

ANTON SAVCHENKO

Taxonomic studies in Dacrymycetes:
Cerinomyces and allied taxa



DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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LIST OF ORIGINAL PUBLICATIONS

- I Savchenko A, Zamora JC, Shirouzu T, Spirin V, Malysheva V, Köljalg U, Miettinen O. 2021. Revision of Cerinomyces (Dacrymycetes, Basidiomycota) with notes on morphologically and historically related taxa. *Studies in Mycology* 99: 100117 [1–72],
<https://doi.org/10.1016/j.simyco.2021.100117>
- II Zamora JC, Savchenko A, González-Cruz Á, Prieto-García F, Olariaga I, Ekman S. 2022. Dendrodacrys: a new genus for species with branched hyphidia in Dacrymyces s.l., with the description of four new species. *Fungal Systematics and Evolution* 9: 27–42,
<https://doi.org/10.3114/fuse.2022.09.04>
- III Savchenko A, Zamora JC, Alvarenga R, Köljalg U, Miettinen O. 2022. Additions to Dendrodacrys and outline of taxa with branched hyphidia in Dacrymycetes (Basidiomycota). *Fungal Systematics and Evolution* 10: 103–126, <https://doi.org/10.3114/fuse.2022.10.04>

Papers are cited throughout the thesis with the corresponding Roman numerals. The author's contribution to the publications is shown below.

	I	II	III
Idea and study design	++	+	++
Fieldwork and sampling	+	-	+
Laboratory work and microscopy	++	+	++
Phylogenetic analyses	++	-	++
Writing and manuscript preparation	++	+	++

ABBREVIATIONS

12S	Mitochondrial ribosomal small subunit
5.8S	Nuclear ribosomal 5.8S gene
<i>C.</i>	<i>Cerinomyces</i>
<i>Ca.</i>	<i>Calocera</i>
<i>Ce.</i>	<i>Ceracea</i>
CB	Cotton Blue
CR	Congo Red
<i>Da.</i>	<i>Dacrymyces</i>
<i>De.</i>	<i>Dendrodacrys</i>
ITS	Internal transcribed spacer, consists of ITS1, 5.8S, ITS2
LSU	Nuclear ribosomal large subunit
nrDNA	Nuclear ribosomal DNA (SSU, ITS, LSU)
PCR	Polymerase chain reaction
RPB1	RNA polymerase II largest subunit
RPB2	RNA polymerase II second largest subunit
<i>s.l.</i>	<i>sensu lato</i> (Lat.), in a wide sense
<i>s.s.</i>	<i>sensu stricto</i> (Lat.), in a strict sense
SSU	Nuclear ribosomal small subunit
TEF1- α	Translation elongation factor 1-alpha

INTRODUCTION

Fungi represent one of the largest and most diverse kingdoms of eukaryotes. About 100,000 fungal species have been described so far, but according to the recent estimations the real number of extant fungi is between 2.2 and 3.8 million species (Hawksworth and Lücking, 2017). In this kingdom, the most species-rich groups are Ascomycota and Basidiomycota. The latter group, also called “basidial fungi”, dominates decomposition of wood in terrestrial ecosystems (Riley et al., 2014). Despite the ecological importance, its diversity and taxonomy are insufficiently known (Zhao *et al.*, 2017). Meanwhile, many branches of biology depend on an accurate identification of taxa and, ever more often, require an understanding of their phylogenetic relations (Godfray, 2005). For example, inadequate taxonomic data impede ecological research and disrupt nature conservation efforts (de Carvalho *et al.*, 2008; Molina *et al.*, 2011). Therefore, advances in systematics not only expand our understanding of biodiversity but can have positive impact on biological sciences in general.



Fig. 1. Basidiocarps of selected dacrymycete members. **A.** *Calocera furcata* (H6012626). **B.** *Cerinomyces borealis* (GB-0071203). **C.** *Dacrymyces grandinoides* (= *Cerinomyces grandinoides*, H7008841). **D.** *Dacrymyces adpressus* (H6012680). **E.** *Dacryonaema rufum* (H:Poelt, Fungi 242). **F.** *Dendrodacrys laetum* (TUF135263). **G.** *Ditiola radicata* (H6012689). **H.** *Unilacryma unispora* (H6012675). Scale bars: A, B, D, E, G, H ≈ 1 mm; C, F ≈ 5 mm.

This thesis presents taxonomic studies in a group of basidial fungi called dacrymycetes, specifically in the genus *Cerinomyces* and related taxa. Among the wood rotting basidiomycetes, dacrymycetes is a relatively small but well-established taxonomic class with clear morphological and phylogenetic boundaries.

It diverged from other extant fungi approximately 340 million years ago (Zamora and Ekman, 2020) and is known as one of the earliest-diverged groups causing brown rot of wood, i.e., a type of rot that primarily targets cellulose (Floudas *et al.*, 2015; Nagy *et al.*, 2016). In nature dacrymycetes occur exclusively on dead wood and usually produce gelatinous yellow fruitbodies (also called basidiocarps, Fig. 1). The group was studied from the beginning of systematic mycology, but until the end of 19th century dacrymycetes were often treated in a mix with other gelatinous fungi, e.g., within the genus *Tremella* (Persoon, 1801). Definition of dacrymycetes has narrowed and stabilized with progress in microscopy techniques. Brefeld (1888) introduced the name and concept of Dacrymycetaceae and provided images of the main microscopic feature that characterizes the group – bisterigmate Y-shaped basidia (Fig. 3D, lower). During the 20th century dacrymycetes were extended with many new genera and species, as reviewed in a series of monographs by McNabb (1973, 1966, 1965a, 1965b, 1965c, 1965d, 1965e, 1964). When molecular methods were applied to dacrymycetes, phylogenetic trees confirmed that the group is distinct from relatives and covers a strongly supported clade – a sister to the class Agaricomycetes (Weiβ and Oberwinkler, 2001). Later, after more developed phylogenies of the group appeared, it often has been formally called the class Dacrymycetes (e.g., Hibbett *et al.*, 2007).

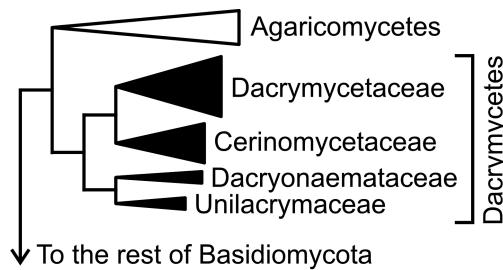


Fig. 2. Family arrangement of dacrymycetes (not to scale).

