Mycoscience (2007) 48:388–394
DOI 10.1007/s10267-007-0378-0

FULL PAPER

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Sequence analyses of the 28S rRNA gene D1/D2 region suggest *Dacrymyces* (Heterobasidiomycetes, Dacrymycetales) is polyphyletic

Received: May 1, 2007 / Accepted: August 15, 2007

Abstract For the purpose of determining phylogenetic relationships within the Dacrymycetales, we conducted molecular phylogenetic analyses based on sequences of the 28S rRNA gene D1/D2 region using neighbor-joining and maximum-likelihood methods. Although the phylogenetic relationships at higher taxonomic levels were not resolved, we obtained some new information about inter- and intrageneric relationships in this order. *Dacrymyces punctiformis* formed a clade with *Cerinomyces* spp., and *D. stillatus*, *D. minor*, *D. chrysospermus*, and *D. subalpinus* constituted a clade with *Guepiniopsis buccina*. These clades and other *Dacrymyces* species were scattered over the Dacrymycetales lineage. The results suggest that *Dacrymyces* is polyphyletic. Our study suggests that basidiocarp morphology has limited taxonomic value at the generic or familial level and that there is a need for a taxonomic reassessment of this order, including a redescription of *Dacrymyces*.

Key words *Dacrymyces* · Dacrymycetales · Molecular phylogenetics · Polyphyletic · 28S rRNA gene

Introduction

Members of the Dacrymycetales (Basidiomycota, Heterobasidiomycetes) are brown-rot fungi and characterized by yellow to orange firm-gelatinous or soft-waxy basidiocarps and forked basidia, except for *Dacrymyces unisporus* (L.S. Olive) K. Wells. The order was composed of the single family Dacrymycetaceae with several genera until Jülich (1981) erected an additional family Cerinomycetaceae to accommodate the genus *Cerinomyces* G.W. Martin that produces resupinate basidiocarps. The order was inferred as monophyletic based on phenetic characters (Oberwinkler 1993; Wells and Bandoni 2001). Previous morphological and molecular studies have suggested that dacrymycetalean fungi are closely related to the Homobasidiomycetes as well as the Tulasnellales and Ceratobasidiales heterobasidiomycetous fungi (Lowy 1968; Weiß and Oberwinkler 2001; Weiß et al. 2004). Therefore, we estimate that the order occupies an important position in studying the phylogeny of Homobasidiomycetes.

Traditionally, generic classification in this order has been mainly based on morphological characters of basidiocarps such as shape, presence, or absence of a specialized cortex and internal hyphal texture (McNabb and Talbot 1973). Oberwinkler (1993) discussed the generic concept in Dacrymycetales based on many morphological characters. However, phylogenetic relationships among genera within this order have not been resolved. In general, to study this problem molecular phylogenetic techniques will be useful, but the number of species used for molecular phylogenetic analyses are still limited (Weiß and Oberwinkler 2001; Weiß et al. 2004).

In this study, phylogenetic relationships within the Dacrymycetales were analyzed using molecular phylogenetic methods. We sequenced the 28S rRNA gene D1/D2 region of 37 newly isolated dacrymycetalean strains and analyzed them with 13 sequences obtained from Genbank.

Materials and methods

Collection and culture establishment

All 37 Japanese dacrymycetalean strains used in this study are listed in Table 1. Fungal fruit bodies were collected with part of the substratum, air-dried in the laboratory, and stored at room temperature. When examined in the laboratory, a portion of the fruit body was soaked into distilled water. Fully hydrated fruit bodies were sectioned with a freezing microtome (RUB-2100, MC-802A; Yamato Kohki, Saitama, Japan). Sections were placed on a microscopic slide and mounted in Neo-Shigaral (Shiga Konchu

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Table 1. List of sequenced strains in this study

