Dacrymycetes

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Abstract

The Dacrymycetes, a morphologically, chemically, and ecologically well defined monophyletic group of wood decaying Basidiomycota, is reviewed in this article. The life cycle of *Dacrymyces stillatus* is considered as representative for all members of the class. Traditional taxonomy is based on morphologcial characters. This classification is compared with molecular phylogenies. Evolutionary trends of dacrymycetaceous fungi are discussed.

Content

I. Introduction

Dacrymycetes is a well defined class in the Agaricomycotina, Basidiomycota. **The most important characteristic is the unique basidial ontogeny and morphology** (Fig. 1d). Young basidia grow slightly clavate and expand apically to produce two thick, cylindrical and long sterigmata which taper abruptly to form spicula on which asymmetrically attached, large spores develop. Between the sterigmata the original apex of the young basidium remains visible, a characteristic which is

morphologically rather distinctive. Most species have curved-cylindrical basidiospores, typically transversely septate when mature (Fig. 1e-g). Commonly, basidiospores germinate with microconidia (Fig. 1e, f), but germ-tube formation is also widespread (Fig. 1g). Production of secondary spores is not known in the Dacrymycetales. Several species of *Dacrymyces, Femsjonia*, *Guepiniopsis*, and *Calocera*, which we have studied extensively in pure culture, produce **limited yeast colonies**, originating from microconidia (Fig. 1f). Microconidium formation does occur also on hyphae (Fig. 1h), functioning as additional asexual reproduction. In *Dacrymyces stillatus,* hyphal fragmentation, also considered as a conidial stage, is rather common and is an effective dispersal mechanism (Fig. 1i). Hyphal walls partly gelatinize, thus forming a soft waxy to gelatinous, sometimes tough consistency. **Basidiocarp morphology** varies from strictly corticioid to pustulate, cupulate, cyphelloid, stalked-capitate, or clavarioid. The abhymenial surfaces often produce strongly differentiated "marginal-hairs", terminal hyphal cells which are characteristic for certain taxa. Cystidia are absent in the hymenia, but conspicuously branched dikaryophyses often occur. Predominantly, Dacrymycetes species form gelatinous, **mostly bright yellowish to orange basidiocarps**, pigmented by carotenoids. Most fructifications have root-like bases in the wood; rarely they are broadly attached to the substrate. An intensive brown-rot is associated with growth in coniferous and angiosperm wood, but lignin decomposition may occur, too.

II. Ontogeny

The life-cycle of *Dacrymces stillatus* (Fig. 1) is taken as a representative example for the Dacrymycetes to illustrate the most important developmental stages. The morphology of basidiocarps (Figs. 2, 5), however, is rather variable. Usually, the hyphal context of the trama and the subhymenium (Fig. 1c, 3a) is gelatinous due to gelatinizing outer hyphal walls, and depending on the water content of the fructifications. Hymenia are one-layered in young stages and may develop into mutlilayered thickening ones in older basidiocarps (Fig. 1c). **A typical basidial ontogeny** is illustrated in Fig. 1d. Only in rare cases, basidia are three- or one-sterigmate, the latter as in *Unilacryma unispora* (Fig. 8e). In most cases, mature basidiospores are transversely septate (Fig. 1e) and germinate with microconidia that appear to reproduce by budding (Fig. 1e), however limited in time and space. Spore germination with hyphae, illustrated from *D. palmatus*, but also occurring in *D. stillatus*, is common, and microconidia can develop on these haploid hyphae (Fig. 1g). Fragmented hyphae are capable to produce microconidia, too (Fig. 1h). **Fragmenting hyphae** (Fig. 1i) normally occur in asexual fructifications, but occasionally also in basidiocarps (Fig. 1a, b). Asexual fructifications are common in *D. stillatus* but rare or lacking in other species of the Dacrymycetes.

