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## Genera in a Monophyletic Group: The Dacrymycetales \*)

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**Summary** The *Dacrymycetales* is taken as an example of a monophyletic group to explain generic concepts in the *Heterobasidiomycetes*. Known characters are discussed and so far proposed genera evaluated taxonomically. Phenetic and cladistic methods are used to prove the naturalness of the taxa. A key to genera is provided to test the practical applicability. General conclusions are: Profound knowledge of species characters is mandatory for the establishment of sound generic concepts. Genera should represent natural units. If the naturalness is not proved, not likely or not given, they cannot be used for phylogenetic interpretations. The delimitation of a genus is subjective, even when the claims for naturalness are strictly applied. A well founded generic concept has a key-function for identification, taxonomic and systematic groupings, as well as ecological studies. Genera should only be accepted when the descriptions include detailed analyses of differentiating characters, and adequate illustrations, at least, of the type-species.

### INTRODUCTION

Generic concepts play an important role in systematics. Quite often overviews of certain organismic groups are presented as "The genera of abc". In practice of training programs and identification work dealing with biodiversities, the first question most often is: what genus is it? The reason for this is that many easily recognizable, suprageneric monophylies do exist whose generic classifications are not evident, consider for example the grasses, Compositae or Cruciferae. In other cases, first, rapid and easy sorting leads to paraphyletic groups or assumed but not proved monophylies, e.g. pyrenomyces and discomycetes, clavarioid and gilled fungi. Also in these cases the key question is the one for the genus.

Secondly, any kind of detailed and meaningful phylogenetic systematics has to consider the generic level, i.e. the grouping of species in monophyletic entities.

There is a third fact why genera appear to be so important in taxonomy. They are those taxa with whom the easiest shifting games can and have been played.

No doubt for those who are interested in organismic diversities, they have to get familiar with the generic classification of the group they are dealing with.

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The *Dacrymycetales* are used in a case study for the evaluation of generic concepts in the *Heterobasidiomycetes* for several reasons: they represent a monophyly and generic concepts have been applied rather diversely in this order. Also non-specialists of *Heterobasidiomycetes* know these fungi and monographic treatments are available. Finally, I could study a representative number of *Dacrymycetales* species on a world wide scale in the laboratory and in the field, and the data of these studies, accumulated over 30 years, are used here for comparative evaluations. In addition, few data are taken from literature.

General remarks

### Theses

#### **1. Profound knowledge of species characters is mandatory for the establishment of sound generic concepts.**

There is general agreement in whatever method is applied for evaluation of taxa, the quality of characters used is delimiting the interpretation. Consequently, most careful attention should be paid for character analyses. In contrast, however, many examples, even in recent publications show that characters and character sets are accumulated from literature search only or predominantly, and critical interpretations are avoided because of lacking expertise.

#### **2. Genera should represent natural units.**

If the naturalness is not proved, not likely or not given, they cannot be used for phylogenetic interpretations. — How can naturalness be proved? Let's consider two examples: a) When J. Eriksson (1950) monographed Bourdot and Galzin's Sect. *Coloratae* of the "genus" *Peniophora*, he selected and characterized a group which following mycologists accepted as the "natural genus" *Peniophora*. Species of the genus s.str. share a certain number of combined features which do not occur in other sections of the genus s.l. nor in other genera. Which of these characters can be assigned as apomorphies has to be proved. b) I selected the *Dacrymycetales* for the present study, i.a. because of the monophyly of order. There is "one" character, the basidium, which is unique, therefore derived and the apomorphy for the taxon, and there are no other characters which interfere. Many other examples exist in which natural taxa are known for a long time, well characterized by differentiating features which are unique and which can, if necessary, be called apomorphies. Even when the two examples mentioned are quite different in circumscription and rank, in both cases many characters and character states are well studied and adequately interpreted and therefore usable for defining natural taxa.

**3. A paraphyletic genus has to be split in monophyletic taxa.**

If two taxa result, they are genera. One includes the type species of the original genus; it should be named for some time "genus s.str." The second genus is not the most closely related to the first one.

**4. The homogeneous appearance of a genus which can only be characterized by plesiomorphies is no proof for a monophylum.**

If monophyly is required, but cannot be determined by an apomorphy, only the type species, which then represents a monophylum, has to be considered.

**5. In a first step, generic concepts can be based on generic types.**

Additional species to be included in a given genus have to share the derived generic characters.

The huge number of species for which only insufficient data are available prohibits meaningful classifications. Therefore, selected species have to be used for overviews. At first and at least, generic types have to be studied so carefully that they can be used for comparative evaluations.

**6. The delimitation of a genus is subjective, even when the claims for naturalness are strictly applied.**

Genera can comprise several or many species, or they simply are monotypic. They can intergrade step by step into other, closely related genera or they can be separated by big distances. There is no common scale for measuring or recommending generic distances. In phenetic schemes there is some kind of an agreement to use several distinguishing characters for the separation of closely related other genera. Even when no supraspecific or infrageneric taxa would be accepted, a case in which the generic concept would be a very narrow one, no general objective generic concept could be achieved.

**7. The number of species considered has an impact on the generic concept and the phylogenetic interpretation of the given monophylum.**

The generic concept of a monotypic genus is easily derived from the specific characters which have to enter a generic comparison. The more species are included in a genus, the more variation of characters will occur, thus also influencing the character state explanations.

**8. A well founded generic concept has a key position for identification, taxonomic and systematic groupings, as well as ecological studies.**

For species identification a crucial question commonly concerns the generic affiliation. Often suprageneric taxa, irrespective of naturalness, are easy to be recognized, and genera quite often not. It is not surprising that also natural



genera exist which are more difficult to be recognized by simple methods than paraphyletic ones. Phylogenetic interpretations of higher taxa always have to refer on genera as monophyletic entities.

**9. For practical purposes of classification and identification, unnatural genera have to be accepted as long as natural ones are wanting.**

The splitting of a heterogeneous taxon into a natural and a remaining unnatural one should be accepted when a careful comparison with all related genera is provided. In the case that the generic type, alone or together with other species, can be reinterpreted as a natural genus, the remainder should not be renamed. The given name has to be used for the monophyletic group (genus s.str.) and should further be used for the paraphyletic remaining species (same genus name s.l.) as long as they cannot be resolved. The genus *Dacrymyces* can be taken as an example.

**Recommendations**

1. For establishing an acceptable generic concept, the following proceeding is recommended: a) proof the monophyly of the genus. Is it a monophyletic one, it can be applied. b) Before a monophyletic genus is split into two or more monophyla, the improvements for taxonomic purposes should be evident, e.g. easier handling of genera with not too many species. c) Avoid to create monotypic genera. d) Before genera are united, it has to be proved that they are the closest related monophyla, i.e. sister groups. The improvements for taxonomic purposes should be evident as in splitting genera. e) If the paraphyletic condition of a genus is recognized, attempts should be made to split it in monophyletic taxa (see thesis 3)
2. Genera should only be accepted when the descriptions include detailed analyses of differentiating characters, and, at least, adequate illustrations of the type-species.
3. Publication of new taxa should only be accepted as valid in a certain number of international journals with high quality reviewing systems.
4. These journals should be subsidised to such an amount by national and international sources that they can be afforded by all mycological institutions.
5. An attempt should be made to initiate international cooperation of experts to develop projects for world wide generic monographs of all fungal groups. The lack of taxonomists and of regional floristic inventories should not impede but inforce rapid activities for initiatives to improve the present unsatisfactory situation.

6. Forced efforts are needed for intensified studies of fungal biodiversities. This can only be achieved with the expertise of well trained taxonomists.

### CASE STUDY: GENERA OF DACRYMYCETALES

When introducing the *Dacrymycetaceae*, Brefeld (1888) distinguished 4 genera. Martin & Fisher (1933) were the first to publish a generic survey recognizing 9 genera. Swedish *Dacrymycetales* were monographed by Neuhoﬀ (1936). He accepted only two genera, *Dacrymyces* and *Calocera*. Brasfield (1938a, b) studied the species of temperate and subtropical North America, Kobayasi (1939a, b) those of Japan, and Martin (1952) treated the north central taxa of North America. The genera of the *Dacrymycetaceae*, 9 being accepted, were again surveyed by Kennedy (1958a). In a series of monographs, McNabb (1964, 1965a, b, c, d, e, 1966, 1973) presented detailed taxonomic studies on a world wide scope, recognizing 8 genera. In a key to the *Heterobasidiomycetes* of the U.S.S.R., the *Dacrymycetales* were included by Raitviir (1967). Lowy (1971) treated neotropical taxa, and Reid (1974) monographed the British species. Donk (1966) compiled an annotated check of European species. A short description of the order and a key to 9 genera were given by McNabb & Talbot (1973).

The order *Dacrymycetales* represents a natural taxon, as can be derived from the stability of several important characteristics: 1) ontogeny and morphology of the basidium; 2) morphology and germination of basidiospores; 3) septal pore type; 4) pigmentation of basidiocarps; 5) wood-decay properties.

The taxon is a good example for a homogeneous group in which further subdivisions are rather difficult. Morphology of the basidiocarps and the marginal hairs are commonly used for generic delimitations. Patouillard & Lagerheim (1895) stated “Les genres de la série des Dacrymycètes étant établis presque exclusivement d’après la forme de réceptacle, sont bien peu distincts les uns des autres et devraient peut-être considérés comme des simples sections d’un type unique...”. Donk (1966) quoted this opinion as well that of Neuhoﬀ (1936) who believed that generic characteristics overlapped to an extent that single features cannot be used to distinguish any genera.

### DISCUSSION OF GENERA

The numbers in brackets refer to characters used in the data matrix and the cladogram.

### CERINOMYCES MARTIN

There are several unique characteristics in the type species, *C. pallidus*, and the closely related *C. crustulinus*: 1) basidiocarps not orange; 2) totally adnate

to the substratum; 3) not gelatinous; 4) the basidia comparatively short and stout, and 5) basidiospores apparently not transversely septate even when mature.