Species	Specimen no.[a]	Shape of basidiocarps	Locality	Substrae[b]	Reference	TNS no.[c]	MAFF no.[d]	DDBJ accession no.
Calocera cornea	HNo. 267	Clavate	Mt. Shirami, Wakayama	B	McNabb (1965a)	TNS-F-15701	MAFF240116	AB299068
Calocera cornea	HNo. 358	Clavate	Mt. Daimonji, Kyoto	C	McNabb (1965a)	TNS-F-15702	MAFF240117	AB299076
Calocera cornea	HNo. 376	Clavate	Takaraga-ike, Kyoto	B	McNabb (1965a)	TNS-F-15703	MAFF240118	AB299077
Calocera viscosa	HNo. 175	Dendroid	Sugadairakougen, Nagano	C	McNabb (1965a)	TNS-F-15704	MAFF240119	AB299048
Calocera viscosa	HNo. 466	Dendroid	Chichibu, Saitama	C	McNabb (1965a)	TNS-F-15705	MAFF240120	AB299082
Cerinomyces albosporus	HNo. 191	Resupinate	Mt. Daimonji, Kyoto	C	Boidin and Gilles (1986)	TNS-F-15706	MAFF240121	AB299050
Dacrymyces capitatus	HNo. 182	Turbinate or cushion	Mt. Daimonji, Kyoto	C	McNabb (1973)	TNS-F-15707	MAFF240122	AB299049
Dacrymyces capitatus	HNo. 192	Turbinate or cushion	Mt. Daimonji, Kyoto	C	McNabb (1973)	TNS-F-15708	MAFF240123	AB299051
Dacrymyces capitatus	HNo. 212	Turbinate or cushion	Takaraga-ike, Kyoto	B	McNabb (1973)	TNS-F-15709	MAFF240124	AB299055
Dacrymyces capitatus	HNo. 222	Turbinate or cushion	Kasuga shrine, Nara	B	McNabb (1973)	TNS-F-15710	MAFF240125	AB299058
Dacrymyces chrysospermus	HNo. 215	Turbinate or brain	Midoroga-ike, Kyoto	B	McNabb (1973)	TNS-F-15711	MAFF240126	AB299057
Dacrymyces chrysospermus	HNo. 320	Turbinate or brain	Sugadairakougen, Nagano	C	McNabb (1973)	TNS-F-15712	MAFF240127	AB299073
Dacrymyces chrysospermus	HNo. 468	Turbinate or brain	Sugadairakougen, Nagano	C	McNabb (1973)	TNS-F-15713	MAFF240128	AB299083
Dacrymyces chrysospermus	HNo. 486	Turbinate or brain	Kijimadaira, Nagano	B	McNabb (1973)	TNS-F-15714	MAFF240129	AB299084
Dacrymyces lacrymalis	HNo. 209	Cushion, sessile	Takaraga-ike, Kyoto	B	McNabb (1973)	TNS-F-15716	MAFF240131	AB299053
Dacrymyces lacrymalis	HNo. 235	Cushion, sessile	Oodaigahara, Nara	B	McNabb (1973)	TNS-F-15717	MAFF240132	AB299062
Dacrymyces lacrymalis	HNo. 261	Cushion, sessile	Mt. Tamaki, Nara	B	McNabb (1973)	TNS-F-15718	MAFF240133	AB299066
Dacrymyces lacrymalis	HNo. 281	Cushion, sessile	Sugadairakougen, Nagano	B	McNabb (1973)	TNS-F-15719	MAFF240134	AB299069
Dacrymyces minor	HNo. 224	Cushion, sessile	Mt. Kasuga, Nara	W	McNabb (1973)	TNS-F-15720	MAFF240135	AB299059
Dacrymyces minor	HNo. 237	Cushion, sessile	Kasuga shrine, Nara	C	McNabb (1973)	TNS-F-15721	MAFF240136	AB299063
Dacrymyces minutus	HNo. 282	Turbinate or disc	Sugadairakougen, Nagano	C	McNabb (1973)	TNS-F-15722	MAFF240137	AB299070
Dacrymyces punctiformis	HNo. 196	Cushion, sessile	Mt. Daimonji, Kyoto	C	Reid (1974)	TNS-F-15723	MAFF240138	AB299052
Dacrymyces punctiformis	HNo. 213	Cushion, sessile	Takaraga-ike, Kyoto	B	Reid (1974)	TNS-F-15724	MAFF240139	AB299056
Dacrymyces punctiformis	HNo. 285	Cushion, sessile	Shioda, Nagano	C	Reid (1974)	TNS-F-15725	MAFF240140	AB299071
Dacrymyces san-augustinii	HNo. 441	Cushion, sessile	Mt. Shirami, Wakayama	W	Kobayasi (1939)	TNS-F-15726	MAFF240141	AB299081
Dacrymyces stillatus	HNo. 233	Cushion, sessile	Kasuga shrine, Nara	C	McNabb (1973)	TNS-F-15727	MAFF240142	AB299061
Dacrymyces stillatus	HNo. 256	Cushion, sessile	Mt. Tamaki, Nara	C	McNabb (1973)	TNS-F-15728	MAFF240144	AB299065
Dacrymyces stillatus (anamorph)	HNo. 252	Cushion, sessile	Mt. Tamaki, Nara	B	McNabb (1973)	TNS-F-15729	MAFF240143	AB299064
Dacrymyces subalpinus	HNo. 228	Turbinate or brain	Mt. Kasuga, Nara	C	Kobayasi (1939)	TNS-F-15730	MAFF240145	AB299060
Dacrymyces unisporus	HNo. 332	Cushion, sessile	Sugadairakougen, Nagano	C	Olive (1944)	TNS-F-15731	MAFF240146	AB299074
Dacrymyces variisporus	HNo. 263	Turbinate or disc	Mt. Tamaki, Nara	C	McNabb (1973)	TNS-F-15732	MAFF240147	AB299067
Dacrymyces variisporus	HNo. 300	Turbinate or disc	Sugadairakougen, Nagano	C	McNabb (1973)	TNS-F-15733	MAFF240148	AB299072
Dacrymyces variisporus	HNo. 352	Turbinate or disc	Mt. Daimonji, Kyoto	C	McNabb (1973)	TNS-F-15734	MAFF240149	AB299075
Dacryopinax spathularia	HNo. 379	Spathulate, stipitate	Midoroga-ike, Kyoto	C	McNabb (1965b)	TNS-F-15735	MAFF240150	AB299078
Dacryopinax spathularia	HNo. 398	Spathulate, stipitate	Kasuga shrine, Nara	C	McNabb (1965b)	TNS-F-15736	MAFF240151	AB299079
Femsjonia pezizaeformis	HNo. 439	Turbinate or disc	Sugadairakougen, Nagano	C	McNabb (1965d)	TNS-F-15737	MAFF240152	AB299080
Guepiniopsis buccina	HNo. 562	Cup, stipitate	Mt. Tamaki, Nara	B	McNabb (1965c)	TNS-F-15738	MAFF240153	AB299085

