**INTRODUCTION**

*Dacrymyces* s.l. is currently treated as a genus of saprotrophic jelly-fungi distributed worldwide, and comprises about half of the species of the class *Dacrymycetes* (McNabb 1973, Reid 1974, Shirouzu *et al.* 2009, 2017). The distinction between genera in *Dacrymycetes* has traditionally been based on the macro- and micromorphological characters of the basidiocarps. Within the series of monographic studies on *Dacrymycetes* carried out by R.F.R. McNabb, the genus *Dacrymyces* seemed to be particularly difficult to circumscribe (McNabb 1973), especially against the genus *Heterotextus* (McNabb 1965). In fact, *Dacrymyces* has frequently been treated as a hotchpotch to include any taxa that could not be properly placed in other, well-characterised genera in the *Dacrymycetes*. As a result, this generic name is often applied to any species producing gelatinous to cartilaginous, cushion-shaped or turbinate basidiocarps, with a rather homogeneous hyphal structure, and either with an amphigenous hymenium or a sterile cortex of cylindrical to moderately differentiated, inflated cells (less so than in *Heterotextus*).

The phylogenetic relationships in *Dacrymycetes* have been re-evaluated with molecular data, and numerous independent studies have shown *Dacrymyces* to be highly polyphyletic (e.g. Shirouzu *et al.* 2007, 2013a, 2017, Zamora & Ekman 2020, Savchenko *et al.* 2021). Recent taxonomic revisions have focused on *Dacryonaemataceae* and *Unilacrymaceae* (Zamora & Ekman 2020) and on *Cerinomycetaceae* (Savchenko *et al.* 2021). In these revisions, several species with dacrymyces-like basidiocarps, not closely related to the type of *Dacrymyces*, *Da. stilillus*, have already been clarified and combined into monophyletic genera. On the other hand, the generic boundaries within *Dacrymycetaceae* are far from clear, because phylogenetic relationships among several groups of *Dacrymyces* s.l. and other genera (e.g. *Calocera*, which is also polyphylectic) are not currently well-supported, and phenotypic characters distinguishing the different clades overlap considerably. As a result, mycologists studying this class have been very cautious not to make the taxonomy of the group more intricate, avoiding unnecessary splitting and further creation of difficult-to-diagnose genera.

In the course of several sampling campaigns in various European countries during the last 12 yr, we found some specimens of *Dacrymyces* s.l. with conspicuous and often branched hyphidia that turned out to be undescribed species. Our aim is to describe these new species, providing both morphological studies and phylogenetic analyses, as well as a comparison with other morphologically similar species.

Preliminary DNA-based phylogenetic analyses placed them in the same clade as a specimen identified as *Da. dendrocalami*, a species with conspicuously branched hyphidia (Oberwinkler & Tschen 1989). The presence of these branched hyphidia seems to be a rather uncommon character within the family.
Dacrymycetaceae, according to Zamora & Ekman (2020). We will therefore evaluate whether this clade merits recognition at generic level, as a further step to solve the polyphyly of Dacrymyces s.l.

MATERIAL AND METHODS

Sampling

Specimens were collected in the field in both hydrated and dry states. Some fresh specimens were kept in a refrigerated humid chamber up to 2–3 d in order to study the macro- and micromorphological structures of the living basidiocarps. Otherwise, samples were dried at room temperature and kept as fungarium specimens in CWU, G, H, and UPS (Thiers 2021) for subsequent morphological study. We selected 17 of these newly collected specimens, representing five putative new species, for molecular study.

We chose a subset of representative taxa from all main clades in Zamora & Ekman (2020) to investigate the phylogenetic placement of the target group within the class Dacrymycetes. We selected up to two samples per species with at least two unlinked DNA regions available to minimise missing data. For the species delimitation analyses, we restricted the sampling to species in the target clade (putative new genus), and included the only other additional sample (Da. cf. adpressus, TNS-21069, AB472729) with DNA data available in GenBank. Nomenclature has been updated following Zamora & Ekman (2020) and Savchenko et al. (2021).

Morphology

The morphological methods largely follow Zamora & Ekman (2020) and are thus only briefly summarised below. Basidiocarps were photographed when fresh or after being hydrated, with either a Canon EOS 700D or an Infinity 1 macro camera coupled with a Leica MZ 75 dissecting microscope. The micromorphology was studied with a Zeiss Axios Imager A1 compound microscope by mounting hand-cut sections in water and 5 % KOH, and photographs were taken in the latter medium with an AxioCam ICc3 digital camera, using differential interference contrast (DIC). Microscopic structures were measured in KOH solution at 630×, either directly or with the aid of Piximètre v. 5.10 (Henriot & Cheyve 2016). Hyphidium width was measured in the upper half, basidium length was considered from the apex (excluding sterigmata) to the basal septum, and basidiospore length from the most protuberant part near the hilar appendix (considered subterminal and measured separately) to the opposite pole; the largest perpendicular dimension to these lengths was treated as the width. The basidiospore length/width ratio is expressed as Q. Terminology for the basidium apex follows Van de Put (2014).

General protocols for laboratory work were explained in detail in Zamora & Ekman (2020); Ukrainian samples were processed following Savchenko et al. (2021). DNA extractions were always carried out from a single basidiocarp using Chelex 100, following the protocol of Ferencova et al. (2017). We amplified fragments of the nrDNA (18S, ITS, nrLSU), RPB1, RPB2, TEF-1α, and 12S (mtSSU) DNA regions using the following primer combinations: The 18S was amplified in two parts with the primer pairs NS1/NS4 (White et al. 1990) and NS21UCBC/SR6 (Gargas & Taylor 1992, Vilgalys unpubl.). The ITS + nrLSU (D1–D3) region was amplified using ITS1F/LRS (Gardes & Bruns 1993, Vilgalys & Hester 1990). The RPB1 was amplified with DacryRPB1-1F/DacryRPB1-2r (Zamora & Ekman 2020). The RPB2 was amplified either with DacryRPB2-6F/DacryRPB2-11aR, or with DacryRPB2-6.2F/DacryRPB2-11bR (Zamora & Ekman 2020), sometimes using nested PCR. The TEF-1α was amplified using EF1-1018F/EF1-2218R (Stelio et al. 2015, Rehner & Buckley 2005) and Efdf/EF1-1953R (Rehner unpubl.). Finally, for the 12S we used either the primers DacryMS1 combined with Dacry12S-2r or Dacry12S-4r (Zamora & Ekman 2020), or substituted the forward DacryMS1 with an external newly designed primer, Dacry12S-1F (5′ AGGTAGTTGRTAGTGTAA 3′), combined with Dacry12S-2r. PCR programmes followed Zamora & Ekman (2020). Sequencing was done by Macrogen using the amplification primers, except for the RPB1 for which we mostly used the internal DacryRPB1-A and DacryRPB1-C (Zamora & Ekman 2020).