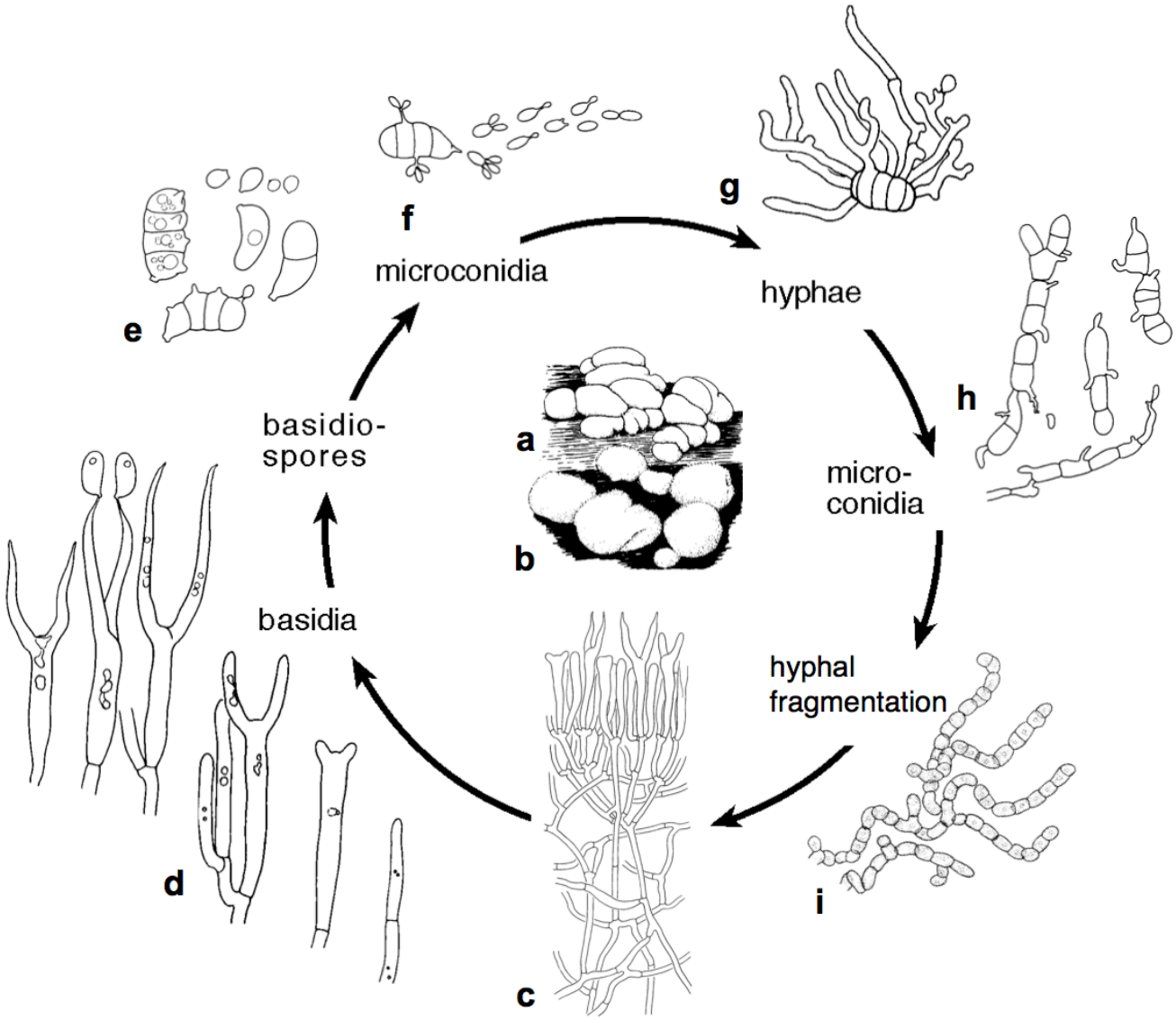


Fig. 1 Life cycle of *Dacrymyces stillatus*. a. Basidiocarps. b. Fructification with fragmenting hyphae (i). **c.** Detail of hymenium and subhymenium. d. Basidial ontogeny showing stages of nuclear divisions in the basidia. e. Basidiospores and spore germination. f. Yeast like budding of microconidia. g. Spore germination with hyphae, illustrated from *D. palmatus*, but also occurring in *D. stillatus*. h. Fragmented hyphae producing microconidia. **i.** Short celled fragmentation of peripheral hyphae from anamorph fructification (b). Figs. not to scale; from Oberwinkler (2012).

Fig. 2 Basidiocarps and anamorph fructification (b) of Dacrymycetales species. a, b**.** *Dacrymyces stillatus*. a. Basidial stage with the hymenium covering the whole upper side. b. Conidial stage with hyphal fragmentation in the whole fructification. c. *Dacrymyces variisporus*, well developed basidiocarp. d. *Dacrymyces palmatus*, hymenium on the upper, folded surface of the basidiocarp. e. *Ditiola haasii*, note hyaline basidiocarps without carotenoids, hymenia marked by light greyish and slightly rough lower surfaces. f. *Dacrymyces chrysospermus*, hymenium covering the folded upper surface of the basidiocarp. g. *Dacryopinax spathularia*, hymenia on the underside of bent basidiocarps. h. *Heterotextus alpinus*, cone-like basidiocarps with hymenia on the flattened underside. i. *Guepiniopsis buccina*, hymenia in the cups, geotropically positively oriented. j. *Dacryonaema rufum*, young basidiocarps on exposed, hard coniferous wood together with crustose lichens. k. *Calocera cornea* with mostly unforked clavarioid basidiocarps on hardwood. l. *Calocera viscosa*, coralloid basidiocarp with a long root inserted in coniferous wood. Bars, 5 mm. All figs. originals F. Oberwinkler.

III. Basidiocarp morphology

Basidiocarp morphology is distinct in most Dacrymycetes species (Figs. 2, 5), but variation during ontogenetic development has to be considered. The **traditional generic concept** is predominantly based on morphology of basidiocarps (Fig. 5). In contrast to all other Dacrymycetes, species of *Cerinomyces* (Fig. 8a) have corticioid (resupinate) growth without definite margins. The flat to slightly cupulate fructifications of *Arrhytidia* have rooting bases and distinct margins. Basidiocarps of other

cupulate genera (Fig. 5), like *Ditiola, Heterotextus, Femsjonia, Guepiniopsis,* and *Dacryopinax* can be characterised by growth direction, stipe morphology and cell differentiations of marginal hairs. Other stalked species are grouped in *Dacryonaema* with globose fertile parts, *Calocera* with simple or forked clavarioid basidiocarps, and *Dacryomitra* with a minute morchelloid habit.

IV. Hyphal systems, hyphae, marginal hairs, and hyphal septa

The reason behind jelly fructifications with a soft or tough context in Dacrymycetes is a **strong tendency of outer hyphal wall layers to gelatinize**. In addition, thin-walled and hyaline hyphae are rather common, but various kinds of wall thickenings and carotenoid pigmentations do occur, too. Especially terminal cells or cell chains of marginal hyphae are often very characteristically structured and therefore used for traditional generic delimitations, as in *Dacryonaema, Guepiniopsis,* and *Heterotextus* (Fig. 7). Hyphal clamps are present or lacking, and as such consistent specific characters. All Dacrymycetes studied so far show dolipores with continuous parenthesomes except for a tiny central pore (Fig. 4).

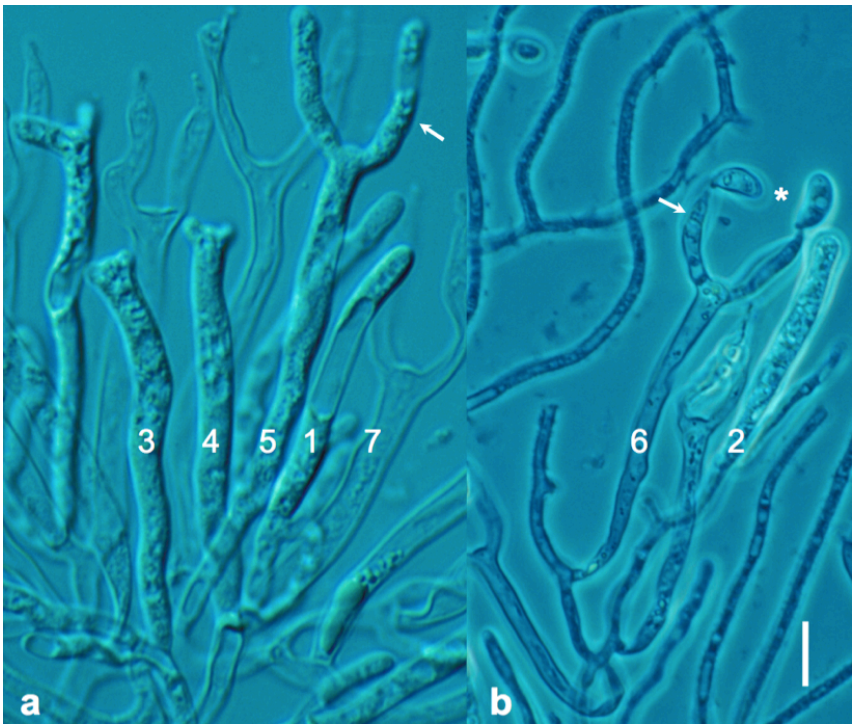
V. Hymenia, dikaryophyses, basidia, and basidiospores

The normal hymenial surface in dacrymycetaceous species is smooth. However, well developed hymenia may become cerebriform to irregularly flabellate. Luxuriantly growing hymenia will alter the original shape of basidiocarps considerably.

Usually, the **hymenial layer** is composed exclusively of basidia in different developmental stages (Fig.3). Some species, like *Dacrymyces estonicus* possess slender, unbranched dikaryophyses (hyphidia). Branched dikaryophyses are known, e.g., in *D. enatus*, and *D. ovisporus* (Fig. 8d). Conspicuously branched dikaryophyses, dendrohyphidia, are found in *D. dendrocalami* (Fig. 8b), *D. macnabbii* (REID 1974), *D. paraphysatus*, and *Unilacryma unispora* (Fig. 8e).

