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Two New Species of *Dacrymyces* (*Dacrymycetales*, *Basidiomycota*) from Southwestern China

Ya-Ping Lian [1,2], Ablat Tohtirjap [1] and Fang Wu [1,*]

[1] Institute of Microbiology, School of Ecology and Nature Conservation, Beijing Forestry University, Beijing 100083, China; ayqmher@163.com (Y.-P.L.); ablat31@bjfu.edu.cn (A.T.)
[2] College of Forestry, Beijing Forestry University, Beijing 100083, China
* Correspondence: fangwubjfu2014@bjfu.edu.cn

Abstract: Two new species of *Dacrymyces*, *D. cerebriformis* and *D. sinostenosporus*, are presented from southwestern China, based on morphological characteristics and phylogenetic analyses. *Dacrymyces cerebriformis* is characterized by obviously cerebriform basidiomata when mature, hyphae without clamp connections, and hyaline, thin-walled, allantoid, 0–7-septate basidiospores (18.4–23.1 × 5.5–7.7 µm). *Dacrymyces sinostenosporus* is characterized by discoid and applanate basidiomata when mature, hyphae without clamp connections, and hyaline, thin-walled, cylindrical to allantoid, 0–7-septate basidiospores (18.0–23.5 × 6.3–8.0 µm). *Dacrymyces cerebriformis* can be distinguished from *D. sinostenosporus* by the narrower thin- or thick-walled terminal cells in the marginal hyphae of the sterile surface (1.7–3.5 µm vs. 3.5–6.0 µm in diameter) and thinner basidiospores (Q = 3.14–3.28 vs. Q = 2.63–2.77). A phylogenetic analysis of *Dacrymyces* is performed by using a dataset composed of concatenated internal transcribed spacer regions (ITS) and a large subunit (nrLSU) of ribosomal DNA gene, and two new species nested in two distinct lineages with robust support. A full description and illustrations of the two new species are provided here.

Keywords: *Dacrymycetaceae*; morphology; phylogeny; taxonomy

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1. Introduction

Dacrymyces Nees was established to accommodate a single species, *D. stillatus* Nees, which is characterized by sessile, pustulate to pulvinate, yellowish, gelatinous basidiomata when fresh, hyphae without clamp connections, bifurcate basidia, and septate basidiospores [1]. Plenty dacrymycetous fungi with bifurcate basidia and septate basidiospores have been found, some related to genera including *Ditiola* Fr., *Femsjonia* Fr., *Cerinomyces* (G.W. Martin), and *Dacryopinax* (G.W. Martin et al.), having been established and recognized [2–9]. Some new species were described in *Dacrymyces*, and its generic limit became broader [10–13]. Nowadays, a total of 114 *Dacrymyces* taxa has been accepted according to Index Fungorum, and they have been found to be widely distributed around the world, mostly in Europe, America, Asia, and Oceania [10–18]. Species in the genus usually inhabit dead trees, stumps, fallen trunks, or branches of angiosperms or gymnosperms, and play a key role in the wood decomposition process, causing a brown rot [14,17].

In addition, species of *Dacrymyces*, in the present sense of the genus, have diverse basidiomata, and several species with clamped hyphae have been described in the genus [14–18]. In the phylogenetic analysis, *Dacrymyces* was suggested to belong to a polyphyletic group through sequence analyses of the D1/D2 domains of the large subunit (nrLSU) of ribosomal DNA gene [19]. Most species in *Dacrymyces* are found nested in *Dacrymycetaceae*, and a few species nest in *Cerinomycetaceae* or form a separate clade in Dacrymycetes [14,19]. Those species that nest out of *Dacrymycetaceae* transfer to *Cerinomyces* or *Unilacryma* (Shirouzu et al. [15,18]). However, *Dacrymyces* is still of polyphyletic origin, scattering in *Dacrymycetaceae* in the phylogeny, and no phenotypic features can be used to classify

Dacrymyces and its related genera [14,16,18,19]. Therefore, the genus is still ambiguous in taxonomy and phylogeny.

In the present study, five specimens with typical characteristics of *Dacrymyces* are collected from Yunnan province in southwestern China, which is rich in gelatinous wood-decaying fungi [20,21]. In the phylogenetic analyses of *Dacrymyces,* using a dataset composed of concatenated ITS and nrLSU genes, the sequences of four specimens collected by us form two distinct lineages with strong support. Although another specimen's, Dai 19805, DNA sequence extractions failed, the five specimens were identified as two new species, viz. *D. cerebriformis* and *D. sinostenosporus,* based on their morphological characteristics and a phylogenetic analysis. The aim of this article is to provide detailed information on the phylogenetic position and morphological characteristics of the two new species.