McNabb (1964) broadened the scope of the genus to include *Ceracea lagerheimii*, *Cerinomyces grandinioides*, and *C. altaicus*, species with mature septate spores and partly orange basidiocarps. Ginns (1982) described a new species, *C. ceraceus*, and reported spore germination by budding and a conidial stage in culture which is similar to those of other species of the *Dacrymycetales*. Apart from *Cerinomyces*, effused corticioid, dacrymycetaceous basidiocarps are known only in *Arrhytidia*. However, species of *Arrhytidia* are not fully adnate to the substratum; each single basidiocarp is attached to the wood centrally by a root-like base.

Development and morphology of the basidia in species of *Cerinomyces* are typically dacrymycetaceous: A narrowly clavate basidium with two stout sterigmata, their bases separated by the rounded basidial apex. The differentiation of the basidial apex during sterigma formation is rather unique in all taxa of *Dacrymycetales*, and no significant deviation is found in *Cerinomyces*. Other two-sterigmate species in *Heterobasidiomycetes*, like *Ypsilonidium sterigmaticum*, and *Homobasidiomycetes*, e.g. *Clavulicium macounii*, certain *Athelia* and *Clavulina* species, and others are quite distinct in basidial morphology. However, McNabb (1964), and Donk (1972) believed that *Clavulicium* closely resembles *Cerinomyces*. Eriksson (1958; Fig. 5.e-g) published an excellent illustration of *Cerinomyces crustulinus*, a species which he tentatively placed in the *Corticiaceae*. Eriksson & Ryvarden (1973) were of the opinion that *Cerinomyces* is "an intermediate between *Corticiaceae* and *Dacrymycetaceae*". Martin (1952), Kennedy (1958.a), Parmasto (1961), and McNabb (1964) included the genus in the *Dacrymycetaceae*.

In conclusion, *Cerinomyces* may serve as a good example for an easily circumscribed group, characterized by fully adnate and marginally indefinitely growing basidiocarps. However, these plesiomorphic characters do not allow to prove the monophyly of the genus.

#### *ARRHYTIDIA* BERKELEY & CURTIS

The type species, *Arrhytidia flava*, is separated by several important characters from *Dacrymyces stillatus*: 1) Basidiocarps are flat-discoid with rooting bases; 2) they have prominent, fimbriate marginal zones, composed typically of partly spreading hyphae with specially structured terminal cells; 3) the hymenium contains basidia and rather narrow, unbranched hyphidia; 4) the basidia are stout and slightly swollen basally; 5) anamorphs are unknown,

and may be assumed to be lacking. This phenetic character set includes the apomorphy of flat, but centrally rooted basidiocarps (8). However, the rooting base may be hidden in old and confluent specimens.

The introduction of the genus *Arrhytidia* has caused considerable confusion in the taxonomy of the Dacrymycetales. Martin & Fisher (1933), Brasfield (1938 a), Martin (1949), Kennedy (1958 a), and Lowy (1971) accepted the genus, while Donk (1966), McNabb (1973), and Reid (1974) included it in *Dacrymyces*. However, the broadly conceived scope of *Dacrymyces* easily leads to a heterogeneous assemblage which makes it rather difficult to group related species.

The above circumscription may serve as a basis for separating *Arrhytidia* from *Dacrymyces*. Kennedy (1958 a) included one taxon, *Arrhytidia involuta*, "with certainty" in the genus. Martin & Fisher (1933) used *Arrhytidia* on the basis of their study of *Ceracea aureo-fulva*, a species which fits the generic concept rather well. At present, at least *Arrhytidia fulva* and *A. corticioides* could be accepted as typical species of *Arrhytidia*.

*Dacrymyces estonicus* is a pustulate species, but it agrees with *A. flava* essentially in the composition of the hymenium and in basidial morphology. The spore morphology appears to be different. According to McNabb (1973), many-septate spores are present in the type of *A. flava*. Although differing in basidiocarp form, *D. estonicus* seems to be more closely related to *Arrhytidia* than to *Dacrymyces* s.str.

We are dealing here with a mixed character set of macroscopic and microscopic features which appear to be applicable for a generic circumscription. Even when a basidiocarp feature is used as a derived character, hyphal differentiations should be considered as a possible tool for better generic characteristics.

#### DACRYMYCES NEES: FRIES

The type species, *D. stillatus* is a wide-spread, presumably cosmopolitan, and regionally common species which, at least in north temperate regions, appears to be usually associated with arthrosporous fructifications. It is suggested that *Dacrymyces* as a natural genus is restricted to a few species with pustular basidiocarps (10), unspecialized, sterile marginal hyphae, amphigeneous hymenia, and arthrosporic conidial fructifications (12). Therefore *D. aquaticus* is considered to be a representative of *Dacrymyces* s.str., which, according to the authors (Bandoni & Hughes 1984), differs from *D. stillatus* in "...having both basidia and arthroconidia regularly produced in the

same basidiocarp", in its 1-celled arthroconidia, the aseptate or 1-septate basidiospores, and in its being "...restricted to sodden wood or wood floating in water". Hyphal fragmentation can also be found in cultures of various *Dacryomyces* species, e.g. *D. capitatus*, and *D. minor*. These are regarded as being closely related to species of the type group, especially since they coincide in nearly all basidiocarp features. Such conidial stages were once reported for *D. elisii* by Olive (1958), who examined the type, and who then treated the name as a synonym of *D. stillatus*. Kennedy (1958b) interpreted the taxon as not producing arthrospores, and being only a variety of *D. stillatus*. McNabb (1973), who also studied a part of the type, found no arthrosporic anamorphs. He included the name *D. elisii* in the synonyms of *D. capitatus*.

The only world-wide and comprehensive monograph of the genus *Dacryomyces* is that of McNabb (1973). He recognized 30 species which were grouped in the two subgenera, *Dacryomyces*, and *Turbinaster*, which were originally introduced by Kobayasi (1939a). The subgenera are mainly circumscribed by characteristics of basidiocarps and hymenial configurations. Species of subgen. *Dacryomyces* have non-turbinate fruitingbodies with amphigenous hymenia, while those of subgen. *Turbinaster* are characterized by turbinate to pezizoid basidiocarps with hymenia restricted to apical disks. Species of the subgen. *Turbinaster* could not be included in the cladogram because of unclear characters, character states, and distribution of characters. A detailed comparative morphological analysis of species on a world wide scale is needed to propose a substantial systematic reinterpretation. In addition, studies in developmental stages, life cycles, and ecological properties, and also in culture experiments are needed for a better understanding of specific and supraspecific taxa.

The present example has a more general bearing on the generic concept concerning anamorph-teleomorph connections, but I would not be inclined to derive generalizations in this case. An acceptable solution is, to use *Dacryomyces* in a restricted and in a broad sense until sufficient new data for more conclusive interpretations are available.

#### *DACRYOMYCETOPSIS* RICK

The monotypic genus *Dacryomycetopsis* resembles *Dacryomyces* in gross morphology. The basidiocarp is pustulate, irregularly lobed, and attached to the substrate by a rooting base. The original descriptions of the genus (Rick 1958), and the single recognized species are very scanty. However, Rick mentioned one of the important characteristics, the prominent dendrohyphidia (13) "... setulis longis, valde ramosis ...". Such dendrohyphidia seem

to be rather unusual in *Dacrymycetales*. Similar sterile hymenial elements are known in *Dacrymyces paraphysatus* (Olive 1958), *D. macnabbii* (Reid 1974), and *D. dendrocalami* (Oberwinkler & Tschén 1989). In other *Dacrymyces* species, only sparsely branched hyphidia occur, e.g. in *D. enatus*, and *D. ovisporus*. Loop-like clamps are rather frequently found on thin-walled hyphae. Such clamps have been reported for *D. macnabbii* (Reid 1974), and they can also be found in *Guepinopsis spathularia*. Another, possibly important generic character is the layer of thick-walled hyphae covering the sterile surface of the basidiocarp. This combination of distinct morphological characteristics makes a generic separation desirable. Further studies are needed to elucidate which species of *Dacrymyces* s.l. could be included in *Dacryomycetopsis*.

The question for the generic delimitation in this case is, whether one, two or three apomorphies (dendrohyphidia, loop clamps, thick-walled hyphae of the sterile surface) can or have to be used. An answer may be given when the character distribution in all *Dacrymyces* species is known. Similar problems exist in many other cases of the Heterobasidiomycetes, as well as in other fungal and non-fungal groups.

#### DACRYOPINAX MARTIN

The characteristics of *Dacryopinax elegans*, the type species of the genus, are unique: 1) cyphelloid, dark colored basidiocarps, 2) composed of rather thick-walled hyphae apart from the hymenial region, 3) hairs of fascicled, thick-walled hyphae, and 4) thick-walled, mature basidiospores.

Martin (1948) incorporated also *Guepinia fissa* in *Dacryopinax*. However, McNabb (1965b), who studied the type material, could not separate it from *D. elegans*. Five more species were recognized by McNabb (1965b), viz. *D. aurantiaca*, *D. dennisii*, *D. indacocheae*, *D. petaliformis*, and *D. yungensis*. Though detailed descriptions of these species were given by McNabb (1965b), it is not yet possible to make definite taxonomic conclusions. McNabb himself was uncertain whether to accept Kennedy's (1958a) concept of *Dacryopinax*, basidiocarps of which she described as "... homogeneous, of thick-walled fibrous hyphae ...". McNabb (1965b) suggested that presumably only *D. indacocheae* and *D. dennisii* would fit in this restricted scope of the genus.

McNabb (1965b) was aware of the taxonomic problems in having assembled species with different hyphal arrangements in one genus. On the other hand he was of the opinion that "... there seems to be no satisfactory way of dividing *Dacryopinax* into natural groups".



It is obvious again that not even the morphology of these fungi has been adequately studied. Other important features, such as development, culture characteristics, and ecology are completely unknown.

