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Additions to *Dendrodacrys* and outline of taxa with branched hyphidia in *Dacrymycetes* (*Basidiomycota*)

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Abstract: The genus *Dendrodacrys* is a monophyletic group that belongs to *Dacrymycetes* (*Agaricomycotina*, *Basidiomycota*) and accommodates species distinguished by strongly branched hyphidia in combination with 3-septate basidiospores. While the original circumscription mainly treated European taxa, here we shift the focus to tropical and sub-tropical material and uncover wider variation in morphology within *Dendrodacrys*. Still united by hyphidia shape and basidiospore septation, the genus is expanded with 10 taxa having pustulate, cerebriform, or stipitate basidiocarps of yellow to dark brown colours, cylindrical to ovoid basidiospores, and hyphal septa with or without clamps. Monophyly of the amended *Dendrodacrys* is confirmed with a phylogeny based on six markers (SSU, ITS, LSU, *TEF1-α*, *RPB1*, and *RPB2*). As a result, we describe two new species (*De. laetum* and *De. rigoratum*), transfer three existing species to *Dendrodacrys* (*De. brasiliense*, *De. dendrocalami*, and *De. pezizoideum*), and raise one variety to the species level (*De. kennedyae* ≡ *Dacrymyces enatus* var. *macrosporus*). In addition, we provide descriptions for the earlier combined *De. paraphysatum* and four new informal taxa. Lastly, we present illustrations, a character table, and an identification key that addresses all known dacrymycetes with branched hyphidia.

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INTRODUCTION

A set of traditional morphological characters for identification in the class *Dacrymycetes* has been established for a long time (Kennedy 1958a). From a taxonomist perspective, most of these characters are well expressed and unambiguous – for example, basidiocarp shape or number of basidiospore septa. Nevertheless, it has often been considered difficult to apply them in the delimitation of genera (e.g., Donk 1966). The main reason for this is ubiquitous character homoplasy that became evident as soon as the first phylogenetic studies on dacrymycetes were published (Shirouzu *et al.* 2007, Shirouzu *et al.* 2013a).

To enable morphological identification of monophyletic groups, recent studies focused on combinations of traits rather than on single defining characters. With this approach the authors of the present study revised three of four dacrymycete families: *Cerinomycetaceae*, *Dacryonaemataceae*, and *Unilacrymaceae* (Zamora & Ekman 2020, Savchenko *et al.* 2021). The last and the largest family – *Dacrymycetaceae* – is more difficult to treat as it contains most of the polyphyletic

genera in the class, dominated by the highly diverse *Dacrymyces* (ca. 190 taxon names, here abbreviated as “*Da.*”) and *Calocera* (ca. 80 taxon names). Nevertheless, there are indications that it is possible to tackle polyphyly in the family and at the same time preserve morphologically identifiable genera. To this end, characters that previously have not been widely used for generic delimitation may be re-evaluated as a stable basis for it.

In the most recent “divide and conquer” attempt to address polyphyly in the family, the genus *Dendrodacrys* (here abbreviated as “*De.*”) was created to encompass a well-defined clade of taxa with branched hyphidia, 3-septate basidiospores, and specialized marginal hyphae (Zamora *et al.* 2022). Branched hyphidia (or dendrohyphidia) are relatively common in basidia-bearing fungi (Donk 1964, Cléménçon *et al.* 2004), and in dacrymycetes they occur in all the four recognised families. Prominently branched hyphidia are present in all known species of *Dacryonaemataceae* and *Unilacrymaceae*, as well as in many gelatinous members of *Cerinomycetaceae* (Fig. 1, bold font). Furthermore, weakly branched hymenial structures are known in several corticioid and gelatinous taxa of *Cerinomyces*. However, in *Dacrymycetaceae*

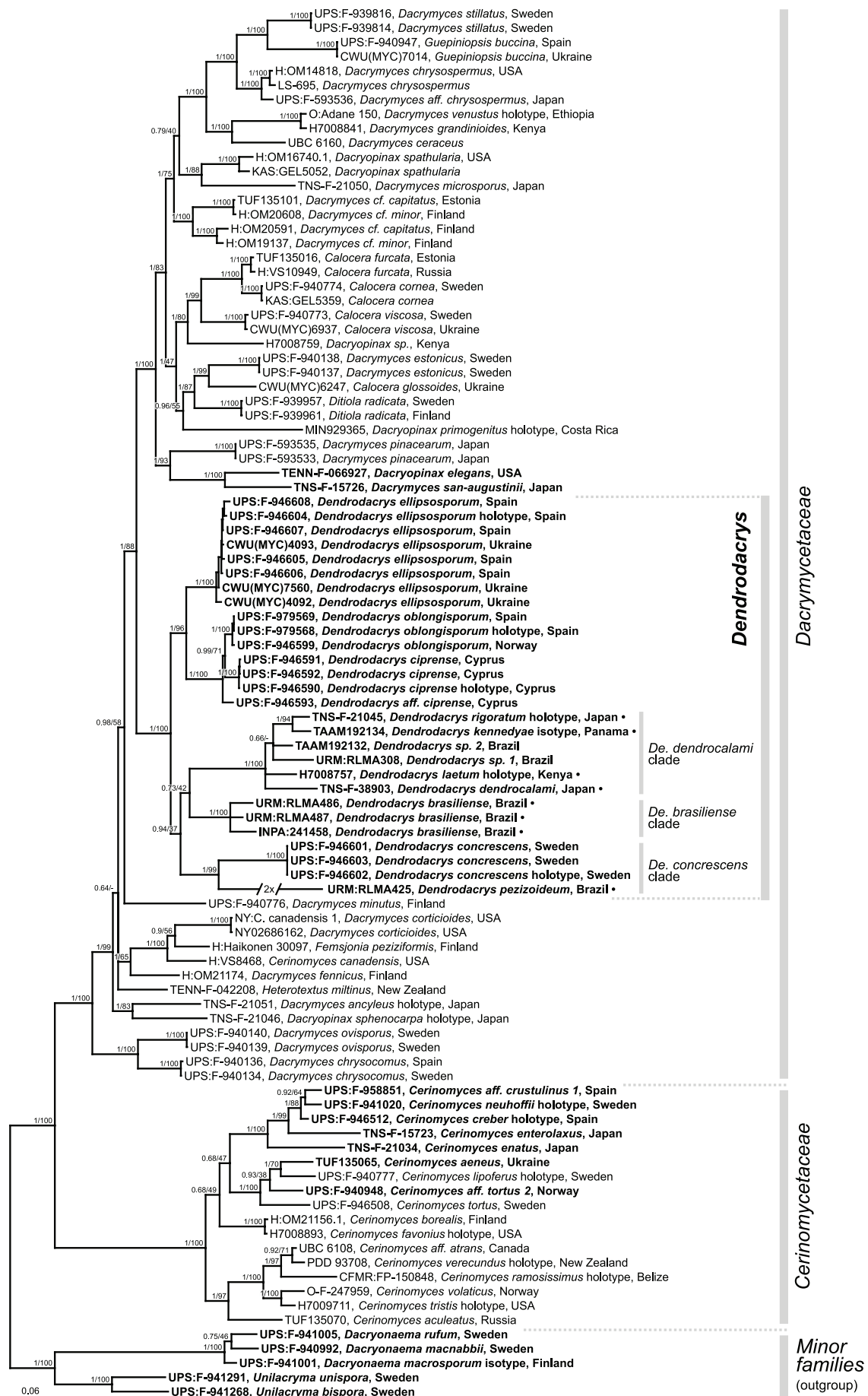


Fig. 1. Phylogeny of the *Dacrymycetes* with focus on *Dendrodacrys*. Taxa with strongly branched hyphidia are marked with bold font. Taxonomic novelties are indicated with a dot (•). Bayesian consensus tree based on SSU, 5.8S, LSU, *RPB1*, *RPB2*, and *TEF1-α* sequences. Numbers before and after slash (/) indicate posterior probabilities of Bayesian analysis and bootstrap support values respectively.

outside of *Dendrodacrys* dendrohyphidia are known only in a few species. Some of them are otherwise easy to tell apart from *Dendrodacrys* spp. (see Discussion), but others show a pattern of morphology characteristic for the genus. To find out if they are related to *Dendrodacrys*, we targeted a number of such taxa, including *Calocera arborea*, *Dacryopinax elegans*, and *Femsjonia pezizoidea*. In addition, we evaluated candidate specimens from the tropics that did not agree with any extant species description. With obtained data, we aim to challenge the definition of *Dendrodacrys*, determine if the studied taxa belong to the genus, and create new species and combinations where needed.

MATERIALS AND METHODS

Morphological study

Specimens were obtained from the herbaria BPI, CWU, EA, FH, H, K, LSU, NY, S, TAAM, TNS, TUF, URM, and UPS, abbreviated following Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>). Collector's numbers are shown without the collector's name abbreviation. Studied type specimens are indicated through the exclamation mark (!), and these specimens are not duplicated under "Material examined". Descriptions are based primarily on sequenced specimens that are marked with an asterisk (*), and specimens without sequences are incorporated only in the absence of sequenced ones or when their morphology agrees well with the adopted species concept. Detailed information on specimens, high-resolution macro photographs, and scanned notes and labels are available under CC BY 4.0 license through individual query via the PlutoF platform (<https://plutof.ut.ee>, Abarenkov *et al.* 2010).

For details on microscopy, slide preparation, measurements, and terminology see Savchenko *et al.* (2021). Illustrations were prepared in Affinity Designer v. 1.10.5.1342. Microscopic studies were performed with Leica DMLB, Leica DM1000 LED, and Nikon Eclipse 80i microscopes under $\times 1\,000$ magnification with phase contrast or differential interference contrast (DIC). Slides were mounted in Cotton Blue in lactic acid or $\sim 1\%$ KOH with Congo Red. Spore statistics were produced in a custom SQLite database. The following abbreviations are used in descriptions: L for mean spore length, W for mean spore width, Q for L/W ratio, and Q' for variation of length to width ratio of individual basidiospores. Basidiospores with Q values of ~ 1.0 are reported as ovoid, ~ 1.5 as ellipsoid, ~ 2.0 as narrowly ellipsoid, and ≥ 2.5 as cylindrical. To show variation in basidiospore dimensions, 5 % of measurements from each end of the range are excluded and given in parentheses. In case of identical values, parts in parentheses are omitted. When not stated explicitly, basidiospores and conidia were measured in Cotton Blue in lactic acid, whereas basidia and hyphidia were measured in $\sim 1\%$ KOH. The total number of measured structures in relation to the number of studied specimens is shown as "n = 30/1". Raw morphometric data for the studied specimens are provided in Supplementary Table S1 and available in the dedicated PlutoF-hosted dataset <https://doi.org/10.1515/BIO/2483910>. Taxonomic novelties were deposited in MycoBank (Robert *et al.* 2013).

DNA extraction, PCR, and sequencing

Detailed protocols for extraction and PCR are provided in Savchenko *et al.* (2021). DNA was extracted with High Pure PCR

template preparation kit (Roche Applied Science, Penzberg, Germany) following the protocol of manufacturer. PCR was performed with the following forward and reverse primers separated with a slash. The whole ITS region with a part of LSU: ITSOF (Tedersoo *et al.* 2008) / LR5 (Hopple & Vilgalys 1994), or LB-W (Tedersoo *et al.* 2008), or ITS4 (White *et al.* 1990); ITS1: ITFOF / ITS2 (White *et al.* 1990); ITS2: 58A1F (Martin & Rygielwicz 2005) / ITS4; LSU, both by Hopple & Vilgalys (1994): LR0R / LR7; SSU, both modified by L. Tedersoo after White *et al.* (1990): NS1a / NS8a; *TEF1- α* , both by Rehner & Buckley (2005): EF1-983F / EF1-1567R; *RPB1*: RPB1-Af (Stiller & Hall 1997) / RPB1-Cr (Matheny *et al.* 2002); *RPB2*, both by Liu *et al.* (1999): fRPB2-5F / fRPB2-7cR. In PCR we used HOT FIREPol Blend Master Mix (with 10 mM MgCl₂; Solis BioDyne) and DNA in 1 \times concentration. Sequencing was done by MacroGen Europe (Amsterdam, Netherlands) using the amplification primers except ITS5 (White *et al.* 1990) for ITSOF products and CTB6 (Garbelotto *et al.* 1997) for LR0R products.

One of the samples, *Dendrodacrys pezizoideum* RLMA425, was sequenced with Illumina NextSeq 500 at the Biomedicum Functional Genomics Unit, University of Helsinki. Read cleaning was done using the FastQC v. 0.11.7 (<https://www.bioinformatics.babraham.ac.uk/projects/fastqc/>). Bowtie2 v. 2.3.4.3 (Langmead & Salzberg 2012) was used to map the reads to a dataset of target markers; alignment was done using the sensitive option. Following the mapping of the reads the aligned read files were assembled using the MEGAHIT assembler v. 1.2.9 (Li *et al.* 2015) with the k-list parameter set to 79,99,119.

Using the metabarcoding approach, we attempted to sequence ITS1 and ITS2 regions of rRNA of three samples, *Dendrodacrys* sp. 3 K(M): 141170 (ITS2 unsuccessfully), *Dendrodacrys* sp. 4 K(M): 64214, and *De. paraphysatum* NY00738304 (both regions unsuccessfully). For ITS1, we used ITS1catta (Tedersoo & Anslan 2019) / ITS2ngs (Tedersoo *et al.* 2018) PCR primers; for ITS2, gITS7ngs (Tedersoo & Lindahl 2016) / ITS4. Amplicons were sequenced with Illumina NovaSeq 6000 (2 \times 250 bp) in a paired-end mode at Novogen Inc., UK. For detailed protocols see Anslan *et al.* (2021).

All the sequences are available in GenBank (Sayers *et al.* 2022) and the accession numbers are shown in the Table 1. GenBank submissions of the protein-coding genes were prepared with nex2tbl tool (<https://github.com/Mycology-Microbiology-Center/nex2tbl>) built for the R environment (R Core Team 2019).

Phylogenetic inference

General sequence management and contig assembly were done in Geneious v. 7.1.3 (<https://www.geneious.com>). Aligning was performed in MAFFT v. 7 online with the automatically selected method (<https://mafft.cbrc.jp/alignment/server/>, Katoh *et al.* 2019). For the phylogenetic analyses, parts of the alignments were excluded by hand (poorly aligned and heterogeneous regions of nrDNA, introns in protein-coding genes). Manual adjustments to alignments were done with AliView v. 1.28 (Larsson 2014). A concatenated dataset for the class-wide tree inference included the following genes: SSU, 5.8S, LSU, *TEF1- α* , *RPB1*, and *RPB2*. Partitioning scheme consisted of nine parts: the first three genes represented one partition each, and the latter three genes were divided into 1st–2nd codon positions vs 3rd position each. For this analysis ITS1 and ITS2 were excluded as difficult to align without violating homology assumptions. Compared to the rest of the class, the amount of sequence data for the new taxa in

Table 1. Specimens and corresponding sequence accession numbers used in this study. Accession numbers of newly generated sequences are indicated in bold.