2. Materials and Methods

2.1. Sample Collection

Samples of dacrymycetous fungi were collected from coniferous, deciduous broad-leaved, and evergreen broad-leaved forests in subtropical Yunnan province, southwestern China. When sampling, basidiomata were collected together with the substrate. When possible, the corresponding tree species to the substrate were identified in the forests. Collected samples were dried by a mushroom dryer at a temperature of approximately 35 °C, and the dry samples were placed in an envelope and transported to the laboratory.

2.2. Morphological Studies

A morphological description was performed following work by Shirouzu et al. [15]. Macro-morphological characteristics were observed and described based on the field-collected fresh specimens and photos, and the color names followed Petersen's [22] work. Micro-morphological characteristics were obtained from dried specimens. Hand-cut sections were rehydrated with 5% KOH and stained with 2% Phloxine B ($C_{20}H_2Br_4C_{l4}Na_2O_5$) reagent. Microscopic structures, such as basidia, basidiospores, and hyphae, were observed and photographed by the Nikon Eclipse 80i microscope (magnifications $\times \leq 1000$) with a Nikon Digital Sight DS-Fi2 camera. The following abbreviations were used: L—mean length; W—mean width; Q—L/W ratio for the given specimen; *n* (a/b)— number of spores (a) measured from given number of specimens (b). The specimens were deposited in the herbarium of Beijing Forestry University (BJFC).

2.3. DNA Extraction, Polymerase Chain Reaction, and Sequencing

Total genomic DNA were extracted from the dried specimens using the CTAB rapid plant genome extraction kit (Aidlab Biotechnologies Co. Ltd, Beijing, China). The DNA sequence data were obtained from two regions. The internal transcribed spacer regions (ITS) were amplified with primer pairs ITS5/ITS4 [23], and the primer pairs LR0R/LR7 were used to amplify the large subunit of nuclear ribosomal DNA gene (nrLSU) [24].

Polymerase chain reaction (PCR) was performed using S1000™ Thermal Cycler (Bio-Rad Laboratories, Hercules, CA, USA). PCR was performed in Eppendorf tubes containing 30 μL of reaction mixture with the following composition: 1 μL extracted DNA, 12 μL ddH_2O, 15 μL 2 × EasyTaq PCR Supermix (TransGen Biotech Co., Ltd., Beijing, China), and 1 μL of each primer. The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles of 94 °C for 40 s, 54 °C for 45 s, and 72 °C for 1 min, with a final extension at 72 °C for 10 min. The PCR procedure for nrLSU was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles of 94 °C for 1 min, 50 °C for 1 min, and 72 °C for 1 min, and a final extension at 72 °C for 10 min. The PCR products were purified and sequenced in Beijing Genomics Institute, China, with the same primers.

2.4. Sequence Alignment and Phylogenetic Analysis

The sequences obtained from this study and downloaded from GenBank are listed in Table 1. Sequences were aligned with the MAFFT version 7 web tool (http://mafft.cbrc.jp/alignment/server/, accessed on 10 March 2022) using the Q-INS-i option for ITS and nrLSU. *Coprinus comatus* (O.F. Müll.) Pers. and *Suillus pictus* (Peck) Kuntze were used as the outgroups following work by Shirouzu et al. [15]. The combined ITS and nrLSU alignment contained 1588 characters (including gaps). Sequence alignment was deposited at TreeBase (http://purl.org/phylo/treebase, accessed on 14 March 2022; submission ID 29541).

Table 1. Taxa information and GenBank accession numbers of the sequences used in this study.