#### *HETEROTEXTUS* LLOYD

Species of *Heterotextus* differ from other taxa of *Dacrymycetales* by the peculiar morphology of terminal cells of sterile basidiocarp surfaces. These cells are typically basally swollen and apically bluntly beaked, and rather thick-walled. In addition, in *H. miltinus* and *H. alpinus*, the swollen part of these cells are rough-walled by narrow teeth. Such structures seem to lack in *H. luteus* and *H. pezizaeformis* (McNabb 1965 d).

By characters of cortical hairs, *Heterotextus* is easily distinguishable from *Guepiniopsis*. Species of the latter genus have catenulate hyphae of sterile basidiocarp surfaces. Reid (1974) kept *Heterotextus* under synonymy of *Guepiniopsis*. He is of the opinion "... that the palisadic elements in *G. alpina* are not basically different from those found in *G. chrysocoma* or *G. buccina*". In *Dacryopinax*, surface hairs are composed of fasciculate, thick-walled hyphae. In *Femsjonina* and *Ditiola* morphologically deviating terminal hyphal cells are lacking.

Difficulties arise for generic delimitations between *Heterotextus* and *Dacrymyces* s.l. *Dacrymyces suecicus* (McNabb 1973) has a basidiocarp gross morphology of *Dacrymyces*, but the marginal hair type of *Heterotextus*. McNabb was not at all certain about the true taxonomic position of this species. From his descriptions it may be derived that the taxon is a member of *Heterotextus* in a natural relationship. However, a detailed, comparative restudy of *D. suecicus* is needed for such a conclusion. Obviously McNabb (1965 d) would have been inclined to treat *Heterotextus* as a third subgenus of *Dacrymyces*.

#### *GUEPINIOPSIS* PATOUILLARD

The genus *Guepiniopsis* contains species with rather distinctive morphological characteristics. These are chiefly the marginal hyphae of sterile basidiocarp surfaces. Such hyphae are catenulately composed of stout, swollen cells. Often the thick walls are conspicuously layered and externally roughened. Marginal hyphae with that morphology occur in the type of the genus, *G. buccina*, and in *G. chrysocoma*. The latter species was not included in *Guepiniopsis* by McNabb (1965 c), though already Brasfield (1938) transferred it into that genus. However, McNabb (1973) argued that Brasfield's concept of *G. chrysocoma* does not agree with that derived from

a study of Friesian material. He supposed that “the obpyriform cortical cells of Brasfield’s fungus indicate that it most probably belongs in *Heterotextus*”. McNabb (1973) included *Peziza chrysocoma* in *Dacrymyces*, thus following Tulasne (1853). The taxon is grouped in subgen. *Turbinaster* of *Dacrymyces*, together with *D. marginatus*, *D. minutus*, *D. pedunculatus*, *D. suecicus*, and *D. variisporus*. *Dacrymyces marginatus* is interpreted here in its original sense, *Arrhytidia flava*, the type of the genus *Arrhytidia*. Certainly *Guepiniopsis minuta* (Olive 1954) is a closely related species which should be maintained in *Guepiniopsis* and not transferred to *Dacrymyces* as proposed by McNabb (1973). It is suggested that also *D. palmatus* is closely related with *Guepiniopsis* species. However, because of the lack of detailed investigations, taxonomic conclusions would seem to be premature.

#### DITIOLA FRIES

Lindau (1894) was the first to describe *Ditiola radicata*, the type species of the genus, in detail. He definitely demonstrated the dacrymycetaceous nature of the species and indicated morphological features usable for a generic circumscription. Kobayasi (1939 a), Kennedy (1964), and McNabb (1966) principally accepted this taxonomic concept. *Ditiola* is a small genus and McNabb (1966) recognized only two species and one variety in his monograph. Oberwinkler (1989) proposed a new species, *D. haasii*, which shows affinities to the *Dacrymyces tortus*-group.

The stalked, capitate to discoid or slightly cyphelloid basidiocarp is present in the type species and in *D. brasiliensis*. Stalked, more or less cyphelloid fructifications are also found in species of *Heterotextus*, *Guepiniopsis*, *Dacryopinax*, and *Femsjonia*. *Heterotextus* and *Guepiniopsis* differ from *Ditiola* in the strongly swollen and often multilayered terminal cells or cell chains of “marginal hairs”. In *Dacryopinax*, these are composed of bundles of thick-walled hyphae; such hyphal fascicles are lacking in *Ditiola*. *Femsjonia* comprises two species, *F. pezizaeformis*, and *F. pezizoidea*, according to the interpretation of McNabb (1965 e). These species have stalked, cupulate basidiocarps similar to those of *D. radicata*. McNabb (1966) mentions “*Ditiola* may be readily distinguished from macroscopically similar species of other genera by the heterogeneous nature of the basidiocarps”. Such differences in hyphal structure are generally accepted for generic delimitations, but microscopic study of the hyphal construction in *Ditiola* and *Femsjonia* species reveals some similarities. In species of both genera, thin- and thick-walled hyphae are present. *F. pezizaeformis* basidiocarps are composed of thin-walled generative hyphae in the hymenium and subhymenium, and thick-walled



hyphae in the remaining parts of the fructification. Nevertheless, *Femsjonia* is said to consist of a homogeneous hyphal system (McNabb 1965 e). However, Reid (1974) was of the opinion that *F. pezizaeformis* has "... an exactly similar construction of the fruitbody ..." as *D. radicata* and he therefore reduced *Femsjonia* to synonymy under *Ditiola*. One of the generically important characteristics of *Ditiola* is the conspicuous rooting base (23) composed of thick-walled hyphae. This structure is lacking in *Femsjonia*.

*Ditiola haasii* shows a similar basidiocarp gross morphology as *D. radicata*. Also the hyphal system is heterogeneous. Thick-walled hyphae are restricted to the root and basal parts of the stipe, other parts of the basidiocarp being composed of thin-walled, fibulate hyphae.

In pure cultures of *D. haasii* mycelial growth of efibulate hyphae was obtained from three strains. These hyphae produce a large number of conidia on lateral outgrowths. The anamorph stage is partly similar with that of *D. radicata*, as described and illustrated by Harmsen (1954). In addition, conidiophores are produced by these hyphae which resemble those of *Femsjonia pezizaeformis* as reported by Yen (1949), and as studied during these investigations.

#### FEMSJONIA FRIES

Kobayasi (1939 b) was the first to give an adequate description of the type species, *F. pezizaeformis*, based on microscopic studies. He found the basidiocarps to be composed mainly of thick-walled hyphae. Consequently Neuhoﬀ's (1936) concept of including *Femsjonia* in *Dacrymyces* did not seem to be appropriate. Later authors unanimously treated *Femsjonia* as a separate genus. However, because of the heterogeneous hyphal construction of *Femsjonia* basidiocarps, Reid (1974) placed the genus under synonymy of *Ditiola*. Certainly, these genera are closely related. They have in common a number of taxonomically important characteristics: 1) Basidiocarps stalked-cupulate to cyphelloid; 2) context of fructifications tough-gelatinous; 3) sterile surfaces of stipe and abhymenial layer of disk composed of thick-walled, but unspecialized hyphae; 4) hyphae in the basidiocarps heterogeneous, i.e. thick-walled hyphae in the stipe, and thin-walled ones in the hymenium, subhymenium and in part below these layers; 5) hymenium restricted to a more or less concave disk; 6) hymenium mainly composed of basidia; conspicuous hyphidia lacking at least in the type species.

However, *Ditiola radicata* is primarily marked by its conspicuous and tough rooting base (23). The stipe of the basidiocarp abruptly expands at the surface of the wood and enlarges conically to form the apical disk. A surprisingly

similar basidiocarp morphology is found in *D. haasii*. In this species the thick-walled hyphae are confined to the root and the basal part of the stipe. Nevertheless, it fits much better into the scope of *Ditiola* than into that of *Dacrymyces*. No adequate studies have been carried out to understand structure, function, development, and origin of rooting bases in basidiocarps of *Dacrymycetales* species.

Stalked-cupulate, cyphelloid basidiocarps are also present in species of the genera *Dacryopinax* s.str., *Guepiniopsis*, and *Heterotextus*. These taxa are mostly well-defined by their specialized marginal hairs.

McNabb (1965 e) recognized two species in his monographic treatment of the genus. *Femsjonina pezizoidea* is known from South America, and *F. orientalis* (Kobayasi 1939 b) from Honshu is suggested to be synonymous (fide McNabb 1965 e). A third species, *F. rubra*, preferably occurring on *Abies*-species in the mountains of Southwest China, was described by Zang mu (1983).

#### CALOCERA (FRIES) FRIES

*Calocera* is circumscribed exclusively by the clavarioid basidiocarps. No detailed anatomical studies have been carried out to prove the generic similarities of species assigned to that genus. The generic concept is derived here from a comprehensive study of the type species, and a taxonomic comparison with clavarioid species included in *Corynoides*.

*Calocera viscosa* has several important characteristics: 1) Fructifications are developing from a large, conspicuous rooting base with a three-zonal hyphal arrangement. 2) Mature basidiocarps are ramified. 3) The hyphal systems of the root are elongating into the basidiocarp, and typically developed at least in the lower parts. 4) The hyphal system is composed of: a) a peripheral layer of thin- to slightly thick-walled hyphae which are loosely interwoven; b) a second, internal layer of densely arranged, thick-walled, and strongly gelatinized hyphae with roughly ribbed outer wall layers; c) a central core of broad, densely packed, thin to slightly thick-walled and scarcely gelatinized hyphae. 5) The hymenium is not markedly separated from the sterile base of the basidiocarp.

A careful comparison with other clavarioid species, which are commonly placed in *Calocera*, as *Corynoides cornea*, and *Dacryomitra pusilla*, reveals a rather unique characterization for *Calocera viscosa*. Therefore the genus *Corynoides* is reintroduced to accomodate at least two species which were investigated in detail for this contribution, *C. cornea* and *Dacryomitra pusilla*. These species do not have conspicuous rooting bases; they lack the hyphal systems which are

present in *Calocera viscosa*, though a two-zonal arrangement (three-zonal inclusive of the hymenial layer) is present. However, these hyphal layers are composed of uniformly thin-walled hyphae. The hymenium is commonly confined to a well marked and separated head, even when it is elongated.

