Insights on The Morphological and Phylogenetic Delimitation of *Dacrymyces* Nees

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Abstract

Dacrymycetes has four families and 13 genera, few of them with molecular data available and then usually polyphyletic in phylogenetic analyses. *Dacrymyces* Nees is one of the polyphyletic genera in Dacrymycetes and it was introduced to accommodate one species, *D. stillatus* Nees. The morphological features of the genus are a homogeneous composition of the intra-structure and an amphigenous or superior hymenium. In this study, we included Neotropical specimens in the phylogeny of the Dacrymycetes and *Dacrymyces* s.s. is emended to include species with resupinate basidiomata, unilateral hymenium and heterogeneous context. In this new delimitation, the new species *Dacrymyces flavobrunneus* is described using morphological and molecular data and three new combinations (*D. ceraceus* comb. nov., *D. maxidorii* comb. nov. and *D. spathularia* comb. nov.) are proposed based on DNA analyses.

Introduction

Dacrymycetes is a class of Basidiomycota characterized by the presence of continuous parenthosomes covering the dolipore septa (Oberwinkler 1993, Wells 1994), long bifurcate basidia, except in *Unilacryma unispora* (L.S. Olive) Shirouzu, Tokum. & Oberw., and basidiospores normally septate (McNabb 1964; 1965a-e;1966; Shirouzu et al. 2013a; Oberwinkler 2014). Mostly of the species are brown-rot (Oberwinkler 1993), although white-rot was also reported (Seifert 1983).

Currently, Dacrymycetes has four families (Cerinomycetaceae, Dacrymycetaceae, Dacryonaemataceae and Unilacrymaceae), all with morphological and molecular support (Zamora and Ekamn 2020), and 13 genera [*Arrhytidia* Berk. & M.A. Curtis, *Calocera* (Fr.) Fr., *Cerinomyces* G.W. Martin, *Dacrymyces* Nees, *Dacryomitra* Tul. & C. Tul, *Dacryonaema* Nannf., *Dacryopinax* G.W. Martin, *Dacryoscyphus* R. Kirschner & Zhu L. Yang, *Ditiola* Fr., *Femsjonia* Fr., *Guepiniopsis* Pat., *Heterotextus* Lloyd, and *Unilacryma* Shirouzu, Tokum. & Oberw.] that are mainly delimited based on morphological features (Oberwinkler 2014). Four genera (*Calocera, Cerinomyces, Dacryopinax* and *Dacrymyces*) in Dacrymycetes have molecular data available and they are usually polyphyletic in the phylogenetic analyses (Shirouzu et al. 2013a; Zamora and Ekamn 2020).

Dacrymyces was introduced to accommodate one species, *D. stillatus* Nees (1816), which presented teleomorphic and anamorphic stage. The morphological features of the genus are a homogeneous composition of the intra-structure, and an amphigenous or superior hymenium (McNabb 1973). The last revision of the genus was performed by McNabb (1973) using morphological features and included 31 species in *Dacrymyces*. Currently, the genus has 131 species names in Index Fungorum, although some of these were considered invalid or synonymized by McNabb (1973).

Recently, some *Dacrymyces* species have been described using molecular and morphological data (Shirouzu et al. 2009, 2017). So far, 29 species have DNA sequences usually from ITS and nc LSU rDNA regions (Shirouzu et al. 2009, 2017; Zamora and Ekamn 2020). For example, Zamora and Ekamn (2020)

showed that the molecular, morphological, cytological and secondary compounds data produced similar phylogenies and, for some species complexes (e.g., *Calocera cornea* complex or *D. stillatus* complex), the inclusion of different approaches would be important to delimit these species.

In the Neotropics, the genus is represented by 12 species [*D. ancoratus* Lowy, *D. bambusae* Rick, *D. capitatus* Schwein., *D. ceraceoides* Rick, *D. chrysospermus* Berk. & M.A. Curtis, *D. dictyosporus* G.W. Martin, *D. enatus* (Berk. & M.A. Curtis) Massee, *D. falcatus* Brasf., *D. punctiformis* Neuhoff, *D. stillatus*, *D. subtristis* Rick, *D. variisporus* McNabb] (Lowy 1971; Sobestiansky 2005; Meijer 2006; Alvarenga and Xavier Santos 2017; Castro-Santiuste et al. 2017), although none of them was confirmed using molecular data and mostly represented by one record. Thus, the aim of the study was to expand the knowledge of *Dacrymyces* s.s. clade based on morphology features and phylogenetic inferences, to describe one new species, and to propose three new combinations.

