (cont.)

		Genbank acession numbers			
Species name	Voucher	ITS	LSU	*RPB1*	TEF-1α
G. curtisii	CBS100132	JQ520164	–	KJ143947	KJ143927
	CBS100131	JQ781848	–	KJ143946	KJ143926
G. enigmaticum	DAI 15970	KU572486	–	–	KU572496
	DAI 15971	KU572487	–	–	KU572497
G. flexipes	WEI5494	JN383979	–	–	–
	WEI5491	JQ781850	–	–	–
G. fornicatum	TN231	FJ655476	–	–	–
	KL231	FJ655471	–	–	–
G. fulvellum	XSD08051	FJ478088	–	–	–
G. gibbosum	XSD34	EU273513	–	–	–
	KUT0805	AB733121	–	–	–
	G1	JN596331	–	–	–
G. hoehnelianum	DAI12096	JN383980	–	–	–
	GDGM25735	JX195203	–	–	–
G. japonicum	AS5.69	AY593864	–	–	–
	AS5.69	AY593865	–	–	–
G. leucocontextum	DAI 15601	KU572485	–	–	KU572495
	GDGM44490	KM396272	–	–	–
G. lingzhi	DAI12574	KJ143908	–	JX029985	JX029977
	DAI12426	JQ781870	–	–	–
	CUI9166	KJ143907	–	JX029982	JX029974
G. lipsiense	NOR5311432	EF060005	–	–	–
	FIN131R610	EF060004	–	–	–
G. lobatum	JV 1212/10J	KF605676	–	–	KU572501
G. lucidum	BEOFB 432	KX371595	–	–	KX371598
	BEOFB 431	KX371594	–	–	KX371597
	K175217	KJ143911	–	KJ143950	KJ143929
	CUI9207	KJ143910	–	KJ143949	KJ143928
	GL16	HM053438	–	–	–
	GL14	HM053436	–	–	–
	GL951	KC311371	–	–	–
G. martinicense	LIPSWMart0844	KF963257	–	–	–
	LIPSWMart0855	KF963256	–	–	–
G. mastoporum	PM21	JQ409361	–	–	–
G. meredithae	ASI7140	JQ5201911	–	–	–
	ATCC64492	JQ520190	–	–	–
G. multipileum	DAI9447	KJ143914	–	KJ143953	KJ143932
	CWN04670	KJ143913	–	KJ143952	KJ143931
	DAI9447	KF494997	–	–	–
G. multiplicatum	DAI12320	KU572490	–	–	KU572500
	DAI13710	KU572489	–	–	KU572499
	URM83346	JX310823	–	–	–
G. orbiforme	URM83334	JX310814	–	–	–
	URM83336	JX310816	–	–	–
G. oregonense	CBS266.88	JQ781876	–	KJ143955	–
	CBS265.88	JQ781875	–	KJ143954	KJ143933
G. parvulum	URM83345	JX310820	–	–	–
	URM80765	JX310822	–	–	–
G. perzonatum	SP445985	KJ792745	–	–	–
	SP4459871	KJ792747	–	–	–
G. pfeifferi	KM120818	AY884185	–	–	–
	GPF1	JN222420	–	–	–
G. philippii	E7098	AJ536662.2	–	–	–
	E7092	AJ608710	–	–	–
G. pudoferreum	CATASGp008	FJ392284	–	–	–
G. pseudoferreum	CATASGp005	FJ392281	–	–	–
G. ramosissimum	XSD08032	EU918700	–	–	–
	XSD08085	FJ478127	–	–	–
G. resinaceum	CBS 194.76	X78737/X78758	–	KJ143956	KJ143934
	IUM3651	JQ520204	–	–	–
	ASI7143	JQ520203	–	–	–
	BR4150	KJ143915	–	KJ143915	–
G. sessile	JV1209/9	KF605629	–	KJ143958	KJ143936
	JV1209/27	KF605630	–	KJ143959	KJ143937
G. sichuanense	CGMCC55331	JN197284	–	–	–
	HMAS1301281	JF915404	–	–	–
G. sinense	XZGC1	HQ235633	–	–	–
	GDGM25829	KC415760	–	–	–
	WEI5327	KF494998	KF495008	–	KF494976
G. sp.	PALCOSTPBP10	KJ792084	–	–	–
	PALCOSTPBP09	KJ792083	–	–	–
	GD026 (HUEFS)	MF436674	MF436671	MF436679	–
G. aff. *steyaertanum*	C17274	EU239388	–	–	–
G. steyaertanum	MEL2382783	KP012964	–	–	–
G. stipitatum	THC16	KC884264	–	–	–
G. subamboinense	GSUB1371	DQ425006	–	–	–
	GSUB1361	DQ425005	–	–	–

Table 1 (cont.)

		Genbank acession numbers			
Species name	Voucher	ITS	LSU	*RPB1*	TEF-1α
G. tornatum	URM82776	JQ514110	–	–	–
	TBG01AM2009	JQ514108	–	–	–
G. tropicum	YUAN3490	JQ781880	–	–	–
	DAI9724	JQ781879	–	–	–
G. tsugae	DAI3937	JQ781853	–	–	–
	AFTOL ID 771	DQ206985	AY684163	–	DQ059048
	DAI12760	KJ143920	–	KJ143961	KJ143940
G. tsunodae	GR3631	FJ154773	–	–	–
	WD2034	AB588989	AB368069	–	–
G. tuberculosum	LIPSWMart0845	KF963258	–	–	–
	LIPRCMart1075	KF963255	–	–	–
G. weberianum	GANOTK16	JN105704	–	–	–
	GANOTK06	JN105703	–	–	–
	GW11	GU726935	–	–	–
	GW10	GU726934	–	–	–
	TN21	FJ491988	–	–	–
	TN15	FJ491986	–	–	–
G. zonatum	FL03	KJ143922	–	–	KJ143942
	FL02	KJ143921	–	KJ143962	KJ143941
Perenniporia medulla-panis	MUCL43250	NR119717	–	–	–
Perenniporiella chaquenia	MUCL49758	NR111365	FJ393857	–	HM467602
P. pendula	MUCL47129	FJ411082	FJ393854	–	HM467600
Tomophagus cattienensis	CT119	JN184398	–	–	–
	CT99	JN184397	–	–	–
T. colossus	TC02	KJ143923	–	KJ143963	KJ143943
	URM80450	JX310825	JX310839	–	–
	URM83330	JQ618247	JX310811	–	–

RESULTS

Molecular Phylogeny

The final ITS dataset (Fig. 1) included sequences from 157 fungal specimens, with 659 characters, of which 320 were constant and 267 parsimony informative. The combined (ITS+LSU+*RPB1*+TEF-1α) dataset (Fig. 2) included sequences from 68 fungal specimens, with 3489 characters, of which 2415 were constant and 813 parsimony informative. The evolutionary models selected for ITS dataset were TIM2+G (ITS1), TIM1ef+I+G (5.8S) and HKY+I+G (ITS2). For the multiloci dataset the selected models were TVM+I+G (ITS1), K80+I (5.8S), TPM3+G (ITS2), TIM2+I+G (LSU), HKY+G (*RPB1* introns), TRN+I (*RPB1* 1st codon), HKI+I (2nd codon), TIM2+G (3rd codon), TPM3u+I+G (TEF-1α introns), GTR+I (TEF-1α 1st codon), TVM+I+G (TEF-1α 2nd codon) and TIM2+G (TEF-1α 3rd codon).

Eleven major lineages were recovered in ITS analyses. Two of them corresponded to the new genera proposed here, i.e., *Furtadoa* (1.0 BPP, 95 % BS) and *Foraminispora* (1.0 BPP, 100 % BS). Three distinct lineages were composed of species currently classified in the genus *Amauroderma*, here named the *Amauroderma* s.str. (1.0 BPP, 63 % BS), 'Amauroderma rude' clade (1.0 BPP) and 'Amauroderma yunannense' clade (1.0 BPP, 99 % BS), which clustered as the sister clade of *Foraminispora* (0.98 BPP). Four distinct lineages were composed of species currently classified in the genus *Ganoderma*, which are *Ganoderma*, 'Ganoderma coffeatum' clade, 'Ganoderma ramosissimum' clade (1.0 BPP, 100 % BS) , 'Magoderna' clade (1.0 BPP, 100 % BS) and 'Trachyderma' clade (1.0 BPP, 100 % BS). Finally, *Tomophagus* (1.0 BPP, 100 % BS) represented an independent lineage composed of two species.

The multiloci dataset recovered nine main clades, which consists of the clades in the ITS dataset, with exception to 'Ganoderma coffeatum' clade and 'Ganoderma ramosissimum' clade which were not included in the analyses. The clades are *Amauroderma* s.str. (1.0 BPP, 89 % BS), *Ganoderma* (1.0 BPP, 90 % BS), 'Magoderna' clade (1.0 BPP, 100 % BS), 'Trachyderma' clade (1.0 BPP, 100 % BS), *Tomophagus* (1.0 BPP, 100 % BS), 'Amauroderma rude' clade (1.0 BPP, 96 % BS), 'Amauroderma yunannense' clade (1.0 BPP, 99 % BS), and the new genera proposed here, *Furtadoa* (1.0 BPP, 92 % BS) and *Foraminispora* (1.0 BPP, 100 % BS). 'Amauroderma yunnanense' clade clustered as the sister clade of *Foraminispora* (1.0 BPP, 96 % BS) and this assemblage as a sister clade of *Ganoderma* (0.98 BPP, 52 % BS).