Sequence alignment

Sequences were assembled and edited in Sequencher v. 4.1.4 (Gene Codes, USA), using IUPAC ambiguity codes for heteromorphic positions. Newly generated sequences are included in Table 1, while information of the remaining sequences can be found in Zamora & Ekman (2020) and in the Joint Genome Institute (Grigoriev et al. 2014). We built two alignments, the first one for inferring a general phylogeny to show the phylogenetic position of the new species and to identify the main clades that may deserve generic recognition, and a second alignment to perform species delimitation analyses, containing only the new species and closely related taxa. Most alignments were inferred using MAFFT v. 7 (Katoh & Standley 2013, G-INS-i option) for the ribosomal regions, or manually in the case of the protein coding genes, back- translating them into nucleotides after having excluded introns and aligned the amino acids (introns were not used in subsequent analyses). Two highly variable regions of the 12S, appearing between the conserved motifs AWTTCCWT and GAAMWATGT, and AGGGTTGCGYRG and GMTWGAATCW, respectively (some base changes in certain species occur in these motifs) were excluded from the analyses. The 12S region was not used for species delimitation since it was available for only two species in the target clade (De. concrescens and De. ellipsosporum). The ITS1 and ITS2 were extremely variable across some of the target species and several trials with MAFFT resulted in substantially different alignments; thus, these regions were only included in the species delimitation analysis and after being aligned with BAli-Phy (Suchard & Redelings 2006). We prepared a backbone alignment with up to two samples per species (the ones with the most dissimilar sequences), and executed four runs with 5 × 105 iterations each. ITS1 and ITS2 were treated as two separate partitions, using the GTR + I + Γ model for nucleotide substitutions and the rs07 model for insertion/deletion events. The first 25 % of the runs were discarded as burn-in and the summarised samples showed an average standard deviation of splits frequencies < 0.005, and effective sample sizes > 7,000, verified using Tracer v. 1.7 (Rambaut et al. 2018). Alignments are available in TreeBASE (TB2:S29109).

Phylogenetic analyses

We tested congruence among unlinked DNA regions by performing a maximum likelihood (ML) phylogenetic analysis using RAxML v. 8.2.8 (Stamatakis 2014), with GTR + I + Γ as the model of substitution. The phylogenetic tree was constructed with the ML method, using the rapid bootstrap algorithm with 1000 replicates. Support values were estimated with the bootstrap test with 1000 replicates.
Table 1. DNA sequences generated in this study, with GenBank accession numbers and voucher information.

| Taxon                  | Country and province          | Voucher                  | 18S  | ITS + nrLSU | RPB1  | RPB2  | TEF-1α | 12S  |
|------------------------|-------------------------------|--------------------------|------|-------------|-------|-------|--------|------|
| *Dendrodacrys ciprense*| Cyprus, Lemesos               | UPS F-946590 (holotype)  | OM515350 | OM519385 | OM502304 | OM502321 | OM502321 | OM502337 |
|                        | Cyprus, Lemesos               | UPS F-946591             | OM515351 | OM519386 | OM502305 | OM502322 | OM502322 | OM502338 |
|                        | Cyprus, Lemesos               | UPS F-946592             | OM515352 | OM519387 | OM502306 | OM502323 - | OM502323 - |
| *Dendrodacrys aff. ciprense* | Cyprus, Lemesos             | UPS F-946593             | OM515353 | OM519388 | OM502307 | OM502324 | OM502324 | OM502339 |
| *Dendrodacrys concrescens* | Sweden, Öland                | UPS F-946601             | OM515354 | OM519389 | OM502308 | OM502325 | OM502340 | OM677448 |
|                        | Sweden, Öland                | UPS F-946602 (holotype)  | OM515355 | OM519390 | OM502309 | OM502326 | OM502341 - |
| *Dendrodacrys ellipsoasperum* | Sweden, Uppland            | UPS F-946603             | OM515356 | OM519391 | OM502310 | OM502327 | OM502342 | OM677449 |
|                        | Spain, Madrid               | UPS F-946604 (holotype)  | OM515357 | OM519392 | OM502311 | OM502328 | OM502343 | OM677450 |
| *Dendrodacrys ellipsoasperum* | Spain, Madrid            | UPS F-946605             | OM515358 | OM519393 | OM502312 | OM502329 | OM502344 | OM677451 |
|                        | Spain, Balearic Islands     | UPS F-946606             | OM515359 | OM519394 | OM502313 | OM502330 | OM502345 | OM677452 |
|                        | Spain, Madrid               | UPS F-946607             | OM515360 | OM519395 | OM502314 | OM502331 | OM502346 | OM677453 |
|                        | Ukraine, Crimea             | CWU(MYC)4092             | OM515362 | OM519397 | OM502316 - | OM502348 - |
|                        | Ukraine, Crimea             | CWU(MYC)7560             | OM515363 | OM519398 | OM502317 | OM502333 | OM502349 - |
| *Dendrodacrys oblongisporum* | Norway, Sogn og Fjordane   | UPS F-946599             | OM515364 | OM519399 | OM502318 | OM502334 | OM502350 - |
|                        | Spain, Madrid               | UPS F-979568 (holotype)  | OM515365 | OM519400 | OM502319 | OM502335 | OM502351 - |

of each dataset using IQ-TREE v. 1.6.12 (Nguyen et al. 2015), running 500 standard bootstrap (bs) replicates. We considered a conflict among topologies when a strongly supported (bs ≥ 75 %) cladode from one phylogeny was contradicted by another strongly supported cladode in another phylogeny (Mason-Gamer & Kellogg 1996). The partitioning scheme and model parameters were calculated based on the Bayesian information criterion with the version of ModelFinder (Kalyaanamoorthy et al. 2017) integrated into IQ-TREE. We used five potential subsets for the nrDNA dataset (18S, ITS1, 5.8S, ITS2, and nrLSU), three for each protein coding gene alignment (codon positions), and left the integrations of each dataset into IQ-TREE. We used five potential subsets for the nrDNA dataset (18S, ITS1, 5.8S, ITS2, and nrLSU), three for each protein coding gene alignment (codon positions), and left the

Maximum Likelihood analyses were performed as indicated above for each single-region alignment, repeating the analyses five times starting from random trees. Brach support was assessed by standard bootstrapping, performing 500 replicates in total. Bayesian analyses were done with MrBayes v. 3.2.6 (Ronquist et al. 2012), using the same partitioning scheme obtained in the ML analysis, with model parameters but not tree topology unlinked across subsets, and using model jumping to sample across models in each subset (Huelsenbeck et al. 2004). We allowed a gamma distributed rate heterogeneity across sites (approximated by four categories) and a proportion of invariant sites. We used the following priors: a (1, 1, 1, 1, 1) Dirichlet prior for the substitution rates, a (1, 1, 1, 1) Dirichlet prior on the state frequencies, and a uniform (0, 1) prior for the proportion of invariable sites. Branch lengths were linked and proportional across partitions, and we used the compound Dirichlet prior Unconstrained:GammaDir (1, 0.158, 1, 1), based on the tree length estimates from the best replicate of the ML analysis. Mixing was considered adequate with the temperature parameter set to 0.2. We executed four runs starting from random trees, each with four chains, for up to 1 × 10⁶ generations and sampling every 1 000th tree. The analyses were automatically stopped when the average standard deviation of split frequencies (ASDSF) dropped below 0.01. The first half of the analysis was discarded as burn-in, and the 50 % majority-rule tree with posterior probabilities (pp, considered significant when ≥ 0.95) and average branch lengths was calculated from the post-burn-in trees. We checked with Tracer v. 1.7 (Rambaut et al. 2018) that effective sample size (ESS) for each parameter was above 200. Trees were visualised in FigTree v. 1.4 (Rambaut 2016) and rooted based on the results from Zamora & Ekman (2020).