[a] Private collection number of T. Shirouzu
[b] C, B, and W represent conifer, broadleaf tree, and woody plant, respectively
[c] Herbarium of the National Museum of Nature and Science (TNS)
[d] Culture collection of National Institute of Agrobiological Sciences (MAFF)

Hukyu-sya, Tokyo, Japan). Prepared slides were observed under an optical microscope in detail and specimens were identified to species based on the descriptions of Kobayasi (1939), Olive (1944), McNabb (1965a–d, 1973), Reid (1974), and Boidin and Gilles (1986). All specimens examined in this study were deposited in the herbarium of the National Museum of Nature and Science (TNS), Tsukuba, Ibaraki, Japan.

Pure cultures were established by a single spore isolation. All strains treated in this study were deposited in MAFF Genebank, National Institute of Agrobiological Sciences, Tsukuba, Ibaraki, Japan.

Molecular techniques, alignment, and phylogenetic analyses

DNA was extracted from mycelia of the dacrymycetalean strains cultured on 2.5% malt extract liquid medium following the modified CTAB method described by Matsuda and Hijii (1999). The 28S rRNA gene D1/D2 region was amplified with primers D1 (Peterson 2000) and NL4 (O'Donnell 1993). Polymerase chain reactions (PCR) were performed using a HotStarTaq Master Mix (Qiagen, Mississauga, Canada). Each PCR tube contained a 50-µl mixture (21 µl distilled water, 25 µl master mix, 3 µl template DNA, and 0.5 µl each primer; final, 0.25 µM). Amplification of each DNA fragment was performed using a PCR thermal cycler (Eppendorf Mastercycler Gradient; Eppendorf, Hamburg, Germany). The thermal cycling schedule was as follows: the first cycle consisted of 15 min at 94°C, followed by 45 cycles of 30 s at 94°C, 30 s at 58°C for annealing, 1 min at 72°C, and the final cycle of 10 min at 72°C. The reaction mixture was then cooled at 4°C for 5 min. PCR products were purified with a QiAquick PCR Purification Kit (Qiagen, Ontario, Canada).

Sequencing reactions were performed using a BigDye Terminator Cycle Sequencing FS Ready Reaction Kit (PE Applied Biosystems, Foster City, CA, USA) and a Eppendorf Mastercycler Gradient according to the manufacturer's instructions. Sequencing reaction products were purified with a DyeEx Spin Kit (Qiagen, Mississauga, Canada), and directly sequenced using an ABI PRISM 377-18 DNA Sequencing System (Applied Biosystems, Foster City, CA, USA). The sequences determined in this study were deposited in the DNA Data Bank of Japan (DDBJ). Their accession numbers are shown in Table 1.

In addition to the sequences we generated, a total of 11 sequences accessed from GenBank belonging to Dacrymycetales were included in the phylogenetic analysis (Table 2). *Auricularia mesenterica* and *Myxarium nucleatum* were used as the outgroup (Table 2).

Preliminary multiple alignments of sequences were conducted using Clustal W version 1.71 (Thompson et al. 1994). Final alignments were manually adjusted. Alignment gaps were treated as missing data, and ambiguous positions were excluded from the analysis. Both neighbor-joining (NJ) (Saitou and Nei 1987) and maximum-likelihood (ML) analyses were carried out using PAUP* 4.0b8 (Swofford 2000). NJ trees were constructed with the HKY 85 model (Hasegawa et al. 1985). ML analysis was performed with the HKY85 +Γ model of nucleotide substitution (Hasegawa et al. 1985). To estimate clade support, the bootstrap procedure of Felsenstein (1985) was employed with 1000 replicates in NJ analyses and 100 replicates in the ML analysis.

Results and discussion

Molecular phylogenetic trees obtained by the methods of NJ and ML are shown in Figs. 1 and 2, respectively. Both methods inferred typologically concordant phylogenetic trees.

High bootstrap values supported a *Cerinomyces albosporus* Boidin & Gilles-*C. crustulinus* (Bourdot & Galzin) G.W. Martin-*Dacrymyces punctiformis* Neuhoff clade, a *Calocera cornea* (Batch) Fr.-*C. viscosa* (Pers.) Fr. clade, a *D. stillatus* Nees-*D. minor* Peck clade, and some other clades such as *D. capitatus* Schwein., *D. lacrymalis* (Pers.) Sommerf., *D. punctiformis*, *D. variisporus* McNabb, *Dacryopinax spathularia* (Schwein.) G.W. Martin, and *Guepiniopsis buccina* (Pers.) L.L. Kenn. (NJ > 90%; ML > 80%). However, except for the branch supporting the Dacrymycetales clade (NJ 77%; ML 88%), phylogenetic relationships