Taxonomy

Foraminispora Robledo, Costa-Rezende & Drechsler-Santos, *gen. nov.* — MycoBank MB819015

Etymology. Referring to the basidiospores with hollow endosporic projections which are continuous until the exospore wall. Foramen means hole, while spora means spore in Latin.

Typification. Porothelium rugosum Berk., Hooker's J. Bot. Kew Gard. Misc. 8: 237. 1856.

Diagnosis — Similar to *Amauroderma*, differing by the spores with endosporic ornamentation as hollow columns, which are continuous until the exospore wall.

Basidiomata annual, stipe pleuropodal to pseudomesopodal, pileus circular to spathulate. *Pilear surface* glabrous, greyish brown to dark brown, concentrically zonate with thin blackish bands, radially rugose. *Context* white, homogenous, in section with a shiny black cuticle. *Tubes* slightly darker than context. *Pore surface* whitish to vivid orange. Pores regular, circular to angular. Dissepiments thick, entire. *Stipe* cylindrical, pale to dark brown, finely tomentose, solid to hollow, context homogeneous, whitish, in section with a shiny dark cuticle. *Hyphal system* dimitic, generative hyphae clamped, arboriform and skeleto-binding hyphae almost hyaline, dextrinoid. Cystidia and cystidioles absent. *Basidia* clavate, with four sterigmata. *Basidiospores* subglobose, hyaline to pale brown, double walled, with conspicuous ornamentation as endosporic projec-

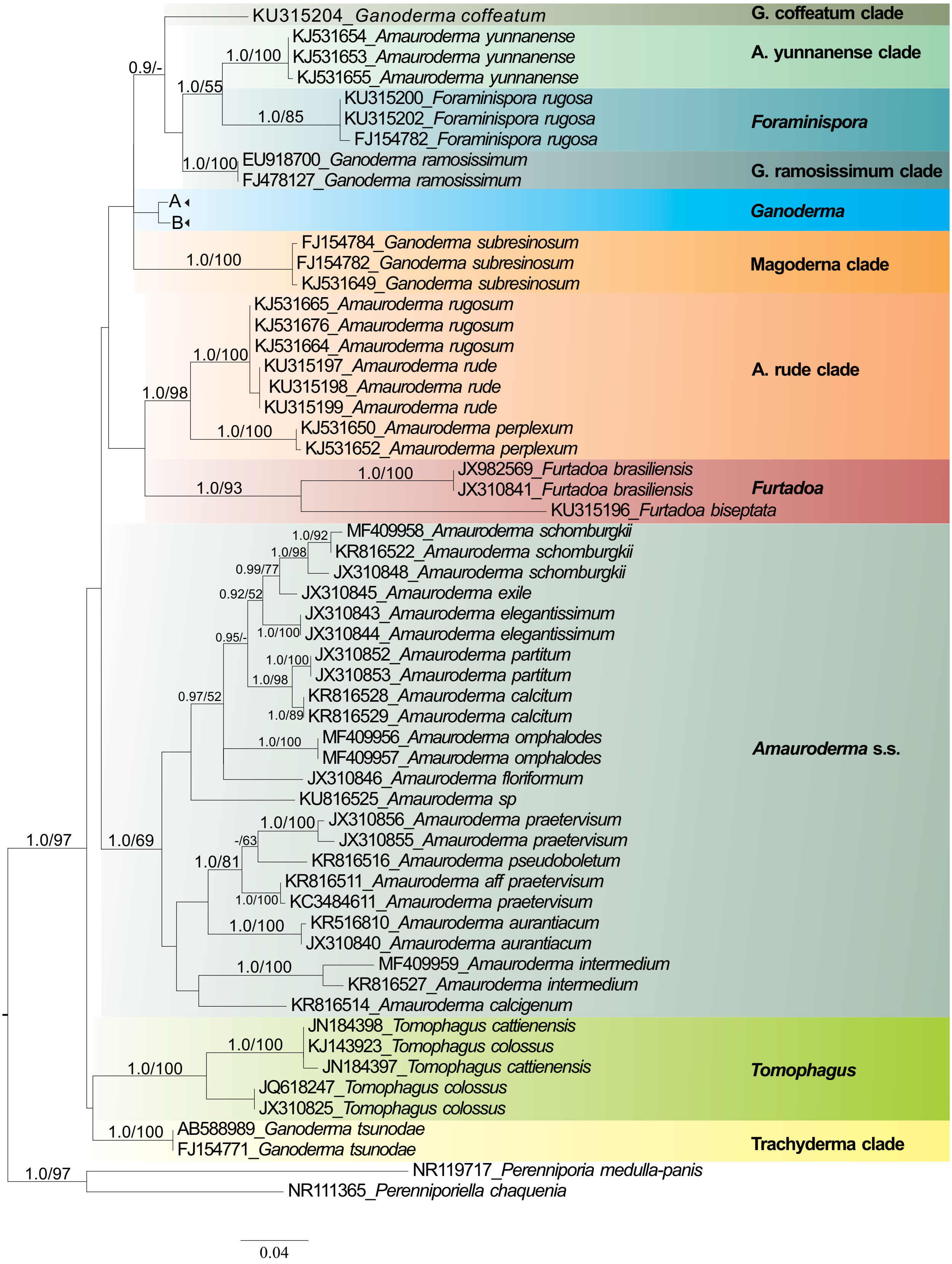
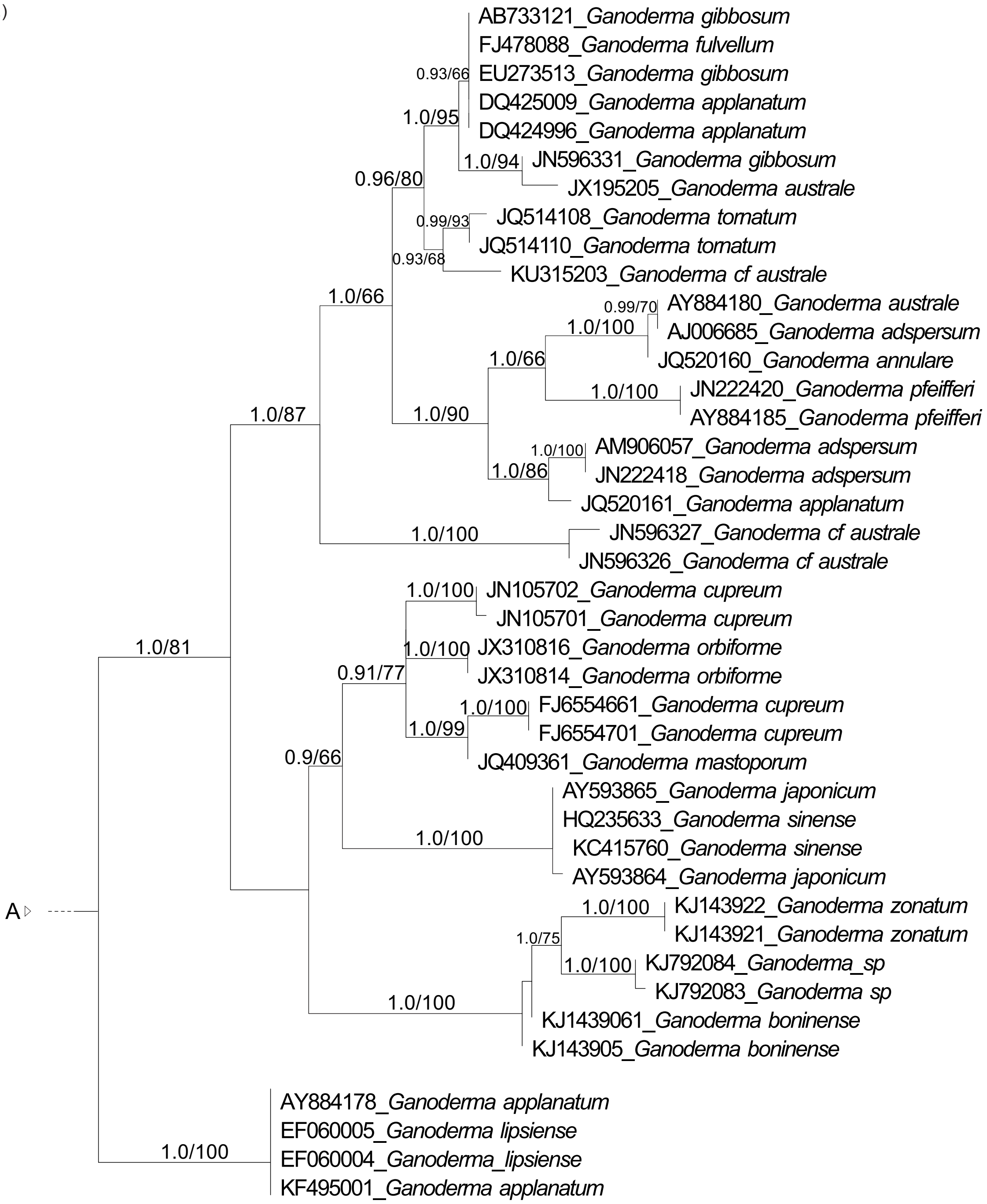


Fig. 1 Maximum likelihood (ML) tree of *Ganodermataceae* based on dataset of ITS sequences. Bayesian posterior probability above 0.7 and Bootstrap values above 50 % are shown.