Species delimitation

Specimens were assigned to putative species using the multispecies coalescent approach implemented in STACEY v.
1.2.4 (Jones 2017) as part of the BEAST2 platform (Bouckaert et al. 2014). Clock and tree model parameters were estimated independently for each of the four unlinked DNA regions. An uncorrelated lognormal relaxed clock model (Drummond et al. 2006) was used. The dataset was divided into eight subsets (two for each non-recombining DNA region, one with lower and the other with higher substitution rates), as follows: (i) 18S + 5.8S + nrLSU, (ii) ITS1 + ITS2, (iii–v) 1st + 2nd codon positions of protein coding regions, (vi–viii) 3rd codon position of protein coding regions. Model parameters were estimated for each DNA subset with bModelTest (Bouckaert & Drummond 2017), allowing all transition/transversion split models. We ran four MCCM parallel analyses for 2 × 10⁸ generations, sampling every 1 × 10⁶th tree. The collapse height parameter was set as ϵ = 10⁻⁴, and we used the Beta (1,1) prior on the collapse weight parameter (ω). We noted some convergence problems in one of the runs for one of the partitions (1st + 2nd codon positions of TEF-1α) and excluded this run for subsequent analyses. The first half of the other three runs was discarded as burn-in. The most likely number of clusters (i.e. putative species) was calculated from the remaining sample using SpeciesDelimitationAnalyzer (Jones et al. 2015). The similarity matrix of pairwise posterior probabilities was visualised and plotted in R (R Core Team 2021) following Jones et al. (2015).

RESULTS

Phylogeny

The best partitioning scheme and models for each subset in the concatenated ML analysis were: (i) 18S, TN + F + I + G4, (ii) 5.8S + 12S, GTR + F + I + G4, (iii) nrLSU, TN + F + I + G4, (iv) RPB1 1st + RPB2 1st, TIM2 + F + I + G4, (v) RPB1 2nd + RPB2 2nd, TIM3 + F + I + G4, (vi) RPB1 3rd + RPB2 3rd, GTR + F + I + G4, (vii) TEF-1α 1st, F81 + F + I + G4, (viii) TEF-1α 2nd, JC + I + G4, and (ix) TEF-1α 3rd, GTR + F + G4. All ML tree replicates had a similar topology, and the likelihood score for the best one was lnL = -73248.971. The concatenated Bayesian analysis halted after 5 × 10⁸ generations (ASDF < 0.01). All parameters had an ESS exceeding 800 in the posterior sample, and all PSRF values were in the range 0.998–1.005. The topologies of the 50 % majority-rule Bayesian consensus tree and of the ML trees were similar, and thus only the best ML tree with bs and pp values is shown in Fig. 1.

The overall topology of the Dacrymycetes tree (Fig. 1) is highly consistent with that reported by Zamora & Ekman (2020). The four families recognized received bs = 100 % and pp = 1.00 support. Within Dacrymycetaceae, we have identified the same 8 main groups (D1–D8), plus Dacrymyces fennicus as sister to D6 (Femsjönio) with high support (bs = 93 %, pp = 1.00). Clades D1, D2, D4–D7 received bs = 100 % and pp = 1.00 support, clade D3 was represented by a single sample, and clade D8 was well-supported (bs = 77 %, pp = 1.00). The target group (clade D5) was sister to clade D8 (clampsless species) with partial support (bs = 58 %, pp = 1.00). Within clade D5, relationships were generally highly supported. Dacrymyces cf. dendrocalami and Da. cf. adpressus were resolved as sister to each other with bs = 100 % and pp = 1.00 support. Four putative new species (see below), named Dendrodacrys ciprense, De. concrescens, De. ellipsosporum, and De. oblongisporum, also received bs = 100 % and pp = 1.00 support. In addition, De. ciprense and De. oblongisporum, together with an isolated sample (De. aff. ciprense) formed a well-circumscribed clade with bs = 100 % and pp = 1.00 support, but the relationships among these three groups only received partial support (bs = 72 %, pp = 0.97).

Species delimitation

SpeciesDelimitationAnalyzer yielded two main species delimitation schemes, one with seven putative species (45.1 % posterior probability), and the other with eight putative species (34.7 % posterior probability). All other delimitation schemes had < 5 % posterior probability. All relevant model parameters in the STACEY analysis had an ESS exceeding 500 in the posterior sample. The topology of the STACEY chronogram is almost fully supported above the species level (Fig. 2). From the root, two main clades can be distinguished; the first is fully supported and includes Da. cf. dendrocalami (one sample estimated as one species) and Da. cf. adpressus (fully supported clade with two samples, estimated as either one or two species). The other main clade is well-supported (pp = 0.97) and includes four putative species, i.e. De. concrescens (fully supported clade with three specimens), De. ellipsosporum (fully supported clade with seven specimens), De. ciprense (fully supported clade with three specimens), De. aff. ciprense (one isolated specimen), and De. oblongisporum (fully supported clade with three specimens). The branches connecting these five putative species received full support except for the sister relationship between De. aff. ciprense and De. oblongisporum, which is unsupported (pp = 0.9).

Within each putative species (cluster) in the scheme of seven species, all included specimens had a high posterior probability (pp > 0.9) of belonging to the cluster they were assigned, except for the two specimens of Da. cf. adpressus. In this case, the probability that they belonged to the same species was pp = 0.54. The posterior probability that any specimen belonged to a different species to which it was assigned was very low (pp < 0.001).

Taxonomy

**Dendrodacrys** J.C. Zamora, A. Savchenko, Á. González-Cruz, Prieto-García, Olariaga & Ekman, [gen. nov.](http://www.mycobank.org/MycoBank) MB 842993.

**Etymology:** From the Greek δένδρον (dendron, branched like a tree) and δάξκυ (dacry, tear), so as to refer to a genus of Dacrymycetaceae with branched hyphidia.

**Typus:** Dendrodacrys ellipsosporum J.C. Zamora, A. Savchenko, Á. González-Cruz, Prieto-García, Olariaga & Ekman

**Description:** Basidiocarps firm- to soft-gelatinous when fresh, xerotolerant or not, ± sessile and with or without a rooting base, pulvinate to depressed, yellow-orange to brown. Hymenium amphigenous or ± confined to the upper part of the fruitbody, then with a distinct sterile cortex. Clamp-connections present except in one of the currently included taxa. Terminal cells of cortical/marginal hyphae ± cylindrical to narrowly clavate, thin- to thick-walled. Internal hyphae and subhymenial hyphae mostly thin-walled. **Basidia** 2-spored, often cylindrical to clavate, more rarely ± urniform; apex U- to W-shaped, rarely Y-shaped. **Hyphidia** present, distinct, simple to moderately branched, reaching or surpassing the level of the young basidia, but only sometimes forming a conspicuous layer on them. Recently
Dendrodacrys gen. nov.