Table 2. List of sequence data from other studies

Species	Locality	References	GenBank accession no.
Auricularia mesenterica	Germany	Weiß and Oberwinkler (2001)	AF291292
Calocera cornea	Germany	Weiß and Oberwinkler (2001)	AF291302
Calocera viscosa	Unknown	Begerow et al. (1997)	AF011569
Cerinomyces crustlinus	Taiwan	Kirschner and Yang (2005)	AY600248
Cerinomyces crustlinus	Norway	Larsson et al. (2004)	AY586643
Dacrymyces chrysospermus	Unknown	Hibbett et al. (2000)	AF287855
Dacrymyces stillatus	Germany	Weiß and Oberwinkler (2001)	AF291309
Dacryomitra pusilla	Germany	Weiß and Oberwinkler (2001)	AF291311
Dacryopinax spathularia	Taiwan	Weiß and Oberwinkler (2001)	AF291312
Ditiola haasii	Germany	Weiß and Oberwinkler (2001)	AF291314
Femsjonia pezizaeformis	Germany	Weiß and Oberwinkler (2001)	AF291330
Guepiniopsis buccina	Germany	Weiß and Oberwinkler (2001)	AF291332
Myxarium nucleatum	Portugal	Weiß and Oberwinkler (2001)	AF291351