Taxon name	Specimen ID	Country	SSU	ITS	LSU	TEF1- α	RPB1	RPB2	Reference
<i>Calocera cornea</i>	KAS:GEL5359 (AFTOL-ID 438)	?	AY771610	AY789083	AY701526	AY881019	AY857980	AY536286	Lutzoni et al. (2004)
	UPS:UPS-F-940774	Sweden	MN593442	MN595626	MN595626	MN580325	MN580225	MN580265	Zamora & Ekman (2020)
<i>Calocera furcata</i>	H:Spirin 10949	Russia	OP456312	MW191975	MW159088	MW130298	—	—	Savchenko et al. (2021), this study
	TUF135016	Estonia	MW158984	MW191958	MW159087	MW130297	MW130380	MW130422	Savchenko et al. (2021)
<i>Calocera glossoides</i>	CWU(MYC)6247	Ukraine	MW159005	MW191968	MW159084	MW130307	MW130388	MW130428	Savchenko et al. (2021)
<i>Calocera viscosa</i>	CWU(MYC)6937	Ukraine	MW158986	MW191970	MW159090	MW130302	MW130382	MW130424	Savchenko et al. (2021)
	UPS:F-940773	Sweden	MN593444	MN595628	MN595628	MN580327	MN580227	MN580267	Zamora & Ekman (2020)
<i>Cerinomyces aculeatus</i>	TUF135070	Russia	MW158954	MW191884	MW159045	MW130322	MW130375	MW130410	Savchenko et al. (2021)
<i>Cerinomyces aeneus</i>	TUF135065	Ukraine	MW158966	MW191919	MW159054	MW130337	MW130367	OP477356	Savchenko et al. (2021), this study
<i>Cerinomyces aff. atrans</i>	UBC 6108	Canada	AB712485	AB712443	AB712423	—	—	AB712527	Shirouzu et al. (2013a)
<i>Cerinomyces borealis</i>	H:Miettinen 21156.1	Finland	MW158963	MW191889	MW159038	MW130344	MW130371	MW130411	Savchenko et al. (2021)
<i>Cerinomyces canadensis</i>	H:Spirin 8468	USA	MW158983	MW191945	MW159069	MW130349	MW130376	MW130419	Savchenko et al. (2021)
<i>Cerinomyces creber</i> (holotype)	UPS:F-946512	Spain	MW159010	MW191985	MW191985	MW130352	MW130394	—	Savchenko et al. (2021)
<i>Cerinomyces aff. crustulinus</i> 1	UPS:F-958851	Spain	MW159011	MW191986	MW191986	MW130353	MW130395	MW130431	Savchenko et al. (2021)
<i>Cerinomyces enatus</i>	TNS-F-21034	Japan	AB712483	AB712441	AB472696	—	—	AB712525	Shirouzu et al. (2009), Shirouzu et al. (2013a)
<i>Cerinomyces enterolaxus</i>	TNS-F-15723	Japan	AB712504	AB712462	AB299052	—	—	AB712546	Shirouzu et al. (2007), Shirouzu et al. (2013a)
<i>Cerinomyces favonius</i> (holotype)	H7008893	USA	MW158962	MW191895	MW159041	MW130347	MW130374	MW130416	Savchenko et al. (2021)
<i>Cerinomyces lipoferus</i> (holotype)	UPS:F-940777	Sweden	MN593436	MN595620	MN595620	MN580319	MN580219	MN580259	Zamora & Ekman (2020)
<i>Cerinomyces neuhoffii</i> (holotype)	UPS:F-941020	Sweden	MN593441	MN595625	MN595625	MN580324	MN580224	MN580264	Zamora & Ekman (2020)
<i>Cerinomyces ramosissimus</i> (holotype)	CFMR:FP-150848	Belize	AB712488	AB712446	AB712426	—	—	AB712530	Shirouzu et al. (2013a)
<i>Cerinomyces tortus</i>	UPS:F-946508	Sweden	MW159020	MW191995	MW191995	MW130359	MW130401	MW130437	Savchenko et al. (2021)
<i>Cerinomyces aff. tortus</i> 2	UPS:F-940948	Norway	MN593437	MN595621	MN595621	MN580320	MN580220	MN580260	Zamora & Ekman (2020)
<i>Cerinomyces tristis</i> (holotype)	H:Miettinen 16934 (H7009711)	USA	MW158958	MW191906	MW159050	MW130325	—	MW130409	Savchenko et al. (2021)
<i>Cerinomyces verecundus</i> (holotype)	PDD 93708	New Zealand	—	MW191930	MW159052	MW130329	—	—	Savchenko et al. (2021)
<i>Cerinomyces volaticus</i>	O-F-247959	Norway	MN593435	MN595619	MN595619	MN580318	MN580218	MN580258	Zamora & Ekman (2020)
<i>Dacryomyces ancyleus</i> (holotype)	TNS-F-21051	Japan	AB712490	AB712448	AB472713	—	—	AB712532	Shirouzu et al. (2009), Shirouzu et al. (2013a)
<i>Dacryomyces cf. capitatus</i>	H:Miettinen 20591	Finland	MW158997	MW191965	MW159079	MW130300	MW130384	MW130426	Savchenko et al. (2021)
	TUF135101	Estonia	MW158995	MW191962	MW159081	—	—	—	Savchenko et al. (2021)
<i>Dacryomyces ceraceus</i>	UBC 6160	?	JGI	JGI	JGI	JGI	JGI	JGI	(Grigoriev et al. 2011)

Table 1. (Continued).

Taxon name	Specimen ID	Country	SSU	ITS	LSU	TEF1- α	RPB1	RPB2	Reference
<i>Dacryomyces chrysocomus</i>	UPS:F-940134	Sweden	MN593446	MN595630	MN595630	MN580329	MN580229	MN580269	Zamora & Ekman (2020)
	UPS:F-940136	Spain	MN593445	MN595629	MN595629	MN580328	MN580228	MN580268	Zamora & Ekman (2020)
<i>Dacryomyces chrysospermus</i>	H:Miettinen 14818	USA	MW159000	MW191961	MW159077	MW130305	OP477350	—	Savchenko <i>et al.</i> (2021), this study
	UPS:F-593536	Japan	MN593447	MN595631	MN595631	MN580330	MN580230	MN580270	Zamora & Ekman (2020)
<i>Dacryomyces corticioides</i>	LS-695 (AFTOL-ID 528)	?	AY705954	DQ205684	AY691892	DQ028587	DQ785785	DQ381845	Lutzoni <i>et al.</i> (2004)
	NY:C. canadensis 1	USA	OP456306	MW191940	MW159067	MW130315	—	—	Savchenko <i>et al.</i> (2021), this study
	NY02686162	USA	MW159006	MW191944	MW159068	MW130314	—	—	Savchenko <i>et al.</i> (2021)
<i>Dacryomyces estonicus</i>	UPS:F-940137	Sweden	MN593448	MN595632	MN595632	MN580331	MN580231	MN580271	Zamora & Ekman (2020)
	UPS:F-940138	Sweden	MN593449	MN595633	MN595633	MN580332	MN580232	MN580272	Zamora & Ekman (2020)
<i>Dacryomyces fennicus</i>	H:Miettinen 21174	Finland	MW158989	MW191957	MW159071	OP477365	MW130378	MW130421	Savchenko <i>et al.</i> (2021), this study
<i>Dacryomyces grandinioides</i>	H7008841	Kenya	MW158994	MW191950	MW159076	MW130312	MW130390	MW130418	Savchenko <i>et al.</i> (2021)
<i>Dacryomyces microsporus</i>	TNS-F-21050	Japan	AB712499	AB712457	AB472712	—	—	AB712541	Shirouzu <i>et al.</i> (2009), Shirouzu <i>et al.</i> (2013a)
<i>Dacryomyces cf. minor</i>	H:Miettinen 19137 (H6013666)	Finland	MW158998	MW191967	MW159080	MW130301	MW130385	MW130427	Savchenko <i>et al.</i> (2021)
	H:Miettinen 20608	Finland	MW158996	MW191963	MW159082	MW130304	MW130383	MW130425	Savchenko <i>et al.</i> (2021)
<i>Dacryomyces minutus</i>	UPS:F-940776	Finland	MN593450	MN595634	MN595634	MN580333	MN580233	MN580273	Zamora & Ekman (2020)
<i>Dacryomyces ovisporus</i>	UPS:F-940139	Sweden	MN593451	MN595635	MN595635	MN580334	MN580234	MN580274	Zamora & Ekman (2020)
	UPS:F-940140	Sweden	MN593452	MN595636	MN595636	MN580335	MN580235	MN580275	Zamora & Ekman (2020)
<i>Dacryomyces pinacearum</i>	UPS:F-593533	Japan	MN593453	MN595637	MN595637	MN580336	MN580236	MN580276	Zamora & Ekman (2020)
	UPS:F-593535	Japan	MN593454	MN595638	MN595638	MN580337	MN580237	MN580277	Zamora & Ekman (2020)
<i>Dacryomyces san-augustinii</i>	TNS-F-15726	Japan	AB712505	AB712463	AB299081	—	—	AB712547	Shirouzu <i>et al.</i> (2007), Shirouzu <i>et al.</i> (2013a)
<i>Dacryomyces stillatus</i>	UPS:F-939814	Sweden	MN593456	MN595677	MN595677	MN580339	MN580239	MN580279	Zamora & Ekman (2020)
	UPS:F-939816	Sweden	MN593458	—	MN593495	MN580341	MN580241	MN580281	Zamora & Ekman (2020)
<i>Dacryomyces venustus</i> (holotype)	O:Adane 150	Ethiopia	MW158993	MW191949	MW159075	MW130311	OP477349	MW130417	Savchenko <i>et al.</i> (2021), this study
<i>Dacryonaema macnabbii</i>	UPS:F-940992	Sweden	MN593475	MN595653	MN595653	MN580356	MN580211	MN580295	Zamora & Ekman (2020)
<i>Dacryonaema macrosporum</i> (isotype)	UPS:F-941001	Finland	MN593481	MN595661	MN595661	MN580361	MN580216	MN580303	Zamora & Ekman (2020)
<i>Dacryonaema rufum</i>	UPS:F-941005	Sweden	MN593469	MN595646	MN595646	MN580349	MN580209	MN580288	Zamora & Ekman (2020)
<i>Dacryopinax elegans</i>	TENN-F-066927	USA	MN593460	MN595640	MN595640	MN580342	MN580242	MN580282	Zamora & Ekman (2020)

Table 1. (Continued).

Taxon name	Specimen ID	Country	SSU	ITS	LSU	TEF1- α	RPB1	RPB2	Reference
<i>Dacryopinax primogenitus</i> (holotype)	MIN929365	Costa Rica	JGI	JGI	JGI	JGI	JGI	JGI	Floudas et al. (2012), McLaughlin et al. (2016)
<i>Dacryopinax spathularia</i>	KAS:GEL5052 (AFTOL-ID 454)	?	AY771603	AY854070	AJ406407	AY881020	AY857981	AY786054	Lutzoni et al. (2004)
<i>Dacryopinax aff. spathularia</i>	H:Miettinen 16740.1	USA	MW158999	MW191973	MW159085	MW130308	MW130389	MW130429	Savchenko et al. (2021)
<i>Dacryopinax sphenocarpa</i> (holotype)	TNS-F-21046	Japan	AB712516	AB712474	AB472708	—	—	AB712558	Shirouzu et al. (2009), Shirouzu et al. (2013a)
<i>Dacryopinax</i> sp.	H7008759	Kenya	MW158992	MW191959	MW159091	OP477364	OP477348	OP477355	Savchenko et al. (2021), this study
<i>Dendrodacrys brasiliense</i> (holotype of <i>Calocera arborea</i>)	INPA:241458	Brazil	—	AB744230	AB723514	—	—	—	Shirouzu et al. (2013b)
<i>Dendrodacrys ciprense</i> (holotype)	URM:RLMA486 (URM 94627)	Brazil	OP456310	OP529839	OP529833	OP477366	OP477353	OP477358	this study
	URM:RLMA487 (URM 94628)	Brazil	OP456311	OP529840	—	OP477367	OP477354	—	this study
	UPS:F-946590	Cyprus	OM515350	OM519385	OM519385	OM502337	OM502304	OM502321	Zamora et al. (2022)
	UPS:F-946591	Cyprus	OM515351	OM519386	OM519386	OM502338	OM502305	OM502322	Zamora et al. (2022)
<i>Dendrodacrys aff. ciprense</i>	UPS:F-946592	Cyprus	OM515352	OM519387	OM519387	—	OM502306	OM502323	Zamora et al. (2022)
	UPS:F-946593	Cyprus	OM515353	OM519388	OM519388	OM502339	OM502307	OM502324	Zamora et al. (2022)
	UPS:F-946602	Sweden	OM515355	OM519390	OM519390	OM502341	OM502309	OM502326	Zamora et al. (2022)
	UPS:F-946601	Sweden	OM515354	OM519389	OM519389	OM502340	OM502308	OM502325	Zamora et al. (2022)
<i>Dendrodacrys dendrocalami</i>	UPS:F-946603	Sweden	OM515356	OM519391	OM519391	OM502342	OM502310	OM502327	Zamora et al. (2022)
	TNS-F-38903	Japan	AB712495	AB712453	AB712428	—	—	AB712537	Shirouzu et al. (2013a)
	UPS:F-946604	Spain	OM515357	OM519392	OM519392	OM502343	OM502311	OM502328	Zamora et al. (2022)
	CWU(MYC)4092	Ukraine	OM515362	OM519397	OM519397	OM502348	OM502316	—	Zamora et al. (2022)
<i>Dendrodacrys ellipsosporum</i> (holotype)	CWU(MYC)4093	Ukraine	—	OP529842	OP529842	—	—	—	this study
	CWU(MYC)7560	Ukraine	OM515363	OM519398	OM519398	OM502349	OM502317	OM502333	Zamora et al. (2022)
	UPS:F-946605	Spain	OM515358	OM519393	OM519393	OM502344	OM502312	OM502329	Zamora et al. (2022)
	UPS:F-946606	Spain	OM515359	OM519394	OM519394	OM502345	OM502313	OM502330	Zamora et al. (2022)
<i>Dendrodacrys oblongisporum</i> (holotype)	UPS:F-946607	Spain	OM515360	OM519395	OM519395	OM502346	OM502314	OM502331	Zamora et al. (2022)
	UPS:F-946608	Spain	OM515361	OM519396	OM519396	OM502347	OM502315	OM502332	Zamora et al. (2022)
	TAAM192134	Panama	—	OP529836	OP529830	—	—	—	this study
	H7008757	Kenya	OP456305	OP529841	OP529841	OP477360	—	—	this study
<i>Dendrodacrys oblongisporum</i> (holotype)	UPS:F-979568	Spain	OM515365	OM519400	OM519400	OM502351	OM502319	OM502335	Zamora et al. (2022)
<i>Dendrodacrys pezizoideum</i>	UPS:F-946599	Norway	OM515364	OM519399	OM519399	OM502350	OM502318	OM502334	Zamora et al. (2022)
	UPS:F-979569	Spain	OM515366	OM519401	OM519401	OM502352	OM502320	OM502336	Zamora et al. (2022)
	URM:RLMA425 (URM 94345)	Brazil	OP456309	OP529838	OP529832	OP477359	OP477352	—	this study

Table 1. (Continued).

Taxon name	Specimen ID	Country	SSU	ITS	LSU	<i>TEF1-α</i>	<i>RPB1</i>	<i>RPB2</i>	Reference
<i>Dendrodacrys rigoratum</i> (holotype)	TNS-F-21045	Japan	AB712489	AB712447	AB472707	OP477362	—	AB712531	Shirouzu <i>et al.</i> (2009), Shirouzu <i>et al.</i> (2013b), this study
<i>Dendrodacrys</i> sp. 1	URM:RLMA308 (URM 94610)	Brazil	OP456308	OP529837	OP529831	OP477363	OP477351	OP477357	this study
<i>Dendrodacrys</i> sp. 2	TAAM192132	Brazil	OP456307	OP529835	OP529829	OP477361	—	—	this study
<i>Dendrodacrys</i> sp. 3	K(M): 141170	Puerto Rico	—	OP456327	—	—	—	—	this study
<i>Dendrodacrys</i> sp. 4	K(M): 64214	Venezuela	—	OP456328 , OP456329	—	—	—	—	this study
<i>Ditiola radicata</i>	UPS:F-939957	Sweden	MN593461	MN595641	MN595641	MN580343	MN580243	MN580283	Zamora & Ekman (2020)
	UPS:F-939961	Finland	MN593462	—	—	MN580344	MN580244	MN580284	Zamora & Ekman (2020)
<i>Femsonia peziziformis</i>	H:Haikonen 30097	Finland	MN593463	MN595642	MN595642	MN580345	MN580245	MN580285	Zamora & Ekman (2020)
<i>Guepinopsis buccina</i>	CWU(MYC)7014	Ukraine	MW159002	MW191971	MW159086	MW130319	MW130386	—	Savchenko <i>et al.</i> (2021)
	UPS:F-940947	Spain	MN593464	MN595643	MN595643	MN580346	MN580246	MN580286	Zamora & Ekman (2020)
<i>Heterotextus miltinus</i>	TENN-F-042208	New Zealand	MN593465	MN595644	MN595644	MN580347	MN580247	—	Zamora & Ekman (2020)
<i>Unilacryma bispora</i>	UPS:F-941268	Sweden	MN593490	MN595672	MN595672	MN580369	MN580255	MN580314	Zamora & Ekman (2020)
<i>Unilacryma unispora</i>	UPS:F-941291	Sweden	MN593486	MN595668	MN595668	MN580365	MN580251	MN580310	Zamora & Ekman (2020)

Dendrodacrys is relatively low, though the 5.8S gene is always used in combination with at least a part of SSU or LSU, and together with protein-coding genes when available. To check if gene trees support similar composition of clades, six gene trees were built with IQ-TREE v. 1.6.12 (Nguyen *et al.* 2015) implemented at W-IQ-TREE server (Trifinopoulos *et al.* 2016) with 1 000 ultrafast bootstrap replications (Minh *et al.* 2013) and automatic model selection. No significant discordance was found when comparing well-supported clades (UFboot \geq 95 %) between the gene trees or multigene phylogenies.

Bayesian inference was performed with MrBayes v. 3.2.7a (Ronquist *et al.* 2012) as implemented at CSC – the IT Center for Science multi-core computing environment (<https://www.csc.fi>), with default priors, nucleotide substitution models estimated with the model jumping method (nst = mixed), with gamma-distributed rate variation across sites, and with an estimated proportion of invariable sites. Analyses were carried out in four parallel runs with six Markov chain Monte Carlo chains each, for 10 M generations, sampling trees every 5 000 generations, with the temperature constant at 0.1. The burn-in was set to 25 %. Runs converged, as indicated by the low average standard deviation of split frequencies (ASDF < 0.01). Mixing and sampling from the posterior probability distribution were assumed sufficient when, respectively, effective sample size (ESS, Ripley 1987) was reaching above 200 and potential scale reduction factor (PSRF, Gelman & Rubin 1992) was approximating to 1. Tracer v. 1.7.1 (Rambaut *et al.* 2018) and RWTY (Warren *et al.* 2017) were used to assess convergence of the model parameters and topologies. The consensus tree was inferred using 50 % majority rule.