Material And Methods

Studied area and morphological analysis

The specimens were collected during the rainy season in the Atlantic Rain Forest (Pernambuco state, Brazil) and Amazon Forest (Amazonas state, Brazil). Microscopical studies were made with preparations mounted in 3% KOH + 1% phloxine, Melzer reagent and cotton blue. Measures followed Miettinen et al. (2012). The following abbreviations were used in morphological descriptions and tables: L = mean spore length, W = mean spore width, Q' = length/width ratio, Q = mean length/width ratio, n = number of measurements per specimen. Color followed Kornerup & Wanscher (1978) and the literature used for identification was Lowy (1971, 1981), Alvarenga and Xavier Santos (2017) and Castro-Santiuste et al. (2020). The specimens are deposited in the Herbarium (URM) of the Departamento de Micologia ate the Universidade Federal de Pernambuco (UFPE) and isotypes in the Herbarium (SP-Fungi) of the Instituto de Pesquisas Ambientais do Estado de São Paulo (Thiers 2016).

DNA extraction, PCR amplification and sequencing

DNA extraction was performed with the DNeasy Plant Mini Kit (Qiagen), following the manufacturer's protocol. Polymerase chain reaction (PCR) was performed to amplify the ITS and nc 28S LSU using the primers ITS1/ITS4 (White et al. 1990; Gardes and Bruns 1993) and LR0R/LR5 (Vilgalys and Hester 1990), respectively. Polymerase chain reaction (PCR) products were purified applying the ExoSAP-IT (Thermo Fisher Scientifc). We used the same primer pairs for amplicon sequencing following the manufacturer's instructions of the BigDye Terminator Cycle Sequencing Kit v.3.1. The sequences were provided by the Plataforma Tecnológica de Genômica e Expressão Gênica do Centro de Biociências at the UFPE, Recife, Brazil.

Phylogenetic analyses

The assembly and editing of sequences were performed in Staden Package 2.0 software (Staden et al. 1998) and MEGA v. 6 (Tamura et al. 2013). Sequences were used to compare with sequences deposited in GenBank of the NCBI. Sequences obtained in this study were deposited in GenBank. For alignments, we followed Shirouzu et al. (2017) and Castro-Santiuste et al. (2020) and included the new sequences from our specimens (Table 1). Sequence alignments were constructed using the online version of MAFFT (Katoh and Toh 2008), using the Q-INS-I option with default parameters. Ambiguously regions in the alignment (e.g., large gaps) were manually removed prior to subsequent analysis.

Phylogenetic reconstructions were inferred by Maximum Likelihood (ML) and Bayesian Inference (BI). The best evolutionary model was estimated for the ITS and nc LSU rDNA datasets based on Bayesian Information Criterion (BIC) using W-IQ-TREE (Kalyaanamoorthy et al. 2017). ML analysis was performed in W-IQ-TREE (Trifinopoulos et al. 2016), using the SYM+I+G4 model, with 1000 bootstrap replicates (Nguyen et al. 2015) and Ultrafast bootstrap (UFBoot2, Hoang et al. 2017). BI analysis was performed in MrBayes v.3.1.2 (Ronquist and Huelsenbeck 2003) by using SYM+I+G as the best model for two independent runs, each with four chains and run for 10 million generations (split frequence = 0.008). The convergence of the runs was checked using TRACER v1.7.1 (Rambaut et al. 2018).

Statistical support for branches was considered informative with Bayesian posterior probabilities (pp) ≥0.95 and bootstrap (bs) and UFBoot2 (ub) values ≥70%. The trees were visualized with FigTree (Rambaut 2014) and the final layout made in Inkscape 2020.

Results

Phylogenetic reconstruction was based on the alignment of the ITS+nLSU dataset (1282 characters, including gaps) of 141 sequences representing eight genera belonging to Dacrymycetes. ML and BI analyses produced trees with nearly congruent topologies and therefore only the ML tree is shown (Fig. 1). The sequences from the studied specimens were grouped within a clade with high support (bp = 98, ub=91 and pp = 0.99), which we treated as the *Dacrymyces sensu stricto* clade.