It is understandable that a simple morphological feature, the clavarioid basidiocarp, is unanimously accepted as the most important taxonomic criterion for a generic concept of *Calocera*. However, as is evident in other genera of *Dacrymycetales*, e.g. in the pustulate or cyphelloid ones, such characteristics are not at all satisfying taxonomically.

Unfortunately, further reliable data are lacking for other species which have been placed in *Calocera*. Thus, the natural relationship of *C. furcata* is uncertain. For *C. pallido-spathulata* (Reid 1974), the description fits better in *Corynoides* than in *Calocera* s.str. *Calocera guepinioides* has been redescribed by McNabb (1965 a). This circumscription reminds to some degree of that of *Guepiniopsis spathularia*.

Anamorph stages, obtained in pure culture of *Calocera viscosa*, were described and illustrated by Yen (1949). His findings could be confirmed in the course of this study. The anamorphs principally correspond with those known from other *Dacrymycetales* taxa.

#### DACRYONAEMA NANNFELDT

*Dacryonaema rufum* is a unique member of the *Dacrymycetales*. It has an uncommon basidiocarp development with long stages of sterile fructifications which may be capable of drying up, and growing under favorable weather conditions. Further, the hyphal composition of the basidiocarp is unusual with its strongly agglutinated hyphae, tough-gelatinous sheaths, cortical elements which are dendroid (26), and intergrading with more or less undifferentiated ones. These finally form a smooth surface. The basidia are remarkably slender. According to Brough & Bandoni (1975) "clamp connections of the medallion type, visible at the bases of young basidia but often obscured during proliferation, sometimes incomplete and resembling false clamps" are present in *D. rufum*. Such structures could not been found in European specimens. Additional investigations are therefore needed to clarify the identity of European and North American taxa.

The anomalous characteristics of *D. rufum* can easily be used for a generic circumscription. On the other hand, this species cannot be affiliated with other dacrymycetaceous taxa into a natural relationship, though there is no doubt that it belongs into the *Dacrymycetales*.

With profound knowledge, Nannfeldt (1947) discussed in detail the differences to other dacrymycetaceous genera. The macroscopically

comparable species of the *Calocera-Corynoides*-complex are markedly different by fruitbody gross morphology and hyphal arrangements.

#### *CORYNOIDES* S.F. GRAY

*Corynoides cornea* is a rather unusual species. Its main characteristics are: 1) Fructifications not conspicuously rooting; 2) basidiocarp composed of a sterile stipe and a fertile, apical portion; 3) head usually sharply separated from stipe; 4) head developing from subglobose to subcylindrical-fusiform; 5) all hyphae efibulate and thin-walled; 6) central hyphae of stipe densely packed, thus forming a compact, but not a tubular core; 7) peripheral hyphal layer of stipe strongly gelatinous to slimy; 8) unbranched, but prominent hyphidia in the hymenium; 9) basidia with an undulating growth of sterigmata.

These characteristics can be used, at least in part, to separate the species also generically from other dacrymycetaceous taxa. The interpretation is primarily based on a comparison of *C. cornea* and *Dacryomitra pusilla* with the type species of *Calocera*, *C. viscosa*. The latter species possesses a long rooting base, and a three-zonal hyphal system reaching into the branches of the ramified basidiocarp. The hymenium covers the clavarioid fructification amphigenously, it is not restricted to head-like, terminal structures. In *C. viscosa* the hyphae of the layer between the peripheral sheath and the core are extremely thick-walled in the root and lower parts of the basidiocarp. In the upper regions these hyphae disappear more and more. Thus, the hyphal system of *C. viscosa* is markedly different from that of *Corynoides* species.

Tulasne (1872) has proposed the genus *Dacryomitra* to accommodate a species which he named *D. pusilla*. Later workers mostly have synonymized this species with *Calocera glossoides*, though obviously no authentic material has been available for a restudy of that taxon (fide Reid 1974). In contrast, Bourdot & Galzin (1928) gave a deviating description of *C. glossoides*. This was accepted by Donk (1966) to keep *D. pusilla* separate from *C. glossoides*. The problem could not be solved in the course of this study.

Most American workers have accepted the genus *Dacryomitra*, mainly recognizing the basidiocarp, differentiated in a sterile stipe and a fertile head as the generic characteristic. McNabb (1965a), Donk (1966), and Reid (1974) did not accept the separation of *Dacryomitra* from *Calocera*.

## CHARACTERS AND CHARACTER STATES

The numbers in brackets refer to characters used in the data matrix and the cladogram.

### **Basidiocarp morphology** (4, 8, 9, 10, 11, 14, 15, 20, 25, 27)

Species and genera of *Dacrymycetales* show a progressive increase in complexity of basidiocarp morphology. *Cerinomyces* species are totally corticioid with apparently unlimited marginal growth. *Arrhytidia* contains flat-discoid taxa (8) with central, root-like hyphal bundles. Such insertion in the wood is more or less present in all other dacrymycetaceous fungi (4). Further morphological evolution of the fructifications leads to pustular *Dacrymyces* and *Dacryomycetopsis* (10), turbinate, cup-shaped, or cyphelloid *Ditiola*, *Femsjonia*, *Dacryopinax*, *Heterotextus*, *Guepiniopsis* to stalked-capitate *Dacryonaema* and *Corynoides* (20), and to branched, clavarioid *Calocera*. These main types of basidiocarps are traditionally considered to be of main importance for the generic concept in the *Dacrymycetales*. The frequency of convergent evolution of the same or similar fruiting structures is not known in these fungi and it is also not known in many other fungal groups.

There are two observations supporting an interpretation in favour of parallel basidiocarp evolution: a) main types of fruiting structures are found in different monophyletic groups, and b) intergrading and variable stages represented by recent species prove the connections of various types.

*Dacrymyces stillatus* is a good example for variable basidiocarp morphology of an individual fungus during its life cycle. In young developmental stages, fruitingbodies are shortly, but distinctly stalked and capitate. Older fructifications are flattening, spreading over the wood and coalescing with neighbouring ones to form confluent crust-like films. Such stages are almost incomparable morphologically with the younger ones. They resemble much more basidiocarps of *Arrhytidia* species. Under optimal growth conditions, *D. stillatus* basidiocarps may develop a somewhat folded, luxuriant hymenium. Such fructifications are typical for e.g. *D. coryneoides*, *D. dacryomitiformis*, *D. novae-zelandiae*, *D. palmatus*, and *Dacrymycetopsis rosea*.

Another example of intergrading fructification types is that which affiliates *Dacrymyces* s.str. with *D. chrysocoma*, and the cyphelloid *Guepiniopsis buccina*. Also *D. suecicus* shares an intermediate position between two genera, *Dacrymyces* and *Heterotextus* (fide McNabb 1973). A further example proves that a continuous line of fructification types leads from corticioid *Arrhytidia* through stalked capitate *Dacrymyces* to stalked cup-shaped *Ditiola*. Such ontogenetic and generic variations deserve some further comments.

A series of species connects *Dacrymyces* s.l. with *Heterotextus*. This is not an argument in favor of combining these taxa, but it is more an indication of a line of morphological types leading from pustulate to cyphelloid fructifications. Though he accepted *Heterotextus* as a genus, McNabb (1965 d) was uncertain about its true taxonomic status; he could have also treated it as a third subgenus of *Dacrymyces*.

The few remarks may point to the weakness of basidiocarp characters applied to supraspecific taxa. This is especially true for the cyphelloid basidiocarps (14), which do not only occur in many different and distantly related basidiomycetous taxa, but also in many discomycetous *Ascomycetes*. Therefore the apomorphy 14 is dubious or even none.

### **Hyphae and hyphal systems (18, 19)**

There is considerable variation of hyphal characteristics in different taxa of the *Dacrymycetales*. Hyphae generally are hyaline, but quite often they can be variously pigmented with carotinoids. Outer hyphal wall layers most often are or become strongly gelatinized, thus causing gelatinous hyphal systems and fructifications.

In thin, adnate fructifications it is often difficult to assess hyphal consistency. Such of *Cerinomyces* species can be considered as arid or waxy, but not gelatinous, in species of *Arrhytidia* it may be waxy to firm-gelatinous. Because of too unprecise character states, variable appearances depending on environmental and ontogenetic conditions, and too scanty knowledge in general, hyphal consistency could not be used in the present evaluation.

*Dacrymyces stillatus* basidiocarps are composed of a simple, homogeneous hyphal system with thin-walled, efibulate, and strongly gelatinizing hyphae. Most other *Dacrymyces* species seem to be constructed of a homogeneous system of hyphae. Unfortunately, adequate anatomical studies are not available for a soundly based comparison with other *Dacrymyces* species.

The genera *Ditiola* and *Femsjonia* (18) show heterogeneous hyphal systems, i.e. basal and central hyphae of the basidiocarp are thick-walled, those of the upper parts of the subhymenium, and hymenium thin-walled. A modified pattern of location of thick- and thin-walled hyphae in the fructification can be found in *Ditiola haasii* (Oberwinkler 1989). In this species only the basal parts of the basidiocarps are composed of thick-walled hyphae, thus forming the immediate connection with the identically structured hyphae of the root. To consider this kind of hyphal systems as an apomorphy is well founded.

More complicated is the three-zonal hyphal arrangement in *Calocera viscosa* (19). This character is certainly derived and can be used as an apomorphy. Not



only for phylogenetic considerations, but also for well founded taxonomic purposes it is important to know that species of *Corynoides* and *Dacryonaema* do not share this character. The densely agglutinated, tough-horny consistency of *Dacryonaema* basidiocarps seems to be unique in the whole group, and therefore justified as an additional apomorphy. It is not used here because other species are not or only insufficiently characterized.

**Rooting bases (4, 23)**

All species of the *Dacrymycetales*, except those of *Cerinomyces*, produce carotinoids, septate basidiospores, and microconidia. They also share the derived structure of a central basidiocarp rooting base (4).