Maximum likelihood (ML) analyses were performed with RAxML-NG v. 1.1.0 (Kozlov *et al.* 2019), implemented at CSC, starting from 10 random and 10 maximum parsimony initial trees, and with 1 000 iterations of standard non-parametric bootstrap. Model parameters for partitions were calculated based on the Bayesian information criterion with ModelFinder (Kalyaanamoorthy *et al.* 2017) at W-IQ-TREE server. Minor families, *Unilacrymaceae* and *Dacryonaemataceae*, were chosen as an outgroup based on results by Zamora & Ekman (2020). The trees were plotted in the R environment v. 4.2.0 (R Core Team 2019) with ggtree package v. 3.4.0 (Yu *et al.* 2017) and manually edited in Affinity Designer v. 1.10.5.1342. The alignment, phylograms, and R scripts used for visualization were deposited to the dedicated PlutoF-hosted dataset <https://doi.org/10.15156/BIO/2483910>.

RESULTS

Phylogeny and morphology

The class-wide phylogenetic analyses of the dacrymycetes based on SSU, 5.8S, LSU, *TEF1-α*, *RPB1*, and *RPB2* markers confirm that *Dendrodacrys* forms a highly supported monophyletic group, sister to the largest clade of *Dacrymycetaceae* that includes majority of *Calocera* and *Dacrymyces* species (Fig. 1). While the new taxa are all strongly supported, their relations within the genus are often not clearly resolved. New taxa are recovered in three clades within *Dendrodacrys*, and only distantly related to the earlier described European species of the genus.

The clade of *De. concrescens* now includes a newly combined *De. pezizoideum*. Basidiocarps of both species demonstrate orange colouration at maturity and readily coalesce into large flattened aggregations. *Dendrodacrys pezizoideum* occupies one of the longest branches in the class owing to the divergence of its DNA sequences from the relatives. On the morphological level, *De. pezizoideum* is distinguished by the presence of prominent white margin. This feature is not observed elsewhere in the genus and rare in the rest of the class. It is known, for example, in *Da. corticioides* and “*Cerinomyces*” *canadensis* that are also similar to *De. pezizoideum* in resupinate basidiocarps.

The second clade encompasses a single species in a wide sense, *De. brasiliense* (= *Calocera arborea*) and introduces a rare macromorphotype into the genus – long-stipitate weakly branched basidiocarps with pulvinate heads. Genetic divergence between the sequenced loci of *De. brasiliense* specimens is higher than within any other *Dendrodacrys* species. Even so, given the scarcity of available material and its high

morphological uniformity, we decided against splitting and treat all the collections of *De. brasiliense* as a single species for the time being.

Finally, the *De. dendrocalami* clade includes a variety of species from tropical and sub-tropical climates: the eponymous *De. dendrocalami* and *De. rigorum* (Japan), *De. kennedyae* (Panama), *De. laetum* (Kenya), *Dendrodacrys* sp. 1 and 2 (Brazil), *Dendrodacrys* sp. 3 (Puerto Rico), and *Dendrodacrys* sp. 4 (Venezuela). The morphology in the clade is diverse: there are pustulate, cerebriform-lobate, and spatulate-foliose basidiocarps of colours ranging from transparent yellow to dark brown; clamped and clampless hyphal septa; cylindrical to narrowly ovoid basidiospores; and different variations of dendroid hyphidia, either having thickened bases and thin apical parts or almost evenly wide throughout their length. We do not describe most of the aforementioned taxa as new species considering the scanty material and other reasons laid out in the notes and Discussion.

Key and identification table

The presence of branched hyphidia is one of the most prominent microscopic features in dacrymycetes. In the key below we address all the groups known to have this character, while still focusing on *Dendrodacrys* and species that are easy to confuse with them. We provide references when material was not studied by us personally or was better described elsewhere. A summary of the diagnostic characters of *Dendrodacrys* is presented in Table 2.

1. All or at least a fraction of basidiospores ovoid to ellipsoid	2
1. All basidiospores cylindrical-allantoid and slightly curved	7
2. Basidia unisterigmate	<i>Unilacryma unisporea</i>
2. Basidia bisterigmate	3
3. Mature basidiospores often have longitudinal septa (muriform septation)	4
3. Longitudinal septa in mature basidiospores absent or very rare	5
4. Basidiocarps bright yellow to orange, hyphidia simple or weakly branched, hyphal septa always clamped, basidiospores ovoid to ellipsoid, $Q' = 1.1-1.6$	<i>Dacrymyces ovisporus</i>
4. Basidiocarps brown, hyphidia well branched, on internal hyphae both clamped and simple septa present, basidiospores ellipsoid, more rarely cylindrical-allantoid, $Q' = 1.4-2.4$	<i>Unilacryma bispora</i>
5. Basidiospores narrowly ovoid to narrowly ellipsoid, $Q' = 1.2-2.2$, up to 1-septate	<i>Dendrodacrys ellipsosporum</i>
5. Basidiospores ellipsoid to cylindrical-allantoid, $Q' = 1.6-2.5$, up to 3-septate	6
6. Basidiocarps pustulate to applanate, from yellow and dull orange to orange brown, up to 1.2 mm diam, rarely coalescing. Known from Europe	<i>Dendrodacrys oblongisporum</i>
6. Basidiocarps pulvinate to cerebriform, from brown to dark reddish brown and black, coalescing up to 1.2 cm in length. Known from Venezuela	<i>Dendrodacrys</i> sp. 4
7. Hyphal septa mostly or always simple	8
7. Hyphal septa always clamped	13
8. Most hyphal septa simple, but elongated medallion-like clamps occur in subhymenium. Mature basidiospores aseptate or very rarely 1-septate	<i>Dacryonaemataceae</i> (Zamora & Ekman 2020)
8. All hyphal septa simple. Mature basidiospores have more than one septum	9
9. Mature basidiospores more than 3-septate	<i>Dacrymyces san-augustinii</i> s.l. (McNabb 1973, Shirouzu <i>et al.</i> 2009)
9. Mature basidiospores up to 3-septate	10
10. Basidiocarps sessile, pustulate, thin, up to 1 mm diam when dried, almost transparent to yellowish white	<i>Dendrodacrys dendrocalami</i>
10. Basidiocarps stalked, usually higher than 5 mm, coloured	11

11. Fertile areas yellow to yellowish brown, basidiocarp stipe bears one or many pulvinate heads, basidiospores have attenuated ends *Dendrodacrys brasiliense*
11. Fertile areas brown to vinaceous brown, basidiocarps stiped cupulate to foliaceous, basidiospores have rounded ends 12
12. Basidiocarps long-stalked and deep cupulate. Stem hirsute to strigose, especially towards the base, whitish to orange brown, lighter than the hymenium *Dacryopinax elegans* s.l. (McNabb 1965a, Castro-Santiuste *et al.* 2020)
12. Basidiocarps short-stalked, spatulate, shallow cupulate, foliaceous. Stem tomentose and of the same colour as hymenium *Dendrodacrys* sp. 1
13. Mature basidiospores aseptate or extremely rarely 1–3-septate *Cerinomycetaceae* (Savchenko *et al.* 2021)
13. Mature basidiospores have 3 or more septa 14
14. Mature basidiospores up to 7-septate, hyphidia only weakly branched or simple *Dacryomyces nigrescens* (McNabb 1973)
14. Mature basidiospores up to 3-septate, hyphidia well branched 15
15. Basidiocarps with white hirsute stalk or margin. Known from South America *Dendrodacrys pezizoideum*
15. Basidiocarp stalk or margin not distinguished in colour 16
16. Mature basidiocarps early coalesce to form thin resupinate masses (< 2 mm thick) 17
16. Mature basidiocarps often remain solitary, develop more robust thick aggregations if coalesce 18
17. Aggregations display shapes of fused pustulate basidiocarps, remain orange brown and relatively light coloured when dry. Clamps on internal hyphae of regular shape. Conidia cylindrical, 5.0–7.0 × 2.0–3.0 µm. Known from Europe *Dendrodacrys conrescens*
17. Aggregations are slightly cerebriform, become dark reddish brown when dry. Clamps on internal hyphae often swollen. Conidia cylindrical to ellipsoid, 2.9–3.6 × 1.2–1.8 µm. Known from French Polynesia *Dendrodacrys paraphysatum*
18. Basidiocarps remain yellow even when dry. Yellow carotenoid contents conspicuous in hyphae. Crystals present *Dendrodacrys laetum*
18. Basidiocarps become light brown to black upon drying. Pigments in hyphae brown if present. Crystals absent 19
19. Basidiocarps pustulate to pulvinate, applanate, and discoid, < 5 mm in the longest dimension 20
19. Basidiocarps vary in shape, from pulvinate and applanate to cerebriform and lobate, ≥ 5 mm in the longest dimension 21
20. Basidiospores 16.4–20.1 × 6.0–8.9 µm. Known from Cyprus *Dendrodacrys ciprense*
20. Basidiospores 13.0–15.5 × 5.0–6.1 µm. Known from Puerto Rico *Dendrodacrys* sp. 3
21. Basidiocarps light brown when fresh, dark brown when dry, cerebriform to lobate. Coalesce infrequently. Known from Japan *Dendrodacrys rigorum*
21. Basidiocarps dark brown when fresh, almost black when dry, pulvinate to cerebriform. Can coalesce into masses several cm long and a few mm thick. Known from South and Central America *Dendrodacrys kennedyae* and *Dendrodacrys* sp. 2

Taxonomy

Dendrodacrys brasiliense (Lloyd) A. Savchenko, Shirouzu & J.C. Zamora, **comb. nov.** MycoBank MB 844755. Figs 2A, 3.

Basionym: *Dacryopsis brasiliensis* Lloyd, *Mycol. Writings* **V** (60): 874. 1919.

Synonyms: *Ditiola brasiliensis* (Lloyd) McNabb, *New Zealand J. Bot.* **4**: 551. 1966.

Calocera arborea Shirouzu, *Mycoscience* **54**: 253. 2013.

Typus: **Brazil**, Bahia, *C. Torrend* 377, Lloyd cat. 33552 (**lectotype** BPI703017!)

Description: *Basidiocarps* firm-gelatinous when fresh, scattered or in groups on decorticated wood, prominently stipitate, stipe simple cylindrical or with short branches at the top, carrying pulvinate to slightly cerebriform caps, up to *ca.* 1 cm in total height (*vide* Shirouzu *et al.* 2013b), stipe with slightly roughened

surface, cap smooth, when fresh brownish yellow at base and getting gradually yellow towards caps, when dry brown to dark brown. *Hyphae* clampless. Stem organised in three zones: internal, of densely arranged hyphae mostly parallel to the main axis, 1.1–3.5 µm diam, with walls up to 1 µm in width and agglutinated gelatinous layer up to 6 µm in width, with some hyphae extending towards surface; medial, of loosely interwoven anastomosing hyphae 1.8–2.4 µm diam, with thin walls and smooth or roughened gelatinous layer, radiating from the central core; external, narrow and dense coat layer, of simple to branched cylindrical hyphal endings up to 1.2 µm diam with thin walls, mixed with clavate hairs up to 3.5 µm diam, thick-walled and gelatinized. Subhymenial hyphae similar to medial, but less gelatinized and usually smooth. *Hymenium* consists of basidia and slender dendroid hyphidia 1.1–2.7 µm diam, width decreases from the base towards the top, either abruptly or gradually, up to 90 µm in length, thin-walled, sometimes growing through collapsed basidia. *Basidia* 13–58 × 3.0–7.0 µm

Table 2. Summary of morphological characters for *Dendrodacrys* taxa. Notable characters marked with bold font. In the basidiospore description, “small” and “large” mean < 5 mm or ≥ 5 mm respectively and refer to singular, not coalesced, mature basidiocarps.

Group	Taxon	Basidiocarp shape	Basidiocarp colour	Clamps	Basidiospore shape	Basidiospore size, µm	Basidiospore septa number	Q	Conidia size, µm	Region	Additional notes
clampless hyphae	<i>Dendrodacrys brasiliense</i>	stipitate with pulvinate heads , large, sparsely gregarious	yellow to brown	no	cylindrical, both ends often tapered	(9.1–)9.8–13.7(–15.4) × (3.1–)3.2–4.6(–5.2)	3	2.4–3.7		South America	Basidiospore distal end often includes solidified contents
	<i>Dendrodacrys dendrocalami</i>	pustulate, small, gregarious	almost transparent to yellowish white	no	cylindrical, both ends often tapered	(17.0–)17.7–23.0(–23.1) × (5.7–)5.9–7.3(–7.5)	3	2.6–3.9		East Asia	The thickest basidiospore walls in the genus (≤ 1 µm)
	<i>Dendrodacrys</i> sp. 1	stipitate, spatulate, shallow-cupulate, and foliaceous , large, sparsely gregarious	reddish or vinaceous brown	no	cylindrical	(12.1–)13.0–16.4(–16.8) × (5.4–)5.5–6.8	3	1.9–2.8		South America	Dense hymenium. Bases of hyphidia embedded in thick gelatinous layer (≤ 1 µm)
ellipsoid spores	<i>Dendrodacrys ellipso sporum</i>	pustulate to slightly pulvinate and applanate, small, gregarious	orange yellow to brown	yes	narrowly ovoid to narrowly ellipsoid	13.9–25.7(–26.8) × (7.0–)9.7–14.2(–15.5)	1(–3)	1.2–2.2	5.0–6.0 × 2.0–2.5	Southern Europe	Some of the largest basidiospores in the genus
	<i>Dendrodacrys oblongisporum</i>	pustulate to slightly pulvinate, small, gregarious	orange yellow to brown	yes	ellipsoid to cylindrical	13.5–18.5(–19.0) × 6.3–9.4	3	1.6–2.4		Europe	
	<i>Dendrodacrys</i> sp. 4	pustulate to cerebriform, small, sparsely gregarious to coalescing	brown to dark reddish brown and almost black	yes	ellipsoid to cylindrical	(11.8–)12.3–15.1(–15.6) × (5.8–)6.0–7.6(–7.9)	3 + very rarely transverse	1.6–2.5	1.5 × 1.5?	South America	Wide gelatinous layer on subhymenial hyphae (≤ 5 µm)
cylindrical spores	<i>Dendrodacrys ciprense</i>	pustulate to slightly pulvinate and applanate, small, gregarious	light orange brown to brown	yes	cylindrical	(13.6–)16.4–20.1 × (5.5–)6.0–8.9	3	2.2–3.2		Southern Europe	Conspicuously brown-pigmented hyphae present
	<i>Dendrodacrys con crescens</i>	pustulate to slightly pulvinate, small, usually coalesced	yellow and orange to orange brown	yes	cylindrical	12.0–16.2(–18.1) × 4.8–6.3	3	2.0–3.3	5.0–7.0 × 2.0–3.0	Northern Europe	
	<i>Dendrodacrys kennedyae</i>	pulvinate and centrally depressed to cerebriform, large, sparsely gregarious to coalescing	dull yellow to dark brown and almost black	yes	cylindrical	13.1–15.1(–15.4) × (5.3–)5.4–6.6(–6.8)	3	2.2–2.6		Central America	

Table 2. (Continued).

