INTRODUCTION

Ganodermataceae is mainly characterized by pileate basidiomata, sessile to stipitate, hyphal system dimorphic, with arboriform and skeleton-binding hyphae and double-walled basidiospores with a coloured endosporium ornamented with columns and 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). Furtado et al. propose to accommodate species with monomorphic context: F. biseptata, F. brasiliensis and F. calvata. Molecular phylogenetic analyses confirm that both genera grouped as strongly supported distinct lineages out of the Amauroderma s.str. clade.

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In this current classification into five genera, several taxa are considered ‘deviating elements’ either by their microscopic characters (basidiospore shape and ornamentation or hyphal system), macroscopic 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. brasiliensis (Robledo et al. 2015), as well as species with basidiospores with reticulate endosporium (A. deviatum) (Ryvarden 2004).
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/). Microscopical 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 exospor 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$_2$CrO$_4$) crystal, covered by enough water 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.

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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 LRS. 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$^6$th 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 GTR+GAMMA 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/phylo/phyllows/study/TB2:S20193).
Table 1  Species, vouchers and accession numbers of the specimens used in phylogenetic analyses.

| Species name          | Voucher          | ITS     | LSU     | RPB1   | TEF-1α  |
|-----------------------|------------------|---------|---------|--------|---------|
| Amauroderma aurantiacum | FLOR52205        | KR816510| KU315205| –      | –       |
|                       | DHCR504 (HUEFS)  | MF409961| MF409953| MF436687| –       |
|                       | URM78847         | JX310840| –       | –      | –       |
| A. calcigenum          | FLOR52315        | KR816514| –       | –      | –       |
| A. calcitum            | FLOR50931/DHCR538 (HUEFS) | KR816528| KU315207| MF436690| –       |
|                       | FLOR52230        | KR816529| –       | –      | –       |
| A. elegansissum        | URM82769         | JX310844| KT006617| –      | –       |
|                       | URM82787         | JX310843| KT006616| –      | –       |
| A. exile               | URM82794         | JX310845| –       | –      | –       |
| A. florentinum          | URM83250         | JX310846| –       | –      | –       |
| A. intermedium         | GASS910 (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           | CJU6496          | KJ531650| KU220001| –      | –       |
|                       | WEI5662          | KJ531652| –       | –      | –       |
|                       | DAI01081         | KJ531651| KU220002| –      | –       |
| A. aff. praetervisum   | FLOR52249        | KR816511| –       | –      | –       |
| A. praetervisum        | REC18707         | JX310855| –       | –      | –       |
|                       | URM84230         | KC348461| –       | –      | –       |
|                       | GOMES SILVA 909  | JX310856| –       | –      | –       |
| A. pseudoboletum       | FLOR52318        | KR816516| –       | –      | –       |
|                       | CANB643174       | KJ315197| –       | –      | –       |
|                       | CANB597582       | KJ315198| –       | –      | –       |
|                       | CANB359451       | KJ315199| –       | –      | –       |
| A. rugosum             | CJU9012          | KJ531665| KU220011| –      | KU572503|
|                       | ZHOU547          | KJ531675| –       | –      | –       |
|                       | CIIU501          | KJ531664| KU220010| –      | KU572504|
| A. schomburgii         | DHCR504 (HUEFS)  | MF409958| –       | MF436684| –       |
|                       | FLOR52177        | KR816522| KU315215| –      | –       |
|                       | URM83226         | JX310848| –       | –      | –       |
| A. sp.                 | INPA249751       | KR816525| –       | –      | –       |
| A. subraesinosum       | WEI5669          | KJ315649| –       | –      | –       |
|                       | TPH48            | FJ154784| –       | –      | –       |
|                       | TPH16            | FJ154782| –       | –      | –       |
| A. yunnanense          | CJU7974          | KJ531653| KU220013| –      | –       |
|                       | DAI3021          | KJ531654| –       | –      | –       |
|                       | YUAN2253         | KJ531655| –       | –      | –       |
| Furtadoa brasiliensis  | URM83578         | JX310841| –       | –      | –       |
|                       | TKG58            | JX682569| –       | –      | –       |
| F. biezeta             | FLOR50932        | KU315196| KU315206| –      | –       |
| Foraminisporus spucei  | FLOR52191        | KU315200| KU315216| –      | –       |
|                       | FLOR52184        | KU315201| –       | –      | –       |
|                       | FLOR52195        | KU315202| –       | –      | –       |
|                       | DHCHR512 (HUEFS) | MF409960| MF436686| MF421240|
|                       | DHCHR505 (HUEFS) | MF409962| MF436688| MF421241|
|                       | DHCHR560 (HUEFS) | MF409963| MF436689| MF421239|
| Ganoderma adspersum    | RJ1212           | AJ006685| –       | –      | –       |
|                       | GATO00           | AM900657| –       | –      | –       |
|                       | GAD3             | JN222418| –       | –      | –       |
| G. annulare            | KCTC1803         | JQ582160| –       | –      | –       |
| G. aplanatum           | KM120830         | AY884178| –       | –      | –       |
|                       | GA185            | DG425009| –       | –      | –       |
|                       | GA117            | DG424996| –       | –      | –       |
|                       | ATCC44063        | JDG52016| –       | –      | –       |
|                       | WEI5677          | KF495001| KF495011| KF494978| –       |
|                       | Dai 12439        | KF494999| KF495009| –      | KF494977|
| G. aridicola           | DAI 12588        | KJ572491| –       | –      | KU572502|
| G. cf. australe        | DAI 12588        | KJ572491| –       | –      | KU572502|
|                       | JS51             | JN596327| –       | –      | –       |
| G. australe            | DCRH411 (HUEFS)  | MF436675| MF436672| MF436680| MF436677|
|                       | DHCHR417 (HUEFS) | MF436676| MF436673| MF436681| MF436678|
|                       | GDCM25745        | JX195805| –       | –      | –       |
| G. austrolex           | HMAS8958         | AY884180| –       | –      | –       |
|                       | GMW41454         | JM053724| –       | –      | –       |
| G. boninense           | WD2085           | KJ143906| KJ143945| KJ143925|
|                       | WD2028           | KJ143905| KJ143944| KJ143924|
| G. camnosus            | KM109415         | AY884175| –       | –      | –       |
| G. chalceum            | URM80457         | JX310812| –       | –      | –       |
| G. coffeatum           | FLOR50933        | KJ315204| –       | –      | –       |
| G. cupreum             | GANOTK7          | KJ572491| –       | –      | –       |
|                       | GANOTK4          | KJ572491| –       | –      | –       |
|                       | KRE1             | JF655470| –       | –      | –       |
|                       | KL161            | JF655466| –       | –      | –       |