The *Dacrymyces s.s* clade comprises 18 species, including the specimens studied in the current work: the new species *D. flavobrunneus* (bp = 100, ub = 100, pp = 1) and the new combination *D. maxidorii* (bp = 98.1, ub = 100, pp = 1). In addition, sequences of materials previously identified as species of *Cerinomyces* [*C. ceraceus* Ginns, *C. lagerheimii* (Pat.) McNabb and *C. grandinioides* McNabb], as *Guepiniopsis buccina* (Pers.) L.L. Kenn. and as *Dacryopinax spathularia* (Schwein.) G.W. Martin] clustered with high support in this clade (bp = 100, ub = 100, pp = 1) and, except for the sequences identified as *C. lagerheimii*, *C. grandinioides* and *G. buccina*, were transferred to *Dacrymyces*.

Taxonomy

Dacrymyces Nees [as '*Dacryomyces*'], *emend.* Alvarenga

MycoBank: MB17455

Description: Basidiomata originating as pustules, becoming pulvinate discoid, subglobose, lobed, cerebriform turbinate, pezizoid or resupinate, often stipitate becoming spathulate to flabellate, usually attached to substratum by a point or rooting base, occasionally broadly attached. Consistency soft gelatinous to firm gelatinous. Context hetero or homogeneous, gelatinized, clamp connections absent. Cortex present or absent, when present composed of a palisade of thin or thick-walled, septate hairs, terminal cells cylindrical, subclavate, ovate, globose to sub-globose or obpyriform. Hymenium amphigenous, superior or unilateral. Basidia cylindrical-subclavate, occasionally obclavate or urniform, becoming bisterigmated. Dikaryophyses (hyphidia) present or absent. Basidiospores cylindrical, curved cylindrical, allantoid, occasionally broadly and bluntly fusiform, ovate or sub-globose, apiculate, septate at maturity. Germination by conidia and/or germ tubes.

Type species: *Dacrymyces stillatus* Nees, Syst. Pilze (Würzburg): 89 (1816) [1816-17].

Remarks: *Dacrymyces* is traditionally recognized by the homogeneous composition of the intra-structure and an amphigenous hymenium (McNabb 1973). Previously, the species with unilateral hymenium were placed in *Dacryopinax*, with a heterogeneous composition in *Ditiola*, and resupinate in *Cerionomyces* (McNabb 1964, 1965a, 1966, 1973). However, the morphological features do not agree with the phylogenetic analyses, and it cannot be used separately to recognize or distinguish the genera in Dacrymycetaceae (Shirouzu et al. 2013, 2017; Zamora and Ekamn 2020).

Based on our phylogenetic analyses (Fig. 1), species with resupinate basidiomata, heterogeneous composition of the context and unilateral hymenium are grouped in the *Dacrymyces* s.s. clade clade with high support (bp = 100, ub = 100, pp = 1). Thus, we emend the genus description to comprise species with these morphological features.

Dacrymyces flavobrunneus Alvarenga *sp. nov.*, Fig. 2

MycoBank: MB841253

Etymology: *flavobrunneus* (Lat.) = Adj. “flavus-” referring to yellow basidioma when fresh; Adj. “-brunneus” referring to brown basidioma when dry.

Holotype: BRAZIL: Rondônia, Estação Ecológica de Cuniã. Angelina Meiras-Ottoni,11 Feb. 2017, AMO789, (URM). GenBank: ITS = OK257533, LSU = OK257540.

Description: Basidiomata 3–24 mm long, pileate-stipitate, cartilaginous, orange (6A7) when fresh, yellow brown (6F7) when dry. Pileus 3–13 mm in diameter, spathulate; sterile side velutinous, with pale white to brownish hairs. Stipe up to 10 × 1–2 mm, cylindrical, central, velutinous, with greyish hairs when dry. Hymenium unilateral, smooth, glabrous. Marginal hyphae (hairs) of stipe and abhymenium hyphae (abhymenium hairs), 15 µm wide, globose to subglobose, pyriform, septate, thick-walled (4 µm), hyaline to yellowish. Context gelatinized, heterogeneous with two types of hyphae: thin-walled, 1.2 – 3.0 µm

diameter, and thick-walled, 4–5(–7) µm diameter, both branched, septate, without clamp connections. Basidia 20–27 × 3–4 µm, cylindric to clavate, becoming bifurcate when mature; sterigmata up to 7–11 µm, often collapsed after spores' liberation, hyaline, guttulate (carotenoid pigments), hyphidia absent or mixed into the hymenium. Basidiospores (7–) 9–10.3 (–11) × (2.8–) 3.2–4 (–4.2) µm, Q = 2.33–3.66, Q' = 2.89, L = 9.38, W = 3.24, ellipsoid to allantoid slight curved, aseptate to 1-septate, hyaline, guttulate, smooth.