Species	Locality	Sample No.	GenBank Accession No.	
			ITS	nrLSU
Calocera arborea	Brazil	INPA 241458	AB744230	AB723514
Calocera cornea	Canada	CBS124.84	AB712437	AB472738
Calocera fusca	New Zealand	PDD 107930	LC131405	LC131364
Calocera guepinioides	New Zealand	PDD 107969	LC131411	LC131370
Calocera lutea	New Zealand	PDD 107841	LC131413	LC131372
Calocera pedicellata	New Zealand	PDD 107830	LC131415	LC131374
Calocera viscosa (Type species)	Japan	AFTOL-ID 1679	DQ520102	DQ520102
Cerinomyces albosporus	Japan	TUFC12991	AB712440	AB299050
Cerinomyces canadensis	Japan	TUFC12876	AB712441	AB472696
Cerinomyces crustulinus	Canada	TUFC 30545	AB712443	AB712423
Cerinomyces pallidus (Type species)	Belize	FP-150848	AB712446	AB712426
Dacrymyces adpressus	Japan	TUFC12845	AB712447	AB472707
Dacrymyces ancyleus	Japan	MAFF241177	AB712448	AB472713
Dacrymyces capitatus	Canada	CBS293.82	AB712450	AB472741
Dacrymyces ceraceus	USA	HHB-8969	AB712442	AB712422
Dacrymyces cerebriformis	**China**	**Dai 19826**	**OM955201**	**OM955196**
Dacrymyces cerebriformis	**China**	**Dai 19832**	**OM955202**	**OM955197**
Dacrymyces chiangraiensis	Thailand	MFLU:16-0572	KY498587	–
Dacrymyces chrysocomus	Spain	UPS F-940136	MN595629	MN595629
Dacrymyces chrysospermus	Japan	TUFC 13115	AB712452	AB299073
Dacrymyces cylindricus	New Zealand	PDD 105052	LC131419	LC131378
Dacrymyces cyrtosporus	New Zealand	PDD 107952	LC131421	LC131380
Dacrymyces dendrocalami	Japan	TUFC13914	AB712453	AB712428
Dacrymyces dictyosporus	USA	HHB-8618	AB712454	AB712429
Dacrymyces estonicus	Sweden	UPS F-940137	MN595632	MN595632
Dacrymyces flabelliformis	New Zealand	HHB-18308	AB712455	AB712430
Dacrymyces intermedius	New Zealand	PDD 107939	–	LC131385
Dacrymyces intermedius	New Zealand	PDD 107851	–	LC131384
Dacrymyces invisibilis	Chile	14617MD	MH230101	MH230103
Dacrymyces lacrymalis	Japan	TUFC13327	AB712456	AB299069
Dacrymyces lagerheimii	USA	RLG-13487	AB712445	AB712425
Dacrymyces longistipitatus	New Zealand	PDD 107996	LC131425	LC131386
Dacrymyces microsporus	Japan	TUFC 13032	AB712457	AB472712
Dacrymyces minor	Japan	TUFC 12836	AB712458	AB299063
Dacrymyces novae-zelandiae	New Zealand	PDD 107892	LC131427	LC131390
Dacrymyces ovisporus	Sweden	UPS F-940139	MN595635	MN595635
Dacrymyces pachysporus	New Zealand	PDD 105004	LC131429	LC131392
Dacrymyces parastenosporus	New Zealand	PDD 104960	LC131431	LC131394
Dacrymyces pezizoides	Japan	TNS-F-54909	LC386890	LC386894
Dacrymyces pinacearum	Japan	UPS F-593533	MN595637	MN595637
Dacrymyces puniceus	Japan	TUFC 12833	AB712449	AB299057
Dacrymyces san-augustinii	Japan	MAFF240141	AB712463	AB299081
Dacrymyces sinostenosporus	**China**	**Dai 20003**	**MW540888**	**MW540890**
Dacrymyces sinostenosporus	**China**	**Dai 20008**	**MW540889**	**MW540891**
Dacrymyces stenosporus	New Zealand	PDD 105018	LC131433	LC131396
Dacrymyces stenosporus	New Zealand	PDD 107970	LC131434	LC131397

Table 1. *Cont.*

Species	Locality	Sample No.	GenBank Accession No.	
			ITS	nrLSU
Dacrymyces stillatus (Type species)	Sweden	UPS F-939814	MN595677	MN595677
Dacrymyces subalpinus	Japan	TUFC 12834	AB712465	AB299060
Dacrymyces subantarcticensis	New Zealand	PDD 107988	LC131436	LC131400
Dacrymyces subarcticus	Japan	TNS-F-21067	AB712467	AB472727
Dacryomitra pusilla (Type species)	Sweden	UPS F-176774	MN595639	MN595639
Dacryonaema macnabbii	Sweden	UPS F-940949	MN595650	MN595650
Dacryonaema macrosporum	Finland	UPS F-940998	MN595660	MN595660
Dacryonaema rufum (Type species)	Sweden	UPS F-941003	MN595645	MN595645
Dacryopinax elegans (Type species)	USA	HHB-18731	AB712471	AB712433
Dacryopinax indacocheae	Venezuela	CRM-72	AB712472	AB712434
Dacryopinax spathularia	Japan	AFTOL-ID 454	AY854070	AY701525
Dacryoscyphus chrysochilus (Type species)	China	KUN F45014	–	AY604567
Ditiola radicata (Type species)	Sweden	UPS F-939957	MN595641	MN595641
Femsjonia peziziformis	Finland	H Haikonen 30097	MN595642	MN595642
Femsjonia uniseptata	Japan	TNS-F-54019	LC222844	LC222843
Guepiniopsis buccina	Spain	UPS F-940947	MN595643	MN595643
Heterotextus miltinus	New Zealand	TENN 42208	MN595644	MN595644
Unilacryma bispora	Sweden	UPS F-941254	MN595673	MN595673
Unilacryma unispora (Type species)	Sweden	UPS F-941277	MN595665	MN593500
Coprinus comatus	USA	AFTOL-ID 626	AY854066	AY635772
Suillus pictus	USA	AFTOL-ID 717	AY854069	AY684154

Note: newly generated sequences for this study are in bold.

Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian inference (BI) methods based on the combined ITS and nLSU dataset. All characters were equally weighted and gaps were treated as missing data. The optimal substitution model suitable for the combined dataset was determined using the AIC (Akaike information criterion) implemented in MrModeltest 2.3 [25]. The model GTR + I + G was selected for the combined ITS and nLSU dataset. RAxMLGUI 1.2 was used for ML analysis [26,27]. All parameters in the ML analysis used default settings. Statistical support values were obtained using non-parametric bootstrapping with 1000 replicates. The BI analysis was conducted using MrBayes 3.2.5 [28]. Two independent runs were performed, each starting from random trees with four chains for five million generations. Trees were sampled every 1000 generations. The first quarter of sampled trees was discarded as burn-ins, and the remaining trees were used to construct a 50% majority consensus tree and calculate BPP (Bayesian posterior probabilities). A majority rule tree consensus of all remaining trees was calculated. Branches were considered as significantly supported if they received bootstrap support (BS) for ML analysis and Bayesian posterior probabilities (BPP) greater than or equal to 75% (BS) and 0.90 (BPP).

3. Results

3.1. Phylogenetic Results

Sixty-seven fungal sequences that represented 63 species were included in the combined ITS and nrLSU dataset to construct the phylogenetic tree. The newly generated sequences of four Chinese specimens were included in the combined ITS and nrLSU dataset, because extracting DNA from specimen Dai 19805 failed. The BI analysis resulted in a similar topology as the ML analysis; thus, only the BI tree was presented (Figure 1). The phylogeny (Figure 1) demonstrated that samples of 35 *Dacrymyces* species were gathered into *Dacrymycetaceae*. The four specimens representing two new species, *Dacrymyces cerebriformis* and *D. sinostenosporus*, belonged to two distinct lineages with robust supports (100% BS, 1.00 BPP; 100% BS, 1.00 BPP) in *Dacrymycetaceae*. *Dacrymyces sinostenosporus* was found to be closely related to *D. stenosporus* with high support (100% BS, 1.00 BPP).