Fig. 1. Maximum likelihood phylogram of the class Dacrymycetes, with bootstrap (bs) and posterior probabilities (pp) values indicated at species level or above. Thickened branches are considered well-supported (bs ≥ 75 % and pp ≥ 0.95), asterisks (*) denote full support (bs = 100 %, pp = 1.00), and other values are included only when bs ≥ 60 % and pp ≥ 0.9. Notation D1–D8 in Dacrymycetaceae follows Zamora & Ekman (2020) for convenience, and the new genus Dendrodacrys is highlighted. Samples with newly generated data are indicated in bold.
Figure 2. STACEY species delimitation analysis. Chronogram with posterior probabilities at and above species level, and similarity matrix. Clusters separated by lines indicate the scheme of putative species with highest posterior probability.

discharged and still aseptate basidiospores uninucleate. Mature basidiospores 0–3-septate, thin- to thick-walled, hyaline, subglobose to cylindrical-allantoid. Spore print cream to orange, also visible from the spore pruinescence on the basidiocarps (e.g. Fig. 3C). Microconidia infrequent, ellipsoid to cylindrical. Cell cytoplasm with abundant lipid bodies, and with carotenoids ± visible under the light microscope, sometimes inconspicuous. Brownish diffuse parietal pigments sometimes visible in the cortical/marginal hyphae.

Included species: Dendrodacryis ciprense, De. concrescens, De. oblongisporum, De. paraphysatum. Two additional species provisionally identified as “Da. cf. dendrocalami” and “Da. cf. adpressus” are also included here.

Dendrodacryis ciprense J.C. Zamora sp. nov. MycoBank MB 842994. Fig. 3.

Etymology: The adjetival specific epithet refers to the country where the known specimens were found.

Typus: Cyprus, Lemesos, Mesa Potamos, picnic area, on Pinus brutia branches, 2 Dec. 2017, J.C. Zamora (holotype UPS F-946590).

Description: Basidiocarps gelatinous, (0.2–)0.4–1.5(–1.8) mm in diam, slightly erumpent and pustulate when very young, becoming pulvinate to appinate, often with an inconspicuous central root-like projection, gregarious and sometimes partially coalescing but retaining evidence of the individual origin; in hydrated state amber coloured to orangish when young, soon orangish brown to brown, ± dark brown when old; dark brown to blackish When dried. Hymenium ± confined to the upper part of the basidiocarps, irregularly spreading to the margins; sterile cortex often distinct, or at least with a sterile area in the lower part of the basidiocarps. Terminal cells of cortical/marginal hyphae narrowly clavate to slightly fusiform or almost cylindrical, 5.4–9.0 µm diam, ± thick-walled, with walls not clearly gelatinised but cells often embedded in a gelatinous matrix, sometimes with secondary simple septa, with a brownish, diffuse parietal pigmentation well-visible especially in the darkest basidiocarps. Internal hyphae 1.8–5.0 µm diam, thin- to slightly thick-walled, clamped, some with roughened walls. Hyphidia frequent, conspicuous, moderately to densely branched, rarely simple, 2.1–4.4(–5.7) µm diam (wider towards the base and becoming thinner in the upper half or third), often with 1–2 clamped septa throughout their length, reaching or surpassing the level of the young basidia but not forming a layer on them. Young basidia cylindrical to narrowly clavate; mature basidia 49.5–74.4 × 4.4–9.5 µm, with two subapical sterigmata, 16.5–34.0 × 3.9–6.0 µm; basidium apex often slightly protruding. Basidiospores thin-walled, (13.6–)16.4–20.1 × (5.5–)6.0–8.9 µm, 2.2 ≤ Q ≤ 3.2 (n = 20), cylindrical-allantoid to slightly arachiform, becoming 3-septate at maturity, not constricted at septa or only slightly constricted, uninucleate prior to septation; hilar appendix conspicuous, ca. 1 µm long. Basidiospore germination not seen. Carotenoid contents present in the cytoplasm of most cells but rather inconspicuous, not bright yellow-orange.

Ecology and distribution: Only known from Pinus brutia forests in Cyprus. For a more accurate knowledge of its ecological preferences, the species should be looked for in other areas where the host is present (northeastern Mediterranean basin). Probably at least partially xerotolerant.
Fig. 3. *Dendrodacrys ciprense*. A–D. Macromorphology; basidiocarps in fresh conditions. E–N. Micromorphology. E, F. Terminal cells of cortical hyphae. G–I. Hyphidia. J–M. Basidia. N. Basidiospores. A–C, F–H, J–N from UPS F-946590 (holotype); D, E, I from UPS F-946592. Scale bars: A–D = 1 mm; E–N = 10 µm.
Notes: This species can be easily distinguished by the combination of dark basidiocarps, often with distinct brownish parietal pigments but not very conspicuous carotenoids, distinctly branched hyphidia, and cylindrical–allantoid, thin-walled, 3-septate mature basidiocarps. There are very few Dacrymyces s.l. described with branched hyphidia, 3-septate ± allantoid basidiocarps, and non-yellow basidiocarps. We studied part of the type material of Dacrymyces paraphyatus (the holotype, NY00738304, and one isotype, K[M] 8355) and Da. enatus var. macrosorus (the holotype, BPI725717, and four isotypes, NY03684200, LSU00135945, TAAM192134, and K[M] 95953, the last one annotated as “Dacrymyces dendrophyllid P. Roberts”, nom. herb.). These taxa clearly differ from De. ciprese by having distinctly thick-walled and differently sized basidiocarps: in Da. paraphyatus 12.8–16.0 × 5.2–6.0 μm measured in cotton blue from the holotype, (13.4–)13.9–17.6(–22.1) × 5.7–7.4(–7.9) μm measured in KOH from the isotype; 13.5–17.5(–21) × 5–7 μm from McNabb (1973); in Da. enatus var. macrosorus 13.1–15.1(–15.4) × (5.3–)5.4–6.6(–6.8) μm measured in cotton blue from BPI725717, NY03684200, LSU00135945, and TAAM192134, (10.1–)12.1–16.6 × 5.4–7.2 μm measured in KOH from K[M] 95953; 11–15.5 × 4.5–5.5(–6.5) μm from McNabb (1973). In addition, in these taxa some basidiocarps are constricted at septa and pigmented, the hyphidia are 1–2(–2.5) μm wide (rather constant through their length), heavily branched, forming a conspicuous layer on the hymenium, sometimes pigmented, and the basidiocarps are either individually larger or may form masses of some cm in extent (McNabb 1973, and own observations). Furthermore, Da. paraphyatus and Da. enatus var. macrosorus seem to be restricted to tropical areas, occurring on angiosperm wood (McNabb 1973). These two taxa clearly belong to the new genus Dendrodacrys, and we have combined Da. paraphyatus for being the one validly published at species level.

We have found one specimen (UPS F-946593), inhabiting a Cistus branch, that is morphologically and phylogenetically close to De. ciprese, but differs by having paler coloured basidiocarps, with almost indistinct brownish parietal pigments, barely inflated and ± thin-walled terminal cells of cortical hypheae, slightly narrower basidia (4.2–6.8 μm wide), slightly smaller basidiocarps (14.5–17.2(–19.1) × 5.7–7.3 μm), and simple to sparingly branched hyphidia. Also, all sequenced DNA regions place it as close but substantially different from De. ciprese, and the STACEY analysis considered it as another putative species (Fig. 2). These results suggest that this sample probably represents a different species, but we cannot properly evaluate its intraspecific variation based on a single specimen and refrain from describing it here.

Dendrodacrys concrescens J.C. Zamora & Ekman, sp. nov. MycoBank MB 842995. Fig. 4.

Etymology: The specific epithet is an adjectival form based on the participle of the Latin verb concresco (“grow together”), and it refers to the habit of the basidiocarps, growing closely aggregated.