Nowadays, taxonomy of dacrymycetes is in a state of reformation: some taxonomic ranks and groups received revisions just recently, while others were not updated since 1960s. Structure at the higher ranks was generally agreed upon during the last decade. Four families are recognized now, as shown on the Fig. 2: Dacrymycetaceae and Cerinomycetaceae include the vast majority of species, while Unilacrymaceae and Dacryonaemataceae contain only five species in total. Unilacrymaceae was raised to accommodate *Unilacryma unispora* – the only species with unisterigmate basidia (Fig. 3D upper; Shirouzu *et al.*, 2013). In the same work the authors defined position of the earlier proposed family Cerinomycetaceae and retained the rest of the class in Dacrymycetaceae. After that, Zamora and Ekman (2020) made the latest addition up to date, establishing the new family Dacryonaemataceae. It constitutes a sister clade to *Unilacryma* and encompasses three species of the genus *Dacryonaema*.

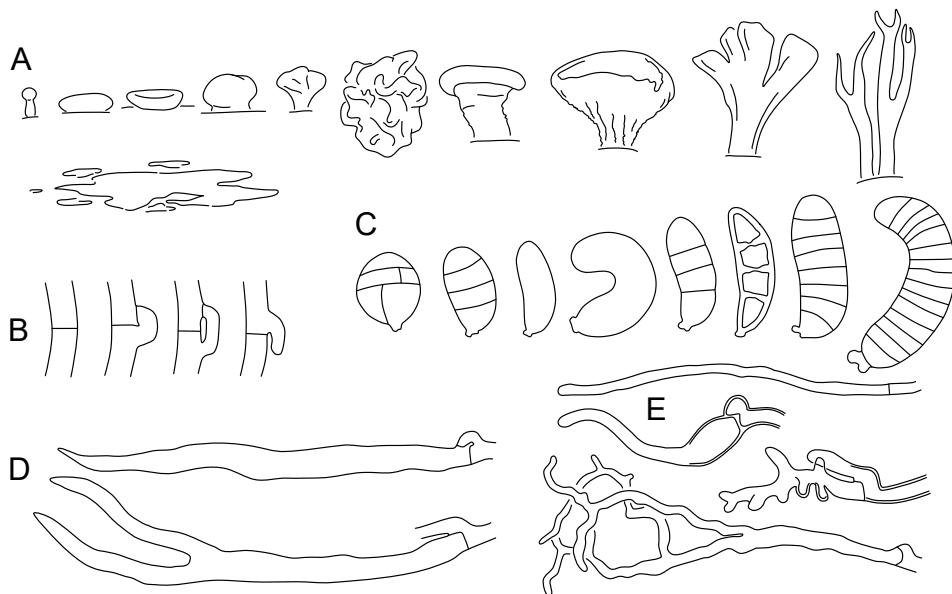


Fig. 3. Morphological characters commonly used in identification of dacrymycetes. Not to scale, arranged from left to right and top to bottom. **A.** Basidiocarp types, above: synnematous, pustulate, pustulate and centrally depressed, pulvinate, capitate with simple stem, cerebriform, capitate with distinguished stem, cupulate, spathulate, cylindrical-dendroid; below: resupinate or corticioid. **B.** Hyphal septa: simple, clamped, with medallion-shaped clamp, with unfinished clamp. **C.** Basidiospores: ovoid (muriform septation), ellipsoid (only transverse septation), cylindrical (from aseptate to >7 transverse septa, slightly or strongly bent, thin- or thick-walled). **D.** Basidia: uni- and bisterigmate. **E.** Hyphidia: simple, simple with thickened base, weakly branched, strongly branched.

At the same time, generic rearrangement for the class is far from completion. All in all, 25 genera were described with more or less clear relations to dacrymycetes, hosting at least 475 names at sub-generic ranks (Table 1). Thirteen genera are currently recognized and cited in the modern literature, and the largest of them in terms of proposed species names are highly morphologically and phylogenetically heterogenous *Dacrymyces* and *Calocera* of Dacrymycetaceae.

Struggle to establish meaningful generic boundaries and to keep them from constant erosion has been a perpetual theme in the studies of dacrymycetes (Donk, 1966). These difficulties originate from a tradition to tie generic definitions to a specific basidiocarp shape (Fig. 1, 3A). It is known now that particular shapes, like most of the other character states in the class, appeared in dacrymycetes multiple times independently. Therefore, genera defined through these characters are resolved as polyphyletic (I, Shirouzu *et al.*, 2013; Zamora and Ekman, 2020). A solution to this problem is to find new combinations of traits for group identification and reshape genera to minimize conflict between morphology and phylogeny.

Table 1. Summary of genera mentioned in relation to dacrymycetes. Numbers of taxa names summarize all published species, forms, or varieties (numbers of included combinations are given in parentheses) except autonyms, orthographic synonyms, illegitimate and not valid names. Notes include outcomes of the recent phylogeny-based revisions or the author's unpublished opinions.

TAXON	YEAR	N OF TAXA NAMES	NOTE
<i>Arrhytidia</i> Berk. & M.A. Curtis	1849	10 (3)	Probable synonym to <i>Femsjonia</i> (I). Rarely used name.
<i>Calocera</i> (Fr.) Fr.	1825	84 (16)	Recognized name in dacrymycetes.
<i>Calopopsis</i> Lloyd	1925	2	Probable synonym to <i>Calocera</i> (McNabb, 1965a). Rarely used name.
<i>Ceracea</i> Cragin	1885	12 (1)	Type species is an ascomycete. Most species are related to <i>Cerinomyces</i> (I).
<i>Cerinomyces</i> G.W. Martin	1949	37 (6)	Recognized name in dacrymycetes, genus consists of 29 formal and 6 informal species (I).
<i>Cerinosterus</i> R.T. Moore	1987	2 (2)	Probable synonym to <i>Femsjonia</i> . Rarely used name.
<i>Corynoides</i> Gray	1821	4 (4)	Probable synonym to <i>Calocera</i> (McNabb, 1965a). Rarely used name.
<i>Dacrymyces</i> Nees	1817	187 (35)	Recognized name in dacrymycetes. Partially recombined to <i>Cerinomyces</i> (I), <i>Dendrodacrys</i> (II, III), <i>Dacryonaema</i> and <i>Unilacryma</i> (Zamora and Ekman, 2020).
<i>Dacryomitra</i> Tul. & C. Tul.	1872	17 (10)	Recognized name in dacrymycetes.
<i>Dacryomycetopsis</i> Rick	1958	1	Type species is likely dacrymycetous. Rarely used name.
<i>Dacryonaema</i> Nannf.	1947	3 (2)	Recognized name in dacrymycetes, genus consists of 3 formal species (Zamora and Ekman, 2020).
<i>Dacryopinax</i> G.W. Martin	1948	23 (7)	Recognized name in dacrymycetes.
<i>Dacryopsella</i> Höhn.	1915	3 (2)	Type species is a <i>Typhula</i> s.l. and does not belong to dacrymycetes.
<i>Dacryopsis</i> Massee	1891	9 (4)	Probable synonym to <i>Ditiola</i> (McNabb, 1966). Rarely used name.