Remarks: The new species *D. flavobrunneus* is similar to *D. maxidorii*, but it can be differentiated by the spathulate pileus, globose to subglobose hairs, heterogenous context, absence of hyphidia and smaller basidia (30–36.5 × 4.5 µm) (Lowy 1981). *Dacrymyces flavobrunneus* differs from other species in *Dacrymyces* due to the unilateral hymenium and heterogeneous context.

Distribution: This specie is known so far from the Brazilian Amazon Forest.

Material examined: Brazil: Amazonas, Presidente Figueiredo, Gruta da Judeia, Tatiana B. Gibertoni, 21 July 2019, DNA21025 (URM); Ibid, Floresta Nacional do Jamarí. Angelina Meiras-Ottoni, 06 Feb. 2016, AMO703, (URM); Ibid, 17ª Brigada de Infantaria de Selva. Angelina Meiras-Ottoni, 20 Dec. 2016, AMO721 (URM).

Dacrymyces ceraceus (Ginns) Alvarenga, comb. nov.

MycoBank: MB841254

Basionym: *Cerinomyces ceraceus* Ginns, Canadian Journal of Botany 60 (4): 519 (1982) [MB110534]

Description: Ginn (1982).

Remarks: *Dacrymyces ceraceus* can be easily recognized by the resupinate basidiomata, presence of spines on hymenophore, basidiospores 12–17 × 4.5–5(–6) µm and with 0–3 septa. The species was originally collected in the USA and the available sequences are from the holotype (Ginn 1982).

Distribution: This species is only known from the USA.

Dacrymyces maxidorii (Lowy) Alvarenga, comb. nov.

MycoBank: MB841255

Basionym: *Dacryopinax maxidorii* Lowy, Mycotaxon 13 (2): 428 (1981) [MB112260]

Description: Lowy (1981).

Remarks: *Dacrymyces maxidorii* is characterized by the presence of cylindrical hairs with globose to subglobose inflated parts forming chains in abhymenial surface (Lowy 1981). In Dacrymycetaceae, four species have inflated abhymenial hairs (*Dacryopinax indacocheae* Lowy, *Dacryopinax primogenitus* D.J. McLaughlin & E.G. McLaughlin, *Dacryopinax lowyi* S. Sierra & Cifuentes, and *Dacrymyces flavobrunneus*

Alvarenga), all with Neotropical distribution, although only *D. flavobrunneus* is, so far, phylogenetically close to this species (Fig. 1).

Dacryopinax indacocheae was described using samples from Bolivia and differs from *Dacrymyces maxidorii* due to presence of conidiophore in the basidiomata (Lowy 1959). *Dacryopinax lowyi* was described from material collected in Mexico and has larger spores (13–17 × 5.6–7.5 µm) with 3 septa when mature (Sierra & Cifuentes 2005), while *D. maxidorii* has smaller spores [(7.0–) 8–10 (–11.0) × 4.5–5 µm] and 1 septum (Lowy 1981). *Dacryopinax primogenitus* is a recently described species from Costa Rica and it was the first Dacrymycetes to have its genome sequenced. The species differs from the Brazilian's species due to the smaller pileus and few inflated cells in the abhimenial surface (Mclaughlin et al. 2016).

Distribution: This species is so far recorded only in Brazil in almost all Brazilian's biomes (Amazon Forest, Atlantic Forest and Cerrado).

Material examined: Brazil: Acre, RESEX Cazumbá-Iracema/Sena Madureira. Angelina Meiras-Ottoni, 11 April 2019, AMO1396 (URM); Pernambuco, Reserva Biológica de Pedra Talhada. Renato L. M. Alvarenga, 10 July 2017, RLMA479 (URM); Ibid, leg., 10 July 2017, RLMA480 (URM); Ibid, leg., Vitor Xavier de Lima, 14 May 2018, VXLF58 (URM); Ibid, leg., 25 June 2018, VXLF320 (URM); Ibid, leg., 06 July 2017, JPT02 (URM); Reserva Ecológica de Saltinho. Angelina Meiras-Ottoni, 15 May 2018, AMO1156 (URM); Ibid, leg., 11 April 2016, RLMA305 (URM); Ibid, leg., 11 April 2016, RLMA306 (URM); Rondônia: Parque Natural de Porto Velho. Angelina Meiras-Ottoni, 03 Jan. 2018, AMO877 (URM); Ibid, leg., 16 Jan. 2016, AMO510 (URM); Sergipe: Parque Nacional da Serra de Itabaiana. Cléverton Oliveira Mendonça 15 June 2018, DNA21031 (URM).