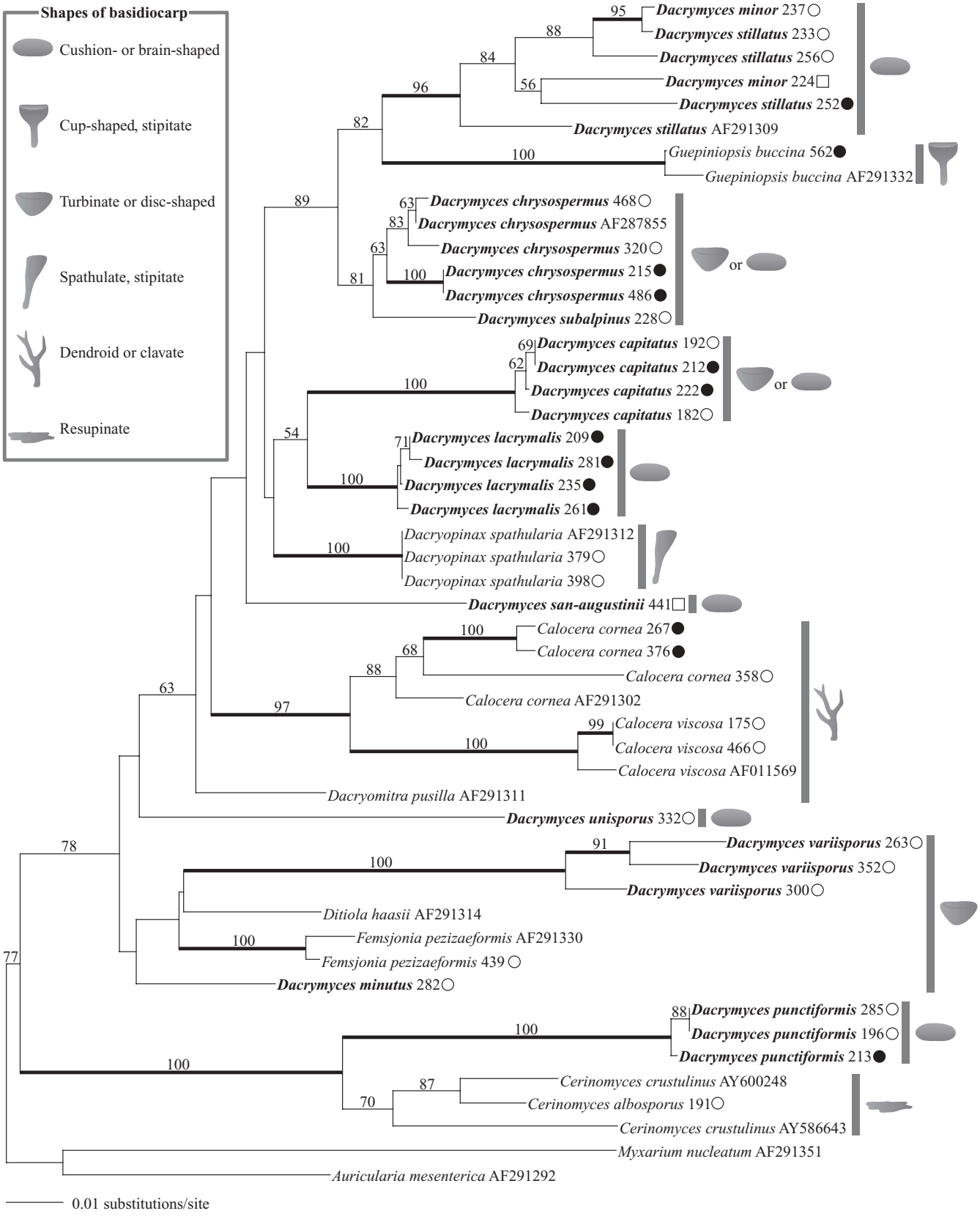

Fig. 1. Neighbor-joining tree constructed based on analysis of the D1/D2 region 28S rRNA gene sequences. The topology was rooted with two Auriculariales, *Auricularia mesenterica* and *Myxarium nucleatum*. *Numbers on branches* are bootstrap values. Species of *Dacrymyces* are shown in *bold type*. The symbols ○, ●, and □ indicate conifer, broadleaf tree, and woody plant as the substrate, respectively