Typus: Sweden, Öland, Böda par., Lindreservatet, on a fallen Pinus sylvestris trunk, 3 Oct. 2017, J.C. Zamora, (holotype UPS F-946602; isotypes in G and H).

Description: Basidiocarps gelatinous to soft-gelatinous, 0.2–1 mm diam, erumpent when very young and later spreading on the substrate, pustulate to pulvinate, growing in densely aggregated groups and coalescing to form masses of several cm², partially retaining evidence of pustular origin at least when fresh; orange to yellowish orange or ochraceous orange in hydrated state, becoming orangish brown when dried and being reduced to a varnish-like layer on the substrate. Hymenium ± amphigenous, irregularly spreading to the margins; sterile areas around the margin often visible in young basidiocarps, becoming inconspicuous when basidiocarps coalesce. Terminal cells of marginal hypheae ± cylindrical, 3.3–6.3 μm diam, thin-to ± thick-walled, apex sometimes pointed, with hyaline walls and some cytoplasmic, yellow-orange carotenoids. Internal hypheae (1.5–)2.0–4.0 μm diam, mostly thin-walled, clamped. Hyphidia unevenly distributed, conspicuous only in some areas, moderately to densely branched, transitioning to simple towards the margin, 2.8–3.4 μm diam (wider towards the base and becoming thinner in the upper third); often with 1–2 clamped septa throughout their length, reaching ± the same level of young basidia, or some surpassing them. Young basidia cylindrical to narrowly clavate; mature basidia (27.3–)29.3–49.3(–52.1) × 4.5–6.2 μm, with two apical or subapical sterigmata, 16.3–36.5 × 2.7–3.9 μm, apex of the mature basidium rarely protruding. Basidiocarps thin-walled, 12.0–16.2(–18.1) × 4.8–6.3 μm, 2.0 ≤ Q ≤ 3.3 (n = 40), cylindrical-allantoid to slightly arachiform, becoming 3-septate at maturity, not visibly constricted at septa, uninculate prior to septation; hilar appendix conspicuous, ca. 1 μm long. Germinating basidiocarps producing cylindrical microconidia, ca. 5.0–7.0 × 2.0–3.0 μm (few germinating basidiocarps seen). Carotenoid contents very conspicuous in the majority of the cells of the basidiocarps, bright yellow-orange.

Ecology and distribution: All studied specimens come from the hemiboreal zone in Sweden, but one GenBank accession (LC492199, released after our datasets were compiled) corresponds to a nrLSU sequence identical to ours of De. concrescens, having been generated from a Japanese specimen (HNo1210, Shirouzu et al. 2020). Even if the species grows on a relatively common substrate, i.e. ± old, decorticated logs of Pinus sylvestris, it seems to be rare, since it was only encountered three times during intense sampling between 2017 and 2020. We have not found any additional specimens in GB, H, O, S, or UPS herbaria. It does not seem to tolerate desiccation well, as the cells of the collected specimens quickly died when the samples were dried.

Additional specimens studied: Sweden, Öland, Böda par., Trollskogens NR, on a fallen Pinus sylvestris trunk, 5 Oct. 2017, J.C. Zamora, UPS F-946601; Uppland, Uppsala, Norra Lunsen NR, on an old, fallen Pinus sylvestris log, 19 Nov. 2017, J.C. Zamora, UPS F-946603.

Notes: Dendrodacrys concrescens is easy to recognise in the field by its conspicuous and dense masses of fused small basidiocarps, on decorticated Pinus logs. When dried, it resembles a thin layer of varnish and the individual basidiocarps become indistinguishable. Two species share some morphological similarities with De. concrescens according to the literature, viz.
Fig. 4. *Dendrodacrys concrescens*. A–C. Macromorphology; basidiocarps in fresh conditions. D–N. Micromorphology. D, E. Terminal cells of marginal (D) and submarginal (E) hyphae. F, G. Hyphidia. H–L. Basidia. M, N. Basidiospores. A, B, E–I, M from UPS F-946602 (holotype); C, D, J–L, N from UPS F-946603. Scale bars: A–C = 1 mm; D–N = 10 µm.
Dacrymyces adpressus and Da. fennicus. We have studied type material of both. Dacrymyces adpressus has simple or indistinct hyphidia and larger individual basidiocarp, not so conspicuously fusing as they grow, and the lectotype was collected on angiosperm wood (Grognot 1863, McNabb 1973). Dacrymyces fennicus, considered as a synonym of Da. adpressus by McNabb (1973), shares the habitat with De. concrescens, and we have even found both species growing on a single log. However, Da. fennicus produces larger, well-separated basidiocarps that are normally not appланate and only sometimes coalesces. In addition, the hyphidia are often indistinct and always simple. Specimens identified as Da. adpressus from Japan (that likely do not represent Da. adpressus s.str.), and a specimen of Da. fennicus with a sequenced genome are well-distinguished from De. concrescens based on the available molecular data (Fig. 1). In particular, the ITS1 sequences of De. concrescens are highly deviant from those of any other species in the Dacrymycetes. In Shirouzu et al. (2020), HNo1210 (see “Ecology and distribution” above) was considered to be an unidentified clade (Clade O).

Dendrodacrys ellipsosporum J.C. Zamora, A. Savchenko, Á. González-Cruz, Prieto-García, Olariaga & Ekman, sp. nov. MycoBank MB 842996. Fig. 5.

Etymology: The specific epithet is a compound adjective referring to the shape of the basidiocarpes, based on the ancient Greek ελλειψοειδή (ellipsoid) and σπορά (spora).

*Typus:* Spain, Madrid, Becerril de la Sierra, on *Juniperus thurifera* exposed branches, 30 Dec. 2017, J.C. Zamora et al. (holotype UPS F-946604; isotypes in G and H); *idem,* on *Juniperus oxycedrus* wood, UPS F-946610 (isotype).

Description: Basidiocarps gelatinous to firm-gelatinous, (0.3–) 0.5–2.0 mm diam, at first erumpent, pustulate or pulvinate, but soon becoming apllanate and slightly pezizoid when dried, often with a central root-like projection, gregarious but sometimes partially coalescing; in hydrated state orangish yellow when young, soon amber coloured to dull orange or brownish orange, chestnut brown when old; orangish brown to blackish when dried. *Hymenium* confined to the upper part of the basidiocarps or sometimes spreading to the margins, sterile cortex more or less distinct, or at least always with a sterile area in the lower part of the basidiocarps. Terminal cells of cortical/marginal hyphae ± cylindrical to irregularly dilated, (3.3–)4.1–7.6–(9.0) µm diam, thin- to more or less thick-walled, often with secondary simple septa, with a brownish, diffuse parietal pigmentation especially in the darkest basidiocarps. Internal hyphae 2.0–6.0 µm diam, thin- to slightly thick-walled, clamped, some with a roughened surface. Hyphidia rather common, distinct, most of them sparingly branched but varying from simple to rather densely branched, 2.1–3.6 µm diam (rather constant throughout their length or somewhat wider towards the base), often with 1–2 clamped septa throughout their length, reaching or surpassing the level of young basidia but not forming a conspicuous layer on them. Young basidia cylindrical to narrowly clavate or narrowly obpyriform; mature basidia (33.5–)40.0–73.0 (–82.0) × (5.3–)6.3–12.8 µm, with two subapical sterigmata, 18.0–44.0 × 4.7–6.8 µm, apex of the mature basidium often slightly protruding. Basidium wall sometimes thickened. Basidiocarps thin-walled, 13.9–25.7–(26.8) × (7.0–)9.7–14.2–(15.5) µm, 1.2 ≤ Q ≤ 2.2 (n = 50), commonly ellipsoid to narrowly ovoid, but rather variable from almost subglobose to lacrymiform/pyriform, 0–1(–3)-septate at maturity, not to sometimes slightly constricted at septa, uninucleate prior to septation; hilar appendix conspicuous, ca. 1.0–1.5 µm long. Basidiospore germination by the formation of hyphae or, more frequently, producing ellipsoid to narrowly ellipsoid conidia, ca. 5.0–6.0 × 2.0–2.5 µm (few germinating basidiospores observed). Carotenoid contents present in the cytoplasm of most cells, but particularly visible at basidia and basidiose, sometimes inconstant and often of a dull orangish powder to moderately orange.