As mentioned above, basidial ontogeny and morphology is the most distinctive character of Dacrymycetes (Figs. 1, 3, 7). Deviations, as in *Unilacryma unispora*, are very rare. *Dacrymyces ovisporus* (Fig. 8d) clearly bridges the gap to typical dacrymycetaceous basidia.

Also, the majority of **basidiospores** share common characters, i.e., transverse septation in mature stages and germination with microconidia and/or hyphae but not with secondary spores (Fig. 9b-f, h). Exceptionally, septation of basidiospores is lacking, as in *Cerinomyces crustulinus* (Fig. 9a), *C. canadensis*, and *C. pallidus*. In addition, most species share cylindrical to allantoid basidiospores, while subglobose ones are restricted to *D. ovisporus* and *Unilacryma unispora* (Figs. 8e, 9d). The latter species have oblique to muriform spore septations.



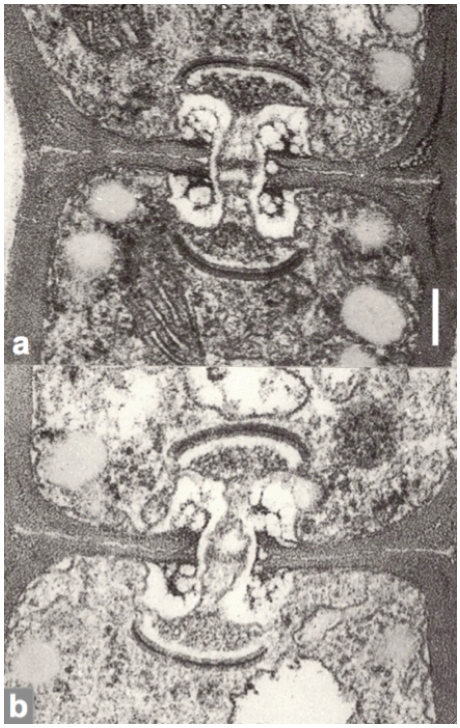


Fig. 3 Light microscopy of *Dacrymyces stillatus* showing a sequence of ontogenetic steps, 1-7, in basidial development. a. Nomarski contrast. b. Transmitted bright-field microscopy. Note long basidial bodies in which nuclear divisions occur, and two long sterigmata (arrows) with terminally narrowing spicula on which basidiospores (asterisk) develop. Bar, 10 µm. Originals F. Oberwinkler.

Fig. 4 a, b. Transmission electron micrographs showing dolipores of *Dacrymyces stillatus* with continuous parenthesomes on both sides of the pores and central bandings of different electron-dense structures inside the pores. a. The upper parenthesome contains a central pore. Bar, 0.5 µm. Originals F. Oberwinkler.

VI. Anamorph stages

Microconidial formation during germination of basidiospores and on monokaryotic hyphae appears to be an **effective dispersal strategy** in the haplophase (Fig. 9e-h). However, it requires the fusion of compatible cells to establish the dikaryophase. Disarticulation of dikaryotic cells along septa to form arthroconidia is characteristic for few dacrymycetaceous taxa. Though it is a very significant distribution mechanism in *D. stillatus*, even in the closely related *D. minor* arthrospore production is not known.

Recently, **additional anamorph fructifications** of Dacrymycetes have been described. *Dacryoscyphus chrysochilus* (Fig. 6) has been introduced by Kirschner and Yang (2005), and two anamorphic *Dacrymyces* species, *D. pinacearum* and *D. subarcticus*, proposed by Shirouzu and Tokumasu (Shirouzu et al. 2009) were transferred into *Dacryoscyphus* (Kirschner et al. 2010).

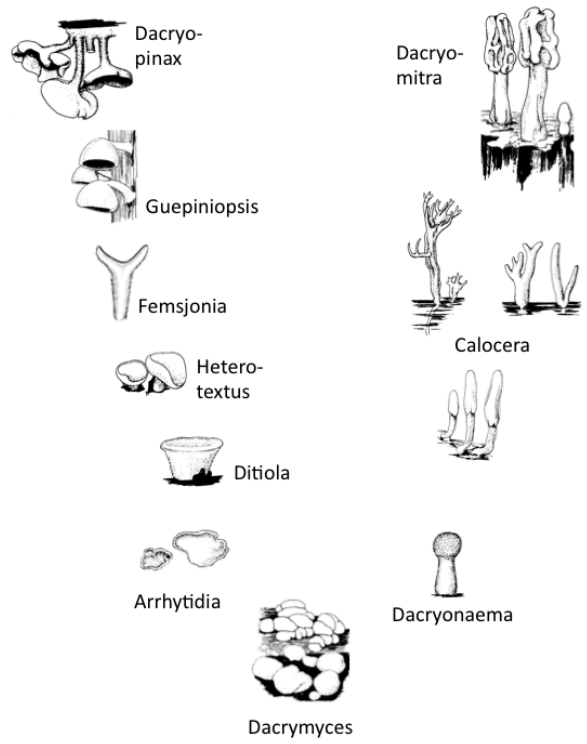
VII. Wood decay, substrate specificity, and distribution

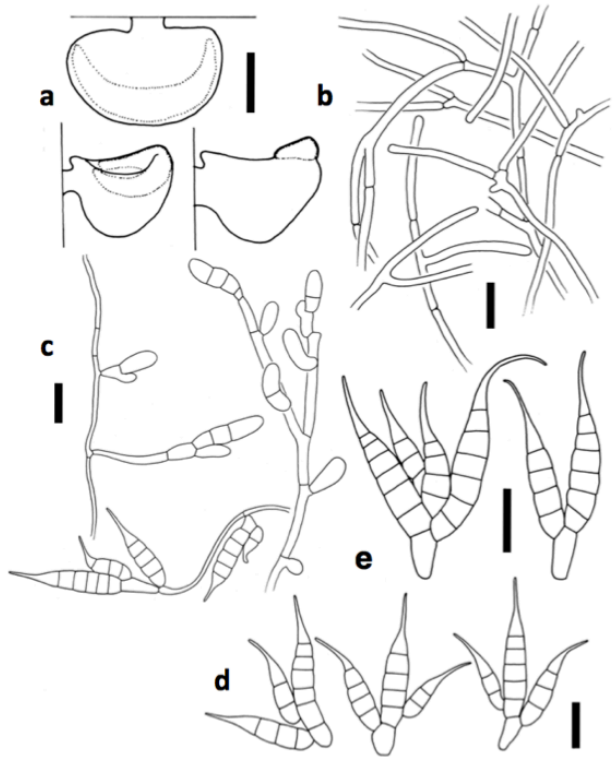
All Dacrymycetes species grow on wood and presumably all are more or less **strong brown-rot fungi** in coniferous and angiosperm wood, but lignin decomposition may occur, too (Seifert 1983). Brown-rot is considered as an evolutionarly old form of wood decay (Floudas et al. 2012).