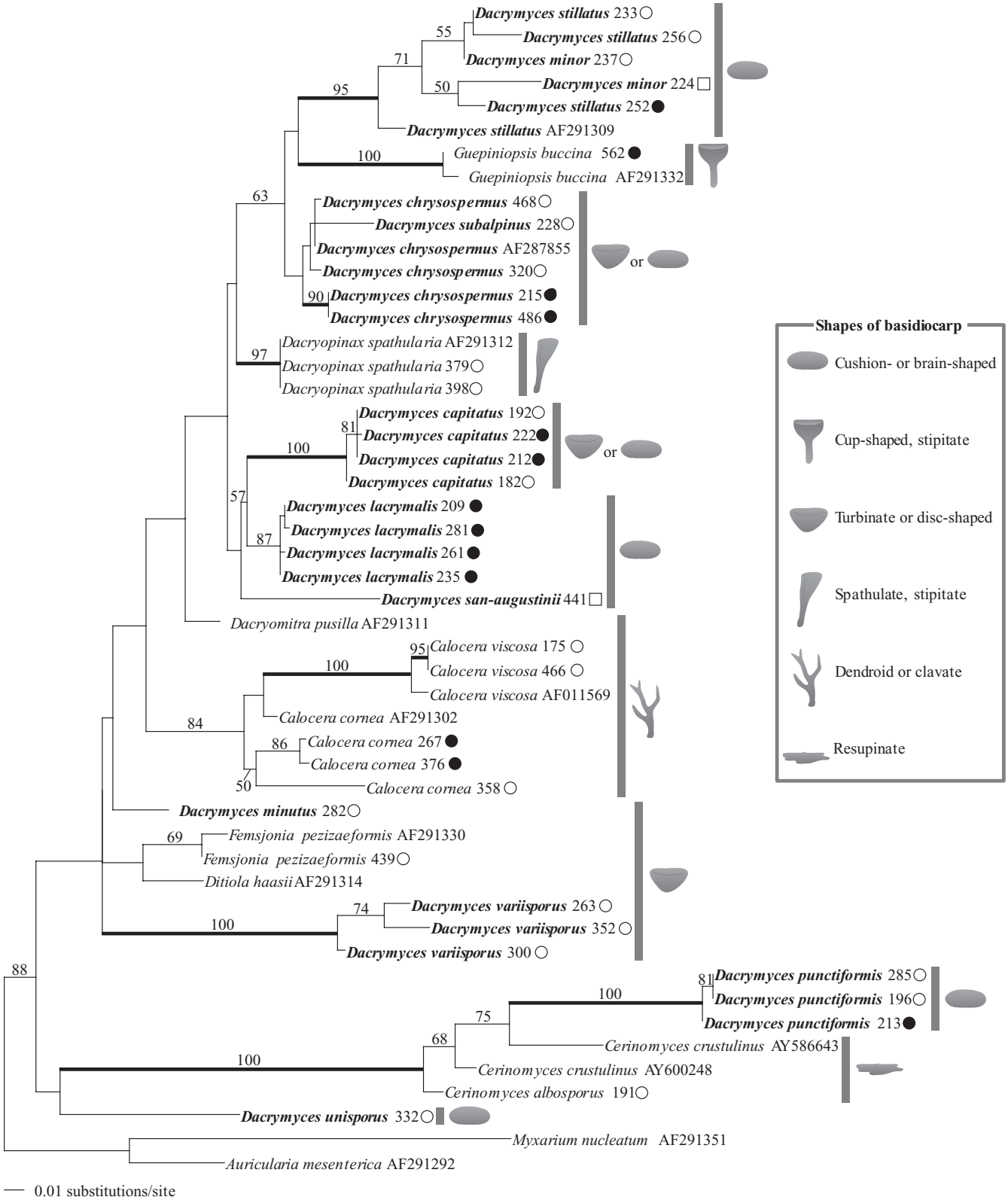

Fig. 2. Maximum-likelihood tree constructed based on analyses of the D1/D2 region 28S rRNA gene sequences. The topology was rooted with two Auriculariales, *Auricularia mesenterica* and *Myxarium nucleatum*. *Numbers on branches* are bootstrap values. Species of *Dacrymyces* are shown in *bold type*. The symbols ○, ●, and □ indicate conifer, broadleaf tree, and woody plant as the substrate, respectively

at high hierarchal levels were unresolved, particularly in the ML tree. To obtain a more robust phylogenetic hypothesis, additional molecular markers and more strains need to be analyzed.

The range of dacrymycetalean species used in previous molecular phylogenetic studies was insufficient (Weiß and Oberwinkler 2001; Weiß et al. 2004), so that phylogenetic relationships within this order are still unresolved. However, we obtained some new information on phylogenetic relationships in this order by analyses using more dacrymycetalean taxa as follows.

Species of the genera *Ditiola* Fr. and *Femsjonia* Fr. have been confused because of their morphological similarities (Reid 1974; Oberwinkler 1993), and the genus *Femsjonia* was synonymyzed under *Ditiola* because of the possession of heterogeneous hyphal construction in common (Reid 1974). Weiß and Oberwinkler (2001) suggested the affinity of *Ditiola haasii* Oberw. and *Femsjonia pezizaeformis* (Lèv.) P. Karst. based on analyses of 28S rRNA D1/D2 region sequences. In our results, *D. haasii* and *F. pezizaeformis* were included in the same clade, but with poor bootstrap support. The monophyly of two *Calocera* (Fr.) Fr. species was supported (NJ 97%; ML 84%), as shown by Weiß and Oberwinkler (2001).