Ecology and distribution: Rather common in the Mediterranean forests, woodlands, and scrub biome of the Iberian Peninsula and Balearic Islands, always associated with *Juniperus spp.* Also found in the southern coast of Crimea. The species is highly xerotolerant and prefers exposed branches, undergoing repeated cycles of dryness and hydration.

Additional specimens examined: Spain, Balearic Islands, Ibiza, Alla dins, Pollença, on *Juniperus phoenicea* wood, 7 Dec. 2018, I. Olariaga, UPS F-946606; Castilla-La Mancha, Guadalajara, Tamajón, near ermita de la Virgen de los Enebrales, on *Juniperus thurifera* branches, 28 Dec. 2019, J.C. Zamora, J. Señoret, B. Zamora, P.L. Aznar & S. Pardillo, UPS F-979748; Guadalajara, Turmiel, entre Anquela del Ducado y Turmiel, junto a la carretera CM-2107, fallen *Juniperus thurifera* log, 24 Jan. 2016, I. Olariaga, UPS F-946613; Madrid, Becerril de la Sierra, on unidentified wood, 16 Jan. 2010, J.C. Zamora, J.C. Campos, Á. González, F. Prieto & G. Sánchez, UPS F-946609; Madrid, Colmenarejo, colada de Cabeza Aguda, on *Juniperus oxycedrus* branches, 28 Dec. 2012, J.C. Zamora, F. Prieto & Á. González, UPS F-946608; Madrid, Colmenarejo, Cercados del Huerto, on *Juniperus oxycedrus* dead branches, 24 Dec. 2019, J.C. Zamora, I. Olariaga, Á. González, F. Prieto & B. Zamora, UPS F-979765; Madrid, Colmenarejo, Presa Vieja, on *Juniperus oxycedrus* branches, 24 Dec. 2019, J.C. Zamora, I. Olariaga & B. Zamora, UPS F-979756; Madrid, Hoyo de Manzanares, Finca La Ladera, on *Juniperus oxycedrus* exposed branches, 11 Jan. 2018, I. Olariaga, J.C. Zamora, F. Pencorbo & L.A. Parra, UPS F-946605; ibid., on *Juniperus oxycedrus* branch, still attached to the tree, 4 Jan. 2018, I. Olariaga, UPS F-946611; Madrid, Hoyo de Manzanares, Finca Las Viñas, on *Juniperus oxycedrus* branch, still attached to the tree, 19 Dec. 2017, M. Prieto & I. Olariaga, UPS F-946612; Madrid, Lozoya, on *Juniperus thurifera* wood, 13 Dec. 2009, Á. González, F. Prieto, B. Zamora & J.C. Zamora, UPS F-946607.

Ukraine, Crimea, Greater Yalta, Myś Martyan Nature Reserve, on *Juniperus excelsa* twig, 1 Jul. 2004, A. Bereznitsky, CWU(MYC)4092, LE262836; ibid., 30 Jun. 2004, S. Klimova, CWU(MYC)4093, LE262830; ibid., Myś Martyan Nature Reserve, cape Nikitin, unidentified wood, 2 Jun. 2004, S. Klimova, A. Bereznitsky, CWU(MYC)7560.

Notes: This species is easily distinguished by its ovoid to cylindrical-ellipsoid, thin-walled basidiocarps with 0–3 transverse septa at maturity that never become muriform, a morphology that is unique in *Dacrymyces s.l.* Besides, the combination of relatively large and dull-coloured basidiocarps, large basidia, conspicuous hyphidia, and xeric habitat on exposed *Juniperus* wood further distinguishes it from any other known species. There are, however, two other accepted species in the *Dacrymycetes* with typically ovoid to ellipsoid basidiocarps. The first is *Dacrymyces ovisporus*, which has shorter, subglobose to broadly ovoid basidiocarps, becoming muriform at maturity due to the formation of transverse, longitudinal and oblique septa (Brefeld 1888, McNabb 1973), simple hyphidia, and larger basidiocarps that are bright orangish
Fig. 5. *Dendrodacrys ellipsosporum*. A–C. Macromorphology of fresh basidiocarps. D–O. Micromorphology. D. Terminal cells of cortical hyphae. E–G. Hyphidia. H–L. Basidia. M–O. Basidiospores. A, B, D, F, G, I, J, M from UPS F-946604 (holotype); C, O from UPS F-946607; E, K, L, N from UPS F-946610 (isotype); H from UPS F-946605. Scale bars: A–C = 1 mm; D–O = 10 µm.
yellow. This species is typically found in Pinus wood and stains the substrate yellow (Torkelsen 1997). In addition, the specimens of Da. ovisporus included in the phylogenetic analyses show no close relationship with our samples of De. ellipsosporum (Fig. 1). Two of the Ukrainian studied specimens (CWU[MYC]4092 and CWU[MYC]4093) were indeed cited as Da. ovisporus in MalySheva & Akulov (2011). The second species with similarly shaped basidiospores is Unilacryma bispora. The dull colours and the presence of branched hyphidia are reminiscent of De. ellipsosporum, but the basidiocarps of the latter are larger, some carotenoid pigment is usually visible in the cytoplasm contents, the basidiospores never become muriform as in U. bispora, and septa in internal hyphae are always clamped. This species is also not closely related to De. ellipsosporum, belonging to a different family (Fig. 1).