Calocera cornea (Fig. 2k) preferably grows on angiosperm wood while *C. viscosa* (Fig. 2l) is wide-spread on coniferous wood. There are **no reliable data on distribution patterns** because species identification is unclear in many cases. *Dacrymyces stillatus* (Fig. 2a, b) is considered a species of cosmopolitan distribution (McNabb 1973), while *D. dendrocalami* (Fig. 8b) is only known from Taiwan and Japan (Shirouzu et al 2009), and *Ditiola haasii* (Fig. 2e) from the Northern Alps (Oberwinkler 1989). Both data on subtrate specificity and species distribution suffer heavily because of inadequate samplings. This may be examplified by *Dacryonaema rufum* (Figs. 2j, 7c, d), a species, originally described from Sweden with a wide distribution in northern and central parts of the country (Nannfeldt 1947). When Brough and Bandoni (1975) reported the species from British Columbia, they considered it as relatively common. A similar observation was made by Poelt and Michelitsch (1982) who collected the species in the Austrian Alps, and by the author who recorded it in the Bavarian Alps (unpublished).

VIII. Traditional taxonomy

The Dacrymycetales represents a natural taxon, which is suppported by the stability of several **important characteristics**: (1) the ontogeny and morphology of the basidium (Fig. 1d); (2) the morphology and germination of basidiospores (Figs. 1e-g, 9a-f, h); (3) the septal pore type (Fig. 4); (4) the pigmentation of basidiocarps by yellowish to orange carotenoids (Gill and Steglich 1987; Goodwin 1953; Fig. 2a-d; f-l); exceptions are *Ditiola haasii* (Fig. 2e) and *Cerinomyces* species, and (5) the predominantly brown-rotting wood decay. In a few earlier publications (Donk 1966; Eriksson and Ryvarden 1973), species of the genus *Cerinomyces* have been considered to be intermediate between the Dacrymycetales and the Aphyllophorales. However, all molecularly based phylogenetic hypotheses including *Cerinomyces* spp. cluster them with the Dacrymycetales.





Figs. 5 Basidiocarps of Dacrymycetales. Figures not to scale, modified from Oberwinkler (2012).

Fig. 6 *Dacryoscyphus chrysochilus.* a. Habit of conidiomata, the upper one seen from above, the lower left from the side, the lower right in a median section, bar 2 mm; all other bars 10 µm. b. Hyphal arrangement in the centre of the conidioma. c. Conidiophores with developing conidia. d. Conidia with three arms. e. Conidia with two arms (right) and four arms (left). From Kirschner and Yang (2005).

The following is an account of the **accepted genera** (compare Fig. 5). Brefeld (1888) introduced the Dacrymycetaceae and recognized four genera. A generic survey of Martin and Fischer (1933) comprised nine genera, but Neuhoff (1936) accepted only two genera. The treatment of nine genera of North Central North American Dacrymycetes by Martin (1952) was again surveyed by Kennedy (1958). A comprehensive study of Dacrymycetes on a worldwide scope has been carried out by McNabb (1964, 1965a, b, c, d, e, 1966, 1973) dealing with eight genera. A key for nine genera of Dacrymycetales was provided by McNabb and Talbot (1973). Twelve genera were treated by Oberwinkler (1994).

Martin (1949) erected the genus ***Cerinomyces*** with three species and *C. pallidus* as the type (Fig. 8a). Originally, the genus comprised corticioid and non-orange coloured species with nonseptate basidiospores. This narrow scope of the genus has been broadened by McNabb (1964) and Ginns (1982), including species with orange basidiocarps and septate basidiospores.

Based on micromorphological characters, Eriksson (1958) tentatively placed *Cerinomyces* in the Corticiaceae and Eriksson and Ryvarden (1973) considered it of intermediate position between the

Dacrymycetaceae and Corticiaceae. McNabb (1964) and Donk (1972) assumed a close relationship with the two-sterigmate *Clavulicium*. However, Martin (1952), Kennedy (1958a), Parmasto (1961), McNabb (1964), and Oberwinkler (1994) kept *Cerinomyces* in the Dacrymycetaceae.

The type species of ***Dacrymyces**, D. stillatus* (Figs. 1, 2a, b, 3, 4, 5) is widespread and very common on coniferous wood in North Temperate regions. Commonly it is associated with anamorphic fructifications. Thus, together with micromorphological features, a concept for *Dacrymyces* s.str. is available, containing *D. aquaticus* (Bandoni and Hughes 1984) and possibly also *D. capitatus* and *D. minor* (Oberwinkler 1994). McNabb (1973) accepted 30 species in his monograph of the genus, and recognized two subgenera, *Dacrymyces* and *Turbinaster*, that were already introduced by Kobayashi (1939). Species of the subgen. *Dacrymyces* have pustular basidiocarps with amphigeneous hymenia; those of subgen. *Turbinaster* are turbinate to pezizoid with hymenia restricted to the apical, disc-like parts, a distiction in accordance with practical classificatorial principles, but with a questionable systematic meaning. A detailed study on selected species of *Dacrymyces* with comprehensive micromorphological illustrations has been carried out by Göttel (1983).

Dacrymyces ovisporus, described by Brefeld (1888), has subglobose to ovoid basidiospores, with cruciform to muriform septations in mature stages (Fig. 9d), and a mixture of two- and one-sterigmate basidia. Oberwinkler (1994) restudied the type of *Platygloea unispora* (Olive 1947) and considered it as closely related to *D. ovisporus*, deviating by a high percentage of unisterigmate basidia, but identical in basidiocarp and spore morphology and germination, and in simple dikaryophyses with short ramifications.

Arrhytidia flava, the type of ***Arrhytidia*** (Berkeley and Curtis 1849), has flat-discoid basidiocarps, attached to the wood by root-like bases, and fimbriate margins, composed of hyphae with morphologically distinct terminal cells. Berkeley (1860) himself was uncertain about the taxonomic meaning of the new genus, and later workers did not come to a conclusive solution due to insufficient documentation of micromorphological characters. Coker (1928) synonimized *A. flava* with *Dacrymyces corticioides*, and Kennedy (1958) was of the opinion that the type species might be identical with *A. involuta* sensu Coker and restricted the genus to the latter species. Lloyd (1919), Brasfield (1938), Martin (1949), Donk (1966), and MacNabb (1973) did not recognize *Arrhytidia* as being generically different from *Dacrymyces*, a view that was critically questioned by Oberwinkler (1994).