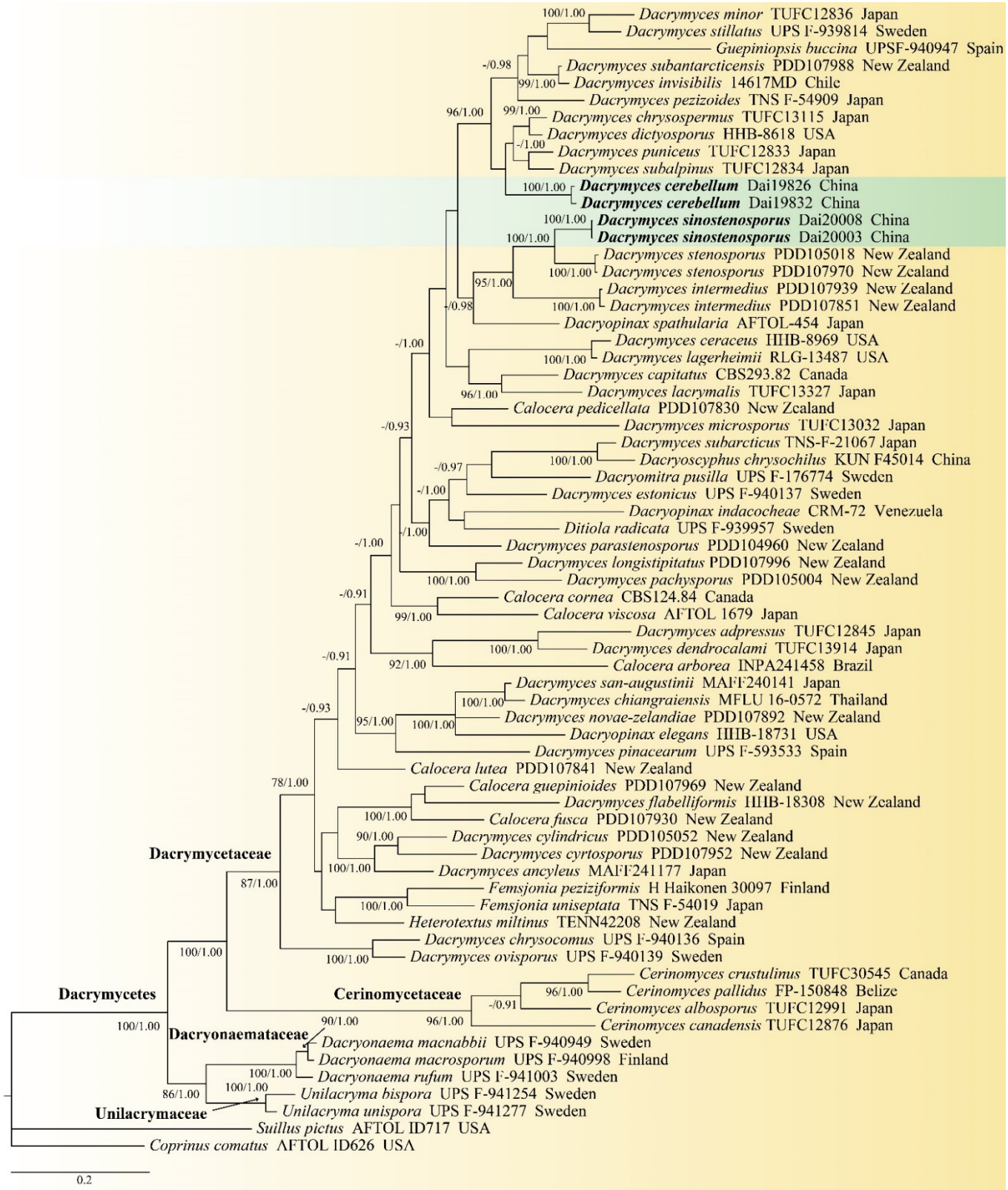

Figure 1. Phylogeny of *Dacrymyces* and related species generated by BI analysis based on the combined ITS and nrLSU dataset. Bootstrap support values for ML $\geq$ 75% and BI $\geq$ 0.90 were given near nodes, respectively. Two new species are in bold. Note: "-" means bootstrap without robust support (BS < 75%, BPP < 0.90); the arrows pointed the nodes.

3.2. Taxonomy

Dacrymyces cerebriformis F. Wu and Y.P. Lian sp. nov. Figure 2.