Among other species names described in the literature for taxa that could be closely related to the new species, we found the old name Da. castaneus (Rabenhorst 1844). The data from the protologue are vague, but there are three characteristics that may agree with De. ellipsosporum. The first and most important one is the spore shape, which is defined as ovoid. In addition, the sporocarps are said to be brownish (hence, the epithet), and were found on a dry, dead branch. Unfortunately, no further data on the substrate or the ecology were indicated, and no iconography or specimens are cited. On the other hand, there are some characters that do not match well with De. ellipsosporum, and even raise doubts about the belonging of Da. castaneus to Dacrymycetaceae. The spores are said to have a dark central part and a bright edge, as if the cytoplasm was dark and the wall hyaline, something remarkably unusual for a species in Dacrymycetaceae. The hyphae are also said to have brown areas. The sporocarps are described as rounded, but the dimensions indicate they can be up to twice longer than wide when fresh, almost disappearing when dried, while in De. ellipsosporum they are almost circular and remain very conspicuous when dried, being easily visible in the field. It should be taken into account that Rabenhorst included in his concept of Dacrymyces (as “Dacryomyces”) species that nowadays we know belong to other groups, e.g. Da. violaceus and Da. fragiformis, which are most likely members of the Tremellomycetes. Therefore, the name Da. castaneus could refer to a non-Dacrymycetaceae jelly fungus. The dark interior of the spores already caused Fries (1874) to express doubts about its classification. The name Da. castaneus has not been in use during the last century and was interpreted differently by other mycologists in the past. For example, Saccardo (1888) suggested that the spores mentioned in the protologue could actually be conidia, and also indicated that the species was found on lemon tree branches in Portugal and Germany, a substrate on which we would never expect De. ellipsosporum to occur. Neuhoff (1936) suggested that it may represent Exidia badio-umbrina, while Kennedy (1958) listed it as a possible, yet dubious, synonym of Dacrymyces enatus var. enatus. McNabb (1973) agreed with Kennedy (1958) while noting that original material could not be traced. Donk (1966) considered it a nomen dubium, and judging by the information indicated above, we agree with this decision and do not see any advantage to rescuing this name. A possible neotypification of Da. castaneus, the only currently possible choice to fix the application of the name, would be difficult and subjective, since the lack of original material and the insufficient data contained in the diagnosis do not allow to make an informed and objective decision. For all these reasons, we prefer to describe De. ellipsosporum as a well-defined new species, and to reject Da.

castaneus as a nomen dubium and ambiguum for the time being, at least until any original material could be found.

Dendrodacrys oblongisporum J.C. Zamora & Ekman, sp. nov. MycoBank MB 842997. Fig. 6.

Etymology: The specific epithet is a Latin compound adjective of oblongus and spora (with a Greek origin but treated as Latin), and refers to the shape of the basidiospores.

Typus: Spain, Madrid, Bustarviejo, close to Puerto de Canencia, on Juniperus communis subsp. alpina dead branches, 28 Dec. 2019, J.C. Zamora, P.L. Aznar, S. Pardillo, J. Señoret & B. Zamora (holotype UPS F-979568); idem, UPS F-979569 (isotype). Note – the holotype and isotype are two different individuals, collected in well-separated bushes but treated as duplicates following Art. 8.2.

Description: Basidiocarps gelatinous to firm-gelatinous, (0.2–) 0.4–1.2 mm diam, barely erumpent when young, pulvinate to applanate, some becoming ± pezizoid when drying up, gregarious or in small groups, rarely coalescing; yellowish orange, ochraceous orange to amber coloured in hydrated state, becoming orange to orangish brown when dried. Hymenium ± confined to the upper part of the basidiocarps, irregularly spreading to the margins; sterile cortex often distinct, or at least with a sterile area in the lower part of the basidiocarps. Terminal cells of marginal hyphae narrowly clavate to cylindrical, 3.9–6.9 µm diam, ± thick-walled, with hyaline walls and some cytoplasmic, often not very conspicuous, yellow-orange carotenoids. Internal hyphae 1.5–4.0 µm diam, mostly thin-walled, clamped. Hyphidia present, often moderately branched but varying from simple to ± densely branched, 2.0–3.8 µm diam (width rather constant throughout their length or somewhat wider towards the base; bumps sometimes present), often with 1–2 clamped septa throughout their length, reaching the level of basidia or some surpassing them. Young basidia cylindrical to narrowly clavate; mature basidia 42.5–70.0(–92.0) × 5.0–7.8 µm, with two subapical sterigmata, 17.0–34.5 × 3.8–6.2 µm, apex of the mature basidium slightly protruding or not. Basidiospores thin-walled or with walls slightly thickened when old, 13.5–18.5(–19.0) × 6.3–9.4 µm, 1.6 ≤ Q ≤ 2.4 (n = 41), often oblong but varying from ellipsoid, narrowly ovoid, to ± cylindrical-allantoid, becoming 3-septate at maturity, not constricted at septa or only slightly, uninnucleate prior to septation; hilar appendix conspicuous, ca. 1.0 µm long. Basidiospore germination not seen. Carotenoid contents visible in the majority of the cells but especially in the basidia, cream-orange to yellow-orange.

Ecology and distribution: Insufficiently known. This species has been found in only two distant localities, one in the Mediterranean forests, woodlands and scrub biome (central Iberian Peninsula, submediterranean climate due to the high elevation), and the other in the taiga biome (southwestern Scandinavia, hyperhumid southern boreal to hemiboreal coniferous forests). In both places, De. oblongisporum inhabited thin branches of coniferous trees and bushes, still attached to the living plants. It may be a widespread but uncommon species, or overlooked due to its small size and macroscopic similarity with many other Dacrymyces s.l. species. At least partly xerotolerant.

Additional specimen studied: Norway, Sogn og Fjordane, Førde, Viafjellet, on Pinus sylvestris branches, 5 Jul. 2018, S. Ekman, UPS F-946599.
Fig. 6. *Dendrodacrys oblongisporum*. A–E. Macromorphology; hydrated (A–C) and dried (D, E) basidiocarps. F–O. Micromorphology. F, G. Terminal cells of cortical hyphae. H, I. Hyphidia. J–M. Basidia. N, O. Basidiospores. A–C, G–I, K–M, O from UPS F-979568 (holotype); D–F, J, N from UPS F-946599. Scale bars: A–E = 1 mm; F–O = 10 µm.
Notes: Dendrodacrys oblongisporum resembles Dacrymyces adpressus and Da. fennicus based on literature. However, both species lack branched hyphidia, Da. adpressus occurs on angiopsperm wood (Grognot 1863), and Da. fennicus typically grows on thick branches or logs of Pinus, not on thin branches or twigs as De. oblongisporum. The basidiospores in both Da. adpressus and Da. fennicus are also more distinctly allantoid, and the terminal cells of the cortical/marginal hyphae thin-walled. Finally, molecular data clearly separate Da. fennicus and De. oblongisporum, and the available DNA sequences from specimens identified as Da. adpressus from Japan (that probably do not represent Da. adpressus s.str.) also distinguish these species into well-separated clades (Fig. 1). From other species of Dendrodacrys, the combination of the basidiospore shape, presence of clamp-connections, and isolated, small yellow-orange basidiocarps is diagnostic. Specifically, De. cipreense produces darker, more brownish basidiocarps, and cylindrical-allantoid basidiospores (2.2 ≤ Q ≤ 3.2). Basidiocarps of De. concrencens are smaller and coalesce to form extense masses, the basidiospores are smaller and especially narrower (4.8–6.3 µm wide), and the ecology is also different, growing on fallen pine logs. Dendrodacrys ellipsosporum has larger and especially broader basidiospores ([7.0–9.7–14.2–15.5] µm wide), slightly broader basidia, and often darker basidiocarps. Finally, Da. cf. dendrocalami lacks clamp-connections and the basidiospores are thick-walled.

DISCUSSION

Is a new genus needed in Dacrymycetaceae?