No comparative studies have been carried out in species of *Dacrymyces* to obtain information on how basidiocarps are anchored in the wood, and whether or not this rooting base is composed of different hyphal systems. It appears at least in *D. stillatus* that also the basal hyphae of both the teleomorph and anamorph fructifications, are thin-walled, as are all other hyphae.

There are conspicuous rooting bases in two different taxa, *Ditiola* and *Calocera*. Macroscopically they appear similar, but in hyphal construction patterns they are considerably different. Hyphae in the root of *Ditiola* are thick-walled (23), in *Calocera* they have three-zonal arrangement of the basidiocarp. Therefore, both rooting types appear to be different apomorphies. The root of *Calocera* has not been used as an additional apomorphy, as well as inconspicuous rooting bases. They cannot yet be evaluated because data from other taxa are lacking.

**Marginal hairs (16, 17, 21, 22, 26)**

Marginal hyphae of sterile surfaces vary considerably in different taxa of the *Dacrymycetales*. Within the traditional range of the genus *Dacrymyces*, e.g. in *D. minor*, these hyphae are conspicuously thick-walled. It is uncertain whether this is a constant characteristic, nor is it known whether *D. stillatus* invariably forms a peripheral layer of unthickened marginal hyphae. For *D. capitatus*, McNabb (1973) reported thin- or thick-walled hairs of the stipe. An almost continuous chain of species may be found in which marginal hyphae become more and more thick-walled, and morphologically structured. In an unidentified species (FO 13868), terminal cells of marginal hyphae have strongly thickened walls and only thin, central cytoplasmic lumina. A number of species, grouped in *Dacrymyces* develop "marginal hairs" composed of chains of thick-walled cells, as in *D. intermedius*. This species was placed close to *D. stillatus* by McNabb (1973). Marginal hairs of that type (fide McNabb 1973) appear to occur also in *D. coryneoides*, *D. dacryomitiformis*, and *D. pedunculatus*.

*Dacrymyces palmatus* has marginal hairs which closely resemble those of *D. (Guepiniopsis) minuta* (Olive 1954), and *D. (Guepiniopsis) chrysocoma*. *Dacrymyces dictyosporus* (Martin 1959) is similar not only in the morphology of marginal hyphae but also in that of the basidiospores. *Dacrymyces suecicus* has a "cortex covered with thick-walled, simple or branched, clamped hairs, terminal cells varying in shape from broadly cylindrical to ovate, occasionally obpyriform, often basally roughened..." (McNabb 1973). This description fits well to that of the marginal hairs of *Heterotextus alpinus*, and also to that of the type of the genus, *H. miltinus*. McNabb (1973) was of the opinion that "it is a somewhat arbitrary decision to place *D. suecicus* in *Dacrymyces* rather than *Heterotextus* for in many respects it is exactly intermediate between the two genera". Certainly, the morphology of the marginal hyphae can be used in this case to understand natural relationships.

The examples mentioned illustrate the difficulties to find clear cut borders between supraspecific taxa when these characters are included in the generic concept. On the other hand they appear to be important markers for monophylies. To prove this hypothesis, the data from all species are required.

### Septa

For species delimitation in the Dacrymycetales, the presence or absence of clamps is traditionally used as a valuable taxonomic feature. Occasionally, closely related taxa may coincide in having fibulate or efibulate hyphae. For example, the type group in *Dacrymyces*, *D. stillatus*, *D. aquaticus*, *D. minor*, and *D. intermedius* is uniform.

Loop-like clamps were found in *D. macnabbii* (Reid 1974). Such clamps also occur, however, in *Dacryomycetopsis rosea* and *Guepiniopsis spathularia*, though obviously not at the bases of basidia as in *D. macnabbii*. Another common feature in these taxa is the conspicuous dendrohyphidia, occurring in the hymenium.

Thus, according to the present knowledge, septal types cannot be used for generic descriptions in the Dacrymycetales. They are therefore not included in the data matrix. Information on all species is needed for an overall evaluation.

### Septal pores

The ultrastructure of the septal pore apparatus has been studied in *Dacrymyces stillatus* (Moore & McAlear 1962; Flegler, Hooper & Field 1976; Moore 1978), *D. dendrocalami* (Oberwinkler & Tschen 1989), *Ditiola haasii* (Oberwinkler 1989), and *Calocera viscosa* (Patton & Marchant 1978). All septal pores examined are similar in general ultrastructure, especially the continuous



parenthesome perforated only by a tiny apical pore. In *Cerinomyces crustulinus*, this septal pore type also occurs (K. Wells, pers. comm.). I have studied species of the genera *Dacrymyces*, *Dacryonaema*, *Femsjonia*, *Guepiniopsis*, and *Calocera*, and can confirm that the septal pore apparatus in the Dacrymycetales is uniform.

Though the character of septal porus cannot be used for generic descriptions in the *Dacrymycetales*, it was mentioned because it is an excellent plesiomorphy, defining the *Tulasnellales* as a sister-group. Such types of dolipores are also universal in the *Auriculariales* ss. Bandoni (Bandoni 1984, Oberwinkler 1985).

### Hymenia (27)

In *Dacrymyces stillatus* the hymenium is spread over the hemispherical area of the young basidiocarp. Under favorable growth conditions the basidial layer becomes folded and irregularly shaped; in older and densely crowded specimens, the hymenium flattens to form a coalescing film. Flat hymenia are typical for species of *Arrhytidia* with discrete margins, and for *Cerinomyces* with indefinite marginal growth. Well developed hymenia may become cerebriform to irregularly flabellate, as e.g. in *Dacrymyces dacryomitiformis*, or *D. palmatus* and *Dacryomycetopsis rosea*. Morcheloid hymenia (27) occur in *Dacryomitra pusilla*. "Luxuriantly" growing hymenia will cover and alter the original shape of basidiocarps drastically.

In resupinate and pustulate species, the hymenium is amphigeneous, but does not cover those parts between the hymenial margin and the insertion of the stipe. However, in stalked, cyphelloid, capitate, spathulate, and clavarioid basidiocarps, the hymenium is usually restricted to the upper parts of the fructifications. In the spathulate-flabellate *Guepiniopsis spathularia*, the hymenium is unilateral and confined to the inferior surface of the upper part of the fruitingbody.

The hymenium is composed of basidia in different developmental stages, the fertile hyphae proliferating laterally at the bases of basidia. A slightly thickening hymenium is formed which lacks sterile hyphae in *Dacrymyces stillatus*. Such hymenial structure is found in numerous species, e.g. *D. minor* and in *Ditiola haasii*.

There are contradictory reports as to the orientation of the basidiocarps and the hymenium in several species and genera. *Dacryopinax elegans* was figured with upright growing fructifications by Fisher (1931), and Brasfield (1938 a). McNabb (1965 b) reported young basidiocarps with superior

hymenia, but further on broadly spathulate structures may develop which have unilaterally oriented hymenia. Martin & Fisher (1933) illustrated downwards growing basidiocarps.

*Femsjonia pezizaeformis* was figured growing upright on the wood with superior disks and hymenia by Istvanffi (in Brefeld 1888: Taf. XI, Fig. 3: 1, 2). Buller (1922) reported that the hymenium is always directed downwards. Martin & Fisher (1933) accepted Buller's version.

For better interpretations of cyphelloid species, field observations should be more precise concerning the growth orientation of the basidiocarps and position of the hymenia. Such characters could putatively be useful for improved generic descriptions.

### **Hyphidia (13)**

It can be suggested that an evolutionary trend may have led from species without hyphidia to those with simple ones, and finally those with dendrohyphidia. Whether recent species of the one or other type are closely related has still to be elucidated. Also it is necessary to recognize the fact that young terminal cells of generative hyphae in the hymenium resemble simple hyphidia morphologically. If well developed dendrohyphidia are considered as a generic marker in the Dacrymycetales, it can be used as an apomorphy for *Dacryomycetopsis*. Such dendrohyphidia are present also in *Dacrymyces paraphysatus*, *D. dendrocalami*, and *D. macnabii*. The latter shares loop-like clamps with *Dacryomycetopsis*. Both characters occur also in *Guepiniopsis spathularia*, though inflated clamps seem not to be present at the bases of basidia as in *D. macnabii*. Other species, like *D. estonicus* possess slender, unbranched hyphidia. Branched hyphidia are known e.g. in *D. enatus*, and *D. ovisporus*.

### **Basidia (1)**

Basidia of the unique dacrymycetaceous type are typical for all species of the Dacrymycetales (Oberwinkler 1965, 1977, 1982). It is an excellent feature for characterizing the order with an apomorphy. However, in very rare cases, basidia with abnormal morphology can be found, e.g. with three or four sterigmata, or two-sterigmate ones with abnormally inserted spicula. Three-sterigmate basidia have been reported also for *Cerinomyces crustulinus* by Eriksson & Ryvarden (1973).

In *Dacrymyces ovisporus* a certain percentage of basidia deviate morphologically from the common dacrymycetaceous type in being one-sterigmate. The number of two- and one-sterigmate basidia is varying considerably in different collections. an unusual high percentage of one-sterigmate basidia can be found in *Platygløea unispora* (Olive 1947). A restudy of the type of

*P. unispora* led to the conclusion that this taxon is closely related to *D. ovisporus*. Both *D. ovisporus* and the type of *P. unispora* are identical in the presence of shortly ramified hyphidia in the hymenium.

Specific deviation of basidial morphology is known in a few cases. Basidia of *Dacrymyces estonicus* are basally slightly swollen (Rataviir 1962). Similar basidia can be found in *Arrhytidia flava*. Rataviir (1962) distinguished two additional basidial types, one is characteristic for *D. chrysocomus*, the other one for *Femsjonia luteo-alba*. In *D. dendrocalami* (Oberwinkler & Tschén 1989) basidia are very stout, often thick-walled and transversely septate.

At present, these basidial types cannot be used for generic delimitations.