Guepiniopsis buccina, the type species of the genus *Guepiniopsis*, formed a clade with *D. stillatus*, *D. minor*, *D. chrysospermus* Berk. & M.A. Curtis, and *D. subalpinus* Kobayasi (NJ 89%; ML 63%). This result suggests that *G. buccina*, which is characterized by stipitate cup-shaped basidiocarps and palisaded marginal hyphae on the sterile basidiocarp surface composed of swollen catenulate cells, was derived from a *Dacrymyces* Nees-like ancestor with turbinate or brain- or cushion-shaped basidiocarps and an unspecialized marginal hyphae. Reid (1974) pointed out the artificial separation of the genus *Dacrymyces* and *Guepiniopsis* Pat. by the presence or absence of a cortical layer composed of palisaded marginal hyphae on the sterile surface of the basidiocarps. To resolve the phylogenetic position of the genus *Guepiniopsis*, molecular analyses using more species of *Guepiniopsis* will be useful.

Dacrymyces species were dispersed widely over the Dacrymycetales lineage. *Dacrymyces punctiformis* formed a clade with two *Cerinomyces* species (NJ 100%; ML 100%), although these two genera are distinguished mainly based on quite different shapes of the basidiocarps. Namely, the genus *Dacrymyces* is characterized by cushion-shaped basidiocarps and *Cerinomyces* is defined by resupinate basidiocarps. The result causes doubt as to the validity of the Cerinomycetaceae, and it suggests the necessity to reconsider the traditional taxonomic system in which the shape of the basidiocarp is treated as the main taxonomic criterion at the generic or familial level.