Group	Taxon	Basidiocarp shape	Basidiocarp colour	Clamps	Basidiospore shape	Basidiospore size, μm	Basidiospore septa number	Q	Conidia size, μm	Region	Additional notes
cylindrical spores	<i>Dendrodacrys laetum</i>	pustulate to cerebriform, large, sparsely gregarious to coalescing	yellow	yes	cylindrical	(13.5–)14.9–18.0(–19.1) \times (5.5–)5.7–6.8(–7.0)	3	2.1–3.2	3.6–4.7 \times 1.1–1.6	Africa	Microscopic crystals
	<i>Dendrodacrys paraphysatum</i>	pustulate to cerebriform, small, usually coalesced	orange yellow to dark reddish brown	yes	cylindrical	12.6–16.0(–18.2) \times (5.1–)5.2–6.7(–6.8)	3(–4)	2.0–3.0	2.9–3.6 \times 1.2–1.8	Southern Pacific	
	<i>Dendrodacrys pezizoideum</i>	resupinate to short-stalked , large, coalescing	from light yellow to reddish brown, with distinct white margin	yes	cylindrical	(11.7–)11.8–17.0(–17.7) \times (3.9–)4.0–6.0(–6.2)	3	2.3–3.4	3.0 \times 1.0	South America	Dimorphic basidiocarps
	<i>Dendrodacrys rigoratum</i>	pulvinate to lobate-cerebriform, large, sparsely gregarious	light yellowish brown to dark reddish brown	yes	cylindrical, proximal end often tapered	(15.7–)15.8–19.6(–20.0) \times (5.8–)5.9–7.9	3(–5)	2.3–2.9		East Asia	Strong change in colour from light to dark when drying. Clamps on hyphidia sometimes unfinished
	<i>Dendrodacrys</i> sp. 2	pustulate to cerebriform, large, gregarious to coalescing	reddish brown to almost black	yes	cylindrical	(10.8–)11.4–15.3(–15.4) \times (4.5–)4.7–5.9(–6.2)	3	2.0–3.2	3.3–5.1 \times 1.0–1.6	South America	Conspicuously brown-pigmented hyphae present
	<i>Dendrodacrys</i> sp. 3	pustulate to applanate and centrally depressed, small, gregarious to coalescing	pale yellow to brown	yes	cylindrical	(12.6–)13.0–15.5(–16.0) \times (4.7–)5.0–6.1(–6.3)	3	2.2–2.9		Caribbean	Clamps on hyphidia sometimes unfinished

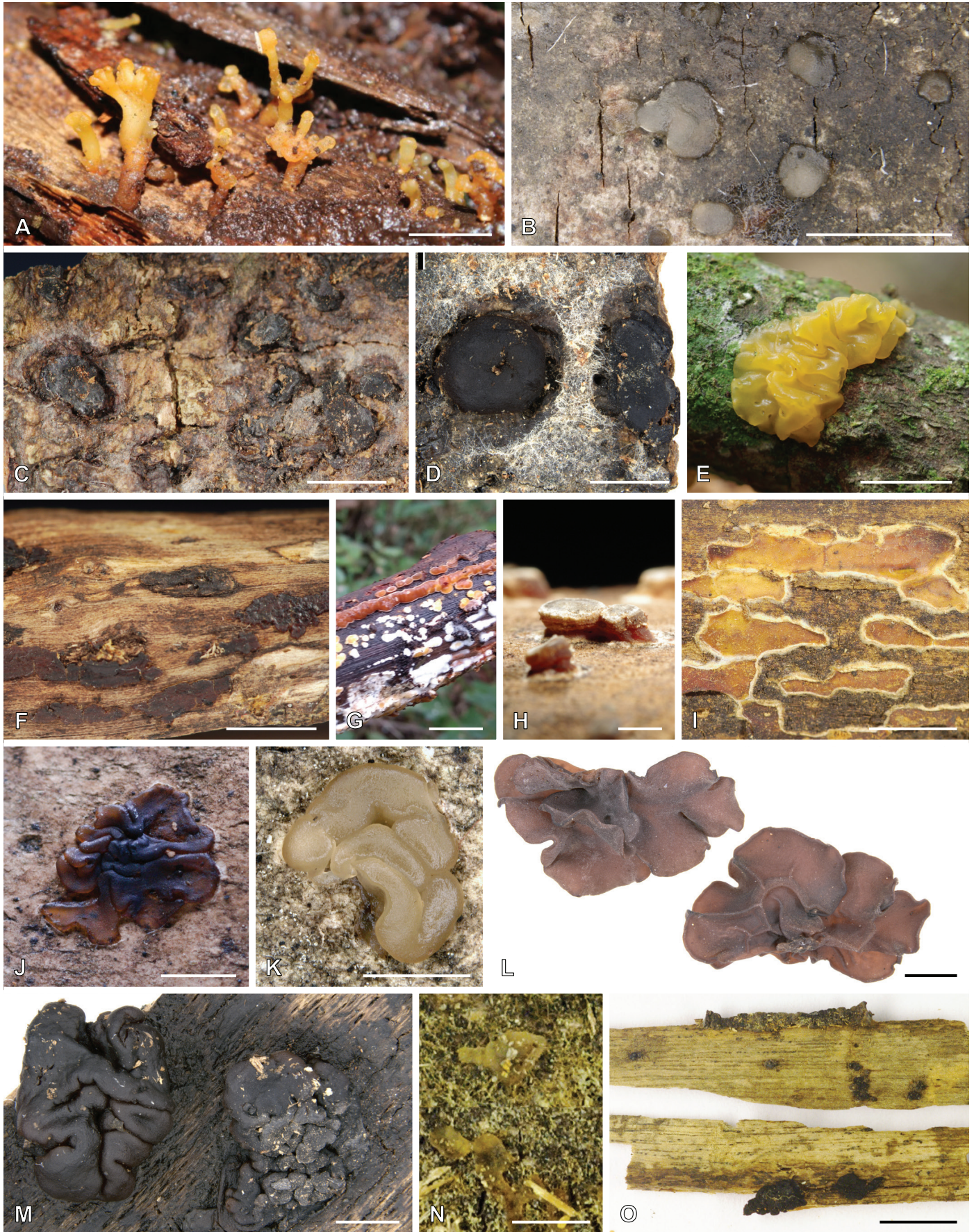


Fig. 2. Basidiocarps of *Dendrodacrys* species. **A.** *De. brasiliense*, RLMA487, fresh. **B.** *De. dendrocalami*, TNS-F-38903, rewetted. **C.** *De. kennedyae*, TAAM192134, dry. **D.** Same species, NY03684200, rewetted. **E.** *De. laetum*, TUF135263, fresh. **F.** *De. paraphysatum*, NY00738304, dry. **G.** *De. pezizoideum*, RLMA425, fresh. **H.** Same species, FH00304806, stalked basidiocarps, dry. **I.** Same species, S: F250650, resupinate basidiocarps, dry. **J.** *De. rigoratum*, TNS-F-21045, dry. **K.** Same species and specimen, rewetted. **L.** *Dendrodacrys* sp. 1, RLMA308, same basidiocarp from fertile and sterile side, dry. **M.** *Dendrodacrys* sp. 2, TAAM192132, rewetted and dry basidiocarps. **N.** *Dendrodacrys* sp. 3, K(M): 141170, dry. **O.** *Dendrodacrys* sp. 4, K(M): 64214, dry, singular and coalesced basidiocarps. Scale bars: A, C, E–G, I, O = 5 mm; B, D, H, J–N = 2 mm.

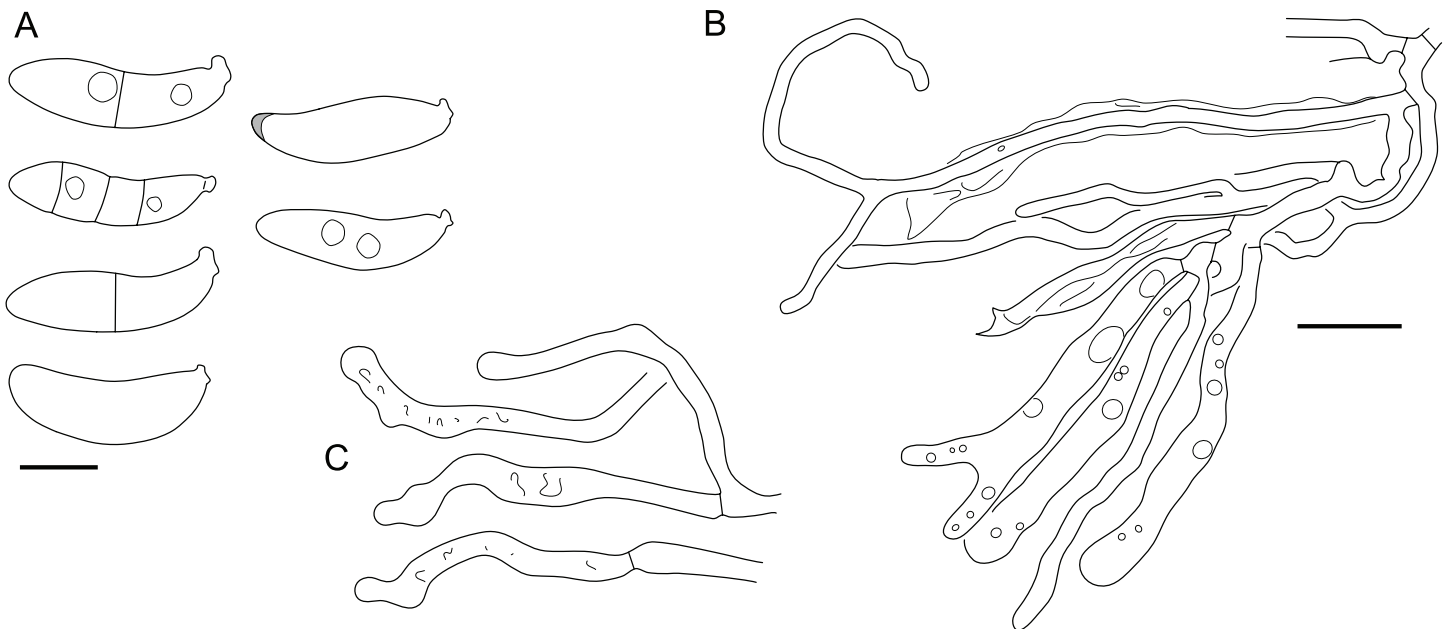


Fig. 3. *Dendrodacrys brasiliense* micromorphology. **A.** Basidiospores. **B.** Basidia, basidioles, and hyphidium growing through a collapsed structure. **C.** Marginal hyphae. Drawn from RLMA486, AMO766. Scale bars: A = 5 μ m; B, C = 10 μ m.

($n = 80/3$), often contain multiple droplets, two sterigmata up to 69 μ m in length. *Basidiospores* cylindrical and slightly curved or rarely sigmoid, often slightly tapered from both ends, up to 3-septate, $(9.1\text{--}9.8\text{--}13.7\text{--}14.1) \times (3.1\text{--}3.2\text{--}4.6\text{--}5.2)$ μ m, $L = 11.6$ μ m, $W = 3.8$ μ m, $Q = 3.1$, $Q' = 2.4\text{--}3.7$ ($n = 82/3$), contain lipid droplets, walls < 0.5 μ m in width, attenuated distal end often includes solidified contents (Fig. 3A, upper right). Basidiospore germination not seen.

Habitat and distribution. The species is known from South America (Brazil), growing on angiosperm wood.

Material examined: **Brazil**, Alagoas, Quebrangulo, Reserva Biológica de Pedra Talhada, 30 Apr. 2018, *R. Alvarenga*, RLMA486* (URM 94627, TUF135215), RLMA487* (URM 94628, TUF135216); Bahia, *C. Torrend*, 414 (BPI702671); Rondônia, Porto Velho, Parque Natural Municipal de Porto Velho, 14 Jan. 2017, *A. Meiras-Ottoni*, AMO766 (URM 94604, TUF135193).

Notes: The pronounced stipe and pulvinate to cerebriform head distinguish basidiocarps of *De. brasiliense*, even though the length of stipe varies from few mm to more than a cm. Together with dendroid hyphidia and tapered spores it makes the species easily recognizable among all dacrymycetes. In several studied specimens we observed that droplets in basidiospores often merge into clots of refractive matter that can alter spore shape or obscure walls, making microscopy more difficult. Protein-coding genes and nrDNA sequences diverge between the specimens, but we could not detect morphological characters to separate these putative species. More sequenced specimens will be needed to make the division justified, and as our data is limited, we prefer to treat the genetic differences as intraspecific variation.

We synonymize *Calocera arborea* to *De. brasiliense* based on the identical morphology of the two species and our material (Shirouzu *et al.* 2013b). Even though the lectotype of *De. brasiliense* displays basidiocarps with shorter stems, all other characters closely resemble *C. arborea* and do not occur

in any other dacrymycete species. Lloyd compared *Dacryopsis brasiliensis* with another of his species, *Dacryomitra depallens*, but the latter develops dacrymyces-like basidiocarps on short stipes and widely cerebriform caps that completely cover the stipes when wet (Lloyd & Stevenson 1919, McNabb 1965b). The name *Dacryomitra cudonia* Bres. (1896) was another possible option for our material, but the type contains small dark brown basidiocarps with short stipes ~ 1 mm in height and discoid to cerebriform caps, looking more like a conventional *Dacrymyces* species. It lacks hyphidia, possesses clampless septa, and has generally smaller microstructures than in *Dendrodacrys* (Brazil, Blumenau, A. Möller no. 24b [or 246?] [holotype S: F19792!]). Lastly, *Coryne gyrocephala* Berk. & Curt. (1849) can be potentially related to the discussed species, but it lacks dendrohyphidia and was collected in North America. Kennedy (1964) and McNabb (1966) worked with types of both *D. brasiliensis* and *C. gyrocephala* and kept them as separate taxa.

Dendrodacrys dendrocalami (Oberw.) A. Savchenko & J.C. Zamora, **comb. nov.** MycoBank MB 844090. Figs 2B, 4.

Basionym: *Dacrymyces dendrocalami* Oberw., *Trans. Mycol. Soc. Japan* **30**: 350. 1989.

Typus: **Taiwan**, Lien-Hua-Chin (?) near Puli, on *Dendrocalamus giganteus*, 26 Mar. 1989, *F. Oberinkler*, *G. Wagner* & *E. Langer*, FO 40725 (**holotype** "in M").

Description. *Basidiocarps* gelatinous when rewetted, growing through cracks of bark in small groups, attached to substrate with a root-like base, sessile, pustulate, with smooth almost amphigenous hymenium, up to 1 mm in the longest dimension when dried; almost transparent to yellowish white or pale yellow in both rewetted and dried state. *Hyphae* clampless. Internal hyphae 2.3–3.3 μ m diam, with slightly gelatinized, smooth or finely roughened walls 0.5–0.8 μ m wide. Subhymenial hyphae of the same type, but with thin smooth walls. Marginal hyphae infrequent, 1.8–4.2 μ m at terminal parts, cylindrical to clavate, sometimes with a pronounced thin long apical part, rarely

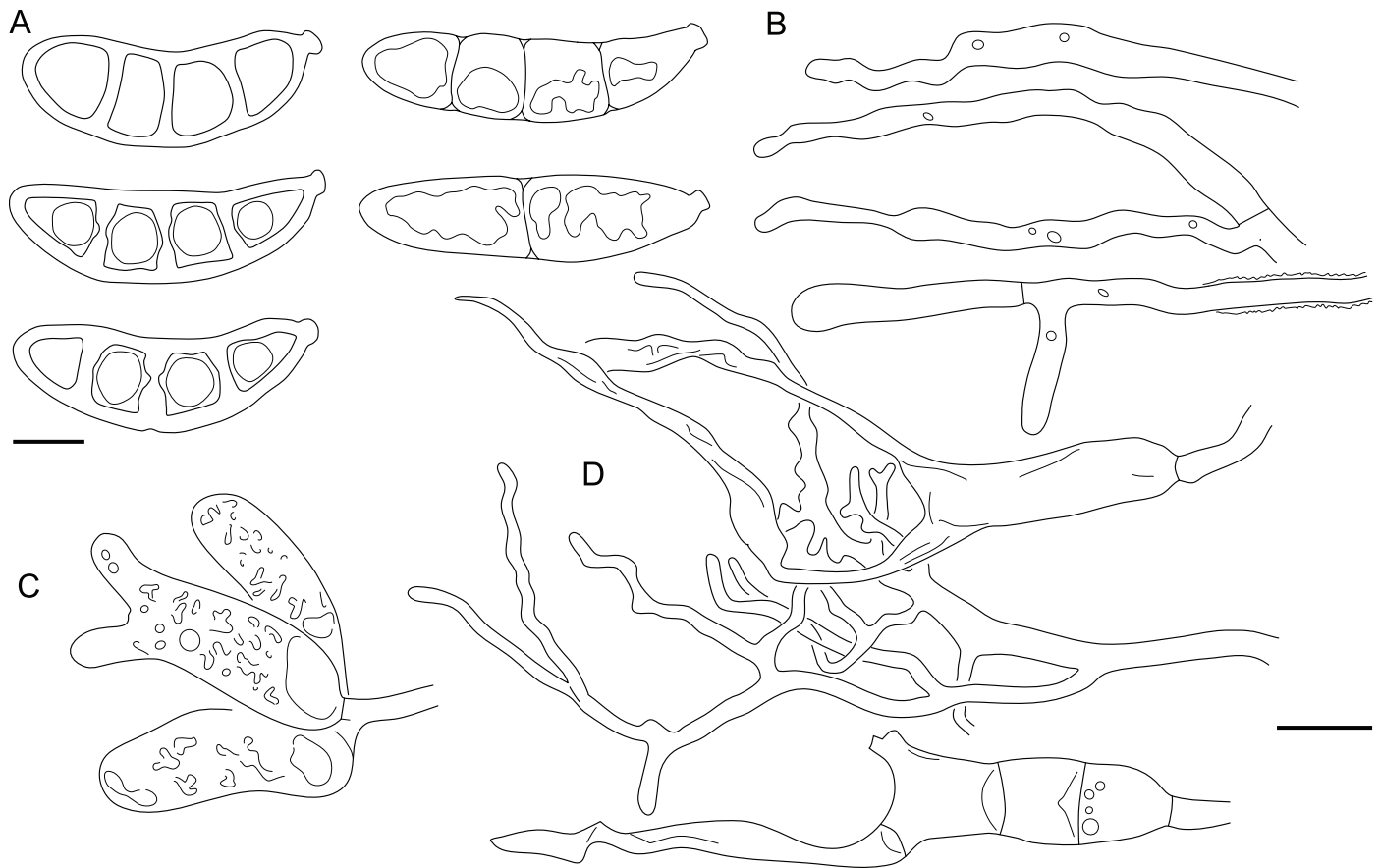


Fig. 4. *Dendrodacrys dendrocalami* micromorphology. **A.** Basidiospores. **B.** Marginal hyphae. **C.** Basidioles. **D.** Basidia (one collapsed and with secondary septa) and hyphidia. Drawn from TNS-F-38903. Scale bars: A = 5 μ m; B–D = 10 μ m.

branched, but often slightly wavy, with thin and smooth walls. *Hymenium* includes frequent dendroid hyphidia 1.4–3.2 μ m diam, getting gradually thinner from the base towards the top, up to 90 μ m in length, thin-walled, often with a few clamps throughout the length, branches abundant and long. Young *basidia* wide cylindrical, up to 10 μ m diam, with numerous lipid droplets, relatively thin-walled; mature basidia of the same shape or widely clavate to obclavate, 25–34 \times 5.8–10.0 μ m ($n = 20/1$), with walls thickening towards the base. Two sterigmata 27–62 μ m in length, normally longer than basidia. *Basidiospores* cylindrical, slightly curved, both ends usually slightly tapered, up to 3-septate, (17.0–)17.7–23.0(–23.1) \times (5.7–)5.9–7.3(–7.5) μ m, $L = 20.3$ μ m, $W = 6.6$ μ m, $Q = 3.1$, $Q' = 2.6$ –3.9 ($n = 30/1$), walls 0.5–1.0 μ m in width. Basidiospore germination not seen.