Genbank accessions:
- ITS: Internal Transcribed Spacer
- LSU: Large Subunit of the Ribosomal RNA Gene
- RPB1: Ribosomal Protein B1
| Species name          | Voucher        | Genbank accession numbers |
|----------------------|----------------|---------------------------|
| **G. curtisi**       | CBS100132      | JQ520164                  |
|                      | CBS100131      | JQ728144                  |
| **G. enigmaticum**   | DAI 15970      | KU572486                  |
|                      | DAI 15971      | KU572487                  |
| **G. flexipes**      | WEIS494        | JN383979                  |
|                      | WEIS491        | JQ781850                  |
| **G. fornicatum**    | TN231          | FJ655476                  |
|                      | KL231          | FJ655471                  |
| **G. fulvellum**     | XSD08051       | FJ478088                  |
|                      | XSD034         | EU273513                  |
| **G. hoehnelianum**  | DAI12096       | JN383980                  |
|                      | DAI12574       | KJ143908                  |
|                      | DAI12426       | JQ781877                  |
|                      | CU19166        | KJ143907                  |
| **G. japonicum**     | AS5.69         | AV593864                  |
|                      | AS5.69         | AV593865                  |
| **G. leucocontextum**| DAI 15601      | KU572485                  |
|                      | DAI 15601      | KM396272                  |
| **G. lingzhi**       | DAI12574       | KJ143908                  |
|                      | DAI12426       | JQ781877                  |
|                      | CU19166        | KJ143907                  |
| **G. lipsiense**     | NORS311432     | EF060005                  |
|                      | FIN131R610     | EF060004                  |
| **G. lobatum**       | JV 1212/10J    | KF605676                  |
|                      | BEOFB 432      | KX371595                  |
|                      | BEOFB 431      | KX371594                  |
|                      | K175217        | KJ143911                  |
|                      | K175217        | KJ143950                  |
|                      | CU19207        | KJ143910                  |
| **G. lucidum**       | GL16           | HM053438                  |
|                      | GL14           | HM053436                  |
|                      | GL951          | KC311371                  |
| **G. martincense**   | LIPSW1amt0844  | KF632527                  |
|                      | LIPSW1amt0855  | KF632526                  |
| **G. mastoporum**    | AS17140        | JQ520119                  |
|                      | ATCC64492      | JQ520190                  |
| **G. multipleum**    | DAI8447        | KJ143914                  |
|                      | DAI8447        | KF494997                  |
| **G. multiplicatum** | DAI12320       | KU572490                  |
|                      | DAI13710       | KU572499                  |
| **G. orbinforme**    | URM83334       | JX310823                  |
| **G. oregonense**    | CBS268.88      | JQ781876                  |
|                      | CBS265.88      | JQ781875                  |
| **G. parvulum**      | URM83346       | JX310823                  |
| **G. perzonatum**    | SP445965       | KJ792745                  |
|                      | SP4459671      | KJ792747                  |
| **G. pfeifferi**     | KM120819       | AY984185                  |
| **G. philippi**      | E7098          | AJ536662.2                |
|                      | E7092          | AJ536671                  |
| **G. pudofermeum**   | CATASGp008     | FJ392284                  |
|                      | CATASGp005     | FJ392289                  |
| **G. ramosissimum**  | XSD08032       | EU918700                  |
|                      | XSD08085       | FJ478127                  |
| **G. resinaceum**    | CBS 194.76     | X78737/X78758              |
|                      | IUM3651        | JQ520204                  |
|                      | AS17143        | JQ520203                  |
| **G. sessile**       | JV1209/9       | KF605629                  |
|                      | JV1209/27      | KF605630                  |
| **G. sicuhanense**   | GC2MC35333     | JN197284                  |
|                      | HM31301281     | JF915404                  |
| **G. sinense**       | XZGC1          | HQ235633                  |
|                      | GDGM25829      | KC415760                  |
|                      | WEIS491        | KJ792284                  |
| **G. sp.**           | PALCOSTBP10    | KJ792084                  |
|                      | PALCOSTBP09    | KJ792083                  |
|                      | GD026 (HUEFS)  | MF436674                  |
| **G. aff. steyaertanum** | C17274        | EU239388                  |
| **G. steyaertanum**  | MEL182783      | KF50008                   |
| **G. stipitatum**    | THC16          | KG824264                  |
| **G. subamboinense** | GSUB1371       | KG425006                  |
|                      | GSUB1361       | KG425005                  |
### Table 1 (cont.)