Fig. 1 (cont.)



tions column-like, some of them with a hole, that persists up to the exospore, IKI-.

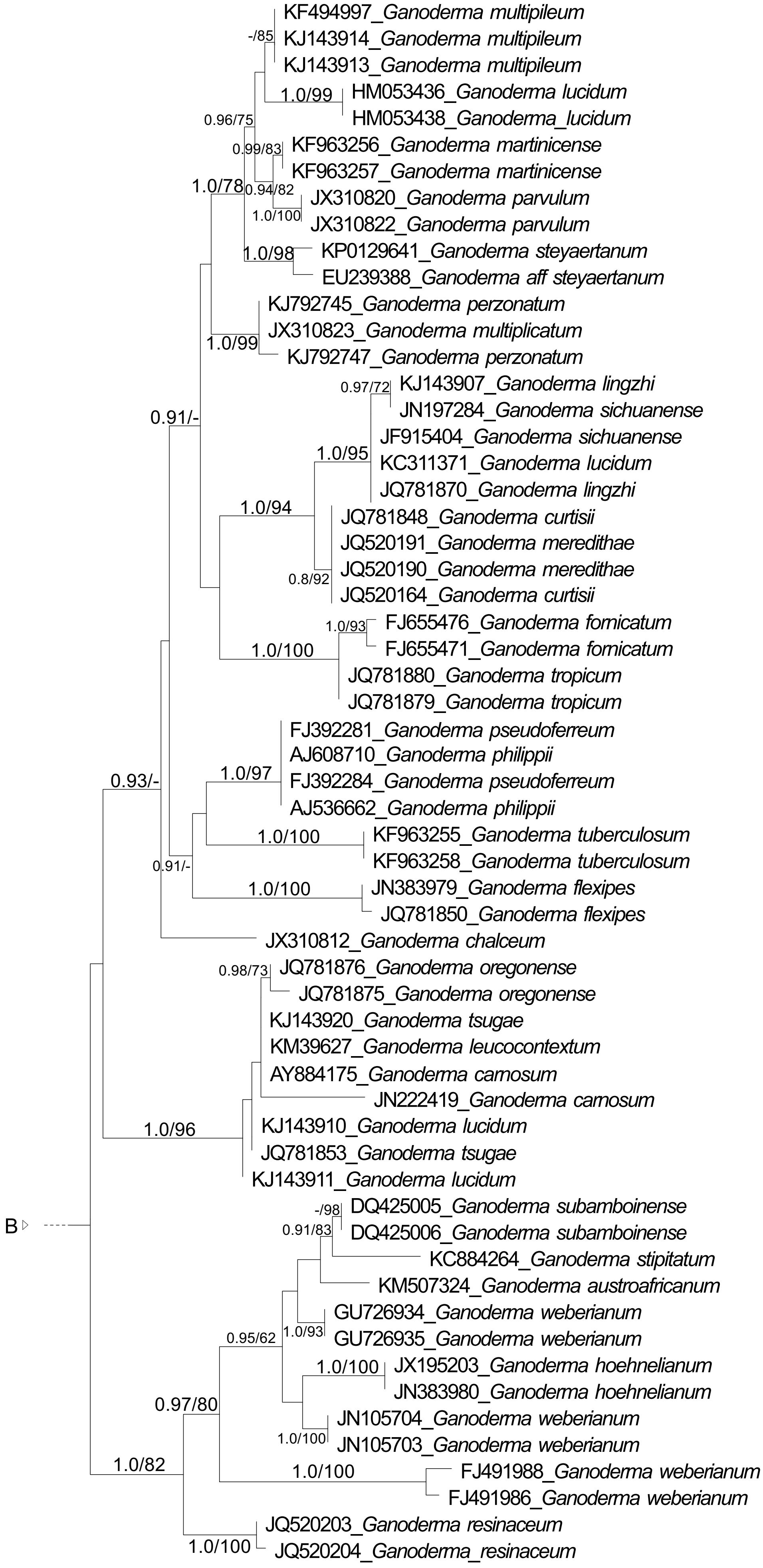
Ecology & Distribution — Specimens growing on the ground or on decayed angiosperm wood in Brazil, Venezuela, French Guiana, Costa Rica and Cuba (Decock & Herrera-Figueroa 2006).

Notes — The new genus is characterized by stipitate basidiomata, dull pilear surface, whitish context, a dimitic hyphal system, skeleto-binding hyphae with lateral and apical branches and arboriform skeletal hyphae, both dextrinoid, and globose to subglobose, hyaline to pale brown spores, with conspicuous endosporic projections. Under SEM, it is possible to observe that some of the columnar endosporic projections are hollow and these holes persist until the exospore wall (Fig. 3). This feature is unique within *Ganodermataceae*, thus, it is considered as an exclusive feature for this genus.

The genus clearly fits into *Ganodermataceae* circumscription, due to its hyphal system with clamped generative and arboriform skeletal hyphae, as well as the double-walled basidiospores, with the inner layer ornamented. Both macro- and microscopic features of *Foraminispora* are shared with the genus *Amauroderma*, i.e., stipitate and annual basidiomata, a dimitic hyphal system and non-truncate basidiospores (Furtado 1962, 1981, Ryvarden & Johansen 1980, Corner 1983, Ryvarden 2004). However, an ultrastructural examination of some species of *Amauroderma* (*A. calcigenum*, *A. pseudoboletus* and *A. schomburgkii*) led us to conclude that the perforated column is absent in this genus (Fig. 4a–f).

Ganoderma also presents species with pale context and double-walled spores with endosporic ornamentation (Ryvarden & Johansen 1980, Corner 1983, Ryvarden 2004, Torres-Torres & Guzmán-Dávalos 2012); however, the absence of the hollow columns (*G. australe;* Fig. 4g–h) and the truncate apex of basidiospores clearly distinguish this genus from *Foraminispora*. *Ganoderma* also has holes in the exospore of some species (*G. lucidum, G. pfeifferi, G. valesiacum*). Nevertheless, the holes are formed among the columns (Pegler & Young 1973).

Fig. 1 (cont.)


KF494997_Ganoderma multipileum
-/85
KJ143914_Ganoderma multipileum
KJ143913_Ganoderma multipileum
1.0/99
HM053436_Ganoderma lucidum
0.96/75
HM053438_Ganoderma_lucidum
0.99/83
KF963256_Ganoderma martinicense
KF963257_Ganoderma martinicense
1.0/78
0.94/82
JX310820_Ganoderma parvulum
1.0/100
JX310822_Ganoderma parvulum
1.0/98
KP0129641_Ganoderma steyaertanum
EU239388_Ganoderma aff steyaertanum
KJ792745_Ganoderma perzonatum
JX310823_Ganoderma multiplicatum
1.0/99
KJ792747_Ganoderma perzonatum
0.97/72
KJ143907_Ganoderma lingzhi
0.91/-
JN197284_Ganoderma sichuanense
JF915404_Ganoderma sichuanense
1.0/95
KC311371_Ganoderma lucidum
JQ781870_Ganoderma lingzhi
1.0/94
JQ781848_Ganoderma curtisii
JQ520191_Ganoderma meredithae
0.8/92
JQ520190_Ganoderma meredithae
JQ520164_Ganoderma curtisii
1.0/93
FJ655476_Ganoderma fornicatum
1.0/100
FJ655471_Ganoderma fornicatum
JQ781880_Ganoderma tropicum
JQ781879_Ganoderma tropicum
FJ392281_Ganoderma pseudoferreum
AJ608710_Ganoderma philippii
1.0/97
0.93/-
FJ392284_Ganoderma pseudoferreum
AJ536662_Ganoderma philippii
1.0/100
KF963255_Ganoderma tuberculosum
0.91/-
KF963258_Ganoderma tuberculosum
1.0/100
JN383979_Ganoderma flexipes
JQ781850_Ganoderma flexipes
JX310812_Ganoderma chalceum
0.98/73
JQ781876_Ganoderma oregonense
JQ781875_Ganoderma oregonense
KJ143920_Ganoderma tsugae
KM39627_Ganoderma leucocontextum
AY884175_Ganoderma carnosum
JN222419_Ganoderma carnosum
1.0/96
KJ143910_Ganoderma lucidum
JQ781853_Ganoderma tsugae
KJ143911_Ganoderma lucidum
-/98
DQ425005_Ganoderma subamboinense
B
0.91/83
DQ425006_Ganoderma subamboinense
KC884264_Ganoderma stipitatum
KM507324_Ganoderma austroafricanum
GU726934_Ganoderma weberianum
0.95/62
1.0/93
GU726935_Ganoderma weberianum
1.0/100
JX195203_Ganoderma hoehnelianum
JN383980_Ganoderma hoehnelianum
0.97/80
JN105704_Ganoderma weberianum
1.0/100
JN105703_Ganoderma weberianum
1.0/82
1.0/100
FJ491988_Ganoderma weberianum
FJ491986_Ganoderma weberianum
JQ520203_Ganoderma resinaceum
1.0/100
JQ520204_Ganoderma_resinaceum