Habitat and distribution: The species is known from East Asia (Japan, Taiwan), growing on angiosperm wood (*Dendrocalamus*, *Parabenzoin*).

Material examined: **Japan**, Nara, Mt. Tamaki, on dead branch of *Parabenzoin trilobum*, 4 Jul. 2009, T. Shirouzu, HNo.888 (TNS-F-38903, culture TUFC13914).

Notes: Among dacrymycetes this species stands out with light-coloured or almost transparent basidiocarps, stout basidia, and thick-walled basidiospores attenuated from both ends (the thickest basidiospore walls seen in all of *Dendrodacrys*). The other two taxa in the genus with similarly clampless septa, *De. brasiliense* and *Dendrodacrys* sp. 1, have prominently stalked basidiocarps and are known only from South America. The

studied specimen TNS-F-38903 agrees well with the protologue of *De. dendrocalami* (Oberwinkler & Tschern 1989). Those authors state that the holotype is in the M herbarium (Botanische Staatssammlung München), but we could not trace it there nor in TUB, KAS, or TNM (respective pers. comms. with D. Triebel of 31 Jan., U. Grünert of 8 Feb., A. Ordynets of 9 Feb., S.-H. Wu of 13 Feb., all in 2022). Besides, the original page mentions the ex-type strain, but it was not found among F. Oberwinkler's cultures from the University of Tübingen that were transferred to DSMZ – German Collection of Microorganisms and Cell Cultures GmbH (pers. comm. with A. Yurkov of 19 Apr. 2022). Usually, we would put off raising a new combination without seeing a type, but in this case the original description permits unambiguous identification. We do not attempt to neotypify the species, hoping that missing specimens of F. Oberwinkler will eventually resurface.

Dacrymyces dendrocalami often shows a palisade layer of swollen young basidioles. To rule out that this feature is common in other known species, we compared the species to *Arrhytidia pustulata*, *Da. nigrescens*, and *Da. coryneoides*, for which McNabb (1973) mentioned that many basidia are “replaced” with thick-walled clavate structures. We studied types of the first two taxa and found them unlikely to be related to *De. dendrocalami*. *Arrhytidia pustulata* lacks hyphidia and has smaller basidiospores, up to 5-septate (holotype FH00304800!, isotype BPI726047!). *Dacrymyces nigrescens* (holotype LSU00135947!) and *Da. coryneoides* produce up to 7-septate spores, and the latter has only infrequent hyphidia that are all simple. European *Da. estonicus* is also distinguished by basidia with thickened base, but the hourglass shape of its basidia and absence of hyphidia clearly tell it apart.

Dendrodacrys kennedyae A. Savchenko, **nom. & stat. nov.** MycoBank MB 844094. Figs 2C, D, 5.

Basionym: *Dacrymyces enatus* var. *macrosporus* L.L. Kenn., *Mycologia* **50**: 902. 1959.

Etymology: In honour of Lorene L. Kennedy, a North American mycologist.

Typus: **Panama**, Canal Zone, Barro Colorado Island, on angiosperm wood, 23 Aug. 1952, G.W. Martin & A.L. Welden, 8662 (**holotype** BPI725717! ex IA, **isotypes** NY03684200!, LSU00135945!, TAAM192134*!).

Description. *Basidiocarps* gelatinous to firm-gelatinous when rewetted, growing through bark with short rooted base, first pustulate, then pulvinate and centrally depressed, flattened, or cerebriform, with smooth surface, up to 6 mm in the longest dimension when dried, coalescing to many cm (*fide* Kennedy 1958); dull yellow to chestnut brown when fresh (*fide* Kennedy 1957), when dried becoming light brown in young basidiocarps to black or reddish black in older ones. *Hyphae* clamped. Internal hyphae parallel and agglutinated, 2.0–5.2 μm diam, walls together with gelatinous layer up to 1 μm wide. Subhymenial hyphae 2.0–4.4 μm diam, walls 0.6–0.8 μm wide. Margins covered with sterile cylindrical, clavate, or of irregular shape hyphae 3–5(–7) μm diam, with gelatinized walls 0.7–2.0 μm wide. *Hymenium* includes abundant finely branched hyphidia, evenly wide or slightly wider at the base, 1.3–1.6 μm diam, up to 90 μm in length. *Basidia* 31–66 \times 3.5–7 μm ($n = 30/1$), sometimes with slightly thickened walls in the base, developing secondary septa, two sterigmata up to 42 μm in length. *Basidiospores* cylindrical, slightly curved, up to 3-septate, 13.1–15.1(–15.4) \times (5.3–)5.4–6.6(–6.8) μm , $L = 14.1$ μm , $W = 5.9$ μm , $Q = 2.4$, $Q' = 2.2$ –2.6 ($n = 30/1$), walls ≤ 0.5 μm in width. Basidiospore germination not seen.

Habitat and distribution: The species is known only from the type locality in Central America (Panama), growing on angiosperm wood.

Notes: The taxon was first proposed as *Da. enatus* var. *brunnescens* (Kennedy 1957), and later effectively published as *Da. enatus* var. *macrospora* (Kennedy 1958b). We prefer to use another epithet to celebrate the work of the taxon's author, L.L. Kennedy, who made significant contributions to the systematics of dacrymycetes.

This species can be identified by pulvinate to centrally depressed or slightly cerebriform basidiocarps becoming dark brown at maturity, with a potential to coalesce into masses of many cm in length. A similar *Dendrodacrys* sp. 2 tends to produce slightly shorter basidiospores and basidia.

Basidiocarps in most type specimens are surrounded with arachnoid clampless sterile mycelium that probably was growing during specimen drying. Boundaries of this mycelium mark the extent from which fresh *De. kennedyae* basidiocarps shrunk down to their current state, implying *ca.* 0.5 mm difference in size (Fig. 2D).

Dendrodacrys laetum A. Savchenko, **sp. nov.** MycoBank MB 844087. Figs 2E, 6.

Etymology: *laetum* (Lat.) – happy, cheerful; referring to the bright colour and presence of crystals.

Typus: **Kenya**, Taita-Taveta, Taita Hills, Ngangao forest, northern part, lat. -3.35311°, lon. 38.33753°, alt. $\sim 1\,820$ m, on angiosperm wood, 23 Nov. 2017, A. Savchenko, 171123/1110 (**holotype** H7008757*!, **isotypes** EA!, TUF135263!).

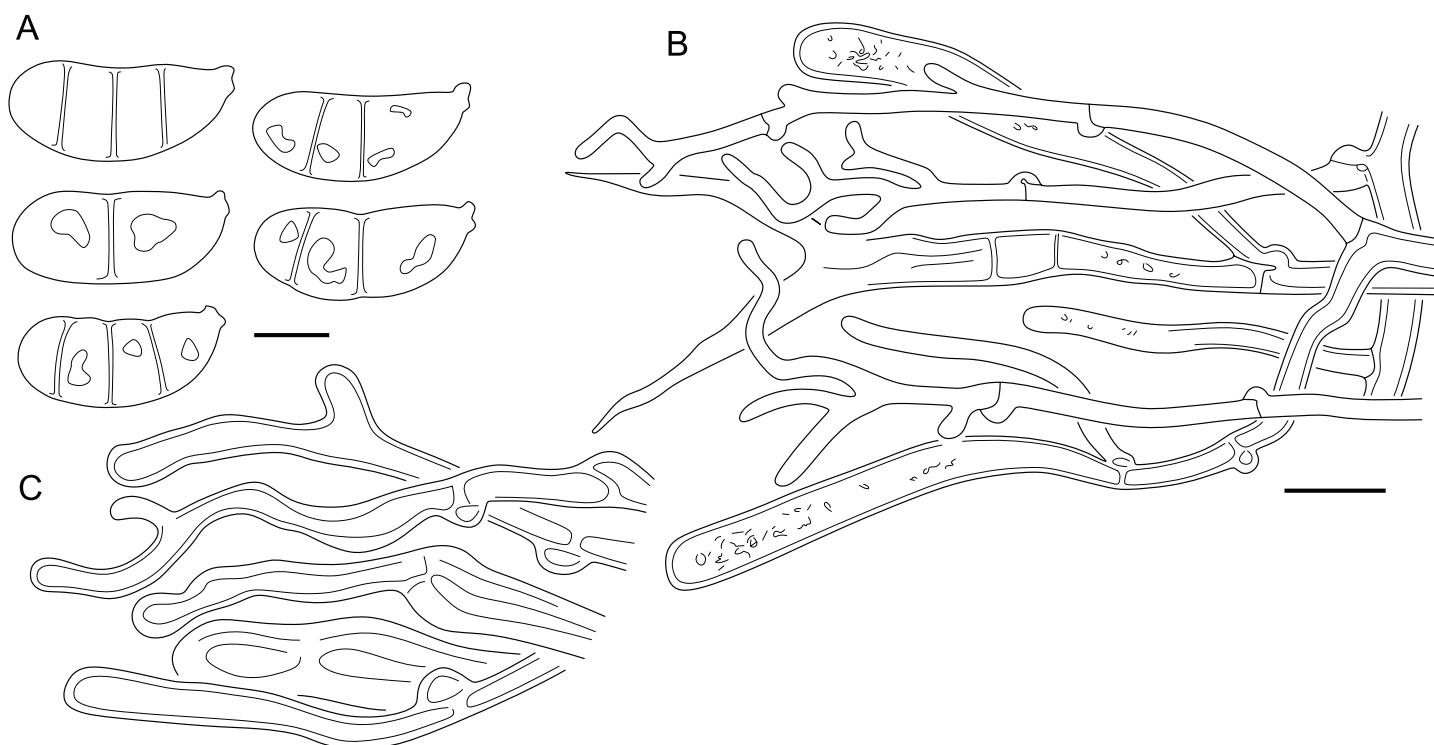


Fig. 5. *Dendrodacrys kennedyae* micromorphology. **A.** Basidiospores. **B.** Basidium, basidioles, and hyphidia. **C.** Marginal hyphae. Drawn from BPI725717. Scale bars: A = 5 μm ; B, C = 10 μm .

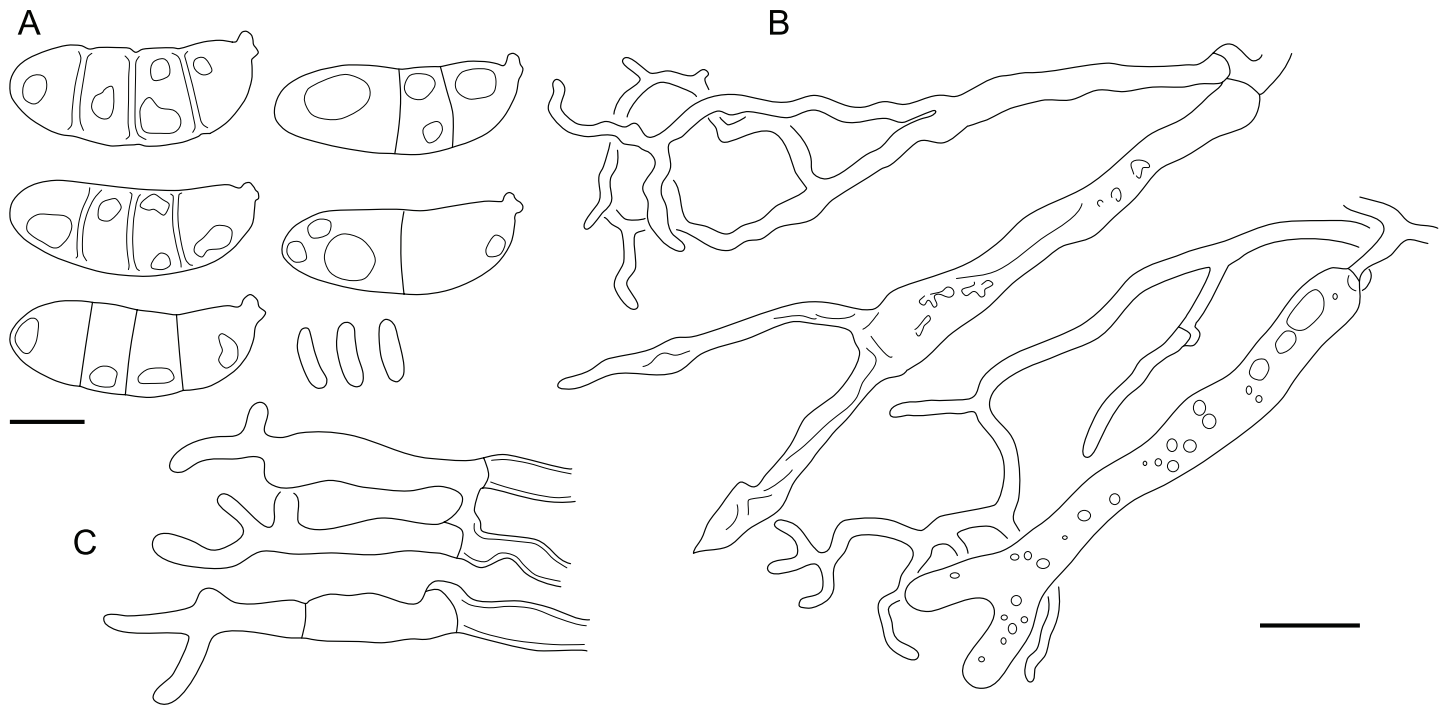


Fig. 6. *Dendrodacrys laetum* micromorphology. **A.** Basidiospores and conidia. **B.** Basidia and hyphidia. **C.** Marginal hyphae. Drawn from TUF135263. Scale bars: A = 5 µm; B, C = 10 µm.

Description: *Basidiocarps* firm-gelatinous when fresh, growing on bark, attached in the central point with a root, first pustulate and applanate, becoming cerebriform, with slightly lobed margin leaning to the substrate, with smooth surface, up to 1.5 cm in the longest dimension when fresh, appearing in sparse groups and coalescing if close; bright yellow when fresh, bleak ochraceous yellow and slightly transparent when dried. *Hyphae* clamped, contain yellow-pigmented drops. Rhomboid or amorphic crystals occur in all parts of basidiocarp. Internal hyphae 2.0–3.0(–4.0) µm diam, with walls ~ 0.5 µm in width, gelatinized; subhymenial hyphae similar. Marginal hyphae of irregular shapes, slightly branched and anastomosing, 2.0–4.0 µm diam, walls ~ 0.5 µm in width, associated with crystals. *Hymenium* includes abundant dendrohyphidia, often deeply branched, in the base 3.0–6.0 µm diam, walls ~ 0.5 µm in width, at the top 1.0–1.5 µm diam, with thinner walls. *Basidia* clavate, 16–38 × 3.9–7.6 µm (n = 45/1), with two sterigmata up to 64 µm in length. *Basidiospores* cylindrical, slightly curved, up to 3-septate, often with lipid drops inside, (13.5–)14.9–18.0(–19.1) × (5.5–)5.7–6.8(–7.0) µm, L = 16.6 µm, W = 6.2 µm, Q = 2.7, Q' = 2.1–3.2 (n = 70/1), walls 0.3–0.5(–0.8) µm in width, germinating with slightly curved-cylindrical *conidia* 3.6–4.7 × 1.1–1.6 µm (n = 10/1).