Dacrymyces spathularia (Schwein.) Alvarenga, comb. nov.

MycoBank: MB841256

Basionym: *Merulius spathularius* Schwein., Schriften der Naturforschenden Gesellschaftzu Leipzig 1: 92 (1822) [MB208187]

Description: Martin (1948) and McNabb (1965a).

Remarks: *Dacrymyces spathularia* differs from other *Dacrymyces* species by the pileate-stipitate basidiomata, with a spatulate to flabelliform pileus, unilateral hymenium, homogenous context, thick-walled hypha, cylindrical abhymenial hairs and basidiospores with (7)8–10.5(11.5) × 3.5–4(4.5), 0–1 septa (McNabb 1965b). The species was described using samples from the USA.

Distribution: This species is recorded in tropical and subtropical regions (GBIF 2021).

Discussion

In our study, the *Dacrymyces s.s.* clade is phylogenetically separated from the *Calocera s.s.* and *Dacryopinax s.s.* clades (bs = 98, ub = 91, pp = 0.99) as well as from other sequences of material identified as *Dacrymyces*. Usually, species in Dacrymycetes with amphigeneous or superior hymenium are placed in *Dacrymyces*; with unilateral hymenium are included in *Dacryopinax*; with coralloid basidiomata are described in *Calocera*, and resupinate species are treated in *Cerinomyces*. The tradition of using morphology to delimitate taxa continued up to recently (e.g., Shirouzu et al. 2009, 2013, 2017), including studies that used molecular data. However, evidences showed that the morphology does not agree with the phylogenetic history of the taxa (Shirouzu et al. 2013, 2017; Zamora and Ekamn 2020). Recently, Zamora and Ekamn (2020) showed similar results on the *Dacrymyces* s.s. clade, although they did not focus in this specific group.

Here, the combinations *D. ceraceus*, *D. maxidori* and *D. spathularia* are proposed based on phylogenetic data, as well as following comments of previous results (Shirouzu et al. 2013, 2017; Zamora and Ekamn, 2020). Other species clearly placed in the *Dacrymyces s.s.* clade, however, were not combined to this genus. *Cerinomyces lagerheinii* was described using samples from Ecuador, but the sequences available are from the USA. This species is reported in Brazil, Ecuador, French Polynesia, Mexico, New Zealand and Venezuela (GBIF 2021). A revision of these samples, older names, and sequencing of the type material or material from the type locality are desirable to know the truly distribution range and boundaries of the species. The sequences used to *C. grandinioides* and *G. buccina* are not either from their types materials or specimens collected in the type locality (Kenya and unknown locality in Europe, respectively), so those sequence may not represent the species (McNabb 1964, 1965b).

The *Dacrymyces s.s.* clade was phylogenetically well delimited and an emend to this genus is herein proposed to include species with resupinate basidiomata, unilateral hymenium and heterogeneous composition, following the morphological features of the new combinations and the new species. In addition, the knowledge about *Dacrymyces* richness in Brazil was updated to seven species by the addition of one new taxon and two combinations of previously described species. Therefore, the inclusion of specimens and sequences from samples collected in the Neotropics can be important to understand the morphological delimitation of *Dacrymyces*, as well as the knowledge about the Dacrymycetes diversity.

Declarations

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Conflicts of interest/Competing interests (include appropriate disclosures) – Not applicable

Ethics approval - Not applicable

Consent to participate - Not applicable

Consent for publication - Not applicable

Availability of data and material – All material is deposited in Herbarium URM. The sequences ares deposited in GenBank. Data will be available online after the acceptance of the manuscript in http://www.splink.org.br/ and https://www.ncbi.nlm.nih.gov/genbank/.

Code availability - Not applicable

Authors' contributions - All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Renato Lúcio Mendes Alvarenga. The manuscript was written by all authors. All authors read and approved the final manuscript. Tatiana B. Gibertoni provided funds and supervised this research.

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Table

Due to technical limitations, table xlsx is only available as a download in the Supplemental Files section.