Table 1. Continued

TAXON	YEAR	N OF TAXA NAMES	NOTE
<i>Dacryoscyphus</i> R. Kirschner & Zhu L. Yang	2005	3 (2)	Recognized name in dacrymycetes.
<i>Dendrodacrys</i> J.C. Zamora, A. Savchenko, Gonz.- Cruz, Prieto-García, Olariaga & Ekman	2022	5 (1)	Recognized name in dacrymycetes, genus consists of 11 formal and 4 informal species (II, III).
<i>Ditiola</i> Fr.	1822	25 (13)	Recognized name in dacrymycetes.
<i>Femsjonia</i> Fr.	1849	11 (3)	Recognized name in dacrymycetes.
<i>Guepiniopsis</i> Pat.	1883	19 (13)	Recognized name in dacrymycetes.
<i>Heterotextus</i> Lloyd	1922	7 (6)	Recognized name in dacrymycetes.
<i>Hormomyces</i> Bonord.	1851	7 (2)	Type species does not belong to dacrymycetes (Mack et al., 2021).
<i>Hydromyces</i> Raf.	1808	0	Not valid name, <i>nom. nud.</i>
<i>Raddites</i> Karst.	1888	1	Type species probably does not belong to dacrymycetes.
<i>Septocolla</i> Bonord.	1851	1	Probable synonym to <i>Dacrymyces</i> (McNabb, 1973). Rarely used name.
<i>Unilacryma</i> (L.S. Olive) Shirouzu, Tokum. & Oberw.	2013	2 (1)	Recognized name in dacrymycetes, genus consists of 2 formal species (Zamora and Ekman, 2020).

Priority for this thesis was to revise a large taxonomic group in dacrymycetes, and at the same time address polyphyly in the class and maintain morphologically identifiable monophyletic genera. The choice of evaluated taxonomic groups was dictated by arguments from both morphology and phylogeny. In terms of phylogeny, when studying a genealogically complex group like dacrymycetes, it is logical to move from the most basal branching event towards the crown of a tree, going through sister clades one by one. In this process authors usually choose a breadth of scope on an *ad hoc* basis. For the first monographic paper (**I**) a choice was made against the large Dacrymycetaceae in favor of its sister family Cerinomycetaceae – strongly supported, dominated by a single genus *Cerinomyces*, and relatively small. Traditionally, *Cerinomyces* was defined by corticioid basidiocarps, in contrast to the rest of the class characterized by gelatinous ones. Similarly to other dacrymycete genera, this emphasis on a single character led to inclusion of unrelated species into *Cerinomyces*, and the genus became overly broad. This problem was addressed the paper **I** where the genus was amended, and taxa related to it historically, phylogenetically, or morphologically were revised.

Developing the subject of morphological similarity, papers **II** and **III** investigated a notable morphological feature called dendrohyphidia (Fig. 3E lower) that is common in *Cerinomyces* but also occur in the rest of the class (Fig. 4). Consequently, the genus *Dendrodacrys* was described in Dacrymycetaceae as the largest group of dendrohyphidia-bearing taxa in dacrymycetes. Over the course of three papers, *Cerinomyces*-like morphologies in the class were thoroughly explored and polyphyletic taxa were reduced.

Aims for the present thesis were:

- 1) to revise and amend *Cerinomyces s.s.* and its respective family Cerinomycetaceae on a basis of phylogenetic analyses and morphological studies involving type specimens and other material from herbarial and field sampling;
- 2) to study and compare taxa related to *Cerinomyces* morphologically;
- 3) to provide nomenclatural solutions for *Cerinomyces*-like taxa in Dacrymycetaceae, including new species and genera if needed;
- 4) to find characteristic morphologies for the recovered phylogenetic clades where possible.

MATERIALS AND METHODS

Morphological studies

The thesis addresses 84 taxa related to the genera *Cerinomyces* and *Dendrodacrys*, including newly described species and informal taxa. Of them, 61 were the target taxa, supplied with detailed descriptions, and 23 were additional ones, provided with smaller notes, studied to assess historical and morphological background. Of the 61 target taxa, 7 were not sequenced. 14 *Cerinomyces* species were described prior to the paper **I**, and the type specimens of 11 of them were accessed. All type specimens of *Dendrodacrys* were seen. Specimens were obtained from the herbaria ARIZ, BPI, CFMR, CWU, EA, FH, G, GB, H, HMAS, ILLS, K, KAS, L, LE, LSU, LSUM, NCSLG, NCU, NY, O, PC, PDD, PRM, S, TAAM, TNM, TNS, TRTC, TU, TUF, UBC, UPS, URM, and personal herbarium of R. Enzlin. Herbaria acronyms follow Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>). Descriptions are based primarily on sequenced specimens, and specimens without sequences are incorporated only in the absence of sequenced ones or when their morphology agreed well with the adopted species concept. Detailed information on specimens, high-resolution macro photographs, and scanned notes and labels for the papers **I** and **III** are available under CC BY 4.0 license via the PlutoF platform (<https://plutof.ut.ee>, Abarenkov *et al.*, 2010). Microscopic studies were performed with various Leika, Nikon, and Zeiss stereomicroscopes and microscopes with phase contrast or differential interference contrast. For slide preparation, measurements, and drawings Cotton Blue in lactic acid or 1–5 % KOH with or without addition of Congo Red were used. Illustrations were produced from microscopic slides using a drawing tube (**I**, **III**) and from integrated camera photos (**I–III**). At least 30 randomly selected mature basidiospores and well-developed basidia were measured when possible. Dimensions were estimated with an accuracy of 0.1 µm. Taxonomic novelties were deposited in MycoBank (Robert *et al.*, 2013). Numbers of taxonomic names in the Table 1 were sourced from MycoBank on 2022-05-14.

Molecular laboratory work and phylogenetic analyses

DNA was extracted from dried basidiocarps or living strains when available. Extractions and PCR for most of UPS and TNS herbaria specimens follow respectively Zamora and Ekman (2020) and Shirouzu *et al.* (2016), while other materials were usually processed as indicated in the paper **I**. Gene regions sequenced for the studies were SSU, ITS, LSU, TEF1- α , RPB1, RPB2 (**I–III**), and 12S (**II**). PCR protocols and sequencing primers are listed in the respective papers. The resulting sequences are available in GenBank. Once produced, the sequences were automatically aligned with MAFFT (Katoh *et al.*, 2019) or BioPhy (Suchard and Redelings, 2006) and additionally edited by hand. Maximum

likelihood phylogeny interference with Felsenstein bootstraps was performed in RAxML (Stamatakis, 2014), RAxML-NG (Kozlov *et al.*, 2019), or IQ-TREE (Nguyen *et al.*, 2015), while Bayesian analyses were done in MrBayes (Ronquist *et al.*, 2012). Species delimitation in the paper **II** was consulted with STACEY analysis (Jones, 2017) as part of the BEAST2 platform (Bouckaert *et al.*, 2014). Final trees were plotted in ggtree (Yu *et al.*, 2017) for R environment (R Core Team, 2019) or in FigTree (<http://tree.bio.ed.ac.uk/software/figtree/>). The alignments and phylogenograms were deposited in TreeBASE (**I**, **II**), and/or published within DOI-index datasets via PlutoF (**I**, **III**).