| Species name       | Voucher | Genbank accession numbers |
|--------------------|---------|---------------------------|
| G. tornatum        | URM82776| JQ514110 – – – |
|                    | TBG01AM2009| – – – |
| G. tropicum        | YUAN3490| JQ514108 – – – |
|                    | DA19724| JQ781880 – – – |
|                    | DA19726| JQ781879 – – – |
| G. tsugae          | DA19397| JQ143920 – KJ143961 |
|                    | AJ2031| FJ154773 – – – |
|                    | WD2034| AB588989 AB368069 – – |
| G. tsunodae        | GR3631| KJ143922 – KJ143962 |
|                    | WD2034| KJ143921 – KJ143963 |
| G. zonatum         | FL03| JQ781879 – – – |
|                    | FL02| JN105704 – – – |
|                    | GW11| JN105703 – – – |
|                    | GW11| JN105703 – – – |
|                    | GW10| JF491989 – – – |
|                    | TN21| JF491986 – – – |
|                    | TN15| JF491986 – – – |
| Perenniporia medulla-paris | MUCL43250| JQ781853 – – – |
| Perenniporia chaquenesis | MUCL49758| – – – |
| P. pendula         | MUCL47129| – – – |
| Tomophagus cattienensis | CT119| – – – |
|                    | CT99| – – – |
| T. colossus        | TC02| – – – |
|                    | URM80450| – – – |
|                    | URM83330| – – – |

#### RESULTS

**Molecular Phylogeny**

The final ITS dataset (Fig. 1) included sequences from 157 fungal specimens, with 659 characters, of which 2415 were constant and 813 parsimony informative. The evolutionarily selected models for ITS dataset were TIM2+G (ITS1), TIM1ef+I+G (5.8S), TPM3+G (ITS2), TIM2+I+G (LSU), HKY+G (RPB1 in-trons), TRN+I (RPB1 1st codon), HK+I (2nd codon), TIM2+G (3rd codon), TIM3u+I+G (TEF-1a in-trons), GTR-I (TEF-1a 1st codon), TVM+I+G (TEF-1a 2nd codon) and TIM2+G (TEF-1a 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, 99 % BS), and this assemblage as a sister clade of *Ganoderma* (1.0 BPP, 100 % BS), which 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 endospore 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 homogenous, 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. _Basidium_ 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.
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. australis; Fig. 4g–h) and the truncate apex of basidiospores clearly distinguish this genus from Foraminispora. Ganoderma also has holes in the exosporium of some species (G. lucidum, G. pfeifferi, G. valesiacum). Nevertheless, the holes are formed among the columns (Pegler & Young 1973).
Haddowia and Humphreya also present species with pale context and double-walled spores with endospore 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, 1976). 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** (Berkl.) Costa-Rezende, Drechsler-Santos & Robledo, *comb. nov.* — MycoBank MB819019; Fig. 3

- *Polypora dubiopansus* Lloyd, Lloyd Myco, Wrt. 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, Brothér. Sér. Bot. 18: 121. 1920
- *Amauroderma dubiopansum* (Lloyd) Ryvarden, Neotropical Polyposes, Syn. Fungorum 19: 52. 2004.