### Karyology

The nuclear behavior of the *Dacrymyces* meiosporangium was investigated by Dangeard (1895). He found dikaryotic stages in the young basidia of *Dacrymyces stillatus* (*D. deliquescens*) and *Calocera viscosa*, fusion of nuclei, one nuclear division, and the migration of only one nucleus into one spore. Istvanffi (1895) noted two divisions of the fusion nucleus in the basidium of *D. chrysocomus* (ss. Brefeld), and the passage of one nucleus into each spore. He postulated the development of a second pair of spores, into which the nuclei, primarily remaining in the sterigmata, would then enter. Juel (1898) studied *D. stillatus* again, confirmed Istvanffi's findings, but did not mention a second generation of basidiospores. The cytological study of *D. stillatus* by Maire (1902) was in general agreement with Istvanffi's and Juel's observations. Two sets of basidiospores were assumed for *Calocera cornea* in the case where four nuclei resulted from the meiotic division. Wager (1914) and Gilbert (1922) investigated unidentified *Dacrymyces* species karyologically. Their accounts agree essentially with those of the earlier workers. Wager did not exclude the possibility that two nuclei may enter one spore, while Gilbert definitely stated that degeneration of the two remaining nuclei occurred in the basidium. His results, obtained obviously from species other than *D. stillatus*, can be confirmed for the latter. Young terminal cells in the hymenium are dikaryotic. A diploid nucleus is found in the young basidium. Meiosis leads to a four-nucleate basidium. One nucleus migrates into each basidiospore, the other nuclei remain and degenerate in the basidial body. Remnants of the basidial nuclei may also be found in the sterigmata.

Bodman (1938) studied the cytology of *Guepinia spathularia*, and found essentially the same nuclear behavior in that species as reported above for other taxa.

From these findings it can be concluded that the karyology of the dacrymycetaceous meiosporangium is rather uniform and quite likely another prove for the monophyly of the Dacrymycetales.

### **Basidiospores (6, 23)**

Spore septation occurs in various taxa of the Heterobasidiomycetes, e.g. in *Septobasidiales*, *Exobasidiales*, and *Cryptobasidiales*. In Homobasidiomycetes, spores are aseptate or, exceptionally, there are some species with spores that become septate immediately before germination, as in *Vuilleminia comedens*. Septate spores therefore are primarily characteristic for heterobasidiomycetous fungi.

Evolutionary tendencies in spore septation are difficult to assess from our present knowledge. It appears that the type species of *Cerinomyces*, *C. pallidus*, and the closely related *C. crustulinus* have constantly aseptate basidiospores. Whether species grouped in that genus, but having septate spores, naturally belong in it is still an open question.

In *Ditiola radicata*, the type of the genus, basidiospores become tardily one-septate; in the obviously closely related *D. radicata* var. *gyrocephala* and *D. brasiliensis*, mature spores are three-septate (McNabb 1966). *Ditiola haasii* has spores that vary from aseptate to one-septate or three-septate. The spores of *Femsjonia* species are mostly three-septate in *F. pezizoidea*, and become many-septate in the type of the genus, *F. pezizaeformis*.

Typically, mature spores in *Dacrymyces stillatus* become thick-walled by apposition of cell wall layers at the inner side of the primary wall. Such thick-walled spores also occur in the obviously closely related *D. intermedius* (McNabb 1973), and in *D. dictyosporus*, *D. enatus* var. *macrosporus*, *D. paraphysatus*, *D. variisporus*, *Guepiniopsis chrysocoma*, and *Heterotextus miltinus*. The significance of thick-walled spores in dacrymycetaceous fungi is not understandable from our present knowledge. It appears that, even in single basidiocarps of *D. stillatus* and *D. variisporus* (McNabb 1973), thin- and thick-walled basidiospores are present. Obviously, further maturation by thickening of spore walls and septa can occur after spore release from the basidia. Under favorable conditions, recently liberated and still thin-walled spores can germinate, without becoming thick-walled. Thick-walled spores of dacrymycetaceous fungi are still capable of germination, although germ pores are lacking. The mechanism of that germination has not been studied.

Species with multiseptate spores can usually be easily recognized, e.g. *Dacrymyces estonicus* and *D. palmatus*.

In *Dacrymyces ovisporus* the basidiospores are approximately subglobose, and mature irregularly muriform. The ontogeny of basidiospore septation has been studied by Bandoni (1963). Bandoni also mentioned the intermediate spore characteristics of *D. dictyosporus*, a species which can be assumed to be related to *D. ovisporus*. Partly muriform spores are also present in *D. variisporus* (McNabb 1973) and *D. (Guepiniopsis) chrysocoma*. Both, *D. dictyosporus* and *D. chrysocoma* sometimes possess subglobose spores (McNabb 1973). It is uncertain at present, whether these species are closely related or not.

In all species, spore morphology and dimensions are essential specific characteristics. More data are necessary, however, to conclude whether spore characteristics also can be used for defining genera.

### **Basidiospore germination (2)**

Basidiospore germination in the *Heterobasidiomycetes* is not fixed. Three different germination types are known: 1) budding, 2) secondary ballistospore production, and 3) germ-tube formation.

In the *Dacrymycetales*, repetitive ballistospores have never been observed, but the formation of microconidia is a very common germination type. Often, spores producing microconidia and those germinating by germ tubes are intermixed in the same spore deposit of various species, thus indicating that it appears to be wide-spread in the *Dacrymycetales*. Germination of *Cerinomyces* species has not been studied so far.

### **Microconidia and yeast budding (7)**

Microconidia are produced blastogenously, and repeatedly through sympodial proliferation of the spicule-like conidioferous branches.

One of the important characteristics of microconidia in *Dacrymycetales* is their capability of yeast-like budding. This could be shown during experimental studies in *D. stillatus*, *D. palmatus*, *Ditiola haasii*, and *Calocera viscosa*. There is evidence that budding of microconidia may be common in dacrymycetaceous fungi. However, under laboratory conditions the yeast phase is usually so short that no yeast colonies develop. Nothing is known about this stage in nature.

Microconidia and microconidiogenesis appear to be unique features and therefore apomorphies for the order, not applicable to generic definitions. Yeasts occur in diverse heterobasidiomycetous groups, thus indicating plesiomorphic conditions without any meaning on generic concepts in this group.

### Conidial stages (12)

Arthrospore formation in *Dacrymyces stillatus* takes place by short-celled fragmentation of hyphae. Adjacent cells are separated by splitting of the outer wall layer. During this process the dolipore protruding from the septal wall becomes occluded. The septum then splits along the innermost layer, and the neighboring cells separate, accompanied by a rounding out of septal walls. Though common in *D. stillatus*, the production of anamorph stages in other species of the order appears to be very rare under natural conditions. Only few observations are available in which asexual fructifications are reported to occur. One of these was the description of arthrospores in *D. ellisii* (*D. capitatus* fide McNabb 1973) by Olive (1958). More careful microscopic studies of fresh collections are needed in order to get a better insight into anamorph-teleomorph correlations.

In pure culture at least two different morphological and developmental stages may be distinguished:

- 1) Hyphal fragmentation which is obviously comparable to that in *D. stillatus* under natural conditions. Similar anamorph stages are produced by *D. ovisporus*, and presumably also by additional species of other genera.

- 2) Conidial formation in dacrymycetaceous fungi is very common in culture. Usually conidia are produced on short, sharply pointed, sympodially proliferating outgrowths of hyphae. It is likely that these outgrowths develop from the simple spicules under favorable growth conditions. Similar anamorph phases appear to be common in other species, e.g. *Ditiola haasii*, *Femsjonia pezizaeformis*, and *Calocera viscosa*. These conidia and the conidiogenesis are similar to microconidia and their production during basidiospore germination. It is unknown what role such anamorph stages play under natural conditions. It is a common feature in the order, as such an ingroup plesiomorphy and not applicable for generic delimitations.

Arthrosporic conidia can be used as an apomorphy in a narrow generic circumscription of *Dacrymyces*.

### Mating systems

The nuclear behavior of *Calocera cornea* was studied by Vandendries (1937), who concluded that the species is homothallic. He found the spores to be binucleate, and dikaryons developed in monospore cultures. Yen (1947) studied *C. cornea* again, and, in addition *Dacrymyces stillatus* and *Femsjonia pezizaeformis*. These species produce mononucleate spores primarily. Before the spore becomes septate and begins to germinate, nuclear divisions occur. Dikaryons were never obtained in monospore cultures. Mating experiments



showed that the species studied are heterothallic and tetrapolar, thus indicating plesiomorphic conditions within heterobasidiomycetous fungi, and without any bearing on the generic concept.

### **Pigments (5)**

Carotenoids are characteristic pigments of Dacrymycetales (Gill & Steglich 1987). There are unusual color changes during the life history in some species, e.g. *Dacrymyces stillatus* develops orange to red colored anamorph stages, while the teleomorph stages usually are yellowish to ochraceous. In most species, the light-dependent pigment production can also easily be observed in basidiocarps growing under natural conditions. Those parts of fructifications which grow in the wood or are covered by other organisms, like mosses or by plant debris, are hyaline or faintly colored; fully exposed parts of the fruitbodies are commonly intense yellowish, orange or reddish.

In outgroup comparison with the *Tulasnellales*, carotenoids can be considered as an apomorphy (5) for the *Dacrymycetales*.