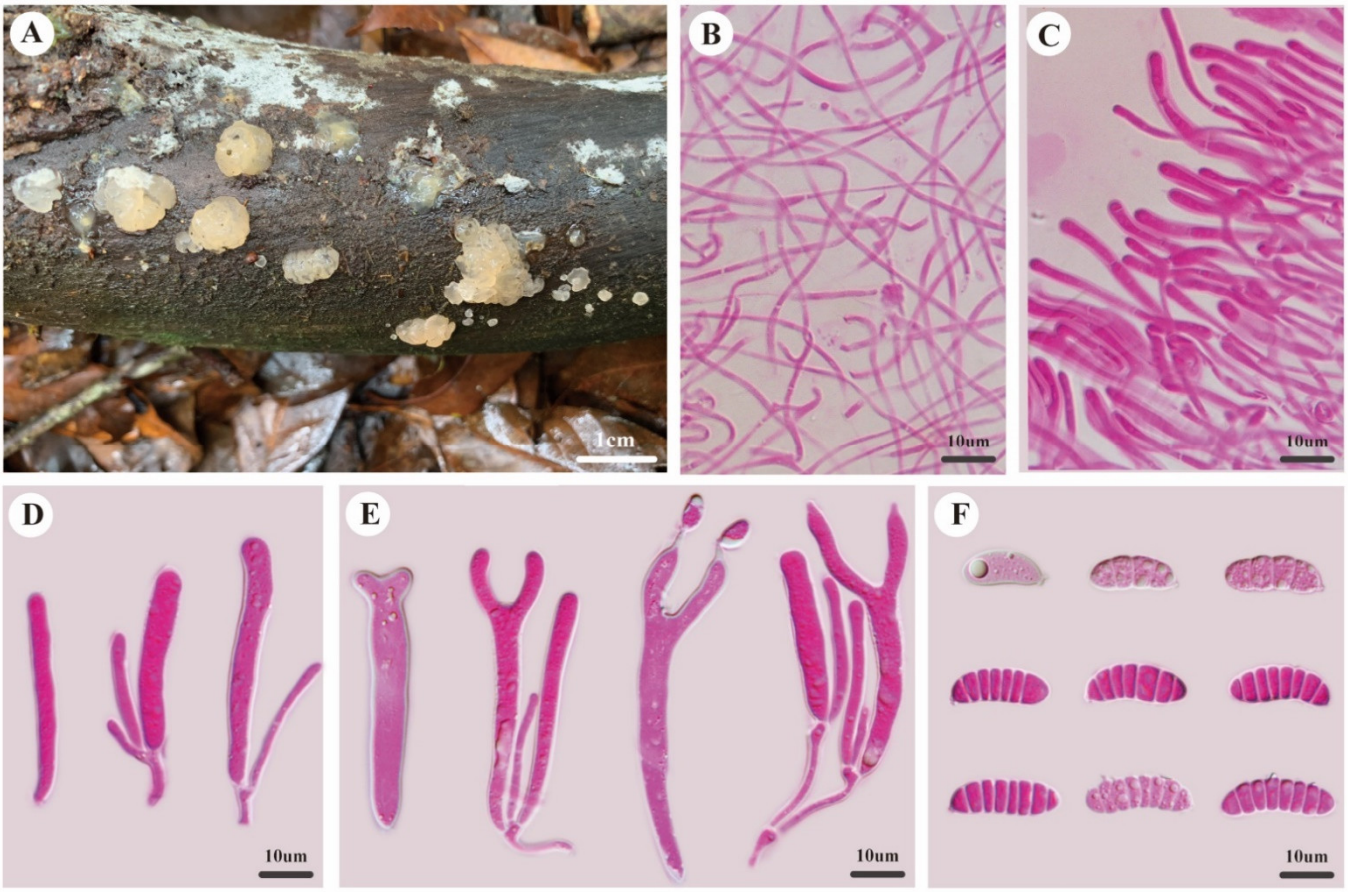

Figure 2. Morphology of *Dacrymyces cerebriformis*. (**A**) Basidiomata. (**B**) Internal hyphae. (**C**) Marginal hyphae. (**D**) Probasidia and hyphidia. (**E**) Developing basidia and hyphidia. (**F**) Basidiospores.

MycoBank no.: 843769

Holotype—China, Yunnan province, Pingbian county, Daweishan National Forest Park, on fallen angiosperm branch, 26 June 2019, Dai 19832 (BJFC031507).

Etymology—Refers to the species having obviously cerebriform basidiomata when mature.

Description—Basidioma sessile, single or caespitose, gelatinous when fresh, cream to buff, pustulate to pulvinate when juvenile, obviously cerebriform when mature, up to 3.0 mm high, 5.0–10.0 mm in diam. Marginal hyphae of sterile surface hyaline, thin- to thick-walled, septate, straight or flexuous, with simple cylindrical thin- or thick-walled terminal cells measuring 11.0–18.0 × 1.7–3.5 µm, without clamp connections. Internal hyphae hyaline, thin-walled, septate, branched, without clamp connections, 1.0–3.0 µm in diam. Hymenium limited to the upper surface of the basidioma, composed of basidia and simple cylindrical hyphidia. Basidia hyaline, thin-walled, cylindrical to clavate, bifurcate when mature, 35.0–50.0 × 4.5–7.0 µm, probasidia similar to basidia in shape, but smaller. Basidiospores hyaline, thin-walled, allantoid, with an apiculum at the base, 0–7-septate, (18.1–)18.4–23.1(–23.8) × (5.4–)5.5–7.7(–8.0) µm, L = 20.7 µm, W = 6.5 µm, Q = 3.14–3.28 (n = 60/2).

Additional specimens examined—China, Yunnan province, Pingbian county, Daweishan National Forest Park, on rotten angiosperm wood, 26 June 2019, Dai 19805 (BJFC031480), Dai 19826 (BJFC 031501).

Notes—*Dacrymyces cerebriformis* is characterized by obviously cerebriform basidiomata when mature, hyphae without clamp connections, and hyaline, thin-walled, allantoid,

0–7-septate basidiospores. The species resembles *D. adpressus* Grognot and *D. sichuanensis* B. Liu and L. Fan by sharing cerebriform basidiomata when mature, but both differ from *D. cerebriformis* by their 0–3-septate basidiospores [13,14].

Dacrymyces sinostenosporus F. Wu and Y.P. Lian, sp. nov. Figure 3.