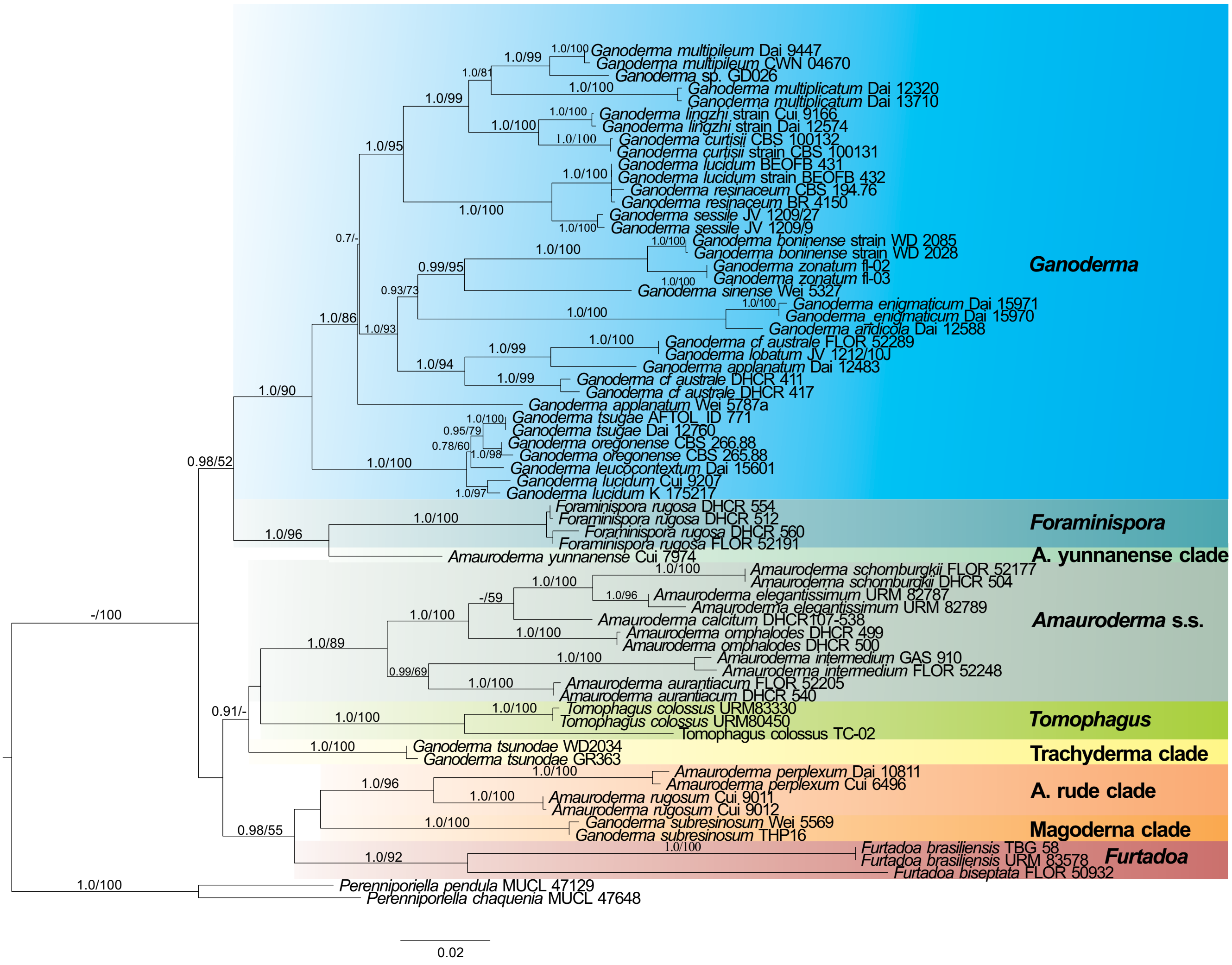


Fig. 2 Maximum likelihood (ML) tree of *Ganodermataceae* based on concatenated ITS, LSU, RPB1, TEF-1α sequence data. Bayesian posterior probability above 0.7 and Bootstrap values above 50 % are shown.

Haddowia and *Humphreya* also present species with pale context and double-walled spores with endosporic ornamentation; however, the ornamentation is formed by ridges. *Tomophagus* mainly differs from *Foraminispora* by its laccate and soft pileus and truncate basidiospores (Murrill 1905, Steyaert 1972, Ryvarden 2004, Tham et al. 2011). Since only *Foraminispora rugosa* is known to bear this feature, its whitish context and the vivid orange pore surface seem to be remarkable features of this genus in its current circumscription.

Foraminispora rugosa (Berk.) Costa-Rezende, Drechsler-Santos & Robledo, *comb. nov.* — MycoBank MB819019; Fig. 3

= *Polyporus dubiopansus* Lloyd, Lloyd Myco. Writ. 3: 125. 1921.

≡ *Porothelium rugosum* Berk., Hooker's J. Bot. Kew Gard. Misc. 8: 237. 1856.

≡ *Ganoderma sprucei* Pat., Bull. Soc. Mycol. France 10: 75. 1894.

≡ *Amauroderma sprucei* (Pat.) Torrend, Brotéria, Sér. Bot. 18: 121. 1920

≡ *Amauroderma dubiopansum* (Lloyd) Ryvarden, Neotropical Polypores, Syn. Fungorum 19: 52. 2004.

Description — Decock & Herrera-Figueroa (2006) as *Amauroderma sprucei*.

Specimens examined. Brazil, Amazonas, Panure, Spruce 44, isotype herb. BPI 237203; Mato Grosso, Chapada dos Guimarães, Parque Nacional da Chapada dos Guimarães, Sítio Vale do Rio Claro, 7 Jan. 2013, *D.H. Costa-Rezende* 113, FLOR52191; ibid., 7 Jan. 2013, *D.H. Costa-Rezende* 114, FLOR 52184; ibid., 7 Jan. 2013, *D.H. Costa-Rezende* 115, FLOR 52192; ibid., 12 Jan. 2014, *L. Pereira-Silva* 21, FLOR52190; ibid., 12 Jan. 2014, *L. Pereira-Silva* 22, FLOR 52189; ibid., 12 Jan. 2014, *L. Pereira-Silva* 58, FLOR52186; ibid., 12 Jan. 2014, *L. Pereira-Silva* 77, FLOR52187; ibid., 12 Jan. 2014, *L. Pereira-Silva* 79, FLOR52185. – Argentina, Jujuy, Depto Ledesma, Parque Nacional Calilegua, Abra de Cañas, S23°40'38.2" O64°53'46.3", alt. 1730 m above sea level, 21 May 2007, *Robledo* 1507, CORD.

Notes — The dull concentric zonate pilear surface, the whitish context, the ochraceous to vivid orange pore surface, the small pores (5–7(–8) pores/mm), a crust with a short trichoderm in the pilear surface, the strongly dextrinoid skeletal hyphae and the predominantly subglobose basidiospores ((7–)8–10 × 7–9 µm), with conspicuous hollow columnar ornamentation are characteristic of this species. The species was described with a di-trimitic hyphal system, with generative and vegetative hyphae in all portions of basidioma, and the trama of tubes as dimitic with arboriform skeletal hyphae (Decock & Herrera-Figueroa 2006). In our observations, the hyphal system is considered dimitic. In the context, we have observed clamped generative hyphae, intercalary skeleto-biding hyphae, with long lateral and apical, thin branches, and skeletal hyphae (up to 7 µm diam), tortuous, with few apical ramifications. The trama of the tubes is composed of clamped generative, arboriform skeletals, and thick-walled skeleto-binding hyphae, formed by a main stalk and very short lateral branches, with or without two thin apical branches.

When *Porothelium rugosum* was combined in *Ganoderma* the epithet 'rugosum' was already occupied by *Ganoderma rugosum*, then the *nome novum Ganoderma sprucei* was proposed.