Figures

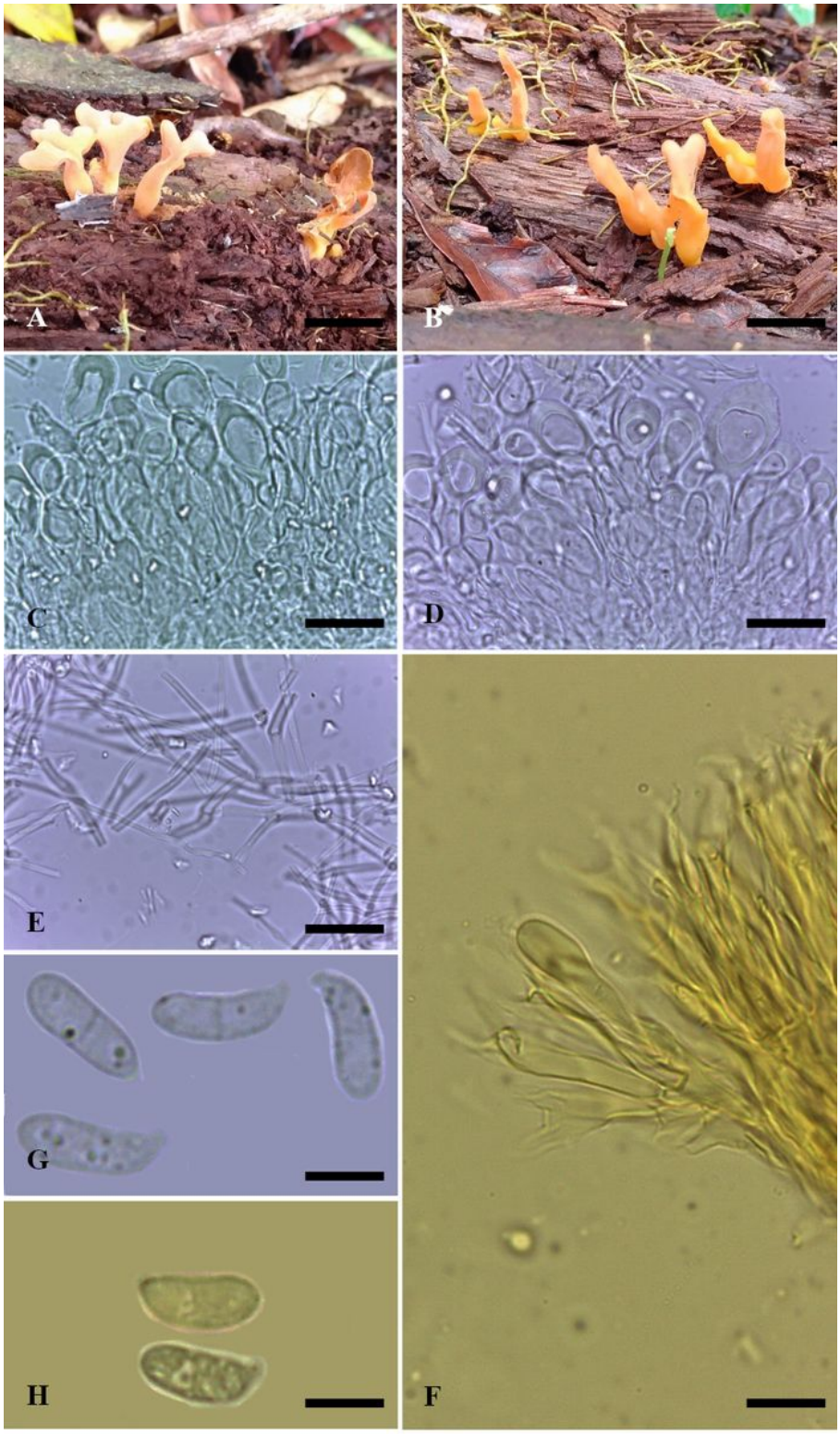

Figure 1

Phylogenetic reconstruction of sequences of Dacrymycetes specimens inferred from a combined dataset of ITS and nLSU. Branches are labeled with ML bootstrap and UFBoot2 equal to or higher than 70%, and BI posterior probabilities equal to or higher than 0.95 respectively. The sequences in bold were generated in this study. The tree was rooted with Corpinus comatus (ALFTOL626) and Suillus pictus (AFTOL717) following Shirouzu et al. (2017).