A detailed study of ***Ditiola** radicata*, the type species of the genus clearly revealed the dacrymycetaceous nature of its basidia (Lindau 1894). The prominent rooting base and the capitate to discoid basidiocarps were used to circumscribe the genus (Kennedy 1964; Kobayasi 1939; McNabb

1966; Oberwinkler 1994) though such character combinations also occur in *Dacryopinax, Femsjonia, Guepiniopsis,* and *Heterotextus*. However, in these genera, marginal hyphae of the sterile basidiocarp surfaces have rather characteristic and distinctive morphological features in comparison with *Ditiola radicata*. Two species were recognized by MacNabb (1966) in his monograph of the genus. A non-pigmented species, *D. haasii* (Fig. 2e), has been described and placed in *Ditiola* by Oberwinkler (1989).

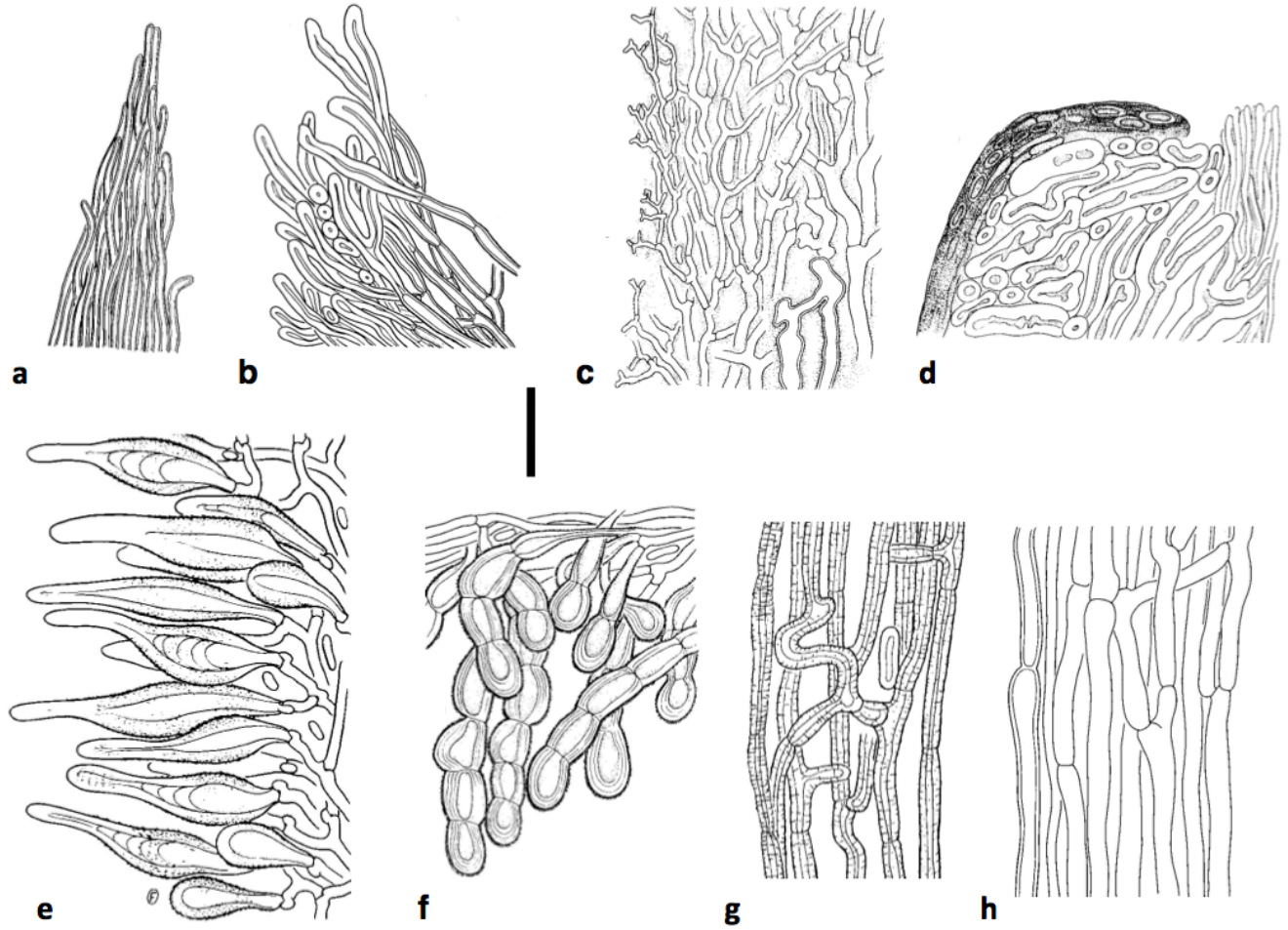


Fig. 7 Hyphal structures in Dacrymycetes. a. *Dacryopinax elegans*, fascicle of thick-walled hyphae forming a marginal hair. b. *Dacrymyces capitatus*, thick-walled marginal hyphae. c, d. *Dacryonaema rufum*. c. Thin and strongly ramified hyphae of sterile basidiocarp surface. d. Thick-walled and agglutinated hyphae of young, sterile ontogenetic stage of the fructification. e. *Heterotextus miltinus*, terminal cells of sterile basidiocarp surface. f. *Guepiniopsis buccina*, cell chains of sterile basidiocarp surface. g, h. *Calocera viscosa*. g. Thick-walled hyphae from outer part. h. Thin-walled hyphae from inner part of rooting base. Bar 20 µm. Originals F. Oberwinkler.

Cortical hairs of ***Heterotextus*** species are thick-walled, basally swollen and apically bluntly beaked (Fig. 7e), thus easily distinguishable from other dacrymycetous genera (compare Fig. 7). However, *Dacrymyces suecicus* shares similar structures of marginal hyphae (MacNabb 1973), indicating that it should be included in *Heterotextus* (Oberwinkler 1994). In his monograph of the genus, MacNabb

(1965d) accepted four species.

According to the generic concept of MacNabb (1965e), ***Femsjonia*** comprises two turbinate to pezizoid species with thick-walled marginal hairs and internal hyphae, bearing conspicuous clamp connections. Allantoid basidiospores are one- to many-septate and germinate with microconidia (Fig. 9f). Microconidia can also develop on haploid hyphae (Fig. 9g). Since then, three additional species have been described from China (Liu et al. 1988; Zang 1983).