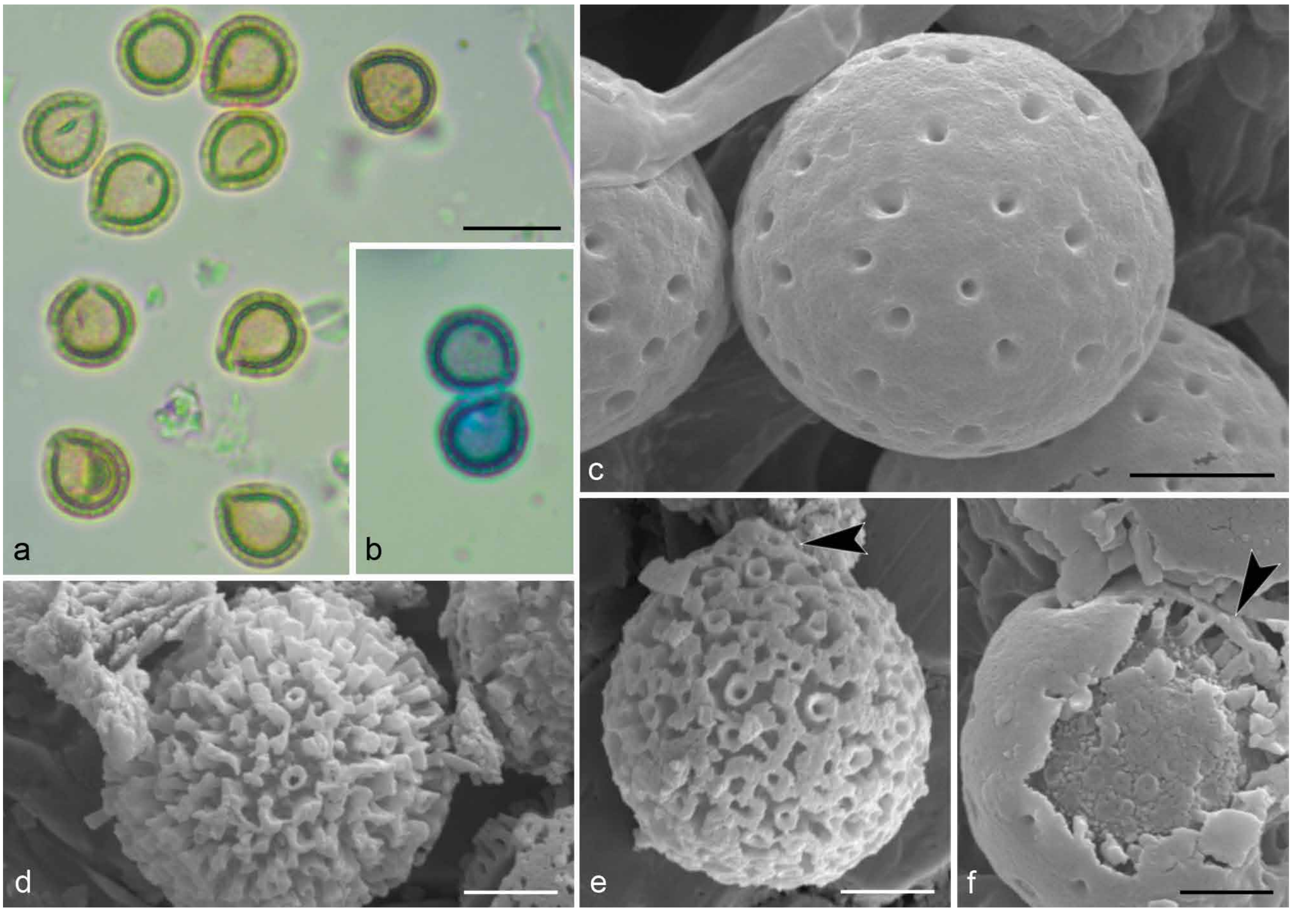


Fig. 3 Basidiospores of *Foraminispora rugosa*. a–b. Optical microscopy (KOH and Cotton blue, respectively). — c–f. SEM micrographs. c. General view showing holes in exospore; d. general view of endospore showing hollow columns; e–f. detail in connection between the hollow columns and exospore holes. — Scale bars: a–b = 10 μm; c = 2 μm; d–f = 1 μm.

The same happened when Torrend combined *P. rugosum* in *Amauroderma*, because the epithet 'rugosum' was occupied as well (*Amauroderma rugosum*). Torrend therefore continued to use 'sprucei', the earliest epithet available in *Amauroderma*. Considering the combination of *Porothelium rugosum* in *Foraminispora* the epithet is available.

Furtadoa Costa-Rezende, Robledo & Drechsler-Santos, *gen. nov.* — MycoBank MB819014

Etymology. Named in honour of Dr. João Salvador Furtado, due to his contribution to the taxonomy of *Ganodermataceae*.

Typification. *Furtadoa biseptata* gen. & sp. nov.

Diagnosis — Similar to *Amauroderma*, differing by presenting a monomitic context.

Basidiomata annual, stipe pleuropodal to pseudomesopodal, soft when fresh, light and fragile when dried, pileus circular to almost flabelliform or funnel-shaped. *Pilear surface* dull, glabrous, greyish brown, azonate. *Context* white to pale brown, homogenous. *Tubes* slightly darker than context. *Pore surface* pale brown. Pores angular, sometimes radially elongated. Dissepiments thin, entire to lacerate. *Stipe* yellowish brown, finely tomentose, solid to hollow, context homogeneous, pale brown. *Hyphal system* dimitic. Context composed of clamped to simple-septate generative hyphae, thin to slightly thick-walled, some distinctly wider, with a swollen apex. Trama of tubes composed of clamped generative and arboriform skeletal hyphae. Cystidia and cystidioles not seen. *Basidia* clavate, with four sterigmata. *Basidiospores* subglobose to ellipsoid, hyaline, double walled, with ornamentation as endosporic projections column-like, IKI-.

Ecology & Distribution — Specimens growing on the ground or on decayed angiosperm wood from Brazil, Guyana and Venezuela (Ryvarden 2004, Coelho et al. 2007, Gomes-Silva et al. 2015, as *Amauroderma brasiliense*).

Notes — This new genus is characterized by a stipitate basidiomata, soft when fresh, dull pilear surface, pale context, a dimitic hyphal system, with a monomitic context, composed of both clamped and simple-septate generative hyphae (Fig. 5), thin to slightly thick-walled and dimitic trama of tubes, composed of clamped generative hyphae and arboriform skeletal hyphae and double-walled, ornamented basidiospores.

Considering the double-walled basidiospores with the inner layer ornamented, the genus fits into *Ganodermataceae* circumscription. Both macro- and microscopic features of *Furtadoa* are shared with the genus *Amauroderma*, i.e., stipitate and annual basidiomata, presence of arboriform skeletal hyphae in the trama of tubes and double-walled, non-truncate basidiospores (Furtado 1962, 1981, Ryvarden & Johansen 1980, Corner 1983, Ryvarden 2004). However, the monomitic context with simple-septate generative hyphae is exclusive of this new genus in the context of the family. Regarding the other accepted genera in *Ganodermataceae*, besides the difference in the hyphal system, *Ganoderma*, *Humphreya* and *Tomophagus* have truncate basidiospores, and *Haddowia* has basidiospores with mainly longitudinal ridges (Steyaert 1972, Ryvarden 2004, Tham et al. 2012).