Zamora & Ekman (2020) and Savchenko et al. (2021) showed that branched hyphidia seemed to be a common feature in Cerinomycetaceae, Dacryonemataceae and Unilacrymaceae, and probably plesiomorphic in the last two families. By contrast, branched hyphidia in Dacrymycetaceae were only found in certain groups and seemed to be a secondary acquisition of this character state or a reversion to the plesiomorphic state. Specifically, until now, branched hyphidia have been found in only two small species groups of Dacrymycetaceae. One is the clade containing Dacryopinax elegans (generic type) and Dacrymyces san-augustini, which is nested in the large group of mostly clumpless species (clade D8). The other clade is D5, where most species have clamp-connections. The group including Dacryopinax elegans and Da. san-augustini is morphologically very heterogeneous and difficult to diagnose, since Dacryopinax elegans has brownish, long-stalked, coellicleariform to auricularioid basidiocarps with unilateral hymenium, and thick-walled, 3-septate basidiospores, while Da. san-augustini (and also Da. novae-zelandiae, which lacks conspicuously branched hyphidia) has ± yellow-orange, sessile, cushion-shaped basidiocarps with a poorly defined sterile cortex, and thin-walled, multisepate basidiospores.

Clade D5, on the other hand, is considerably more homogeneous and easier to diagnose, comprising species with sessile, cushion-shaped to flattened basidiocarps, branched hyphidia, and mature basidiocarps with up to three septa. All known species in this group have clamp-connections, with the exception of Da. cf. dendrocalami, which seems to have lost them. From a phylogenetic point of view, clade D5 and the group containing Dacryopinax elegans are not closely related, so it is not possible to delimit a single, monophyletic genus that would include all Dacrymycetaceae species with branched hyphidia. In addition, it would be difficult to justify the inclusion of species in clade D5 even in a very broad and extended genus Dacrymyces, since that would imply merging well-known genera such as Calocera s.str. with Dacrymyces. Such an assemblage would hardly be diagnosable in terms of the most used characters in Dacrymycetes taxonomy, like the presence or absence of clamp-connections, basidiospore morphology (including shape, wall thickness, and septation), presence or absence of distinct hyphidia, development of a sterile cortex and terminal cells of its hyphae, or the morphology of the basidiocarps. Therefore, the recognition of clade D5 as a distinct genus does not imply oversplitting Dacrymyces, but on the contrary, it increases the diagnosability of the genera in Dacrymycetaceae and partially alleviates the rampant polyphyly of Dacrymyces s.l. Further generic rearrangements are expected in the future, but only after phylogenies with better resolution (especially in clade D8) are obtained and monographic studies of the different clades have been performed. To emphasize the character of branched hyphidia in the species currently included in clade D5, we chose the name Dendrodacrys. None of the included species contain the type of any validly published generic or infrageneric names in Dacrymycetaceae, most of which were already treated by Zamora & Ekman (2020) and Savchenko et al. (2021), so there is no other nomenclatural choice than proposing a new generic name.

Species delimitation in Dendrodacrys

STACEY results showed a rather clear assignment of most specimens to a single cluster (putative species), except for the uncertainty whether the two specimens of Da. cf. adpressus should be considered as one or two putative species. The amount of data for TNS-21069 is much smaller than for the other samples in the dataset, since only nrLSU data was available and only five substitutions separate the two Da. cf. adpressus specimens. This is clearly insufficient to get a reliable estimate of the population structure and possible speciation events within this species or species complex. By comparison, there are seven substitutions and one indel separating the two most distant nrLSU sequences of De. ellipsosporum [obtained from UPS F-946606 and CWU(MYC)4092], but thanks to the information contained in the remaining DNA regions, STACEY did not have problems to suggest that both samples belong to a same cluster, with very high posterior probability. As reported elsewhere, coalescence-based species delimitation is prone to oversplitting (e.g. Jackson et al. 2017, Sukumaran & Knowles 2017, Chambers & Hillis 2020, Leaché et al. 2019). Putative species suggested by such methods should be critically evaluated using all available data and not directly translated to nominal species. This is especially true when the amount of data is small, e.g. few specimens or populations per putative species, and/or few unlinked DNA regions with enough variation. Nevertheless, these two samples were mostly assigned to the same putative species in our analyses, which agrees with a conservative approach.

From a phenotypical point of view, the basidiospore morphology is demonstrated here to be particularly useful to characterise species in Dendrodacrys, being almost like a “fingerprint” for species recognition. In fact, the delimitation of the new species found during our study does not really appear to represent a challenge for the morphology- and coalescence-based species delimitation analyses. Among the proposed
new species, De. concrescens and De. ellipsosporum have a particularly striking morphology and very distinct DNA sequence data, making them unlikely to be confused with any other species. Dendrodacrys ciprense and De. oblongisporum are rather closely related according to our phylogenetic reconstructions, and both species produce non-coalescing, cushion-shaped basidiocarps and somewhat curved, thin-walled basidiospores. However, they are still well-defined and readily distinguishable on account of the colour of the basidiocarps, size and shape of the basidiospores, cell pigments, ecology, and molecular data (see Fig. 2 and observations under the mentioned taxa).

Notes on extra-European taxa

Dacrymyces dendrocalami is easily distinguished from the related taxa by clampless septa, wide basidia, sterigmata exceeding basidia in length, and spore shape. If the Japanese specimens are confirmed to belong to this taxon, then the species would be known from Japan and Taiwan, occurring on angiosperm wood. The characteristic dendroid hyphidia allow identification as Dendrodacrys even on a purely morphological basis, but we prefer to await the revision of the type material before proposing the required combination.

The Japanese Dacrymyces cf. adpressus is most likely an undescribed species. This angiosperm wood-dwelling species differs from the lectotype of Da. adpressus by the presence of abundant dendroid hyphidia. Yet another specimen (Japan, Wakayama, Mt. Shirami, on dead unidentified branches, 12 Oct. 2006, T. Shirouzu HNo. 554, TNS-F-21069) presumably belongs to this taxon, but we did not include it in the analyses due to the lack of data.

Dacrymyces paraphysatus and Da. enatus var. macrosporus are two morphologically close species that clearly belong to Dendrodacrys (see observations under De. ciprense). Dacrymyces enatus var. macrosporus is thus not closely related to Da. enatus var. enatus (syn. Cerinomyces enatus; see Savchenko et al. 2021), but its delimitation against Da. paraphysatus needs to be re-evaluated with additional specimens. Therefore, we do not make the combination in Dendrodacrys for the time being. Concerning Da. paraphysatus, we accept it as an independent species after studying the type material, and since it is already published at the species level, the combination can be safely made without risking the publication of a superfluous name:

Dendrodacrys paraphysatum (L.S. Olive) J.C. Zamora & A. Savchenko, comb. nov. MycoBank MB 842998. Basionym: Dacrymyces paraphysatus L.S. Olive, Bull. Torrey Bot. Club 85: 106. 1958.

Calocera arborea (Shirouzu et al. 2013b), which was considered part of clade D5 in Zamora & Ekman (2020), was not included in the present study pending a morphological revision of the available material, and the generation of additional DNA data. With only ITS and nrLSU sequences currently available, the phylogenetic position of this species varied between studies. For instance, in Shirouzu et al. (2013b, 2016, 2017) it did not form a clade with Da. cf. adpressus and Da. cf. dendrocalami. This species shares with Dendrodacrys the cushion-shaped fertile heads of the basidiocarps and the 3-septate mature basidiospores. However, it has strikingly long and branched stalks, which could be seen as an extraordinary development of the parts that are often rooting into the substrate in several other species of Dacrymycetes. Most importantly, branched hyphidia were not indicated in the protologue, but these structures are not always easy to find. Their absence should be confirmed before taxonomic conclusions are drawn.

Further details on the taxonomy of the cited additional non-European species, as well as an identification key for the genus Dendrodacrys, will be included in a forthcoming study.

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