Habitat and distribution. Known only from the type locality in Africa (Kenya), growing on angiosperm wood.

Notes. The species is distinct by large yellow basidiocarps, branched marginal hyphae, and presence of crystals. Conidia were recorded in close proximity to basidiospores, and we observed spores with conidiogenous scars, but conidia attached to spores were not found. This is the only *Dendrodarys* currently known from Africa.

Dendrodacrys paraphysatum (L.S. Olive) J.C. Zamora & A. Savchenko, *Fungal Syst. Evol.* **9**: 41. 2022. Figs 2F, 7.

Basionym: *Dacrymyces paraphysatus* L.S. Olive, *Bull. Torrey Bot. Club* **85**: 106 (1958).

Typus: French Polynesia, Tahiti, Pirae, trail to Cascades [Fachoda?], on dead limbs of *Citrus limetta*, 8 Apr. 1956, L.S. Olive, T122 [holotype NY00738304!, isotype K(M): 8355].

Description: *Basidiocarps* gelatinous to firm-gelatinous when rewetted, growing on decorticated wood, appearing as small pustules, easily coalescing into resupinate-cerebriform masses, with smooth surface, up to 6 cm in the longest dimension when fresh; from orange yellow when fresh (*vide* Olive, 1958) to dark reddish brown when dried. *Hyphae* clamped. Internal hyphae 2.8–5.1 µm diam, walls with gelatinous layer up to 1.5 µm in width, with occasional hyphal swellings around clamps. Subhymenial hyphae 2.4–3.7 µm diam, with or without thin gelatinous layer. Marginal areas covered with cylindrical to clavate or irregular hyphae, 2.5–4.7(–6.8) µm diam, thin-walled, sometimes heavily gelatinized. *Hymenium* includes conspicuous branched hyphidia 1.5–3.3 µm diam, up to 80 µm in length, getting steadily thinner towards the top, often with several clamps throughout the length, some hyphidia branched only at the top, some branches can be very short. *Basidia* cylindrical to clavate, 39–78 × 3.5–7.2 µm (n = 25/1), with two sterigmata up to 41 µm in length. *Basidiospores* cylindrical, slightly curved, up to 3(–4)-septate, 12.6–16.0(–18.2) × (5.1–)5.2–6.7(–6.8) µm, L = 14.2 µm, W = 5.9 µm, Q = 2.4, Q' = 2.0–3.0 (n = 47/1), walls 0.5–1.0 µm in width. Basidiospores germinate with germ tubes or wide cylindrical *conidia* 2.9–3.6 × 1.2–1.8 µm (n = 12/1, in KOH). Olive (1958) reported conidia 2.7–4.6 × 1.4–2.4 µm.

Habitat and distribution: Known only from the type locality in South Pacific (French Polynesia), growing on angiosperm wood (*Citrus*).

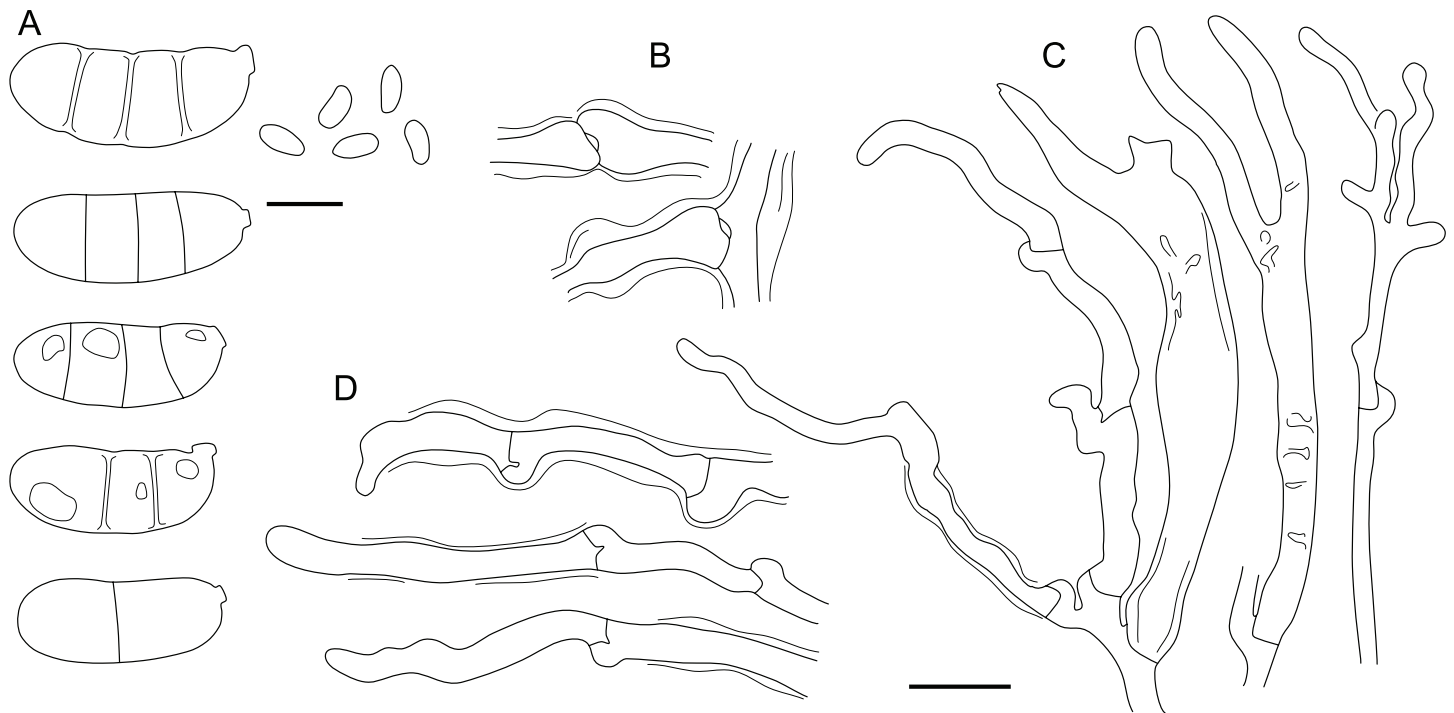


Fig. 7. *Dendrodacrys paraphysatum* micromorphology. **A.** Basidiospores and conidia. **B.** Clamps on internal hyphae. **C.** Basidia (one collapsed) and hyphidia. **D.** Marginal hyphae. Drawn from NY00738304. Scale bars: A = 5 µm; B–D = 10 µm.

Notes: *Dendrodacrys paraphysatum* is notable by thin cerebriform coalescing basidiocarps that in dry state can resemble resupinate gelatinous *Cerinomyces* species such as *C. aeneus*. In contrast to *Cerinomyces*, the former species develops larger basidiospores with up to three or even four septa. *Dendrodacrys conrescens* is most similar to *De. paraphysatum* in basidiocarp type and colour when fresh, but it does not become dark brown upon drying and has longer conidia. Other brown-coloured cerebriform *Dendrodacrys* taxa usually produce thicker basidiocarps that do not coalesce so readily (*De. rigortum*) or become almost black when drying (*De. kennedyae*, *Dendrodacrys* sp. 2).

Dendrodacrys pezizoideum (Henn.) A. Savchenko & Alvarenga, **comb. nov.** MycoBank MB 844092. Figs 2G–I, 8.

Basionym: *Guepinia pezizoidea* Henn., *Hedwigia* **43**: 197. 1904.

Synonyms: *Ceracea rickii* Bres., *Brotéria* **5**: 9. 1906.

Ditiola rickii (Bres.) Bres., *Ann. Mycol.* **18**: 52. 1920.

Femsjonia pezizoidea (Henn.) McNabb, *New Zealand J. Bot.* **3**: 226. 1965.

Typus: **Brazil**, São Paulo, Alto da Serra, Aug. 1902, A. Puttemans, 761 (**lectotype** S:F20949!).

Description: *Basidiocarps* firm-gelatinous when rewetted, appearing as small patches of white mycelium, then pustulate and pulvinate, becoming widely sessile-resupinate or short-stalked, of relatively circular shapes, up to 1.5 cm in the longest dimension, can coalesce to several cm, hymenial surface smooth, slightly convex when fresh, in resupinate basidiocarps flat or concave when dried, from light yellow to orange and reddish brown, stalk and margin fimbriate and white, margin makes a clear outline and appears early. *Hyphae* clamped. Internal hyphae 2.0–4.0 µm diam, walls ~ 0.5 µm in width, gelatinous layer up to 2.0 µm in width. Subhymenial hyphae 2.0–2.5 µm diam, of the same width, less gelatinized. Marginal hyphae

simple cylindrical to slightly clavate or irregularly branched, 2.0–4.0(–6.0) µm diam, walls and gelatinization similar to internal hyphae. *Hymenium* includes abundant frequently branched hyphidia, often occurring in groups, 1.0–3.0 µm diam, getting steadily thinner towards the top, up to 100 µm in length, sometimes with a few clamps throughout the length. *Basidia* cylindrical to clavate 32–65 × 2.5–8 µm (n = 45/4, 15 in CB), with two sterigmata up to 40 µm in length. *Basidiospores* cylindrical, slightly curved, up to 3-septate, (11.7–)11.8–17.0(–17.7) × (3.9–)4.0–6.0(–6.2) µm, L = 13.8 µm, W = 4.9 µm, Q = 2.8, Q' = 2.3–3.4 (n = 63/5), walls < 0.5 µm in width. A single *conidium* was noted germinating from a spore: straight cylindrical, 3.0 × 1.0 µm.

Habitat and distribution: Known from South America (Brazil, Guyana), growing on angiosperm wood (bamboo and unidentified).

Material examined: **Brazil**, Distrito Federal, Taguatinga, Floresta Nacional de Brasília, 12 Jan. 2017, R. Alvarenga, RLMA425* (URM 94345, TUF135190); Rio Grande do Sul, Pareci Novo, 1928, J.E. Rick, 143 (FH00304804), São Leopoldo, on bamboo, 1904, J.E. Rick, 9 (lectotype of *Ceracea rickii*, S:F20231), same loc., on bamboo, no date, J.E. Rick, 28 (S:F20232), no data, J.E. Rick (S:F20233), same loc., on bamboo, J.E. Rick (BPI726062), same loc., on bamboo, 1930, J.E. Rick (FH00304807), Cerro Largo (former Serro Azul), 1928, J.E. Rick, 495 (FH00304806, S:F250650), same loc. and date, J.E. Rick, 413 (FH00304805). **Guyana**, Cuyuni-Mazaruni reg., Koreai Creek, on bamboo, Jan. 1924, D.H. Linder, 708 (FH00304776).

Notes: Basidiocarps of the species vary from flat and resupinate to short-stalked with convex hymenium. Be it margin or stalk, in well-developed dried basidiocarps white hirsute hyphal covering on sterile areas is always visible – a unique feature among *Dendrodacrys* members. Comparable morphology can be found in *Dacrymyces corticioides*, “*Cerinomyces*” *canadensis*, and *Femsjonia* s.s., though all these taxa lack dendrohyphidia.

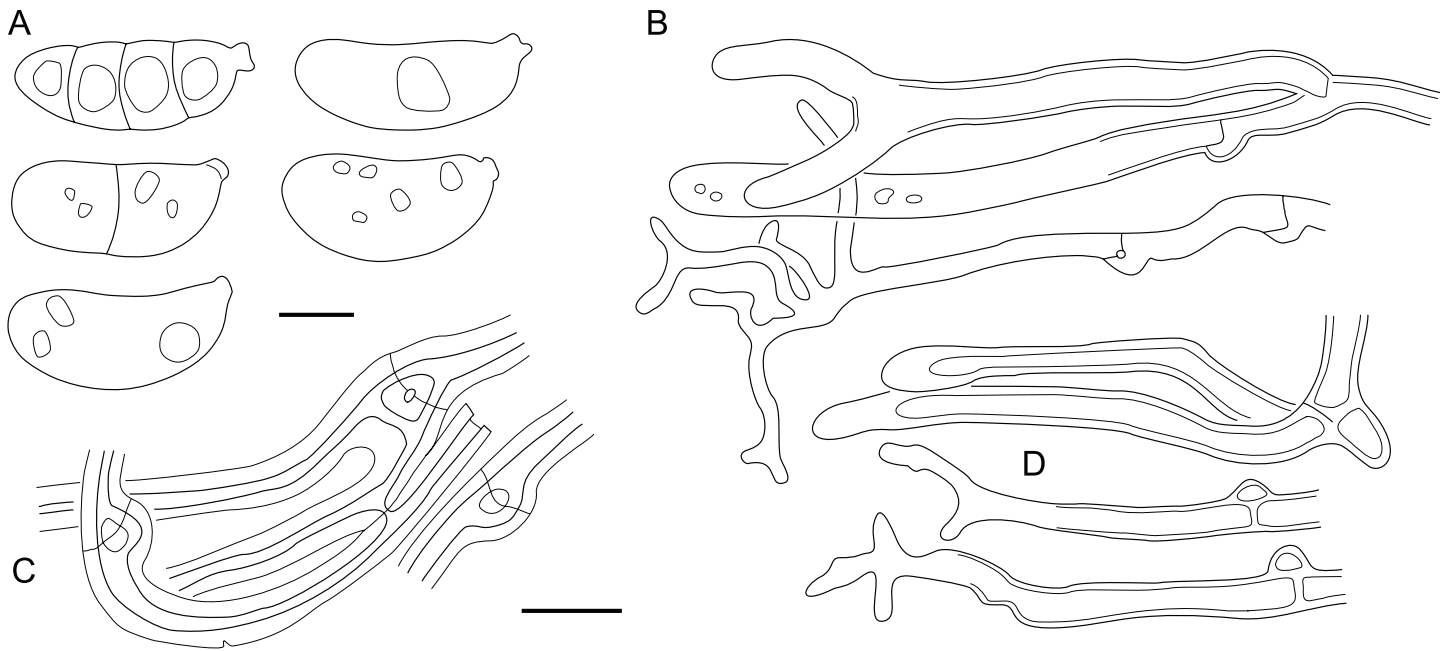


Fig. 8. *Dendrodacrys pezizoidea* micromorphology. **A.** Basidiospores. **B.** Basidium, basidiole, and hyphidium. **C.** Internal hyphae. **D.** Marginal hyphae. Drawn from RLMA425. Scale bars: A = 5 μ m; B–D = 10 μ m.

The holotype of *Guepinia pezizoidea* is scanty and presents slightly immature basidiocarps with underdeveloped margin, but microscopically it conforms to the rich authentic material of *Ceracea rickii*. Hennings (1904) provided a rather accurate description for *G. pezizoidea*, saying that it is “related to *G[uepinia] peziza* Tul. [= *Guepiniopsis buccina*], but completely sessile, slightly tomentose on the outside”.

Among the studied specimens possibly related to *Dendrodacrys* one stood out in that we could not confidently place it the genus. The specimen in question possesses dendroid hyphidia but also aseptate spores and widely resupinate basidiocarps with whitish hirsute margins resembling *De. pezizoidea*. These features would place it somewhere between *Cerinomyces* (with aseptate spores) and *Dendrodacrys* (with hirsute margin). Morphology, measurements, and collection locality did not help to assign it to any known *Cerinomyces* species, and because sequencing attempts of this material failed, the question of its identity remains open (Jamaica, Surrey co., Saint Andrew par., Holywell Park, Fairy Glade Trail, on unidentified wood, 13 Jun. 1999, P.J. Roberts, GA649 [K(M): 116646]).

Extracted from genome assembly, ITS1 of RLMA425 spans ~1500 bp and highly diverges from other dacrymycete sequences, which suggests explanation of the authors’ lack of success in Sanger sequencing of this region. Other genes produced from this sample are also substantially different from the relatives, but never to the extent of ITS1.

Dendrodacrys rigoratum A. Savchenko & J.C. Zamora, *sp. nov.* MycoBank MB 844088. Figs 2J, K, 9.

Etymology: *rigoratum* (Lat.) – provided with rigidity.

Typus: Japan, Kyoto, Mt. Daimonji, on angiosperm branches, 30 Jun. 2006, T. Shirouzu, HNo.355 (**holotype** TNS-F-21045, ex-type cultures TUFC12845, MAFF241172).