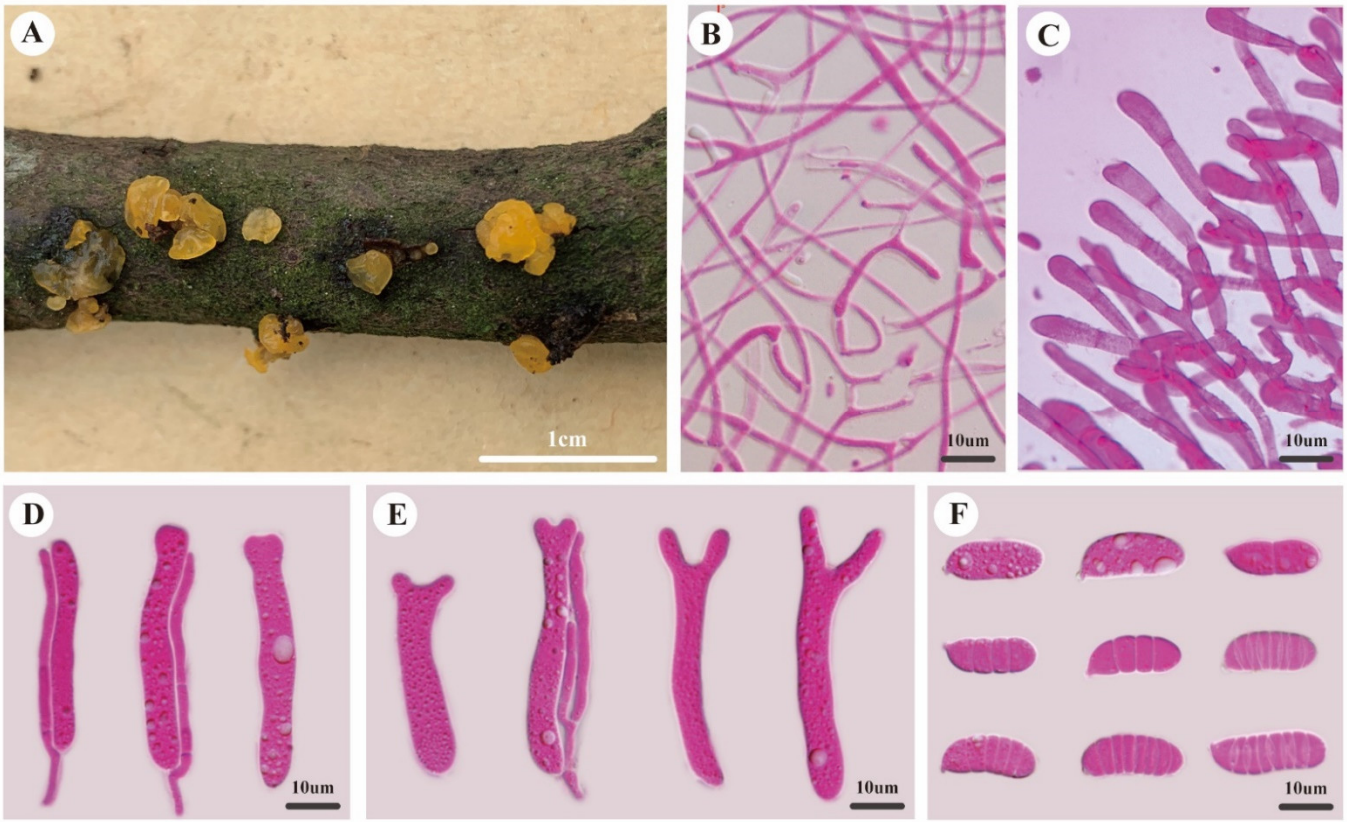

Figure 3. Morphology of *Dacrymyces sinostenosporus*. (**A**) Basidiomata. (**B**) Internal hyphae. (**C**) Marginal hyphae. (**D**) Probasidia and hyphidia. (**E**) Developing basidia and hyphidia. (**F**) Basidiospores.

MycoBank no.: 838634

Holotype—China, Yunnan province, Wenshan county, Laojunshan Nature Reserve, on fallen branch of *Lithocarpus*, 30 June 2019, Dai 20003 (BJFC031677).

Etymology—Refers to the species similar to *Dacrymyces stenosporus*, but occurring in China.

Description—Basidiomata sessile, single or caespitose, gelatinous when fresh, curry-yellow to orange yellow, pustulate to pulvinate when juvenile, discoid and applanate when mature, sometimes slightly cerebriform when coalescing, up to 1.2 mm high, 2–4 mm in diam. Marginal hyphae of sterile surface hyaline, thin- to thick-walled, septate, straight or flexuous, with cylindrical, thin-walled terminal cells measuring 7.0–17.0 × 3.5–6.0 µm, without clamp connections. Internal hyphae hyaline, thin-walled, septate, branched, without clamp connections, 0.8–3 µm in diam. Hymenium limited to the upper surface of the basidiomata, composed of basidia and simple or branched cylindrical hyphidia. Basidia hyaline, thin-walled, cylindrical to clavate, becoming bifurcate when mature, 40.0–60.0 × 4.0–9.0 µm, probasidia similar to basidia in shape, but smaller. Basidiospores hyaline, thin-walled, cylindrical to allantoid, with an apiculum at the base, 0–7-septate, (17.0–)18.0–23.5(–24.0) × (5.9–)6.3–8.0(–8.4) µm, L = 19.3 µm, W = 7.1 µm, Q = 2.63–2.77 (*n* = 60/2).