RESULTS

A dataset of SSU, 5.8S, LSU, TEF1- α , RPB1, and RPB2 genes was used to infer the class phylogeny and resolve the position of *Cerinomyces* – the target genus of the paper I. General arrangement of dacrymycete families presented in this paper confirmed the earlier reported phylogenies of dacrymycetes, with the robustly supported Cerinomycetaceae as a sister clade to the Dacrymycetaceae (I: Fig. 4). Both families comprised the order Dacrymycetales – a sister to a clade that coupled Dacryonaemataceae and Unilacrymaceae.

Following the phylogeny, *Cerinomyces* was reshaped to a stricter circumscription that also makes entirety of its respective family. The study defined a combination of traits that unites *Cerinomyces* and distinguishes it from genera in other families: (a) presence of simple clamps on all hyphal septa; (b) curved-cylindrical thin-walled basidiospores that only rarely and tardily develop up to three transverse septa; (c) low amount of carotenoid pigments in hyphae and basidiospores; and (d) corticioid, resupinate, pustulate, pulvinate and only slightly cerebriform basidiocarps (see examples on Fig. 3). Young basidiospores in selected members of *Cerinomyces* were found to be binucleate, in contrast to the rest of the class with uninucleate spores.

Traditionally, *Cerinomyces* was defined by the arid corticioid basidiocarps. Alongside corticioids, the new circumscription included species with gelatinous pustulate to cerebriform basidiocarps, even though such basidiocarps are typically attributed to *Dacrymyces* (I: Fig. 11–13). To highlight links between phylogenetic and morphological groups, five empirical clades were designated within the *Cerinomyces*. Newly introduced gelatinous members formed two of them (so-called *C. enatus* and *C. tortus* clades), while conventional corticioid species were scattered across another three (*C. pallidus*, *C. albosporus*, and *C. borealis* clades). Each clade was detailed with individual phylogenetic tree based on SSU, ITS, LSU, and more rarely TEF1- α (I: Fig. 5–8); these trees were used as an assistance in species delimitation. In total, 29 species were recognized in *Cerinomyces* s.s., of which 20 were newly described. Additionally, three new combinations were proposed, four informal taxa were designated, and seven species were excluded from the genus.

Most of the excluded species had corticioid morphotype typical to the traditional *Cerinomyces*, but in phylogeny they belonged to Dacrymycetaceae. A clade containing *Dacrymyces grandiniooides* (\equiv *C. grandiniooides*) was resolved as a sister to *Da. stillatus* (type of *Dacrymyces*), *Da. chrysospermus*, and *Guepinopsis buccina*. To reduce polyphyly, all taxa related to *Da. grandiniooides* were formally transferred to *Dacrymyces*. Two other corticioid species, “*Cerinomyces*” *canadensis* and *Da. corticioides*, were recovered in proximity to *Femsjonia peziziformis*. They were not formally recombined, as this action is better suited for a future dedicated study on *Femsjonia*. Aside from corticioid appearance, all these species were morphologically different from *Cerinomyces* s.s.: they had more robust, yellow-tinted basidiocarps with thick light-coloured

subiculum, fimbriate margins, and hymenial surfaces of waxy- to firmly-gelatinous consistency when moisturized (**I**: Fig. 14, 15). In addition, *Dacrymyces grandiniodoides* group lacked clamps and showed 3-septate basidiospores (e.g., **I**: Fig. 59). On the whole, four new species, six combinations and one informal taxon were raised in *Dacrymyces* when tackling *Cerinomyces*-related taxa in Dacrymycetaceae.

While all the corticioid taxa morphologically related to *Cerinomyces* were addressed in the paper **I**, it did not exhaust diversity of gelatinous dacrymycetes with *Cerinomyces*-like appearance. One of the notable microscopic characters found in *Cerinomyces* was sterile hymenial structures called dendrohyphidia or branched hyphidia (lowermost on Fig. 3E). However, it would be wrong to treat dendrohyphidia merely as an identification clue pointing towards *Cerinomyces* – they occur in other dacrymycetes as well, even though they were reported less frequently. All five members of Dacryonaemataceae and Unilacrymaceae have already been confirmed to develop branched hyphidia, but information on this character in Dacrymycetaceae was scanty. Papers **II** and **III** filled this gap.

Three already described members of Dacrymycetaceae with dendrohyphidia were collaterally reviewed in the paper **I**, namely *Da. paraphysatus*, *Da. enatus* var. *macrosporus*, and *Femsjonia pezizoidea*. However, amount of similar material that could not be assigned to any species was growing. The main difference of this group from *Cerinomyces* s.s. was presence of 3-septate basidiospores and overall larger sizes of macro- and microstructures. As a yet unnamed group, it was first approached in the study **II** and shown to form a well-supported clade in Dacrymycetaceae. After considering that undescribed clade has a rather homogeneous morphology, and branched hyphidia are an uncommon character within the family, a new genus called *Dendrodacrys* was established (Fig. 4, **II**). Other characters that bound *Dendrodacrys* together were the abovementioned 3-septate spores of mostly cylindrical and slightly curved shape, and presence of specialized marginal hyphae. Elsewhere in Dacrymycetaceae dendrohyphidia were known for scarcely any species that were easy to tell apart from *Dendrodacrys* (the best known are *Da. san-augustinii* and *Dacryopanax elegans*).

In support to the class tree, a STACEY species-delimitation analysis was carried out. It suggested a scheme of seven putative *Dendrodacrys* species that was generally congruent with morphology and the authors' view on delimitation. Four species were described in a formal way, while the rest remained with informal designations because of the limited data on morphology. One species without sequences, *De. paraphysatum*, was combined to *Dendrodacrys* on morphological grounds (**II**).