### **Wood decay and substrate specificities**

All dacrymycetaceous species are known to grow exclusively on wood. They are very important wood-decay fungi. Shields & Shih (1975) found considerable weight losses of wood during growths of *Calocera cornea*, *Dacrymyces stillatus*, and *D. capitatus*. Siepmann (1977, 1979) reported heart rot in stumps of *Pseudotsuga menziesii* caused by *Calocera viscosa*. This species causes the same decay in *Larix decidua* (Pawsey 1971). Seifert (1983) tested 16 species in the *Dacrymycetales* for the ability to decay wood. He found 4 distinct types of decay on wood blocks: 1) A uniform brown discoloration of the wood was caused by strains of *Cerinomyces ceraceus*, *Dacrymyces capitatus*, *D. dictyosporus*, *D. palmatus*, and *Guepiniopsis spathularia*. 2) In a brown pocket rot, linear to irregular parts of wood, up to 5 mm wide, are discolored brown. The decay is caused by strains of *Calocera cornea*, *Dacrymyces capitatus*, *D. palmatus*, and *D. novae-zelandiae*. 3) In a third type of brown-rot the wood is decomposed successively, finally leaving a brown skeleton. Strains of *Calocera cornea* and *Dacrymyces stillatus* are causing such decay. 4) *Calocera lutea* and *C. viscosa* strains decayed wood blocks without significant discoloration, comparable in appearance to white-rot. Most of these fungi degraded carbohydrates and significant amounts of lignin. Several strains of *Cerinomyces canadensis*, *C. crustulinus*, *Dacrymyces minutus*, *D. palmatus*, *D. punctiformis*, and *Heterotextus luteus*, however, showed little or no capacity to decay wood.

Even such detailed, comparative work does not allow taxonomic interpretation. There appears to be no application for a generic delimitation.

Though the fructifications of Dacrymycetales species usually are developed only under wet or even very wet conditions, mycelia of several species can survive dry periods, reviving extremely rapidly when sufficient moisture is again available. Therefore some species, e.g. *Dacrymyces stillatus* and *Dacryonaema rufum* can colonize fully exposed wood which, after wet periods, dries up immediately. Such species are associated with only some few other highly specialized fungi. No detailed studies on ecological properties of these organisms are available. From occasional observations in the field, a high adaptation to specific environmental conditions can be assumed. *Calocera viscosa* grows preferably on gymnosperm logs of a special degree of decay; *Corynoides cornea* mainly lives in angiospermous hard wood in Europe.

These specific adaptations do not allow a more general application on a generic level.

### Parasites

*Dacrymycetales* species are frequently infected by other fungi. *Chytridiomycetes* are rather common parasites in many soft gelatinous *Dacrymycetales*. Rhizoids of these parasites penetrate the host cell walls, functioning as haustoria.

Host-parasite interactions with tremelloid haustoria are known from the heterobasidiomycetous *Sebacina penetrans* (Hauerslev 1979) and *Occultifur internus* (Oberwinkler 1990), growing in the fructifications of *Dacrymyces stillatus*. Also *Platygløea arrhytidiae* and *P. fungicola* var. *interna* grow internally in dacrymacetaceous hosts (Olive 1958).

Nothing is known on host specificity and therefore, at present, mycoparasitic interactions cannot be applied for generic descriptions.

### Distribution

*Dacrymycetales* have a world-wide distribution. Many species appear to inhabit large areas while others are known only from few localities. In no case sufficient data for specific distribution patterns are known. No data can be used for generic delimitations. Intensified floristic work is required to improve our knowledge.

### CLADISTIC ANALYSIS

Type species of all genera and closely related species are taken for a cladistic interpretation to prove the naturalness of the accepted genera. Because of insufficient data, additional species could not be considered.



Therefore the results cannot be considered as being representative for all taxa of the *Dacrymycetales*.

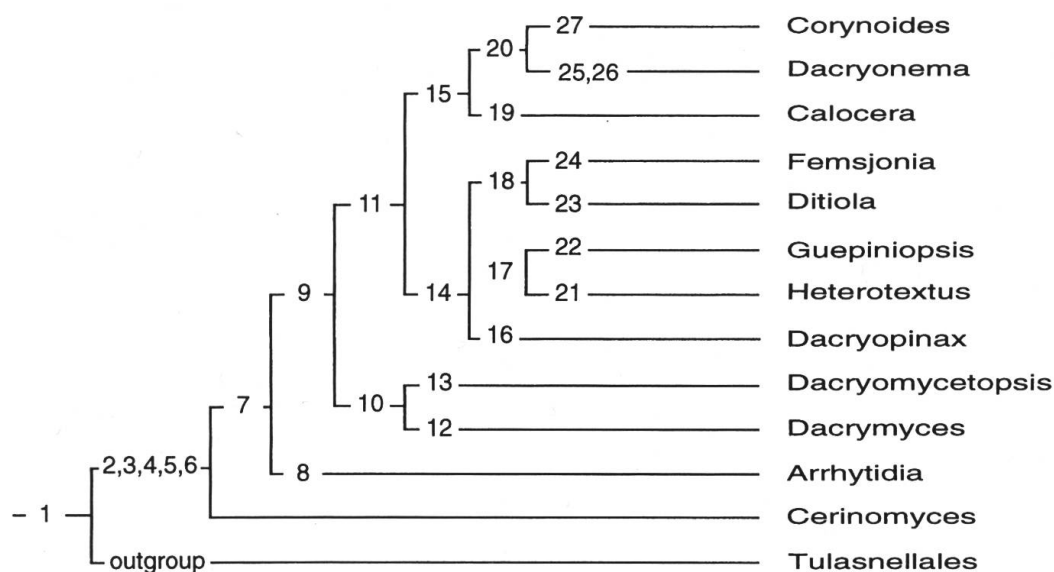
Data matrix for characters and character states:

**Genera:** Tula - *Tulasnella*; Ceri - *Cerinomyces*; Arrh - *Arrhytidia*; Dacm - *Dacrymyces*; Daco - *Dacryomycetopsis*; Hete - *Heterotextus*; Guep - *Guepiniopsis*; Dacp - *Dacryopinax*; Diti - *Ditiola*; Fems - *Femsjonia*; Calo - *Calocera*; Dacn - *Dacryonaema*; Cory - *Corynoides*.

**Characters and character states:** 1 doliporus with continuous parentheses; 2 dacrymycetaceous basidium; 3 loss of secondary spores; 4 carotenoids present; 5 basidiospores septate; 6 spore germination with microconidia; 7 basidiocarp centrally fixed; 8 basidiocarp flat-discoid; 9 basidiocarp efigured; 10 basidiocarp pustulate; 11 basidiocarp conspicuously stalked: 1 stalk simple, 2 stalk usually branched; 12 arthroconidia present; 13 dendrohyphidia present; 14 cyphelloid; 15 clavarioid; 16 hairs fasciculate; 17 terminal hair cells swollen; 18 hyphal system heterogeneous; 19 hyphal arrangement in three zones; 20 basidiocarp stalked-capitate; 21 terminal cells of stipe hairs beaked; 22 hair cells catenulate; 23 homogeneous, long, tough rooting base; 24 stipe surface whitish; 25 head globose; 26 marginal hairs dendroid; 27 head cylindrical, folded to morcheloid.

0 - plesiomorph; 1-3 - apomorph.

	Tula	Ceri	Arrh	Dacm	Daco	Hete	Guep	Dacp	Diti	Fems	Calo	Dacn	Cory
1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	0	1	1	1	1	1	1	1	1	1	1	1	1
3	0	1	1	1	1	1	1	1	1	1	1	1	1
4	0	1	1	1	1	1	1	1	1	1	1	1	1
5	0	1	1	1	1	1	1	1	1	1	1	1	1
6	0	1	1	1	1	1	1	1	1	1	1	1	1
7	0	0	1	1	1	1	1	1	1	1	1	1	1
8	0	0	1	0	0	0	0	0	0	0	0	0	0
9	0	0	0	1	1	2	2	2	2	2	3	3	3
10	0	0	0	1	1	0	0	0	0	0	0	0	0
11	0	0	0	0	0	1	1	1	1	1	2	1	1
12	0	0	0	1	0	0	0	0	0	0	0	0	0
13	0	0	0	0	1	0	0	0	0	0	0	0	0
14	0	0	0	0	0	1	1	1	1	1	0	0	0
15	0	0	0	0	0	0	0	0	0	0	1	1	1
16	0	0	0	0	0	0	0	1	0	0	0	0	0
17	0	0	0	0	0	1	1	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	1	1	0	0	0
19	0	0	0	0	0	0	0	0	0	0	1	0	0
20	0	0	0	0	0	0	0	0	0	0	0	1	1
21	0	0	0	0	0	1	0	0	0	0	0	0	0
22	0	0	0	0	0	0	1	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	1	0	0	0	0
24	0	0	0	0	0	0	0	0	0	1	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	1	0
26	0	0	0	0	0	0	0	0	0	0	0	1	0
27	0	0	0	0	0	0	0	0	0	0	0	0	1



Cladogram for the genera of the Dacrymycetales, based on generic types

#### Discussion of the cladogram

Cladograms derived from selected taxa cannot be expected to explain the phylogeny of the whole group. Unfortunately this is also true when representative species, as the generic types, are used. Therefore all species should be included in the evaluation. This demand is strongly delimited by the incomplete inventory in most fungal groups.

1. The *Tulasnellales* have been selected as an outgroup because they appear to be the sister group of the *Dacrymycetales*. They share the doliporus with continuous parenthesomes and holobasidia. Secondary spore production is a common character in the *Tulasnellales*. It is not found (3) in the *Dacrymycetales*. The *Auriculariales* (ss. Bandoni 1984) could also be used as an outgroup because of the same septal pore type. However, meiosporangia are phragmobasidia, indicating that this order appears to be not so closely related to the *Dacrymycetales*.
2. The dacrymycetaceous basidium only occurs in the *Dacrymycetales*. It is an excellent apomorphy for the order. Variations are discussed under "Characters".
3. Most heterobasidiomycetous species produce secondary spores, e.g. the *Uredinales*, *Septobasidiales*, *Auriculariales*, *Tremellales*, and *Tulasnellales*. Loss of secondary spores is therefore an important systematic character for the *Dacrymycetales*.