Additional specimen examined—China, Yunnan province, Wenshan county, Laojunshan Nature Reserve, on fallen angiosperm branch, 30 June 2019, Dai 20008 (BJFC031682).

Notes—*Dacrymyces sinostenosporus* is characterized by discoid and applanate basidiomata when mature, hyphae without clamp connections, and hyaline, thin-walled, cylindrical to allantoid, 0–7-septate basidiospores. The species is closely related to *D. stenosporus*

in morphology and phylogeny, but *D. stenosporus* has shorter basidia (30–40 × 4 µm vs. 40.0–60.0 × 4.0–9.0 µm), is smaller, has 0–3-septate basidiospores (13–17 × 5–6 µm vs. 18.0–23.5 × 6.3–8 µm) [16], and it shares less than 90% similarity to *D. stenosporus* in ITS sequences.

4. Discussion

In order to improve knowledge on *Dacrymyces*, five specimens of the genus were collected from Yunnan province, China, which were identified as two new species, viz. *D. cerebriformis* and *D. sinostenosporus*, based on morphological characteristics and phylogenetic analyses using the combined ITS and nrLSU dataset. The two new species have typical characteristics of *Dacrymyces*, and they share 0–7-septate basidiospores, but they are phylogenetically distant from each other. *Dacrymyces cerebriformis* can be distinguished from *D. sinostenosporus* by its narrower, thin- or thick-walled terminal cells in the marginal hyphae of the sterile surface (1.7–3.5 µm vs. 3.5–6.0 µm), and thinner basidiospores (Q = 3.14–3.28 vs. Q = 2.63–2.77).

Five *Dacrymyces* species were described from China, but DNA data of these species were not available for a phylogenetic analysis. This study firstly obtained molecular data of *Dacrymyces* samples from China, which contributed to the knowledge of the species diversity in China. Among those previously described, *Dacrymyces* species from China, *D. yunnanensis* (B. Liu and L. Fan), and *D. sichuanensis* were also originally described from southwestern China, but *D. yunnanensis* differed from the two new species by having ellipsoid to subglobose basidiospores, with transverse and vertical septations (15.6–24.7 × 13–16 µm), and *D. sichuanensis* was readily distinguished from the two new species by the presence of clamp connections and 0–3-septate basidiospores [12,13]. Therefore, seven *Dacrymyces* species, including *D. dendrocalami* Oberw., *D. duii* (B. Liu and J.Z. Cao.), *D. cerebriformis*, *D. pengii* (B. Liu and L. Fan) A. Savchenko, *D. sichuanensis*, *D. sinostenosporus* and *D. yunnanensis*, have been found in China to date.

Other species, including *D. stillatus*, *D. lacrymalis* (Pers.) Nees, *D. minor* (Peck), *D. subantarcticensis* (Burds. and Laursen), *D. novae-zelandiae* (McNabb), and *D. san-augustinii* (Kobayasi), may be confused with *D. cerebriformis* and *D. sinostenosporus* due to sharing sessile, pulvinate, yellowish basidiomata when fresh [14,29], but the former four species differ from the two new species by having 0–3-septate basidiospores, *D. novae-zelandiae* differs by its longer basidia (55–72 µm vs. 35–40 µm in *D. cerebriformis*; 40–60 µm in *D. sinostenosporus*), and *D. san-augustinii* differs from *D. cerebriformis* and *D. sinostenosporus* in that it has wider and curved allantoid basidiospores (16–27.5 × 6–10 µm) [14].

The polyphyletic problem of *Dacrymyces* was still not well solved, and species in different genera of *Dacrymycetaceae* overlapped in phylogenies [17,18]. More samples with DNA data from different areas of the world are badly needed, and extensive examinations and phylogenetic analyses on these samples should be carried out in the future. The species presented here were intended to contribute to the understanding of the great diversity and taxonomy of the genus *Dacrymyces*, but further studies should analyze them as a whole.

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Informed Consent Statement: Not applicable for studies involving humans.

Data Availability Statement: All data generated or analyzed during this study were included in this published article.

Conflicts of Interest: The authors declare no conflict of interest.

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