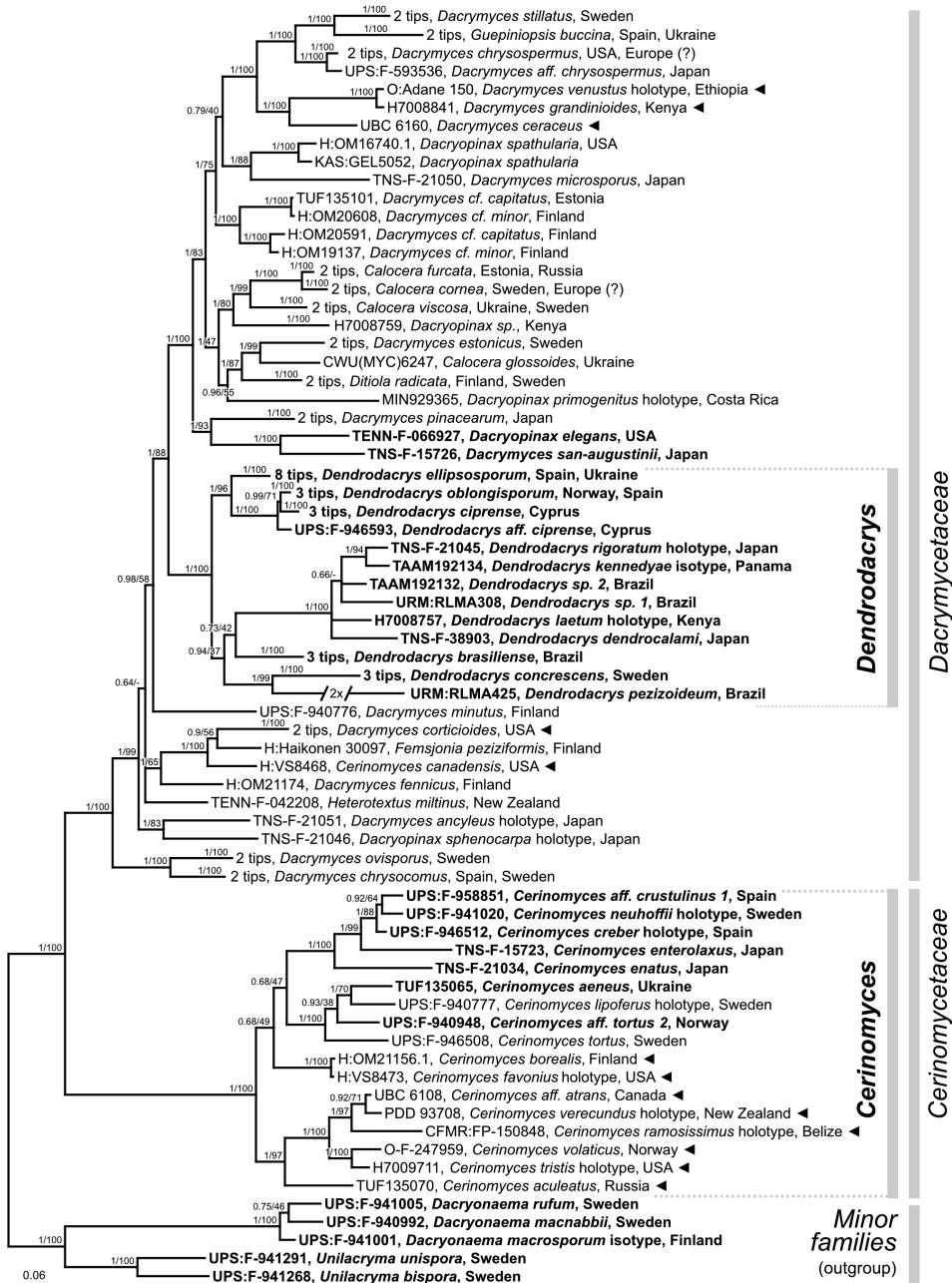


Fig. 4. Phylogeny of dacrymycetes from the paper III (modified; clades with redundant tips are collapsed). Taxa with strongly branched hyphidia are marked in bold font, taxa with corticioid basidiocarps are marked with black triangles (◀). Bayesian consensus tree based on SSU, 5.8S, LSU, RPB1, RPB2, and TEF1- α sequences. Numbers before and after slash (/) indicate posterior probabilities of Bayesian analysis and bootstrap support values.

Data on *Dendrodacrys* in the paper **II** originated from European material. In turn, a follow-up paper **III** communicated tropical and subtropical taxa. It proposed six nomenclatural novelties for *Dendrodacrys* including two new species and four new combinations (of which one is a variety raised to the species rank with a change of name). In total, the number of species in the genus was raised up to 11. Two Japanese taxa that used to be associated with *Dendrodacrys* informally (**II**) now were accepted as a new species and a new combination (**III**). Morphology of *Dendrodacrys* presented in the paper **III** is diverse: there are pustulate, cerebriform, lobate, and spathulate-foliose basidiocarps of colours ranging from transparent yellow to dark brown; clamped and clampless hyphal septa; and different variations of dendroid hyphidia, either having thickened base and thin apical part, or almost evenly wide through the length. Though, even after inclusion of these morphologies, *Dendrodacrys* can still be defined by its key diagnostic features mentioned above.

All taxa presented in the papers **I–III** were accompanied with detailed descriptions, macrophotos, photos of microstructures or line drawings made directly from microstructures, as well as notes aiding identification. In the papers **I** and **III** character tables were provided, and a wide selection of taxa was included in taxonomic keys to help with potentially confusing species groups. Basic ecological and distribution information was presented alongside descriptions.

In the papers **I–III** 42 nomenclatural novelties were published. Listed below, they include one new genus, 27 new species, and 14 new combinations. Notes like “*comb. nov.*” are used here only to showcase results and do not mean that this summary is an actual publication place.

- Cerinomyces aeneus* A. Savchenko, Miettinen & J.C. Zamora, *sp. nov.*
Cerinomyces atrans A. Savchenko, *sp. nov.*
Cerinomyces borealis Miettinen, Spirin & A. Savchenko, *sp. nov.*
Cerinomyces brevisetus Chikowski, Alvarenga & A. Savchenko, *sp. nov.*
Cerinomyces cokeri (McNabb) A. Savchenko & J.C. Zamora, *comb. nov.*
Cerinomyces concretus A. Savchenko, *sp. nov.*
Cerinomyces creber J.C. Zamora, A. Savchenko, Trichies & Olariaga, *sp. nov.*
Cerinomyces enatus (Berk. & M.A. Curtis) A. Savchenko, *comb. nov.*
Cerinomyces enterolactus Shirouzu & A. Savchenko, *sp. nov.*
Cerinomyces favonius Spirin, Miettinen & A. Savchenko, *sp. nov.*
Cerinomyces fugax A. Savchenko, *sp. nov.*
Cerinomyces hesperidis A. Savchenko, *sp. nov.*
Cerinomyces inermis A. Savchenko, *sp. nov.*
Cerinomyces lipoferus J.C. Zamora & A. Savchenko, *sp. nov.*
Cerinomyces nepalensis A. Savchenko, *sp. nov.*
Cerinomyces neuhoffii J.C. Zamora & A. Savchenko, *sp. nov.*
Cerinomyces paulistanus A. Savchenko, *sp. nov.*
Cerinomyces pinguis A. Savchenko, *sp. nov.*
Cerinomyces ramosissimus A. Savchenko, *sp. nov.*