4. The presence of carotenoids is a good apomorphy in this node even when they also occur in rusts, in Tremellales and rather scattered in diverse *Homobasidiomycetes*.
5. In contrast to *Ascomycetes*, septate meiospores are rare in *Basidiomycetes*. They are characteristic for species of the *Septobasidiales*, *Exobasidiales*, and *Cryptobasidiales*. Some other, rare cases are known, e.g. *Waitea*, whose systematic position is not clear and which is not considered a member of the *Tulasnellales* s.str. If it has its correct place in this order, the character could not be used as an apomorphy for the *Dacrymycetales*.
6. In general, spore germination by production of microconidia is very rare in *Basidiomycetes*. Conidiogenesis of the *Dacrymycetales*-type appears to be unique, thus representing an apomorphy.
7. Most corticiaceous (resupinate) species grow marginally indeterminate and they are totally attached to the substrate. Such growth behaviour is found in species of the outgroup and in many other hetero- and homobasidiaceous taxa. It is also characteristic for species of the genus *Cerinomyces*. In contrast, all other species of the *Dacrymycetales* have centrally attached basidiocarps. Because of the plesiomorphic condition of resupinate fructifications, this feature cannot be used for coding *Cerinomyces*. I am not aware of any apomorphy for the genus. Therefore the monophyly is not proved, even when it is most likely that the morphologically very similar species represent a natural genus.
8. Centrally stalked, flat and disk-like basidiocarps are morphologically and ontogenetically quite distinct from adnate ones. Nevertheless, they have to be checked very carefully for proper understanding of its architecture. More problems arise when efigurate basidiocarps, e.g. of *Dacrymyces* species, senesce and spread out on the substrate. Such stages are not identical with mature ones, and cannot be taken for comparison with the *Arrhytidia* type. Some of these problems may be the reason why *Arrhytidia* is commonly not accepted as a genus.
9. The basidiocarp is differently structured but not flat. This stage is an important one for the evolution of more complex fructifications.
10. Pustulate basidiocarps are considered as characteristic for the genus *Dacrymyces* s.l. Form and structure vary considerably in different species and different ontogenetic stages. Similar basidiocarp types occur in many taxa outside the *Dacrymycetales*, but not in the *Tulasnellales*. Concerning microscopic features in all dacrymycetaceous taxa, the pustular organisation is heterogeneous. In the present case of generic types and closely related species, monophyletic groups can be determined.

11. The sterile stalk of the basidiocarp is well developed and present during the whole ontogeny. The stalk has the function to expose the hymenium. There are many similar examples known in other *Basidiomycetes* and *Ascomycetes*, but not in the outgroup. Even when acceptable as an apomorphy formally, the conclusion is weak.
12. Arthrosporic hyphal fragmentation is a clear apomorphy for *Dacrymyces* s.str. The remainder of *Dacrymyces* s.l. cannot be included here.
13. Dendrohyphidia are known from many other hetero- and homobasidiomycetous fungi, and from a few species of *Dacrymyces* s.l. Whether these belong into *Dacryomycetopsis* is not known.
14. Cyphelloid fructifications have been evolved convergently in many *Asco-* and *Basidiomycetes*. However, they do not occur in the *Tulasnellales*. Nevertheless, the character is very weak and must be considered a doubtful apomorphy.
15. Also clavarioid fructifications are most often convergently evolved structures. They occur in many monophyletic groups within the *Basidiomycetes*. In contrast, no clavarioid species are known from the *Tulasnellales*.
16. Fasciculate marginal hairs are unique for *Dacryopinax* within the *Dacrymycetales*. They do not occur in species of the outgroup.
17. Swollen terminal cells of hair-like hyphae, covering sterile surfaces of fruitbodies occur in many unrelated taxa of asco- and basidiomycetes. There is no doubt that hyphae of this type have evolved quite often independently. Such "hairs" are also known from several species of the genus *Dacrymyces* s.l. These species were excluded from the evaluation.
18. Heterogeneous hyphal systems occur in many distinct monophyla, however not in the *Tulasnellales*. Ingroup taxa are not studied sufficiently to clarify which heterogeneous hyphal systems are homologous or not and which eventually could be proved as apomorphies. For the selected taxa presented here, the apomorphic condition seems to be justified, thus supporting proposals to unite *Ditiola* and *Femsjonia*.
19. *Calocera viscosa* has a special type of heterogeneous hyphal arrangement in 3 zones which appears to be quite distinct from that of *Ditiola* and *Femsjonia*. Because it is not known in other genera, it is considered as a proved apomorphy, and a good distinguishing feature from *Corynoides* and *Dacryonaema*. However, not all clavarioid species of the *Dacrymycetales* are studied to understand the distribution of that character.
20. Stalked-capitate fruitingbodies occur in many diverse hetero- and homobasidiomycetous fungi, as well as in *Ascomycetes*. Even when not

- present in the *Tulasnellales*, the proposed apomorphy is questionable. If possible, it should be replaced by a better one.
21. Thick-walled terminal cells of marginal hairs which are basally swollen and bluntly beaked are certainly a good apomorphy for *Heterotextus*. The question remains whether or not identical structures occur in other taxa of the *Dacrymycetales*. Another question is, whether the narrow genus concept is adequate for practical purposes.
  22. *Guepiniopsis buccina*, the type and only species recognized by McNabb (1965c) can be separated from *Heterotextus* by the multicellular marginal hairs which may have layered cell walls, and by the lack of clamps. There are several species in *Dacrymyces* s.l. which come close to the description of *Guepiniopsis*. These are mainly grouped in subgen. *Turbinaster* of *Dacrymyces* by McNabb (1973). He transferred *Guepiniopsis minuta* (Olive 1954) in *Dacrymyces*. On the other hand, Brasfield (1938) placed *Dacrymyces chrysocomus* in *Guepiniopsis*, a taxonomic conclusion which was accepted also by Reid (1974), and which seems to be much more in accordance with a natural classification than a lumping in a broadly conceived *Dacrymyces*. Even *D. palmatus* shares the principal generic characteristics of *Guepiniopsis*, and not those of *Dacrymyces* s.str. It must be admitted, however, that in this case an intergrading series also links a variety of species in which a clear cut generic hiatus is difficult or even impossible to be detected. As mentioned above, species of *Dacrymyces* s.l. have not been included in the data evaluation for the cladogram.
  23. Rooting bases occur in dacrymycetaceous species, except those of the genus *Cerinomyces*. Often, these structures are inconspicuous and therefore easily to be overlooked. Only in species of two genera, *Calocera* and *Ditiola*, rooting bases are prominent and good features for recognizing species. The function of an elongated, hidden stalk certainly is to use differently decayed wood in deeper layers. *Calocera viscosa* has the special type of heterogeneous hyphal arrangement in 3 zones (19) not only in the basidiocarp itself, but also in the very conspicuous rooting base, which therefore is quite distinct from that of *Ditiola*.
  24. The whitish surfaces of the stipes and the sterile surfaces of the cups is due to a special kind of marginal, thick-walled and rough hyphae. It is likely that they are similar in the 3 recognized species of the genus *Femsjonina*. However, detailed comparison is lacking. Such structures causing a unique outer appearance are not known from other taxa of the order. Therefore, the feature appears to be a good apomorphy.

25. Globose heads of stalked fructifications, covered with hymenia, are found in several unrelated hetero- and homobasidiomycetous taxa, and also in the *Ascomycetes*, but it is lacking in the outgroup and in all other taxa of the ingroup, thus being unique for *Dacryonaema rufum* within the *Dacrymycetales*. Therefore, it can be accepted as an apomorphy, even when its status is questionable on a broader scale of comparisons.
26. Dendroid hairs on the stipe surface which are strongly agglutinated, are only known from *Dacryonaema rufum* in the order. I am not aware of other heterobasidiomycetous species with similar features. Certainly, we are dealing here with a good apomorphy, defining *Dacryonaema* as a unique genus.
27. Short cylindrical heads with folded or morcheloid hymenia are only known in *Corynoides* within the *Dacrymycetales*. But it might be difficult to separate such hymenia clearly from some, occurring in *Dacrymyces* s.l. Additional studies are needed to clarify the problem.

#### Key to genera

The genera discussed above are included in the key. Not only generic types are considered. *Dacryomycetopsis* is not dealt with by other workers. *Dacrymyces* s.str. is also not accepted in other investigations. Therefore *Dacrymyces* s.ampl. should be used when species identification is intended.

#### Basidiocarps resupinate.

- Fructification fully adnate; margin irregular, not fimbriate: ..... ***Cerinomyces***  
 Fructification centrally attached; margin fimbriate: ..... ***Arrhytidia***

#### Basidiocarps pustulate, cyphelloid, stalked, clavarioid, old sometimes dissolving.

- Fructification clavate to clavarioid or capitate with a definite stalk.  
 Basidiocarp stalked, clavarioid, with a large rooting base: ..... ***Calocera***  
 Basidiocarp stalked-capitate, not conspicuously rooting.  
 Head globose, hard-horny; marginal hyphae of stipe dendroid: ..... ***Dacryonaema***  
 Head subglobose-subcylindrical-morchelloid; marginal hairs simple: .... ***Corynoides***

#### Fructification pustulate, turbinate, cyphelloid, stalked-spathulate to stalked-capitate.

- Basidiocarps pustulate or irregularly lobed:..... ***Dacrymyces* s.ampl.**  
 Arthrosporic conidia present:..... ***Dacrymyces* s.str.**  
 Arthrosporic conidia lacking.  
 Hymenium composed mainly of basidia: ..... ***Dacrymyces* s.l.**  
 Hymenium with basidia and conspicuous dendrohyphidia: ... ***Dacryomycetopsis***

#### Basidiocarps stalked.

- Terminal cells of sterile surfaces conspicuously swollen.  
 With 1-2 swollen terminal cells; those of stipe bottle-shaped: ..... ***Heterotextus***  
 With more than 2 swollen terminal cells, thick walls layered: ..... ***Guepiniopsis***  
 Terminal cells of sterile surfaces not or only slightly enlarged.  
 Hairs composed of thick-walled hyphae in bundles, up to 500 µm: ... ***Dacryopinax***  
 Hairs of bundled hyphae lacking; sterile surfaces some times rough by hyphae.  
 Basidiocarps deeply rooting; spores with 1-3 septa: ..... ***Ditiola***  
 Basidiocarps not or slightly rooting; spores with 3 or more septa: .... ***Femsjonina***



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