Description: *Basidiocarps* firm-gelatinous when fresh, scattered over bark, attached to the substrate with a root-like base that penetrates the bark, almost sessile, from pulvinate to resupinate and cerebriform with slightly lobed margins, with a smooth surface, up to 5 mm in the longest dimension when dried; orange to amber when fresh (Shirouzu *et al.* 2009), light yellowish brown when rewetted to dark brown with reddish tint when dried. *Hyphae* clamped. Internal hyphae 1.7–4.6 μ m diam, walls 0.5–1 μ m wide, often with roughened gelatinous layer; parts of hyphae sometimes swollen up to 11 μ m diam, with thickened wall. Subhymenial hyphae more uniform, 2.4–4.2 μ m diam, with thin walls and thin gelatinous layer. Terminal cells of marginal hyphae cylindrical to clavate or irregular, barely branching, but often slightly wavy, 1.9–5.6(–7.2) μ m diam, walls from thin to thick, heavily gelatinized, often with rich vacuolar content, embedded in tough gelatinous film that covers the basidiocarp. *Hymenium* includes abundant dendroid hyphidia 1.7–4.1 μ m diam getting gradually thinner from the base towards the top, up to 90 μ m in length, thin-walled, often with a few clamps throughout the length, some clamps “unfinished”. Hyphidia mostly well-branched, branches often bent. *Basidia* clavate 35–59 \times 3.4–8.1 μ m ($n = 45/1$), with two sterigmata up to 52 μ m in length. *Basidiospores* cylindrical, slightly curved, proximal compartment often attenuated, up to 3(–5)-septate, (15.7–)15.8–19.6(–20.0) \times (5.8–)5.9–7.9 μ m, $L = 17.3$ μ m, $W = 6.7$ μ m, $Q = 2.6$, $Q' = 2.3$ –2.9 ($n = 43/1$), walls ~0.5(–0.8) μ m in width. Basidiospore germination not seen.

Habitat and distribution. Only known from East Asia (Japan), growing on angiosperm wood.

Notes: Zamora *et al.* (2022) showed a species delimitation analysis separating this material from the related taxa. Here we supplement their findings with a morphological comparison. Accounting for the cerebriform to lobate brown basidiocarps that are light in wet state and dark brown in dry, and up to 5-septate spores with often attenuated proximal part, we do not

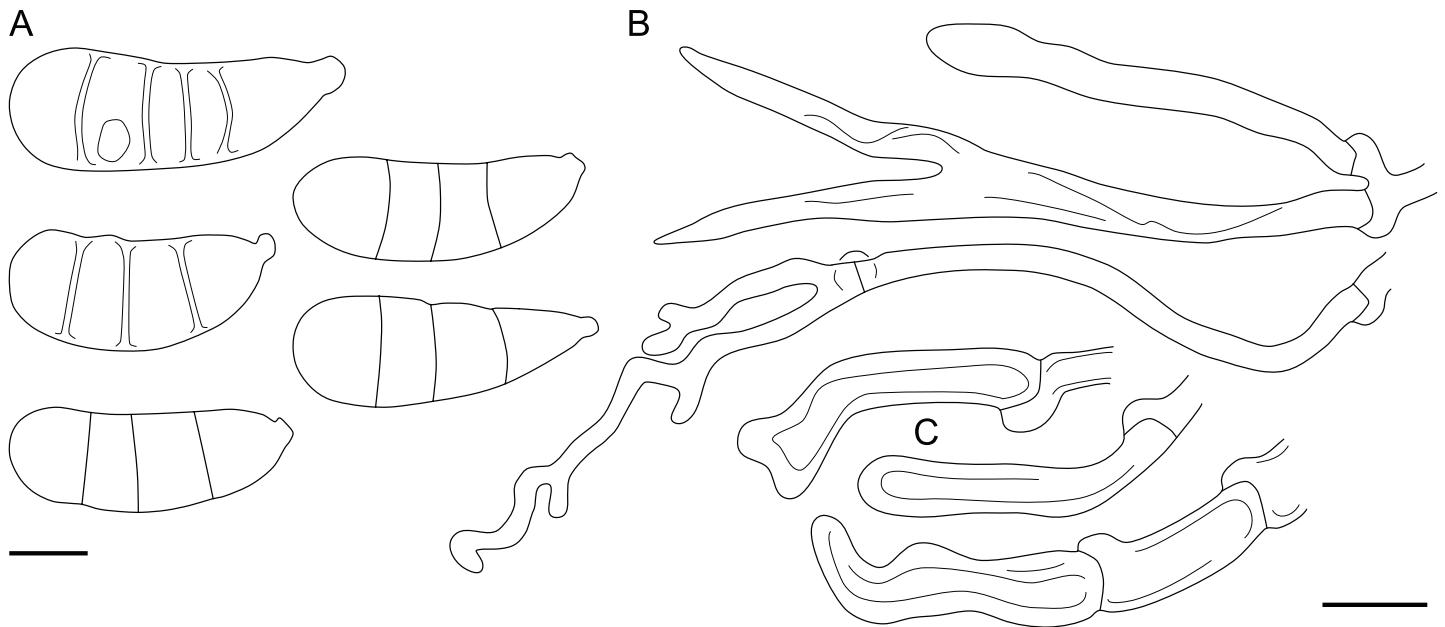


Fig. 9. *Dendrodacrys rigorum* micromorphology. **A.** Basidiospores. **B.** Basidium, basidiole, and hyphidium. **C.** Marginal hyphae. Drawn from TNS-F-21045. Scale bars: A = 5 μ m; B, C = 10 μ m.

know of any published taxon in *Dacrymycetaceae* to which this Japanese material could belong, and therefore designate a new species.

Judging only from its LSU sequence, there is another specimen potentially belonging to this species: Japan, Wakayama, Mt. Shirami, on dead unidentified branches, 12 Oct. 2006, *T. Shirouzu*, HNo.554 (TNS-F-21069). For discussion on that specimen see Zamora *et al.* (2022).

***Dendrodacrys* sp. 1.** Figs 2L, 10.

Description: *Basidiocarp*s firm-gelatinous when rewetted, short-stipitate, first as singular widely-spathulate fronds, then shallow-cupulate and foliaceous, up to 5 mm in height and 1 cm diam; vinaceous brown when rewetted, dark brown when dried. One basidiocarp side bears hymenium, smooth or slightly pruinose

when dried, other one sterile and tomentose, with venous pattern, of the same colour as hymenium. *Hyphae* clampless. Internal hyphae loosely interwoven, 1.7–3.0 μ m diam, with swollen parts up to 7 μ m diam, walls ~ 0.5 μ m wide, gelatinous layer up to 1 μ m wide, smooth or roughened. Subhymenial hyphae similar, without swollen compartments, subhymenial zone narrow. Sterile areas covered with palisade of clavate pigmented hairs up to 6 μ m diam, walls and roughened gelatinous layer difficult to distinguish, up to 3.5 μ m in total width. Border between fertile and sterile areas abrupt. *Hymenium* composed of basidia and branched hyphidia, densely arranged. Hyphidial base 2.5–3.5 μ m diam, with gelatinized walls that easily stain, up to 1 μ m in total width; upper part bears branches 1.0–2.0 μ m diam with thin and not gelatinized walls; transition from base to top usually abrupt; hyphidia up to 80 μ m in total length, sometimes slightly projecting over basidia. *Basidia* clavate, 48–81 \times 4.6–8.0 μ m ($n = 28/1$), with

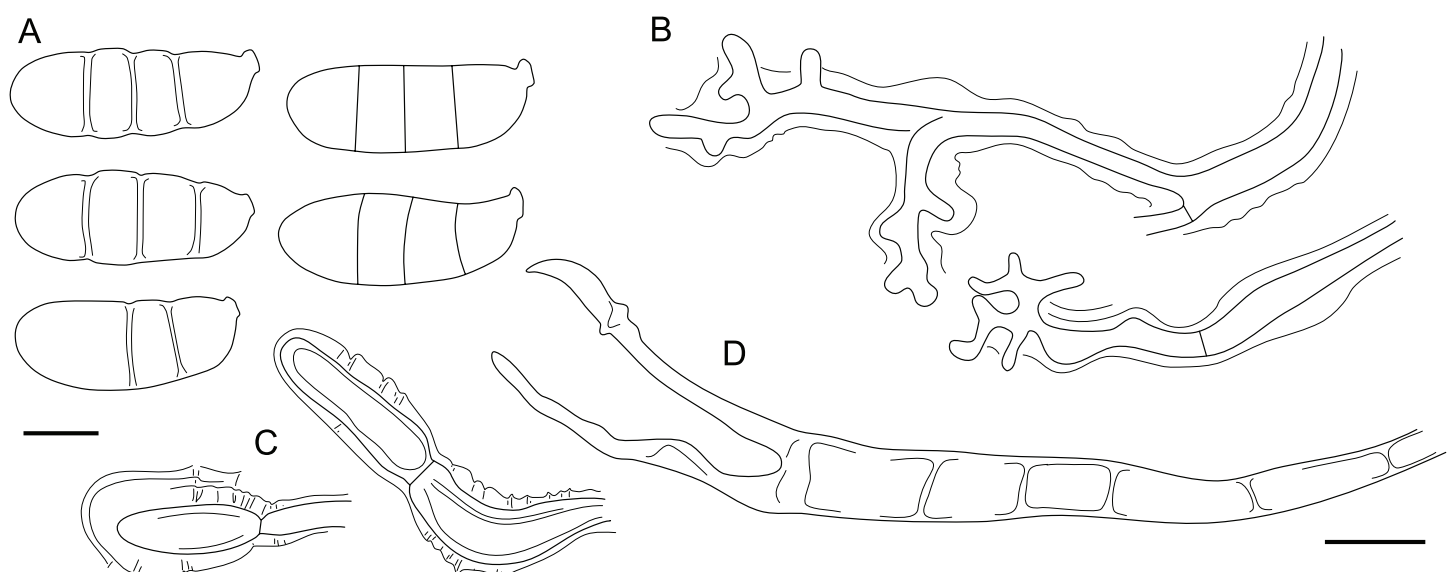


Fig. 10. *Dendrodacrys* sp. 1 micromorphology. **A.** Basidiospores. **B.** Hyphidia in gelatinous layer. **C.** Marginal hyphae. **D.** Basidium with secondary septa. Drawn from RLMA308. Scale bars: A = 5 μ m; B–D = 10 μ m.

large amount of lipid droplets when young, later developing multiple secondary septa; with two sterigmata up to 50 μm in length. *Basidiospores* cylindrical, slightly curved, up to 3-septate, $(12.1\text{--}13.0\text{--}16.4\text{--}16.8) \times (5.4\text{--}5.5\text{--}6.8)$ μm , $L = 15.1$ μm , $W = 6.1$ μm , $Q = 2.5$, $Q' = 1.9\text{--}2.8$ ($n = 48/1$), walls ~ 0.5 μm in width. Basidiospore germination not seen.

Habitat and distribution: The taxon is known from a single locality in South America (Brazil), growing on unidentified wood.

Material examined: **Brazil**, Pernambuco, Tamandaré, Reserva Biológica de Salinho, 4 Nov. 2016, *R. Alvarenga*, RLMA308* (URM 94610, TUF135201).

Notes: Compared to other *Dendrodacrys* members, the taxon has unique spatulate to foliaceous stipitate basidiocarps. We do not formally describe *Dendrodacrys* sp. 1 because it can be identified as *Dacryopinax elegans* s.l., a type species of polyphyletic *Dacryopinax*, whose identity is yet to be established. A studied specimen TENN-F-066927* (USA), that by geographical proximity has a better chance to conform to the type material of *D. elegans*, also demonstrate branched hyphidia, although not as abundant as in our Brazilian material. In addition, there is a number of non-sequenced *Dacryopinax*-related species from South America, e.g., the recently described *D. lowyi* (Sierra & Cifuentes 2005), and our material can potentially belong to them.

***Dendrodacrys* sp. 2.** Figs 2M, 11.

Description: *Basidiocarps* firm-gelatinous when rewetted, sessile and attached to substrate with root or short stipe, cerebriform to weakly lobate, hymenial surface smooth, basidiocarps up to 5 mm in the longest dimension, up to 3 mm in height, coalescing; light to dark brown with reddish tints when rewetted, almost black when dried. *Hyphae* clamped. Internal hyphae 2.0–3.5 μm diam, occasionally swollen up to 6 μm , walls with gelatinous layer up to 1 μm in width, often roughened. Subhymenial hyphae similar to internal. Marginal areas covered with simple or weakly branched, cylindrical, clavate, or slightly moniliform hyphae 2.0–4.0 μm diam, barely gelatinized, with light brown content. *Hymenium*

consists of basidia and hyphidia both containing brown pigments, either evenly distributed inside of structures or in small droplets. Hyphidia branched, of almost even width throughout the length, 1.3–2.2 μm diam and up to 70 μm in length; clamps on hyphidia sometimes unfinished. *Basidia* clavate, 16–42 \times 3.4–6.0 μm ($n = 30/1$), collapsed basidia have secondary septa, two sterigmata up to 47 μm in length. *Basidiospores* cylindrical, slightly curved, up to 3-septate, $(10.8\text{--}11.4\text{--}15.3\text{--}15.4) \times (4.5\text{--}4.7\text{--}5.9\text{--}6.2)$ μm , $L = 12.9$ μm , $W = 5.2$ μm , $Q = 2.5$, $Q' = 2.0\text{--}3.2$ ($n = 40/1$), walls < 0.5 μm in width. *Conidia* cylindrical to fusiform, straight or slightly bended, 3.3–5.1 \times 1.0–1.6 μm ($n = 16/1$), all measured while still attached to basidiospores.

Habitat and distribution: The taxon is known from a single locality in South America (Brazil), growing on unidentified wood.

Material examined: **Brazil**, São Paulo, Parque do Estado, Instituto de Botânica, 10 Jan. 1963, *K. Wells*, 1102 (TAAM192132*).

Notes: *Dendrodacrys* sp. 2 generally resembles *De. kennedyae*, although it produces cerebriform basidiocarps, while the latter species more often develops pulvinate and centrally depressed ones, as well as has slightly larger basidiospores and basidia. The taxon is not formally described in this study, because the scarce material does not allow a reliable comparison to *De. kennedyae*.

***Dendrodacrys* sp. 3.** Figs 2N, 12.

Description: *Basidiocarps* gelatinous when rewetted, attached to substrate with a root-like base, sessile, pustulate to applanate, up to 2 mm in the longest dimension when dried, coalescing when close, with smooth surface; pale yellow to brown when dried. *Hyphae* clamped. Internal hyphae 2.0–4.0 μm diam, walls ~ 0.5 μm wide, gelatinous layer up to 1.0 μm in width, smooth or roughened. Subhymenial hyphae 2.0–4.0 μm diam, walls and gelatinous layer similar to internal hyphae but not roughened. Marginal hyphae cylindrical to clavate, often with pronounced thinner apical part, not branched, but often slightly wavy, 3.0–4.0 μm diam at terminal parts, walls thin and smooth. *Hymenium* includes frequent dendroid hyphidia 1.0–1.5 μm diam, evenly

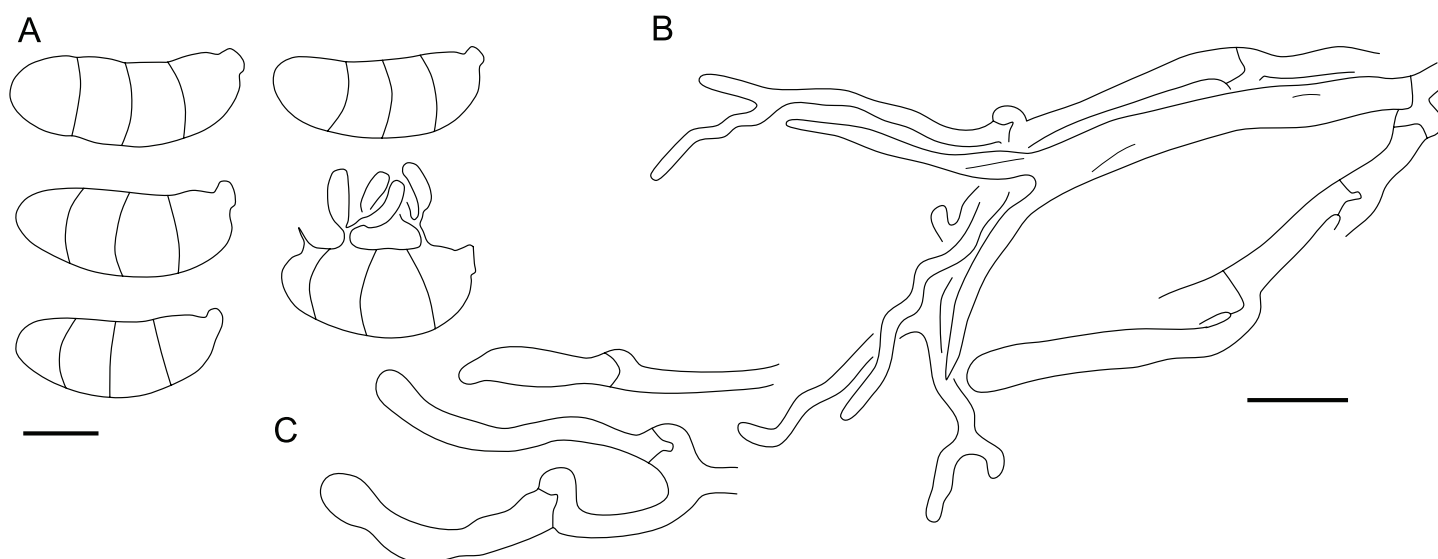


Fig. 11. *Dendrodacrys* sp. 2 micromorphology. **A.** Basidiospores, one bearing conidia. **B.** Basidium, basidiole, and hyphidia. **C.** Marginal hyphae. Drawn from TAAM192132. Scale bars: A = 5 μm ; B, C = 10 μm .