- Cerinomyces tortus* (Willd.) Miettinen, J.C. Zamora & A. Savchenko, *comb. nov.*
Cerinomyces tristis Miettinen & A. Savchenko, *sp. nov.*
Cerinomyces verecundus A. Savchenko, *sp. nov.*
Cerinomyces volaticus A. Savchenko, V. Malysheva & J.C. Zamora, *sp. nov.*
Dacrymyces burdsallii A. Savchenko, *sp. nov.*
Dacrymyces ceraceus (Ginns) A. Savchenko, *comb. nov.*
Dacrymyces cereus (Rick) A. Savchenko, *comb. nov.*
Dacrymyces grandii A. Savchenko & Miettinen, *sp. nov.*
Dacrymyces grandiniooides (McNabb) A. Savchenko, *comb. nov.*
Dacrymyces lagerheimii (Pat.) A. Savchenko, *comb. nov.*
Dacrymyces pengii (B. Liu & L. Fan) A. Savchenko, *comb. nov.*
Dacrymyces pulchrus (Lowy) A. Savchenko, *comb. nov.*
Dacrymyces sobrius A. Savchenko, *sp. nov.*
Dacrymyces venustus A. Savchenko, *sp. nov.*
Dendrodacrys J.C. Zamora, A. Savchenko, Gonz.-Cruz, Prieto-García, Olariaga & Ekman, *gen. nov.*
Dendrodacrys brasiliense (Lloyd) A. Savchenko, Shirouzu & J.C. Zamora, *comb. nov.*
Dendrodacrys dendrocalami (Oberw.) A. Savchenko & J.C. Zamora, *comb. nov.*
Dendrodacrys ellipsosporum J.C. Zamora, A. Savchenko, Gonz.-Cruz, Prieto-García, Olariaga & Ekman, *sp. nov.*
Dendrodacrys kennedyae A. Savchenko, *nom. & stat. nov.*
Dendrodacrys laetum A. Savchenko, *sp. nov.*
Dendrodacrys paraphysatum (L.S. Olive) J.C. Zamora & A. Savchenko, *comb. nov.*
Dendrodacrys pezizoidium (Henn.) A. Savchenko & Alvarenga, *comb. nov.*
Dendrodacrys rigoratum A. Savchenko & J.C. Zamora, *sp. nov.*

When describing nomenclature-complaint species was found premature, or when material was too scanty for typification, provisional “species” were proposed, ten in total: *Cerinomyces aff. aculeatus* 1, *C. aff. crustulinus* 1, *C. aff. tortus* 1, 2, & 3, *Dacrymyces aff. venustus* 1 (**I**), *Dendrodacrys* sp. 1–4 (**III**). Finally, four species were lectotypified: *Ceracea aureofulva* Bres., *Ce. cerea* Rick, *Da. confluens* P. Karst., *Tremella enata* Berk. & M.A. Curtis, and one was neotyped: *Tremella torta* Willd.

DISCUSSION

Taxonomy of dacrymycetes is often characterized as complicated and outdated, but advancements of the last years, including papers presented here, make a promise of stable and natural system. The classic morphology-based studies, such as the series of monographs by McNabb (1964–1973), revised most of the old names and provided comprehensive species lists. In turn, phylogenetic works by Shirouzu *et al.* (2007–2020) established genealogical relations in dacrymycetes. These studies focused on Asian material and thus were somewhat disjointed from the older revisions that usually dealt with European and American taxa. However, a coarse phylogenetic structure of the class was revealed already in the early trees and now remains largely unchanged. Reliable links between the large clades and taxonomic families allowed authors to pay more attention to the fine phylogenetic landscape and move towards generic reassessments. Two factors hamper this work: a) morphological plasticity of dacrymycetes resulting in polyphyly of the traditional genera; and b) lack of type studies and sequenced types. Consequently, description of new species in certain groups is now slowed down because of a high chance to create superfluous names.

Nevertheless, not all the groups are similarly problematic, and some have more concise circumscriptions, lower species numbers, and relatively uniform morphology. Owing to this, three of four dacrymycete families have already received revisions, one of which is presented in this thesis. Revision of Cerinomycetaceae (**I**) was a logical step following the earlier phylogenetic studies that mapped the scope of this family but not ventured into systematic rearrangement. In this treatment, Cerinomycetaceae contains only a single genus *Cerinomyces*. Division into multiple genera was deemed impractical, even though five morphophylogenetic groups were recovered within the family. It was still not possible to identify characters that would unambiguously define every alleged genus, and in addition some of the deeper nodes in the phylogeny showed low support values, obscuring relations of the clades.

After the three families were addressed, the largest and the most polyphyletic Dacrymycetaceae is due for phylogeny-based generic reformation. This process was pioneered with description of a new genus *Dendrodacrys*, which was proposed in the paper **II** of the current thesis and further expanded in the paper **III**. It was decided that the genus is worth raising as it constitutes both a distinct clade and a morphologically-identifiable group, and does not overlap with any older generic types. *Dendrodacrys* took into itself a few species from *Dacrymyces*, *Dacryopsis*, *Calocera*, and *Femsjonia*, which lowered polyphyly in the remainder of the family.

Further work is to be done in clades that diverged both down- and upstream from *Dendrodacrys*. Fig. 5 illustrates two of the many possible scenarios of generic division of Dacrymycetaceae, ruled by the placement of existing types and morphological uniformity. A schema on the left reflects a lumping approach, and on the right – a splitting one. An important consideration for choosing between

them is that the monophyletic state alone is not enough for genus recognition in the utilitarian framework – a genus should be also morphologically distinct and useful in practice. Most likely, future authors will need to find a balance between lumping and splitting to ensure that the delimitation is robust.

There are several questions to be answered before putting forward any kind of a large-scale taxonomic solution for the family. One is how to deal with existing polyphyletic genera that are currently defined through the basidiocarp type. For instance, *Ditiola*, *Heterotextus*, and *Guepiniopsis*, if taken in a strict phylogenetic circumscription, will approach monotypy. As a result, many species will lose their old generic attachments, and the possible new genera erected to host these orphan taxa may appear too inclusive and will be hardly useful in practice.