Dacrymyces unisporus, an exceptional Dacrymycetales species with nonforked basidia, was first described as *Platygloea unispora* (Urediniomycetes; Olive 1944), and it was transferred to *Dacrymyces* by Wells (1994). This morphologically unique species was located within the Dacrymycetales clade, supporting the taxonomic treatment by Wells (1994).

Although the bootstrap support was not high, *D. capitatus* and *D. lacrymalis* were resolved as a clade (NJ 54%; ML 57%). These two species share common morphological characters such as comparatively small basidiocarps, thin-walled 3-septate basidiospores, and the absence of clamp-connections.

Dacrymyces subalpinus comprised a clade with *D. chrysospermus* (NJ 81%). These two species share some morphological characters such as turbinate or brain-shaped basidiocarps, many-septate basidiospores, and the absence of clamp-connections. In the *Dacrymyces stillatus-D. minor* clade (NJ 96%; ML 95%), these two species were paraphyletic. We distinguished these species based on the diameter of basidiocarps and basidiospore wall thickness according to the description of McNabb (1973), but these measurements often overlapped such that the limits of these two species were unclear. Although McNabb (1973) described the presence of an arthroconidial stage in *D. stillatus* that separates it from *D. minor*, *D. minor* also has fragmenting hyphae (Oberwinkler 1993). In addition, many "*D. stillatus*" specimens collected by us lacked an arthroconidial stage. Given the nonmonophyly of these two species, our molecular analyses suggest that their species limits should be reconsidered.

Detailed phylogenetic relationships of other *Dacrymyces* species, *D. san-augustinii* Kobayasi, *D. minutus* (L.S. Olive) McNabb, and *D. unisporus*, were poorly resolved but these species were also nested in the Dacrymycetales clade. Some previous taxonomic studies have pointed out the ambiguous definition of the genus *Dacrymyces*, which was mainly characterized by forming cushion- or turbine-shaped, mostly sessile and homogeneous basidiocarps (McNabb 1973; Reid 1974). As shown in Figs. 1 and 2, species of *Dacrymyces* spanned the breadth of the phylogeny, suggesting that *Dacrymyces* may be polyphyletic.

As already mentioned, the traditional concepts of Dacrymycetales systematics based on basidiocarp morphology appears to be unreliable in defining genera and families. Especially, the cushion-shaped basidiocarps, as a main character of the genus *Dacrymyces*, were observed in all dacrymycetalean genera as an initial developing stage in fruit-body formation. Therefore, cushion-shaped basidiocarps are produced by phylogenetically diverse dacrymycetalean fungi. It is a subsequent problem that taxonomic revaluation of the morphological phenotype such as basidiocarp morphology be used as an important feature at generic or familial level classification.

In the phylogenetic trees, the dacrymycetalean strains that were isolated from broadleaf trees showed a tendency to occupy derived positions in the phylogeny compared with those from conifers (detailed data are not shown, but refer to Table 1 and Figs. 1, 2). Additionally, some inter- or intraspecific subclades composed of strains that occurred on the same wood type were resolved in the *D. stillatus-D. minor* clade, *D. chrysospermus-D. subalpinus* clade, and *C. cornea* clade. In future studies, we will examine ecological properties such as substrate specificity of the dacrymycetalean fungi using the phylogeny to better understand their evolutionary diversification.

Acknowledgments We thank Prof. Tetsuo Hashimoto, Graduate School of Life and Environmental Science, University of Tsukuba, for useful advice concerning the molecular phylogenetic analyses. We also thank Mr. Masateru Hakariya, Sugadaira Montane Research Center, University of Tsukuba, for helping with construction of the molecular phylogenetic trees, and Ms. Yukiko Takahashi, Graduate School of Agricultural and Life Sciences, The University of Tokyo, for sending specimens.

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