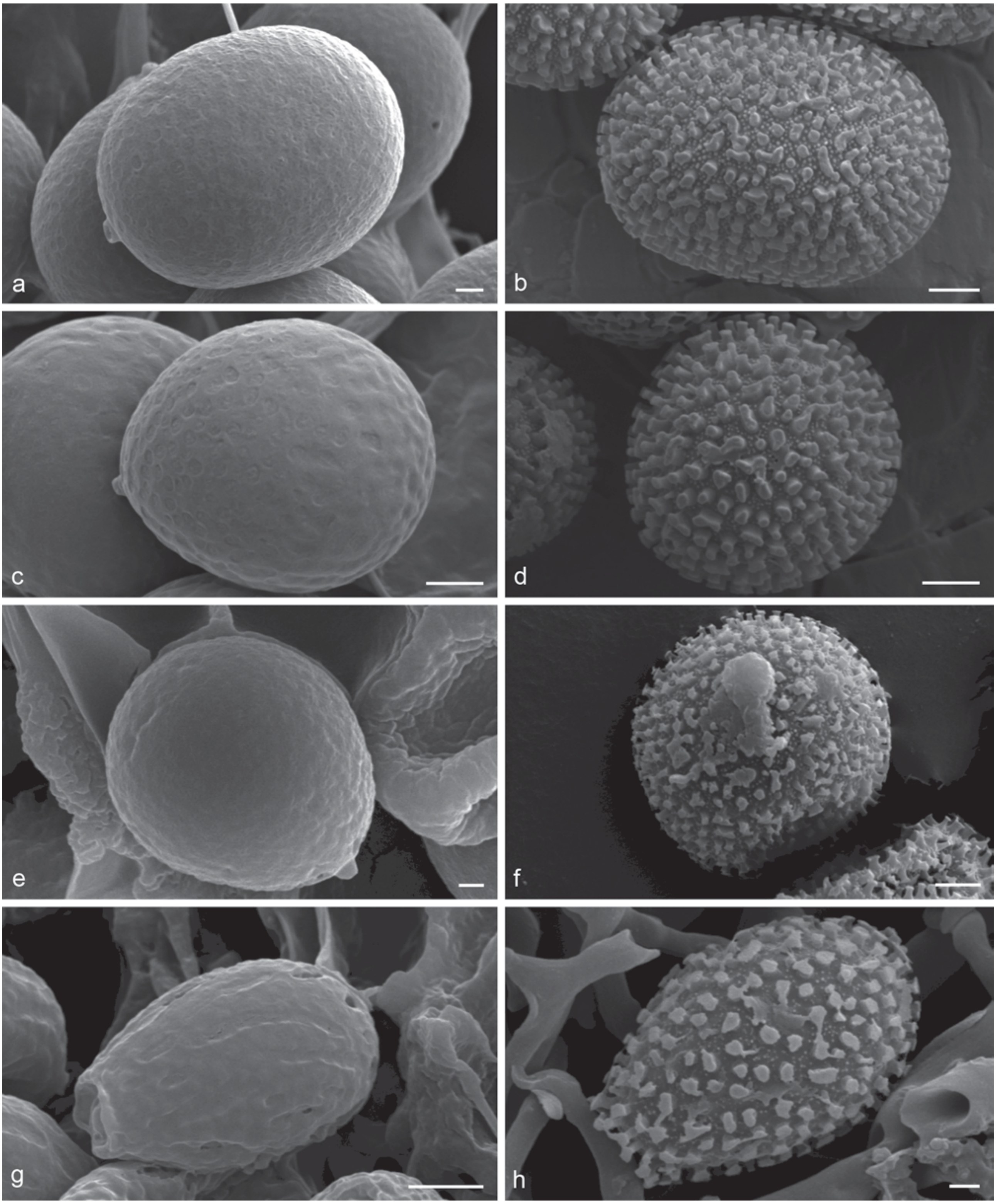


Fig. 4 Scanning Electron Micrograph of basidiospores of *Amauroderma* s.str. and *Ganoderma*. — a–b. *Amauroderma calcigenum* (CORD *Robledo* 394). a. General view showing exospore without holes; b. general view of endospore showing solid columns and smaller secondary ornamentation. — c–d. *Amauroderma pseudoboletus* (CORD *Robledo* 1441). c. General view showing exospore without holes; d. general view of endospore showing solid columns and smaller secondary ornamentation. — e–f. *Amauroderma schomburgkii* (CORD *Robledo* 909). e. General view showing exospore without holes; f. general view of endospore showing solid columns and smaller secondary ornamentation. — g–h. *Ganoderma australe* (CORD *Robledo* 3181). g. General view showing exospore without holes; h. general view of endospore showing solid columns and smaller secondary ornamentation. — Scale bars: a, c, e, h = 1 μm; b, d, f = 2 μm; g = 3 μm.

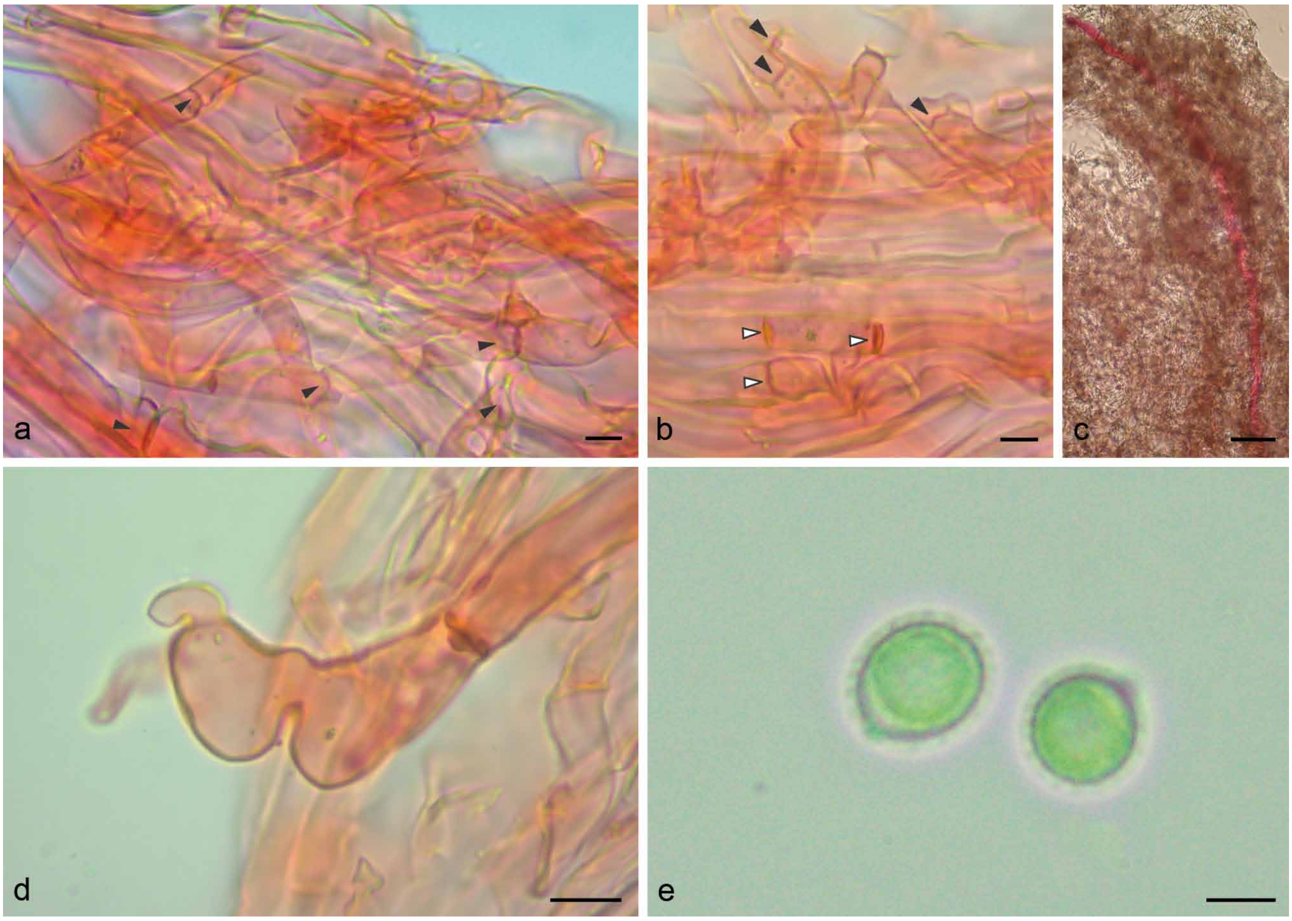


Fig. 5 Micromorphology of *Furtadoa biseptata*. a–b. General view of monomitic hyphal system from context. a. Arrows indicates clamp connections; b. black arrows indicate clamp connections, white arrows indicate simple septate hyphae; c. general view of gloeoporus-like hyphae from context; d. detail in gloeoporus-like hyphae from context; e. basidiospores. — Scale bars: a–b, e = 5 µm; c = 50 µm; d = 10 µm.

Furtadoa biseptata Costa-Rezende, Drechsler-Santos & Reck, *sp. nov.* — MycoBank MB819016; Fig. 5

Etymology. The species epithet refers to the two different septa in the generative hyphae that compose the context of the species.

Type. Brazil, Mato Grosso, Chapada dos Guimarães, Parque Nacional da Chapada dos Guimarães, Sítio Véu da Noiva, on the ground, 26 Mar. 2013, *D.H. Costa-Rezende* 128, holotype herb. FLOR50932.

Diagnosis — This species differs from *F. brasiliensis* by its thinner basidiomata, darker context, and the presence of simple-septate generative hyphae in the context.

Basidiomata stipitate, pleuropodal, single; *pileus* 25–45 mm diam, up to 10 mm thick, almost flattened to slightly convex, soft when fresh, corky when dry; margin incurved and irregular, becoming strongly involute upon dried. *Pilear surface* greyish brown, azonate, radially finely strigose, wrinkled at the center, glabrous. *Context* corky, pale brown, homogeneous, 0.3–5 mm thick, thinner near the margin. *Tubes* slightly darker than context, up to 3 mm long. *Pore surface* concolorous to context; *pores* circular, 3–5(–6) per mm, (200–)250–400 µm diam, (mean = 358.2 µm); dissepiment entire, 90–230 µm thick, (mean = 155.9 µm). *Stipe* solid to hollow, straight to tortuous, up to 50 mm long and 5 mm diam; surface velutinous, longitudinally corrugated, pale brown; context with the same consistency and concolorous with pilear context. Pilear surface composed of generative hyphae, 4–7 µm diam, thin to slightly thick-walled, parallel to the contextual hyphae. *Hyphal system* mono-dimitic; context composed of two kinds of generative hyphae: one clamped to occasionally simple-septate, 3–7 µm diam, hyaline, thin to slightly thick-walled, straight to tortuous, branched; the second gloeopleurous-like, rarely simple-septate, with long stretches without septa (up to 1600 µm), 10–15 µm diam, hyaline, thin to slightly thick-walled, straight to tortuous, mostly unbranched, but eventually presenting some lateral short prolongations; trama of tubes composed of clamped generative hyphae, 3–5 µm diam, hyaline, thin walled; and arboriform skeletal hyphae with few apical, 4.5–6 µm diam in main stalk. *Basidia* subglobose to clavate, 4-sterigmate, 12–15 × 8–10 µm. *Basidiospores* subglobose to ellipsoid, ((6–)7–10 × (5.5–)6–8(–9) µm), (mean = 7.6 × 6.5 µm), Q = 1.07–1.33 (1.36), (mean-Q = 1.18), hyaline, double-walled with the inner layer finely and regular ornamented, verrucose under SEM, IKI-.

Notes — *Furtadoa biseptata* presents macro- and micromorphology that resembles *Furtadoa brasiliensis*, mainly differing by a thinner and darker pileus and by the presence of simple septa (Fig. 5). *Furtadoa corneri* differs from the new species by the funnel-shaped basidiomata and the thinner pileus, as well as by slightly larger basidiospores (8–10 × 6–8(–9) µm, mean = 8.2 × 7.4). *Furtadoa biseptata* was collected just once, even with several field expeditions across four years in the type locality, suggesting it to be a rare species.