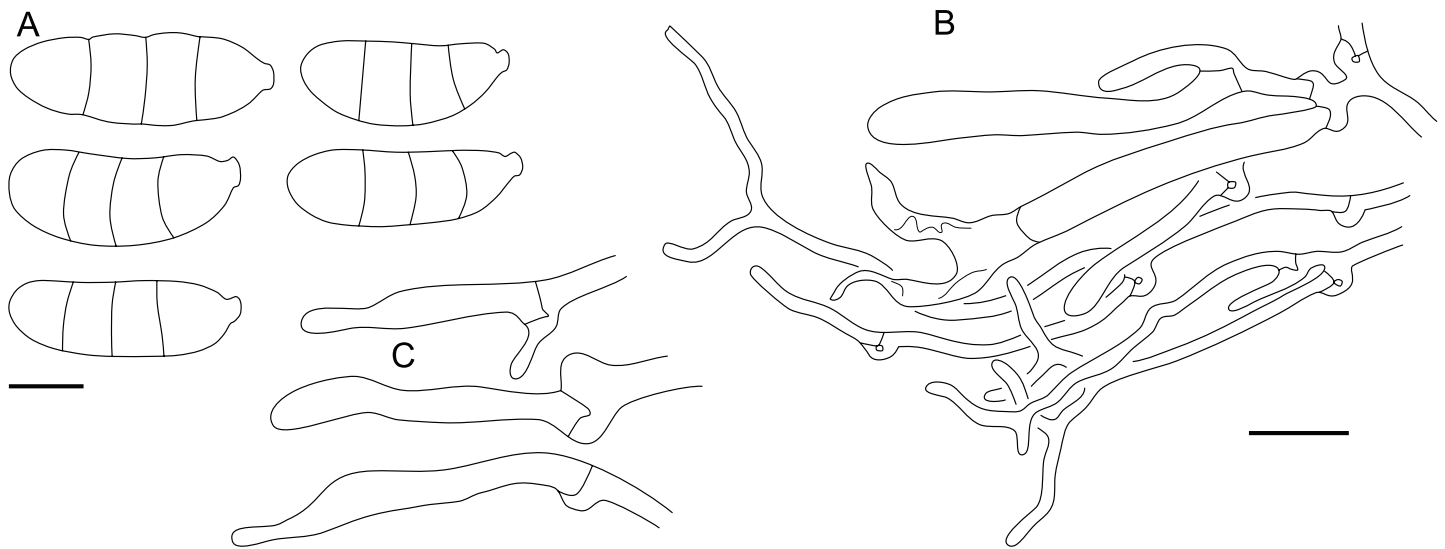


Fig. 12. *Dendrodacrys* sp. 3 micromorphology. **A.** Basidiospores. **B.** Basidium (half-collapsed), basidioles, and hyphidia. **C.** Marginal hyphae. Drawn from K(M): 141170. Scale bars: A = 5 µm; B, C = 10 µm.

wide or rarely gradually thinning from the base towards the top, up to 120 µm in length but usually not protruding throughout hymenium more than 15 µm, thin-walled, often with a few clamps through the length, clamps sometimes “unfinished”. *Basidia* clavate, 26–46 × 4.0–8.2 µm ($n = 37/1$), with two sterigmata up to 35 µm in length. After maturation basidia develop secondary septa. *Basidiospores* cylindrical, slightly curved, up to 3-septate, rarely attenuated from either end, (12.6–)13.0–15.5(–16.0) × (4.7–)5.0–6.1(–6.3) µm, $L = 14.3$ µm, $W = 5.5$ µm, $Q = 2.6$, $Q' = 2.2$ –2.9 ($n = 34/1$), walls < 0.5 µm in width. Basidiospore germination not seen.

Habitat and distribution: Only known from Caribbean (Puerto Rico), growing on bamboo.

Material examined: **Puerto Rico**, Luquillo, El Yunque National Forest (ex Bosque Nacional del Caribe), Bisley, on *Bambusa*, 6 Jun 1998, P.J. Roberts, GA428 (K(M): 141170*).

Notes: Basidiospores of this taxon can be slightly tapered, but they are distinct from similarly shaped spores of *De. dendrocalami* or *De. brasiliense*, being much more thin-walled than in the first, and wider than in the second. We do not describe the taxon formally considering the scanty material.

During the review of this paper, using the metabarcoding approach we obtained sequences of ITS1 region of this taxon. It is not accompanied by other genes and therefore not used in phylogeny inference. The closest BLAST hit to this material is *Dendrodacrys* sp. 2 (TAAM192132) with 87 % identity and 99 % query coverage.

***Dendrodacrys* sp. 4.** Figs 20, 13.

Description: *Basidiocarps* firm-gelatinous when rewetted, growing on decorticated wood, mostly sessile but attached to substrate in a central point, from pustulate to pulvinate, centrally depressed, slightly cerebriform or lobate, with smooth surface, coalescing up to 1.2 cm in the longest dimension when dried; from brown to dark reddish brown when dried. *Hyphae* clamped. Internal hyphae 2.5–5.0 µm diam, walls 0.4–0.8 µm in width, gelatinous layer up to 2.0 µm in width, usually roughened.

Subhymenial hyphae 2.0–4.5 µm diam, with indistinct thin walls, and gelatinous layer that easily swells in KOH up to 5 µm in width, smooth or roughened. Marginal areas covered with cylindrical to clavate hyphae, 2.0–4.0 µm diam, thin-walled, with or without gelatinization up to 1 µm in width. *Hymenium* includes conspicuous well branched hyphidia 1.5–2.7 µm diam, up to 70 µm in length, either getting steadily thinner towards the top or with a more robust gelatinized base, often with several clamps throughout the length, with some clamps “unfinished”. *Basidia* cylindrical to clavate, 31–70 × 4.0–7.8 µm ($n = 34/1$), developing several secondary septa after maturation, with two sterigmata up to 36 µm in length. *Basidiospores* from ellipsoid to cylindrical and slightly curved, up to 3-septate, very rarely with transverse septa, (11.8–)12.3–15.1(–15.6) × (5.8–)6.0–7.6(–7.9) µm, $L = 13.9$ µm, $W = 6.7$ µm, $Q = 2.1$, $Q' = 1.6$ –2.5 ($n = 52/1$), walls ~ 0.5 µm in width. Basidiospore germination not seen.

Habitat and distribution: The taxon is known only from South America (Venezuela), growing on angiosperm wood (*Miconia*).

Material examined: **Venezuela**, Aragua, Henri Pittier National Park, Rancho Grande, on *Miconia*, 29 Aug. 1999, D.J. Lodge, V35 (K(M): 64214*).

Notes: The taxon resembles *De. oblongisporum* in the presence of both cylindrical and ellipsoid basidiospores, though the ones of *Dendrodacrys* sp. 4 are smaller. Additionally, *De. oblongisporum* has small basidiocarps not reaching 2 mm diam. In *Dendrodacrys* sp. 4 a single conidium 1.5 × 3.5 µm was noticed, possibly related to a basidiospore. We do not describe this taxon formally, considering lack of representative material.

During the review of this paper, using the metabarcoding approach we obtained sequences of ITS1 and ITS2 regions of this taxon. They are not accompanied by other genes and therefore not used in phylogeny inference. The closest BLAST hit to this material is *Dendrodacrys* sp. 2 (TAAM192132): ITS1 with 87 % identity and 92 % query coverage and ITS2 with 85 % identity and 100 % query coverage. Similarly obtained ITS1 sequence of *Dendrodacrys* sp. 3 (K(M): 141170) is also different from *Dendrodacrys* sp. 4: 84 % identity and 97 % query coverage.

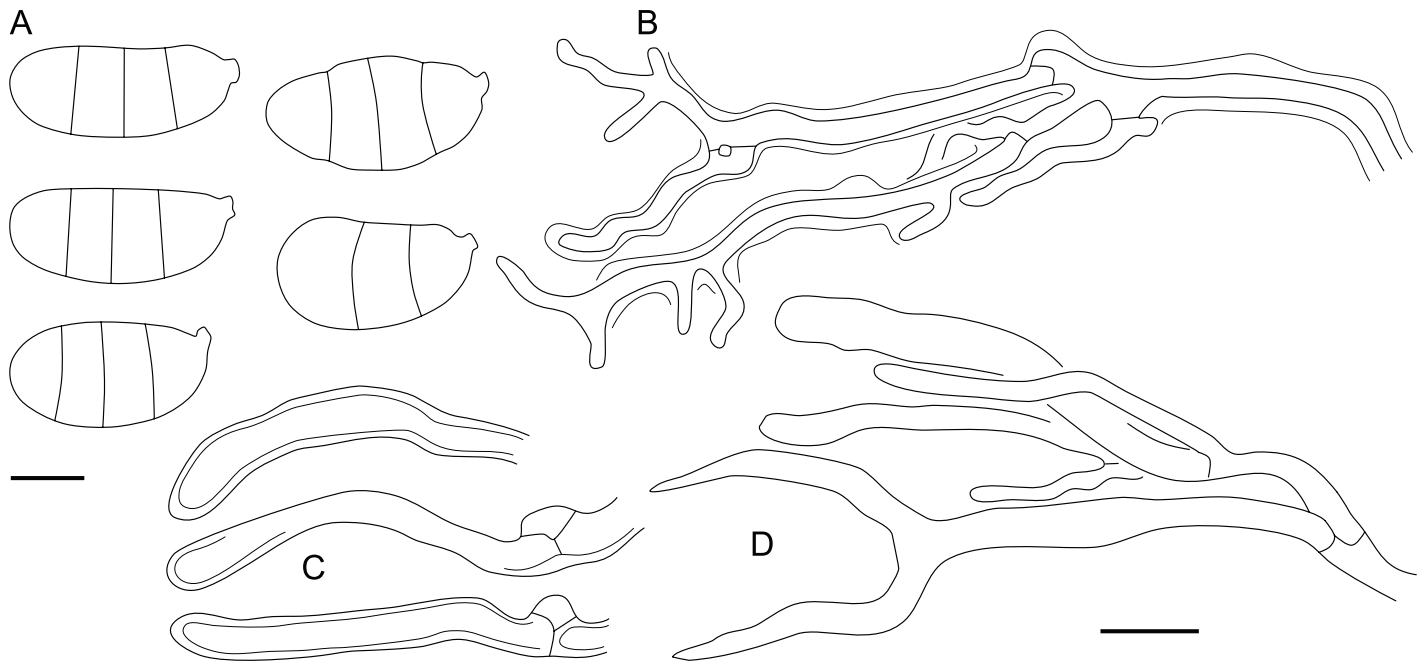


Fig. 13. *Dendrodacrys* sp. 4 micromorphology. **A.** Basidiospores. **B.** Hyphidia in gelatinous layer. **C.** Marginal hyphae. **D.** Basidium and basidioles. Drawn from K(M): 64214. Scale bars: A = 5 µm; B–D = 10 µm.

DISCUSSION

Our study proposes six nomenclatural novelties for *Dendrodacrys* including two new species, three new combinations, and one change of state and name. The study raises the total number of species in the genus to 11. In addition, we informally describe four taxa, of which two yielded enough sequenced markers to be placed in the phylogeny, and provide an extended description for the earlier recombined species *De. paraphysatum*. With the revision of material from tropical and subtropical climates, it becomes clear that the diversity of the genus is only superficially explored. Broad geography of collections and the number of provisional species hint that fresh specimens or discovery of more abundant herbarium material will be needed to better resolve the genus and shed light on its ecology.

Our results have also expanded the morphological limits of the genus: now it includes pronouncedly stipitate basidiocarps with spatulate to foliaceous (*Dendrodacrys* sp. 1) or pulvinate heads (*De. brasiliense*), and also species with simple-septate hyphae (*De. brasiliense*, *De. dendrocalami*, *Dendrodacrys* sp. 1). We also identify two patterns in basidiospore shape that are uncommon in dacrymycetes: first, mixture of cylindrical and ellipsoid basidiospores in one basidiocarp (previously found in *De. oblongisporum* and here in *Dendrodacrys* sp. 4), and second, basidiospore ends that are tapered from both sides (*De. dendrocalami*, *Dendrodacrys* sp. 3), or only from the proximal end (*De. rigoratum*). All these characters are distributed on the phylogenetic tree in a seemingly random fashion. Thus, they are useful only for species identification, and not for clade identification. Nevertheless, even after inclusion of various morphotypes, the genus can still be defined by its key diagnostic features: presence of strongly branched hyphidia, 3-septate spores, and pronounced sterile areas with marginal hyphae.

While species with dendrohyphidia in *Cerinomycetaceae*, *Dacryonaemataceae*, and *Unilacrymaceae* are known relatively well, *Dacrymycetaceae* should be browsed more thoroughly for this character. To be on the safe side, it is worth noting that the

presence of hyphidia should not necessarily invoke the creation of a new species, because relevant taxa may already have been described and then forgotten. For example, *Dendrodacrys* can be a potential destination for some of J.E. Rick's Brazilian species with laconic protologues, like *Da. substritis* that was reported with certain dendrophyses: "Plagulis 0.5–2 cm latis, pulvinatis, cerebriformibus, vitreo-brunneis, demum deliquescentibus, valde gelatinosis. Basidiis 80 × 8–10 my, bisterigmaticis. Dendrophysibus tenuibus, hyalinis. Sporis 15–25 × 9 my, 4-cellularibus, ad septa constrictis, hyalinis. Ad lignum putridum. Fungi Rickiani 20160, S. Salvador 1943: Typus. [...]" (Rick 1958). However, not only terse descriptions can obscure taxa potentially suitable for the genus – hyphidia are not always specified even in detailed studies, *e.g.*, *Calocera arborea* was proposed with only collateral mention of branched structures (Shirouzu *et al.* 2013b).

When it comes to the already reported branched hyphidia, outside *Dendrodacrys* there are at least two well-known species in *Dacrymycetaceae*, but both have a degree of ambiguity to them. They are *Dacrymyces san-augustinii* with multiseptate basidiospores and stipitate-cupulate *Dacryopinax elegans*, both with simple hyphal septa. The type of *Da. san-augustinii* could not be traced either for earlier revision (McNabb 1973), or in a recent study of species described by Y. Kobayasi (Shirouzu & Hosoya 2017). This species' treatments are in discordance between authors: Shirouzu *et al.* (2009) mentioned 7-septate basidiospores in a material from Japan, while McNabb (1973) referred to 12-septate ones from a Hong Kong specimen, and Olive (1958) cited 13-septate spores in a specimen from Tahiti. With this in mind, we believe that a detailed study of *Da. san-augustinii* s.l. may lead to its splitting into several species.

In turn, *Dacryopinax elegans*-like taxa land in several places in phylogenetic trees, both beyond and within *Dendrodacrys*. The holotype of *D. elegans* was collected in the USA, therefore it is unlikely that our Brazilian *Dendrodacrys* sp. 1 belongs to this species in a strict sense. A studied specimen TENN-F-066927, which is likely to be conspecific with *D. elegans sensu typi*, also

carries dendrohyphidia and resides in the same clade as *Da. san-augustinii* sensu T. Shirouzu. We suggest that the original material of *D. elegans* should be studied before describing new taxa related to *Dacryopinax*, especially considering that this species is the type of the genus.

Apart from *Da. san-augustinii* and *D. elegans*, other species of simple-septate *Dacrymycetaceae* reportedly have only simple to sparingly branched hyphidia, like North American *Da. dacryomitiformis* (McNabb 1973) or Asian *Guepiniopsis oresbia* (Rangkuti & Rifai 1975). Finally, non-*Dendrodacrys* species with clamped hyphae are also known only for weakly branched hyphidia. They include *Da. ovisporus* with characteristic muriform ovoid basidiospores, *Da. nigrescens* that by the virtue of 7-septate basidiospores probably does not belong to *Dendrodacrys*, and *Da. sichuanensis*, whose illustration depicts a splitting hyphidium, not elaborated upon in the text (Liu & Fan 1990).

Given the relative simplicity of basidiocarps and hyphal structures in dacrymycetes, finding diagnostic traits in this group is not always easy: every trait should be carefully evaluated in order not to be overly generalizing or idiosyncratic. In this context, branched hyphidia are at a convenient balance, allowing to unite *Dendrodacrys* with support of other characters. Building upon this, we see good prospects for morphological genus delimitation in dacrymycetes when using a combination of traits, as exemplified by *Cerinomyces* and *Dendrodacrys* that host a variety of morphological features, but at the same time are clearly defined by several simple characters each.

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Table S1. Raw microscopic measurements per each spore/basidium.