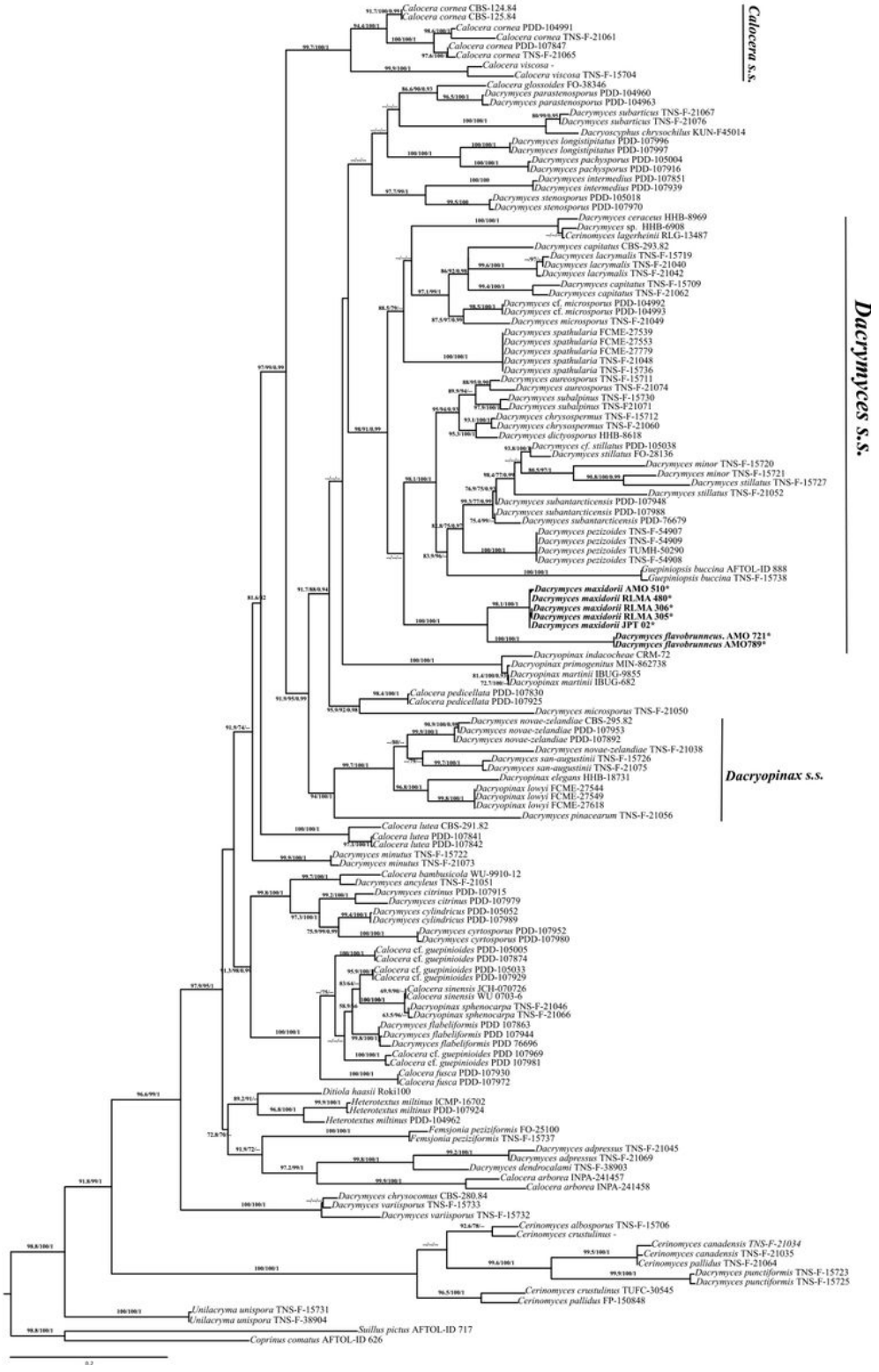

Figure 2

Dacrymyces flavobrunneus Alvarenga sp. nov. a-b. Fresh specimens (AMO789, URM XXXX); c-d. Abhymenium hairs; e. Heterogeneous context (hypha); f. Hymenium; g-h. Basidiospores (g – in water, h – in Melzer's Solucion. Bars: a, b = 1 cm; c,d,e,f = 10 µm; g,h = 5 µm

Supplementary Files

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- Table1.xlsx