Furtadoa brasiliensis (Singer) Costa-Rezende, Drechsler-Santos & Robledo, *comb. nov.* — MycoBank MB819017

≡ *Scutiger brasiliensis* Singer, Nova Hedwigia, Beih. 77: 22, 1983.
≡ *Amauroderma brasiliense* (Singer) Ryvarden, Syn. Fungorum 19: 44, 2004 'as *A. brasilensis*'.

Description — Singer et al. (1983) 22, 'as *Scutiger brasiliensis*'.

Notes — Since *Scutiger brasiliense* was proposed, some different interpretations in its morphology have been raised. *Scutiger brasiliense* was described based on a specimen from Brazilian Amazonia and a specimen from Santa Catarina collected by Rick (Singer et al. 1983), with stipitate basidiomata with a white and soft-flesh context, monomitic hyphal system and inamyloid and ellipsoid to almost subglobose spores (7–9.3 × 6.3–8 µm) as the diagnostic characters. *Amauroderma corneri* was proposed fifteen years later to accommodate another monomitic species with *Amauroderma*-like basidiospores, based on a specimen from Atlantic Rain Forest in Brazil (Gulaid & Ryvarden 1998). However, the species was later considered under synonymy of *A. brasiliense* (Ryvarden 2004, Coelho et al. 2007, Gomes-Silva et al. 2015). In accordance with the morphological differences reported, i.e., *A. corneri* has a thin and funnel- to fan-shaped pileus, whitish when fresh, turning orange to brown when dried and *A. brasiliense* presents a thick and permanently pale basidiomata (Gomes-Silva et al. 2015), we preferred to maintain both taxa as independent species.

Furtadoa corneri (Gulaid & Ryvarden) Robledo & Costa-Rezende, *comb nov.* — MycoBank MB819018

≡ *Amauroderma corneri* Gulaid & Ryvarden, Mycol. Helv. 10 (1): 28. 1998.

Description — Gulaid & Ryvarden (1998) 28, as '*A. corneri*'.

Specimen examined. Brazil, São Paulo, Reg. Santos, Cananeia, Ilha do Cardoso, *L. Ryvarden* 24745, holotype herb. SP 213543.

Notes — *Furtadoa corneri* is characterized by a thin, funnel- to fan-shaped pileus, monomitic context and subglobose to ellipsoid basidiospores (8–10 × 6–8(–9) µm, mean = 8.2 × 7.4), IKI-.

DISCUSSION

Furtadoa, Foraminispora and Amauroderma s.str. within Ganodermataceae

In this work, we presented a molecular phylogenetic overview of the *Ganodermataceae* based on analyses with a wide dataset composed of the majority of the phylogenetic species with ITS sequences available in GenBank (NCBI) and a multiloci dataset (ITS+LSU+*RPB1*+TEF-1α) with a narrower sampling. These analyses, combined with morphological analyses evidenced new ultrastructural characters that enable a better understanding of the generic delimitation in the family. Our results agree with the polyphyletic status of *Amauroderma* previously proposed with morphological and phylogenetic approaches (Steyaert 1972, Gomes-Silva et al. 2015, Costa-Rezende et al. 2016).

A detailed examination of the morphology of some neotropical 'deviating' specimens of *Amauroderma*, previously determined as *A. brasiliense* and *A. sprucei* led us to observe some remarkable morphological features. Our phylogenetic analyses showed that those specimens grouped on different separated lineages, distinct from *Amauroderma* s.str., and, thus, two new genera are proposed to accommodate those species, as well as a new species is proposed. *Furtadoa* is proposed to accommodate 3 monomitic species (*F. biseptata*, *F. brasiliensis* and *F. corneri*) while *Foraminispora* was proposed to accommodate *A. sprucei.* The monomitic context of *F. biseptata* (Fig. 5), *F. brasiliensis* and *F. corneri* may represent a synapomorphy of *Furtadoa*. As *A. trichodermatum* also has a monomitic context, future studies will probably point out that this species should be better placed in *Furtadoa,* as already suggested by Robledo et al. (2015), who speculated that *A. trichodermatum* and *A. brasiliense* could be related. *Furtadoa* appears as not closely related to *Amauroderma* s.str. in both analyses (Fig. 1–2). *Furtadoa brasiliensis* and *F. biseptata* (both as *A. brasiliense*) appeared in a distinct lineage from *Amauroderma* s.str. in previous studies carried out by Gomes-Silva et al. (2015) and Costa-Rezende et al. (2016), supporting our proposition. Furthermore, hyphal system structure has been considered as a character to support the proposition of new genera among Agaricomycetes, especially polypores, such as in *Perenniporiella*, Yuchengia, *Sanghuangporus*, *Tropicoporus* and *Phellinotus* (Decock & Ryvarden 2003, Robledo et al. 2009, Zhao et al. 2013, Zhou et al. 2015, Drechsler-Santos et al. 2016).

The new species (*F. biseptata*) appears in a long branch in the retrieved phylogenetic trees, clustered as the sister clade of *F. brasiliensis*, which represents that there is a high genetic divergence between the taxa, in spite of their morphological similarity.

Foraminispora has a unique morphological feature among *Ganodermataceae*, the hollowed columnar endosporic projections of basidiospores, which is continuous until the exospore wall (Fig. 3). The ontogeny of endosporic ornamentation in *Ganodermataceae* is currently unexplored but it should be investigated in order to contribute to the taxa delimitation, as already observed in other polypore fungi, such as in *Perenniporia* s.lat. (Decock & Ryvarden 2003). Based both in nrITS and combined phylogenies, *Fo. rugosa* is not related to the Amauroderma s.str. clade (Fig. 1–2), as observed by Costa-Rezende et al. (2016, as *A. sprucei*), corroborating the proposition of the new genus. In both phylogenetic analyses *Foraminispora* clustered as a sister group of 'Amauroderma yunannense' clade, which is composed only of *A. yunnanense*. This species also presents a homogeneous whitish to pale yellow context, similarly to *Fo. rugosa* (Li & Yuan 2015). Future studies based on basidiospores ultrastructure may point out that *A. yunnanense* should be placed in *Foraminispora*. Despite presenting basidiospores which are subglobose and not truncate, *Foraminispora* is more related to *Ganoderma* (Fig. 2; 0.98 BPP, 52 % BS) than to *Amauroderma.*

The genus *Amauroderma*, as usually morphologically circumscribed, comprises sessile to stipitate polypores with globose to ellipsoid basidiospores, without a truncate apex, double-walled basidiospores with the inner layer ornamented (rarely smooth, as in *A. coltricioides*), associated with fallen dead wood or roots of living or dead trees, with a tropical and subtropical distribution (Ryvarden 2004). Besides *Furtadoa, Foraminispora* and 'Amauroderma yunannense' clade, species usually included in *Amauroderma* clustered in two unrelated clades in both analysis (Fig. 1–2). One of them is *Amauroderma* s.str., a taxon comprising neotropical species, which shares a sessile to stipitate basidiomata with a di-trimitic hyphal system, composed of clamped generative hyphae, arboriform to skeleto-binding hyphae (both in context and tubes) and non-truncated, double walled spores with solid columnar to semi-reticulate endosporic ornamentation. The second is the 'Amauroderma rude' clade, which is composed of species occurring outside the neotropical region (*A. perplexum*, *A. rude*, *A. rugosum*) and clustered in a distinct lineage from *Amauroderma* s.str., as also observed by Costa-Rezende et al. (2016). Further studies are needed to clarify the taxonomic status of this group since supposedly there are no morphological differences between these species and those of *Amauroderma* s.str.

Comments on Ganoderma, Tomophagus and unresolved taxa

Tomophagus was proposed to accommodate *Polyporus colossus* due to its light weight basidiomata and thick, soft spongy context, differing from *Ganoderma*. The genus was recovered as monophyletic both in the nrITS and combined analysis in the present study, as also observed in earlier studies (Moncalvo et al. 1995, Hong & Jung 2004, Tham et al. 2012, De Lima Júnior et al. 2014). Our results sustain the independency of *Tomophagus* against its synonymy under *Ganoderma*.

The Trachyderma clade is composed only of *G. tsunodae*, which is the type of *Trachyderma*, a genus that was mainly characterized by a fleshy succulent context when growing, differing from *Ganoderma* (Imazeki 1939, 1952). Unfortunately, according to the International Code of Nomenclature for algae, fungi, and plants the name *Trachyderma* is not valid since the name was first given to a lichenized Ascomycota. Therefore, further studies are needed to point out if the taxon is congeneric to *Tomophagus*, or represent a genus that should be properly proposed.