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

Specimens examined. Brus.: Amazonas, Panure, Spruce 44, isotype herb. BP1 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, FLOR5207; ibid., 7 Jan. 2013, D.H. Costa-Rezende 114, FLOR52184; ibid., 7 Jan. 2013, D.H. Costa-Rezende 115, FLOR52192; ibid., 12 Jan. 2014, L. Pereira-Silva 21, FLOR52190; ibid., 12 Jan. 2014, L. Pereira-Silva 22, FLOR52189; 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, FLOR52188 — Amauroderma, 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 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 nomen novum *Ganoderma sprucei* was proposed.
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. 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.](image_url)
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 australis* (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.
**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 thin-ner 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); **dissemination** 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 1 600 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, (8–)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 MB819018

**Scutiger brasiliensis** Singer, Nova Hedwigia, Beih. 77: 22, 1983.

**Amauroderma brasiliense** (Singer) Ryvarden, Syn. Fungorum 19: 44, 2004 ‘as A. brasiliense’.

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 x 6.3–8 μm) as the diagnostic characters. **Amauroderma corneri** was proposed fifteen years later to accommodate another monomorphic 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 x 6–8(–9) μm, mean = 8.2 x 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** 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 monomorphic species (**F. biseptata**, **F. brasiliensis** and **F. corneri**) while **Foraminispora** was proposed to accommodate **A. sprucei**.

The monomictic context of **F. biseptata** (Fig. 5), **F. brasiliensis** and **F. corneri** may represent a synapomorphy of **Furtadoa**. As **A. trichodermatum** also has a monomictic 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 ontology of endospore 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, **F. 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 yunnanense**’ clade, which is composed only of **A. yunnanense**. This species also presents a homogeneous whitish to pale yellow context, similarly to **F. 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. colticioiides**), 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 yunnanense**’ 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 skeletal-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 colos-sus 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. The recovered topologies (Fig. 1–2) does not corroborate the distinction between the genera Ganoderma and Eltingiella, even at subgeneric level (G. subg. Ganoderma and G. subg. Eltingiella) since none of these groups with dull and laccate spores, 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 (Magodera 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 Haddowiella, Humphreya and Magodera, the last one typified by M. subresinosus, and contains two other species (M. infundibiliforme and M. vansteenisii), and was proposed to accommodate species with dimidiate to pleuropodal basidiomata, anticlinal hyphae (hymenioderm) in the pilear surface and ovoid-ellipsoid 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), Magodera might be accepted at generic level. Steyaert (1972) proposed the genus Humphreya to accommodate A. lloydii, P. coffeatus and H. endertii due to their hyphal disposition (peri- or pantocinal) 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.

ANOTATED KEYS 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. Endosporium with complex ornamentation, longitudinal or transversal crests, or a reticulated pattern
3. Basidiospores truncate
4. Basidiospores non truncate
5. Vegetative hyphae brown to pale brown, context hard and fibrous, dark brown, brown to pale brown ...
6. Pilear surface glabrous ...
7. Hyphal system monomitic ...
8. Hyphal system dimitic brown, dark to pale ...
9. Pilear surface hirsute strigose ...
10. Pilear surface hirsute strigose ...

1. Ganoderma includes traditional dull and shiny complexes/groups: Ganoderma australiae/planatum complex, Ganoderma lucidum complex, Ganoderma resineum complex and others.
2. Tomophagus is so far represented by 2 species: T. collosus, the type species, and T. cateniensis. Tomaphagus 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 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 Nom. 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.str. 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 subglosbe spores with conspicuous ornamentation as endosporic projections column-like, some of them with a hole, that persists up to the esporole.
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. Morhologically the genus is characterized by stipitate basidiomata with a d-trimitic hyphal system, composed of clamped generative hyphae, arboriform to skelto-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.
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1 Magoderna is composed by M. subresinosus (type), M. infundibuliforme and M. vansteenisii, and was proposed to accommodate species with dimidiate to pleuropodal basidiomata, antical l hyphe (hymenoidem) in the pilear surface and ovoid-ellipsoid to globose basidiospores without a truncate apex (Steyaert 1972).

2 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.

3 Humphrey was proposed by Steyaert (1972) to accommodate spe- cies 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 Humphrey is uncertain, as previously suggested by Decock & Herrera-Figueroa (2007).

4 Amauroderma s.lat. species. Amauroderma deviatum presents broadly ellipsoid up to subglobose or slightly ovoid spores, with well-marked en- dosporic ridges,reticulated forming a ‘honey-comb’ pattern and secondary, lower ridge forming an irregularly reticulate pattern (Decock & Herrera- Figueroa 2007).
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