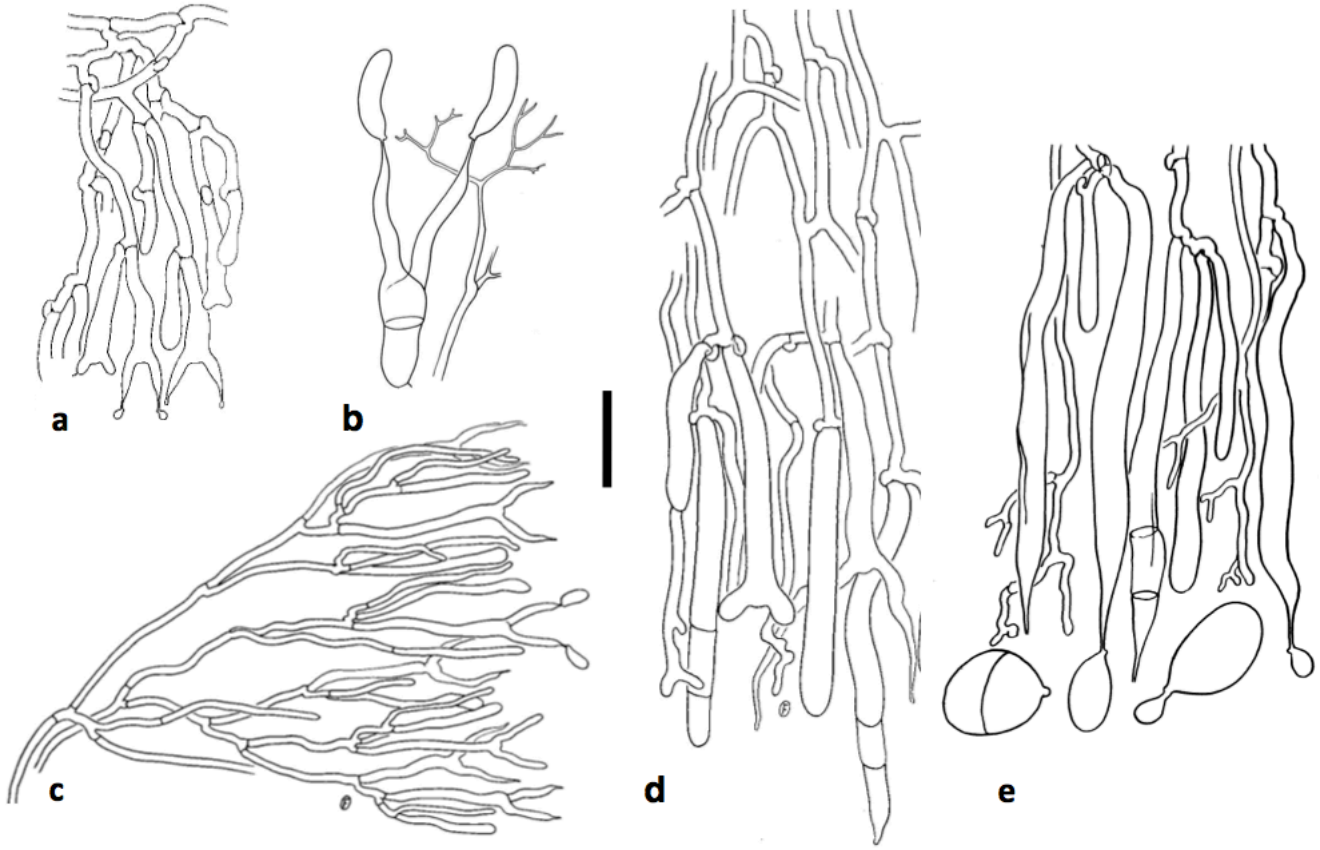


Fig. 8 Parts of hymenia, basidia, basidiospores, and dikaryophyses in Dacrymycetes. a. *Cerinomyces pallidus*, part of hymenium with basidia in different developmental stages. b. *Dacrymyces dendrocalami*, basidium with adventitious septum and two attached basidiospores, and dikaryophysis. c. *Calocera viscosa*, part of hymenium with basidia in different developmental stages. d. *Dacrymyces ovisporus*, part of hymenium with two bisterigmate, two unisterigmate basidia with adventitious septa, and two young basidia. e. *Unilacryma unispora*, part of hymenium with three unisterigmate basidia, two basidiospores, one transversely septate, another with an initial stage of germination. Bar 20 µm. Originals F. Oberwinkler.

In his monograph, MacNabb (1965c) accepted only the type species, ***Guepiniopsis*** *buccina* (Figs. 2i, 5, 7f), defined by catenulate marginal hairs with stout and thick-walled cells, the walls often characteristically layered. The infrageneric taxonomy has been discussed by Oberwinkler (1994).

The cyphelloid basidiocarps of the type species, ***Dacryopinax*** *elegans*, consist of thick-walled hyphae except the hymenium. Also the fascicles of marginal hairs have the same hyphal composition (Fig. 7a). Walls of basidiospores and spore septa are conspicuously thick-walled, too. MacNabb (1965b) broadened the scope of the genus and included six additional species, thus creating a morphologically

heterogeneous assemblage. One of the strongly deviating species is *D. spathularia* (Fig. 2h), a fungus with a widespread distribution in the tropics.