Except for *G. coffeatum*, *G. ramosissimum G. subresinosum* and *G. tsunodae* (treated above), all the *Ganoderma* species clustered in an homogeneous clade (Fig. 1–2) mainly characterized by presenting a coriaceous to wood basidiomata and truncate spores with column-like endosporic projections (Fig. 4g–h), which in future studies could be attributed to *Ganoderma* s.str. The recovered topologies (Fig. 1–2) does not corroborate the distinction between the genera *Ganoderma* and *Elfvingia*, even at subgeneric level (*G.* subg. *Ganoderma* and *G.* subg. *Elfvingia*) since none of these groups with dull and laccate species, respectively, were monophyletic, contrary to previous results, in which the laccate and the dull species appeared as two distinct clades (Moncalvo et al. 1995, Hong & Jung 2004).

Ganoderma subresinosum (Magoderna clade) was recovered in our topologies in a distinct lineage from *Amauroderma* s.str. and *Ganoderma*, as also observed by Gomes-Silva et al. (2015, as *A. subresinosum*) and Costa-Rezende et al. (2016, as *A. subresinosum*). Steyaert (1972) proposed the genera *Haddowia*, *Humphreya* and *Magoderna*, the last one typified by *M. subresinosus*, and contains two other species (*M. infundibuliforme* and *M. vansteenisii*), and was proposed to accommodate species with dimidiate to pleuropodal basidiomata, anticlinal hyphae (hymenioderm) in the pilear surface and ovoid-ellipsoid to spherical basidiospores without a truncate apex. Although the genus has been considered as synonym of *Amauroderma* (Furtado 1981) or *Ganoderma* (http://www.indexfungorum.org/names/Names.asp), according to our topology and the morphological circumscription of Steyaert (1972), *Magoderna* might be accepted at generic level.

Steyaert (1972) proposed the genus *Humphreya* to accommodate *A. lloidii*, *P. coffeatus* and *H. endertii* due to their hyphal disposition (peri- or pantoclinal) and basidiospore ornamentation (reticulate or disjointed cristae). Decock & Herrera-Figueroa (2007) reported that *G. coffeatum* has typical basidiospores with endosporic ornamentation as predominantly longitudinal ridges and with a known distribution in South and Central America. These authors refuted Steyaert's combination since the vicinity of *G. coffeatum* and *H. lloydii* is uncertain. In our work, *G. coffeatum* clustered in an independent clade from the typical *Ganoderma* species (Fig. 1). In this way, the Steyaert's concept of *Humphreya* may represent a genus independent of *Ganoderma*, but, since we have no other sequences from *Humphreya*, we consider that its position at genus level is still uncertain.

ANNOTATED KEY TO GENERA, PHYLOGENETIC CLADES AND GROUPS OF GANODERMATACEAE

This key includes accepted genera in the strict sense and phylogenetic groups as defined in the multigene phylogenetic analyses of this work. Species not included in our analysis that does not fits with any of the defined groups of the key are included in s.lat. genera concepts.

1. Endosporium with simple ornamentation, composed of single columns, occasionally 2–3 columns fused forming short isolated crests 2
1. Endosporium with complex ornamentation, longitudinal or transversal crests, or a reticulated pattern. 11

2. Basidiospores truncate 3
2. Basidiospores non truncate 5

3. Vegetative hyphae brown to pale brown, context hard and fibrous, dark brown, brown to pale brown . . *Ganoderma*[1]
3. Vegetative hyphae hyaline to pale yellowish, context soft, white, creamy white, to very pale brown 4

4. Chlamydospores scattered in the context and trama, globose, reddish brown in KOH, basidiospores > 20 µm long . . . . *Tomophagus*[2]
4. Chlamydospores absent, basidiospores < 20 µm long . . . . Trachyderma clade[3]

5. Hyphal system monomitic 6
5. Hyphal system dimitic brown, dark to pale 7

6. Pilear surface glabrous . . . . *Furtadoa*[4]
6. Pilear surface hirsute strigose . . . . *Amauroderma trichodermatum*[5]

7. Context whitish, spores subglobose 8
7. Context brown to pale, vegetative hyphae brown to pale, IKI-, spores subglobose to ellipsoid or ovoid 9

8. Vegetative hyphae hyaline and dextrinoid *Foraminispora*[6]
8. Vegetative hyphae pale yellow, IKI- . . . . Amauroderma yunnanense clade[7]

9. Neotropical species . . . . *Amauroderma* s.str.[8]
9. Paleotropical species. 10

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[1] *Ganoderma* includes traditional dull and shiny complexes/groups: *Ganoderma australe*/*aplanatum* complex, *Ganoderma lucidum* complex, *Ganoderma resinaceum* complex and others.

[2] *Tomophagus* is so far represented by 2 species: *T. collosus*, the type species, and *T. catienensis*. *Tomophagus collosus* was suggested to be congeneric with *G. tsunodae* (Hattori & Ryvarden 1994). Although our analyses suggest a relationship between these species, whether the taxa are congeneric or not remains unclear.

[3] Trachyderma clade is so far represented by *Ganoderma tsunodae*. Imazeki (1939, 1952) proposed *Trachyderma* as a new genus for this species. However, the generic name is illegitimate as a homonym of *Trachyderma* Norm. 1853 as pointed out by Ryvarden (1991).

[4] *Furtadoa* is distinct from *Amauroderma* s.str. by presenting a monomitic hyphal system in context and a dimitic trama of tubes.

[5] *Amauroderma* s.lat. species. The hyphal system structure and the pale colour of the context suggest a relationship with *Furtadoa* (Robledo et al. 2015).

[6] *Foraminispora rugosa* is so far the only representative of *Foraminispora*, being characterized by a whitish context, dextrinoid vegetative hyphae and subglobose spores with conspicuous ornamentation as endosporic projections column-like, some of them with a hole, that persists up to the exospore.

[7] *Amauroderma* s.lat. species. According to our phylogenetic analyses this species is related to *Foraminisporus* and further ultrastructural examination of basidiospores could prove that the taxa belongs to this genus.

[8] *Amauroderma* s.str. is typified by *A. schomburkii* and as defined phylogenetically is so far restricted to the neotropical region. Morphologically the genus is characterized by stipitate basidiomata with a di-trimitic hyphal system, composed of clamped generative hyphae, arboriform to skeleto-binding hyphae (both in context and tubes) and non-truncated, globose to ellipsoid spores with solid columnar to semi-reticulate endosporic ornamentation. The sessile species of *Amauroderma* were not included in phylogenetic analyses so far, so the inclusion of them in *Amauroderma* s.str. remains uncertain.

10. Basidiomata with whitish context and laccate pilear surface, basidiospores ovoid . . . . Magoderna clade[9]
10. Basidiomata with pale brown context and upper surface dull, basidiospores typically ellipsoid to subglobose or globose . . . . Amauroderma rude clade[10]
11. Endosporium with double longitudinal crests, partly connected by short transverse walls . . . . *Haddowia*
11. Endosporium with crests or ridges ordered in a reticulated, longitudinal, transversal or 'honey-comb' pattern ornamentation 12
12. Basidiospore truncate . . . . *Humphreya*[11]
12. Basidiospore not truncate . . . . *Amauroderma deviatum*[12]

Acknowledgements The authors acknowledge the staff of the Parque Nacional da Chapada dos Guimarães for support in the field expeditions; Luciana Pereira-Silva for specimen collections; herbaria mentioned for the loan of reference material; Connie Baak for advising in the final manuscript editing; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing PhD and PDSE scholarships to DHCR; Fiocruz and LAMOL for performing the molecular sequencing; PPGBot UEFS, PPGFAP and BrBOL for partial financing of the research. GR acknowledges the assistance of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Universidad Nacional de Córdoba for the support facilities used in this work. Financial support was provided by FONCYT (PICT-2015-0830) to G. Robledo. Authors kindly acknowledge Idea Wild for their support with technical equipment; and L. Caeiro (CPA CONICET-UNC) and D. Franchi for their technical support. This study is part of the project Fungos poliporóides (Agaricomycetes) do PARNA Chapada dos Guimarães, Mato Grosso – Políporos PNCG-MT.

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[9] *Magoderna* is composed by *M. subresinosus* (type), *M. infundibuliforme* and *M. vansteenisii*, and was proposed to accommodate species with dimidiate to pleuropodal basidiomata, anticlinal hyphae (hymenioderm) in the pilear surface and ovoid-ellipsoid to globose basidiospores without a truncate apex (Steyaert 1972).

[10] *Amauroderma* s.lat. species. *Amauroderma perplexum*, *A. rude* and *A. rugosum* presents typical morphology of *Amauroderma* s.str.; however, they are restricted to Paleotropics (Furtado 1981, Corner 1983). Further morphological and phylogenetic studies might corroborate the clade as a new genus.

[11] *Humphreya* was proposed by Steyaert (1972) to accommodate species bearing basidiospores with reticulate, honey-comb or cristulate endosporium. Our results showed *G. coffeatum* as an independent clade, i.e., Ganoderma coffeatum clade**.** The relationship of *H. coffeatum* (and *G. flaviporum*, a species recently recovered from synonym of *H. coffeatum*) with *Humphreya* is uncertain, as previously suggested by Decock & Herrera-Figueroa (2007).

[12] *Amauroderma* s.lat. species. *Amauroderma deviatum* presents broadly ellipsoid up to subglobose or slightly ovoid spores, with well-marked endosporic ridges,reticulated forming a 'honey-comb' pattern and secondary, lower ridges forming an irregularly reticulate pattern (Decock & Herrera-Figueroa 2007).

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