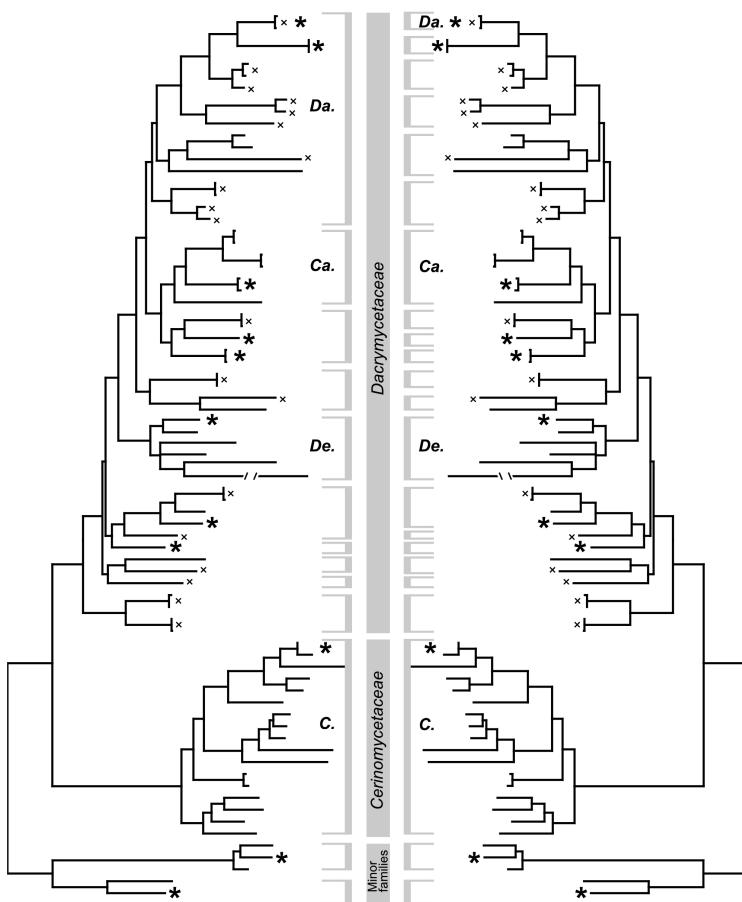


Fig. 5. Phylogeny of dacrymycetes with hypothetical examples of lumping (left) and splitting (right) schemas of generic delimitation. Asterisks (*) mark genus types, crosses (x) – *Dacrymyces* species; *Da.* stands for *Dacrymyces*, *Ca.* for *Calocera*, *De.* for *Dendrodacrys*, *C.* for *Cerinomyces*. Maximum-likelihood consensus tree prepared for the paper III, based on SSU, 5.8S, LSU, RPB1, RPB2, and TEF1- α sequences. Minor families (out-group) are Dacryonaemataceae and Unilacrymaceae.

Other question is how to confront a taxonomic conglomerate of the genus *Dacrymyces*. Historically, species were assigned to *Dacrymyces* by a residual principle, when simplicity of basidiocarps disallowed authors to place them in any other genus. As seen on the Fig. 5, species of *Dacrymyces* (marked with crosses) are currently scattered over the whole Dacrymycetaceae. Broadening the genus to the extent of the family would be the simplest, though unsatisfactory, way to resolve the problem. Other options include narrowing it down to the immediate vicinity of the type species *Da. stillatus* (uppermost clade on the right tree of Fig. 5) or choosing a wider clade that will absorb as little types of other genera as possible (uppermost clade on the left tree of Fig. 5). For the latter solution, it is perhaps reasonable to stop extension in the proximity to the genus *Calocera* s.s., the second-largest conglomerate in dacrymycetes (“Ca.” on the both trees of Fig. 5).

The main obstacle with future revisions of *Dacrymyces* and *Calocera*, as it often happens with long-standing genera, is accumulation of ambiguous species names. Problems with names are usually born from problems with type specimens: the latter can be lost, hardly accessible, too old and scanty for sequencing, or could have never existed. These cases can be approached only with a scrupulous search for authentic materials and careful neo- or epitypification. Therefore, combination of literature surveys, intense herbarium and field sampling, thorough morphological examination, and multigene or genomic sequencing is required to build a modern system of dacrymycetes.

CONCLUSIONS

The given thesis presents taxonomic studies in the fungal class Dacrymycetes. This group is characterized by the general disarray in its taxonomy, which is related to the lack of large-scale modern revisions. The thesis partially closes this gap, and its main results and conclusions are:

- The paper **I** comprehensively revised the second largest dacrymycete family – Cerinomycetaceae. As a result of the revision, the family became monotypic and equal in content to its only genus *Cerinomyces*. Within *Cerinomyces* five clades were inferred, but their morphological differences were found insufficient to split the group into multiple genera. The study implemented a new multi-character definition of the genus because the traditional emphasis on a single character – corticiod type of basidiocarps – has drawn *Cerinomyces* polyphyletic. This defining character was rejected, and species with other, gelatinous type of basidiocarps were introduced to the genus. In the updated definition, *Cerinomyces* is distinguished by presence of simple clamps on all hyphal septa, curved-cylindrical thin-walled basidiospores that only rarely and tardily develop up to three transverse septa, and low amount of carotenoid pigments in hyphae and basidiospores. The paper signified a shift from traditional genus concepts based on macroscopic characters towards phylogenetically meaningful genera defined by microscopic characters.
- The largest dacrymycete family, Dacrymycetaceae, was found to host species that share various morphological traits with *Cerinomyces*. To address such taxa, parts of Dacrymycetaceae were subjected to revisions in the papers **I–III**. Most notably, a new genus *Dendrodacrys* was raised to encompass a phylogenetically strongly supported clade (**II, III**). Species of *Dendrodacrys* are characterized by branched hyphidia, 3-septate curved-cylindrical basidiospores, and presence of specialized marginal hyphae.
- In total, the papers **I–III** proposed 42 nomenclatural novelties, including one new genus, 27 new species, and 14 new combinations. Materials not eligible for formal description were laid out as ten informal taxa. Five species were lectotypified or neoty wholefied. These results once again confirm that museum collections – the main source of material for the thesis – hold a large number of undescribed taxa and can be further used to uncover hidden diversity of dacrymycetes.
- Morphological examination remains the most widely applied and accessible identification method in mycology. With this in mind, all taxa presented in the papers **I–III** were accompanied with detailed descriptions, macrophotos, images of microstructures, and notes. Keys and character tables for both *Cerinomyces* and *Dendrodacrys* were constructed, and basic ecological information was provided.

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SUMMARY IN ESTONIAN

SEENTE PEREKONNA *CERINOMYCES* JA LÄHEDASTE TAKSONITE SÜSTEEMAATIKA NING FÜLOGENEES

Päristuumsete hulgas on seened üks suuremaid ja mitmekesisemaid eluslooduse riike, mille hulka kuuluvad maismaakoosluste surnud orgaanilise aine peamised lagundajad. Vaatamata olulisel ökoloogilisele rollile, on nende taksonoomiat ja ökoloogiat ebapiisavalt uuritud. Käesolev doktoritöö uuris pisarseente klassi *Dacrymycetes* taksonoomiat ning fülogeneesi. See on liigirikkuselt väike, kuid nii morfoloogia kui põlvnemiskäigu alusel selgelt piiritletud ning mükoloogilises kirjanduses küllaltki varakult eristatud rühm. Fülogeneetilised uuringud näitavad, et pisarseened on üks varasemalt lahknenud kandseente rühmi, mis on sösarrühmaks suurimale kandseente klassile *Agaricomycetes*. Klassi *Dacrymycetes* liikidel arenevad kõdupuidul silmaga nähtavad enamasti kollased või oranžid sültjad viljakehad, milles eosed moodustuvad Y-kujulitel eoskandadel.