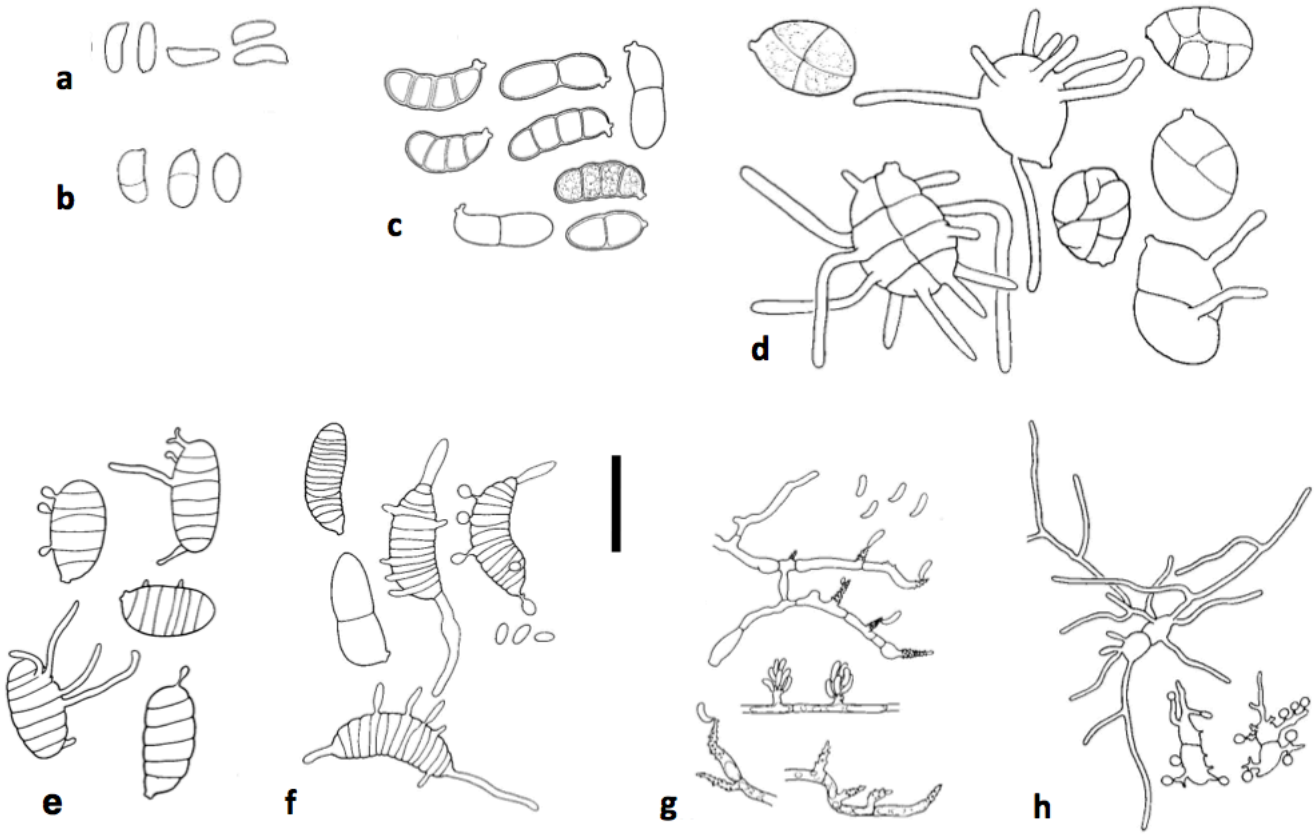


Fig. 9 Germination of basidiospores and microconidia in Dacrymycetes. a. *Cerinomyces crustulinus*, unseptate basidiospores. b. *Dacrymyces minor,* basidiospores with one septum each or unseptate. c. *Dacryomitra pusilla,* slightly thick-walled basidiospores, all septate. d. *Dacrymyces ovisporus*, subglobose basidiospores, septate, except for one spore; three germinating with hyphae. e *Dacrymyces estonicus*, multiseptate basidiospores, three spores germinating with hyphae, two germinating with microconidia. f, g. *Femsjonia peziziformis*. f. Young basidiospore with one septum, four old spores multiseptate, three germinating with hyphae and/or microconidia. g. Haploid hyphae producing microconidia. h. *Calocera viscosa*, three basidiospores, each with one transverse septum; one spore germianting with hyphae, two with microconidia. Bar 20 µm. Originals F. Oberwinkler.

Ontogeny and morphology of ***Dacryonaema*** *rufum* (Nannfeldt 1947), the type and single species of the genus, is unique. There is a primordial cone-like, sterile stage (Fig. 2j, 7c, d), obviously well adapted to extremely dry environmental conditions. The fertile part of the fructification develops into a globose capitulum (Fig. 5).

Commonly, all dacrymycetaceous fungi with clavarioid basidiocarps are included in ***Calocera*** (Figs. 2k, l, 5, 7g, h, 8c, 9h), thus accepting the generic concept of MacNabb (1965a) that considered *Corynoides, Dacryomitra,* and *Calopposis* as synonyms. The type species, *C. viscosa*, has a large rooting base (Fig. 2l) with a dimorphic hyphal arrangement in three zones (Figs. 7g, h) that prolongs into the fructification. Well developed basidiocarps are conspicuously ramified, a character suitable for easy recognition of the species, and the amphigeneous hymenium (Fig. 8c) is not markedly separated

from the sterile base. Basidiospores germinate either with microconidia or with hyphae (Fig. 9h). MacNabb (1965a) recognized eleven species, and three additional ones were described by Liu et al. (1988) from China.

Dacryomitra *pusilla*, the type species of the genus has been introduced by Tulasne and Tulasne (1872) to accomodate a tiny, morel-like fungus with a sterile stalk and a morchelloid hymenium (Fig. 5). In contrast to most American workers, McNabb (1965a), Donk (1966), and Reid (1974) did not accept the genus.

Kirschner and Yang (2005) introduced ***Dacryoscyphus*** *chrysochilus*, an anamorphic species with cupulate conidiomata and staurosporous conidia, growing on dead twigs of *Rhododendron* sp. in Southwest China (Fig. 6). A molecular phylogeny derived from partial LSU rDNA clustered the new species with the Dacrymycetes. Also dolipores with continuous parenthesomes supported this systematic position. Based on comparative morphology, Kirschner et al. (2010) included the anamorphic *Dacrymyces pinacearum* and *D. subarcticus* (Shirouzu et al. 2009) in *Dacryoscyphus*.

IX. Molecular phylogenies

In a study on the phylogenetic relationship of the Auriculariales, Weiß and Oberwinkler (2001) included representative taxa of the Agaricomycotina, inclusive of nine Dacrymycetes species. These clustered in a **well supported monophyletic group**. Similar results were obtained when Sebacinales were studied (Weiß et al. 2004), but only a few members of the Dacrymycetes were included. In proposing *Dacryoscyphus*, Kirschner and Yang (2005) also documented the monophyletic clade of dacrymycetaceous fungi.

The **age of approximately 400 million years** was calculated for Dacrymycetes when tracing the origin of wood decay fungi (Floudas et al. 2012).

Attempts to explore **evolutionary trends** within Dacrymycetes were heavily hampered by inadequate sampling. At present, it appears that species with clamps represent basal relationships while the loss of clamps seems to indicate derived evolutionary stages (Shirouzu et al. 2012). Morphological characters of basidiocarps, basidia, basidiospore septa, and sterile marginal hyphae could not be interpreted in meaningful ancestral state reconstructions.

In an analysis containing the type, ***Cerinomyces*** *pallidus,* and *C. crustulinus, C. albosporus,* and *C. canadensis*, these species clustered in one clade together with *Dacrymyces punctiformis* (Shirouzu et al. 2009; Fig. 10). However, in an extended sampling together with *C. ceraceus, C. grandinioides,* and *C. lagerheimii*, the latter species represented a separate cluster, clearly distinct from the type species group (Shirouzu et al. 2012; Fig. 10). Since a detailed comparative micromorphology of *Cerinomyces* species

is lacking, the two independent clades cannot be characterised with additional features.

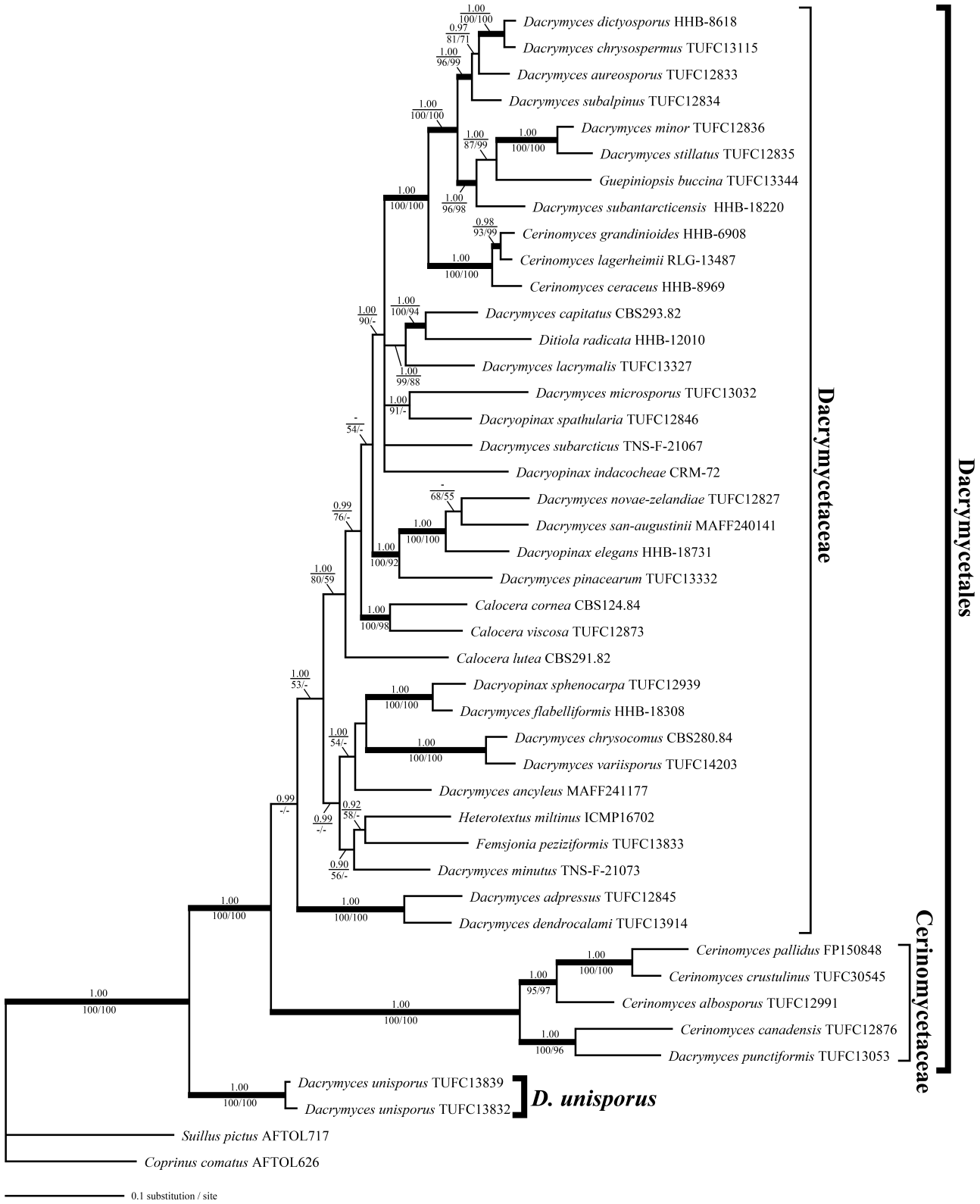


Fig. 10 Bayesian tree of Dacrymycetes based on multigene sequences (3163 bp). Bayesian posterior probabilities PP ≥ 0.90 shown above the branches. Maximum likelihood bootstrapping MLBP ≥ 50% / maximum parsimony bootstrap proportions MPBP ≥ 50% below the branches. Bayesian PP ≥ 0.95, MLBP ≥ 90% and MPBP ≥ 90% indicated by thickened branches. From Shirouzu et al. (2012).

Shirouzu et al. (2007) were the first to document the polyphyletic assemblage of *Dacrymyces* species, using the 28S rRNA gene D1/D2 region. The type species, *D. stillatus*, clustered with *D. minor*, i.e., ***Dacrymyces* s. str.**, with *Guepiniopsis buccina* as sister group. This finding was confirmed in extended samplings with Japanese Dacrymycetes (Shirouzu et al. 2009), and in a comprehensive study on the phylogeny of Dacrymycetes (Shirouzu et al. 2012; Fig. 10). Unfortunately, *D. aquaticus* (Bandoni and Hughes 1984) could not yet be included in molecular analyses.

The minute ***Dacrymyces dendrocalami*** (Oberwinkler and Tschen 1989) has stout basidia, often with adventitious septa, and strongly branched dikaryophyses (Fig. 8b). Basidia and basidiospores often are thick-walled in mature stages. This species clusters with *D. adpressus* in its own clade (Shirouzu et al. 2012; Fig. 10). The micromorphological data available for the latter species (MacNabb 1973; Shirouzu et al. 2009) do not allow a detailed comparison with *D. dendrocalami*.

As discussed above, the type species of ***Femsjonia*** and ***Heterotextus*** differ considerably in structural characters of marginal hairs and the hyphal context of the basidiocarps. Nevertheless, they group as sister taxa in the molecular phylogeny (Fig. 10) of Shirouzu et al. (2012).

The infrageneric taxonomy of ***Guepiniopsis*** has been discussed by Oberwinkler (1994) who considered *G. chrysocoma* as an additional species, and also *Dacrymyces minuta* (Olive 1954) to be closely related. However, in the molecular phylogenies of Shirouzu et al. (2007, 2009, 2012), *G. buccina* is sister of *Dacrymyces* s.str., i.e. *D. stillatus* and *D. minor* (Fig. 10).

Calocera *viscosa* and *C. cornea* show considerable morphological differences, as briefly explained above. Surprisingly, they always cluster together in molecular phylogenies (Shirouzu et al. 2007, 2009, 2012; Weiß and Oberwinkler 2001; Fig. 10).

Dacryomitra *pusilla* is a unique species in Dacrymycetes resembling morchelloid fructifications (Fig. 5). It was included in a sampling by Shirouzu et al. (2009), but unfortunately is omitted in a more comprehensive analysis (Shirouzu et al. 2012). Nevertheless, it supports a generic separation as indicated already by morphological data.

In a four gene (28S, 18S rDNA, ITS, rpb2) phylogeny, Shirouzu et al. (2012; Fig. 10) found *Dacrymyces unisporus* clearly separated from all other dacrymycetaceous taxa but within a well supported monophyletic Dacrymycetes. Considering the unique micromorphology (Fig. 8e), their taxonomic conclusion was to erect a new genus ***Unilacryma***, the family Unilacrymaceae, and the order Unilacrymales for this single species. Unfortunately, the very closely related *Dacrymyces ovisporus* (Fig. 8d) could not be included in this phylogenetic analysis.

Dacryoscyphus *chrysocomus* is an anamorphic dacrymycetaceous fungus with staurosporous conidia (Fig. 6). Micromorphological characters and molecular data indicate close relationship with two

species, originally described as *Dacrymyces pinacearum* and *D. subarcticus* (Kirschner et al. 2010). In an extended sampling, these species cluster with *Dacryopinax elegans* (Shirouzu et al. 2012; Fig. 10).

X. Conclusions

Dacrymycetes constitute a **monophyletic clade in the Agaricomycotina**. Ontogeny and morphology of basidia and basidiospores are the best indicators of these natural relationships. Hyphal context, basidiocarp pigmentation and brown-rot wood decay are additional important characters. All molecular phylogenies available indicate that Dacrymycetes is a well defined taxon. In contrast, traditional taxonomy and molecular phylogenies are mostly contradictory. To solve this dilemma, a comprehensive and detailed comparative micromorphology as well as a considerably enlarged sampling for molecular studies are required.

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