Pisarseente klassis eristatakse traditsiooniliselt neli sugukonda, kuid rühma taksonoomia on ümberkujunemise järgus. Pisarseente sugukonnad *Dacrymyctaceae* ja *Cerinomycetaceae* sisaldavad enamiku kirjeldatud liikidest, sugukondadesse *Unilacrymaceae* ja *Dacryonaemataceae* on arvatud aga vaid viis liiki. Käesolev doktoritöö keskendus sugukonnale *Cerinomycetaceae* ja selle ainsale perekonnale *Cerinomyces* (artikkel I). Liigid, mis on morfoloogiliselt sarnased perekonna *Cerinomyces* esindajatele, aga kuuluvad sugukonda *Dacrymyctaceae*, leiavad käsitlemist artiklites II–III.

Ajalooliselt on perekonda *Cerinomyces* arvatud koorikja viljakehaga liike. Sellise ühe tunnuse põhise süsteemaatika tõttu kuuluvad siia perekonda liigid, mis pole doktoritöö põhjal omavahel lähisuguluses. Pisarseente klassi *Dacrymycetes* fülogeneesi analüüs kasutati kuue geeni nukleotiidseid järjestusi. Saadud tulemuste põhjal esitati artiklis I uus perekonna *Cerinomyces* kontseptsioon. Nüüd kuuluvad siia nii sültja kui liibuva viljakehaga liigid. Lisaks määratleti sama artiklis perekonda *Cerinomyces* kuuluvate liikide tunnuste unikaalne kombinatsioon: (a) lihtsad pandlad kõigis seeneniidi rakuvheseintes; (b) kõver-silinderjad õhukesekestalised kandeosed, milles vaid harva ja hilises arengujärgus areneb kuni kolm ristivaheseina; (c) vähene karotenoidsete pigmentide sisaldus seeneniitides ja eostes; (d) koorikjad, liibuvad, näsa- või padjakujulised ja kergelt aju-taoliste käärudega viljakehad.

Perekonnas *Cerinomyces* eristati ja iseloomustati morfoloogia alusel viis ühis-tekkelist rühma. Nagu mainitud, perekond *Cerinomyces* selle traditsioonilises käsitlusnes koosneb ainult kuivade koorikjate viljakehadega liikidest. Hiljutised uurimused on näidanud, et sellesse perekonda kuulub ka sultjate ja näsjate viljakehadega liike, kuigi taolisi on tavaliselt seostatud hoopis teise pisarseene perekonnaga – *Dacrymycetes*. Käesolevas töös perekonda *Cerinomyces* liidetud sultjate viljakehadega liigid moodustasid kaks iseseisvat evolutsiooni haru, koorikja viljakehaga liigid jagunesid ülejäänud kolme rühma vahel. Rühmas *Cerinomyces sensu stricto* eristati 29 liiki, millega 20 kirjeldati teadusele esmakordselt. Lisaks

esitati kolm uut taksonoomilist kombinatsiooni, eristati neli tõenäoliselt uut liiki, mis vajavad veel uurimist ja seitse liiki arvati sellest perekonnast välja.

Enamus perekonnast *Cerinomyces* välja arvatud liikidest on koorikja morfotüübiga ja kuuluvad fülogeneesi analüüsni alusel pisarseenelistele sugukonda (*Dacrymycetaceae*). Neist üks rühm on lähedane pisarseene perekonna tüüpiliigile – *Dacrymyces stillatus* (tava-pisarseen). Seega, kõik taksonid, mis kuulusid sellesse rühma (nn. *Dacrymyces grandinoides* klaad) viidi üle pisarseene perekonda. Kaks teist koorikjat liiki, *Cerinomyces canadensis* ja *Dacrymyces corticioides* leiti olevalt lähisuguluses liigiga *Femsjonia peziziformis*. Kõik nimetatud liigid erinevad *Cerinomyces* s.s. esindajatest. Nimelt on neil robustsem, paksu heleda subiikulumi ja narmastunud servaga kollakas viljakeha ning niiskena vahajas kuni tugevalt sültjas eoslava pind. Lisaks on *Dacrymyces grandinoides* rühma liikidel kolme vaheseinaga kandeosed, kuid pandlad puuduvad. Kokku kirjeldati perekonnas *Dacrymyces* neli uut liiki, esitati kuus uut taksonoomilist kombinatsiooni ja tuvastati üks veel kirjeldamata takson.

Artikel **I** käsitles kõiki koorikjatele *Cerinomyces* liikidele morfoloogiliselt sarnaseid taksoneid, kuid ei hõlmanud sültja viljakehaga liike, mis on *Cerinomyces* liikidele sarnase välimusega. Heaks morfoloogiliseks tunnuseks *Cerinomyces* liikidel osutusid steriilsed eoslava struktuurid – dendro hüfiidid ehk harunevad hüfiidid. Pisarseeneliste sugukonna taksoneid, mis moodustavad selliseid struktuure käitleti artiklites **II** ja **III**, mis ühtlasi annavad ülevaate dendro hüfiidide esinemisest pisarseente klassis. Harunenud hüfiididega taksonid on koondunud ühte pisarseeneliste klaadi, mida iseloomustab vähene morfoloogiline varieeruvus. Seetõttu eristati selle rühma liigid perekonna tasemel, arvestades ka asjaolu, et sugukonna teistes rühmades moodustavad harunevaid hüfiide vaid üksikud liigid. Uuele perekonnale *Dendrodacrys* iseloomulikeks morfoloogilisteks tunnusteks on hüfiidid, kolme vaheseinaga silinderjad ja veidi kõverdunud kandeosed ning omanäolised servahüüfid.

Artikel **II** kirjeldas Euroopast leitud liike, artikel **III** keskendus aga troopilistest ja subtroopilistest piirkondadest kogutud materjalile. Viimases kirjeldati kaks teadusele uut liiki ja avaldati neli uut taksonoomilist kombinatsiooni, mis töötis perekonnas *Dendrodacrys* liikide arvu ühetestikümnele. Peale ülalmainitud võtmetunnuste iseloomustab selle perekonna liike mitmekesine morfoloogia (artiklid **II** ja **III**): näsajad, ajutaoliste käärudega, hõlmised, pahtlikujulised või lehtjad viljakehad, mille värv ulatub läbipaistev-kollasest tumepruunini; hüüfide vaheseinad kas pannaldega või ilma; dendro hüfiidid eriilmelised – kas paksenenud alusega ja õhukese tipuosaga või siis ühtlase laiusega kogu pikkuses.

Kõikide artiklites **I–III** käsitletud taksonite kohta esitati detailsed kirjeldused, makrofotod, mikrostruktuuride fotod või joonised ning märkused oluliste määramistunnuste kohta. Artiklites **I** ja **III** avaldati tunnuste jaotuste tabelid ning määrajasse kaasati lai valik taksoneid, aitamaks eristada määramisel sarnaseid liigirühmi. Taksonikirjeldustele lisati info liikide ökoloogia ja leviku kohta. Ühtekokku avaldati artiklites **I–III** 42 uut taksononime, sh üks uus perekond, 27 uut liiki ja 14 uut taksonoomilist kombinatsiooni.

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PUBLICATIONS

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