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Dacryoscyphus chrysochilus, a new staurosporous anamorph with cupulate conidiomata from China and with affinities to the Dacrymycetales (Basidiomycota)

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Abstract

An anamorphic fungus forming laterally attached, cupulate, gelatinous, hyaline to white conidiomata with a golden yellow rim producing 2–4-armed stauroconidia from monoblastic conidiogenous cells was collected on dead twigs of *Rhododendron* sp. in southwestern China. Ultrastructure of the septal pore and comparative analysis of the 5′ region of the nuclear large subunit of the ribosomal RNA gene sequence revealed a phylogenetic relationship with members of the Dacrymycetales. Morphological studies and comparison with similar anamorphic fungi indicate the novelty of the taxon, and a new genus and species *Dacryoscyphus chrysochilus* is proposed.

Introduction

Fungi of the order Dacrymycetales are defined by the gelatinous, bright yellow or orange sporomata of most species and the typical basidium with two sterigmata (Oberwinkler 1994). The yellow pigmentation is caused by the presence of carotenoids (Gill and Steglich 1987). Seen with transmission electron microscopy (TEM), septa of the hyphae exhibit dolipores associated with continuous parenthesomes (Oberwinkler 1994; Wells 1994). Additionally, basidiospores become septate after liberation from the basidia and produce minute, one-celled conidia on short denticulate outgrowths of the basidiospores. Hyphae growing out from basidiospores also develop denticulate outgrowths producing conidia. These anamorphs are found in species of several genera of the Dacrymycetales: *Cerinomyces* G.W. Martin (Figure 1), *Dacrymyces* Nees, *Ditiola* Fr., and *Femsjonia* Fr. (Ingold 1983; Maekawa 1987; de Hoog 1993; Oberwinkler 1994). Because of the morphological similarity with members of the genus *Sporothrix* Hektoen and C.F. Perkins, dacrymycetaceous anamorphs were previously assigned to this genus. After recognizing the basidiomycetous nature of these dacrymycetaceous anamorphs, the genus *Cerinosterus* R.T. Moore was proposed to segregate these anamorphs from the remaining *Sporothrix* anamorphs with affinities to the Ascomycota (de Hoog 1993). Sporodochia with arthroconidia occur regularly in the life-cycle of *Dacrymyces stillatus* Nees and perhaps in other species of *Dacrymyces* (Oberwinkler 1994). Apart from this anamorph and the *Cerinosterus* stages, other anamorphs were rarely reported as having affinities

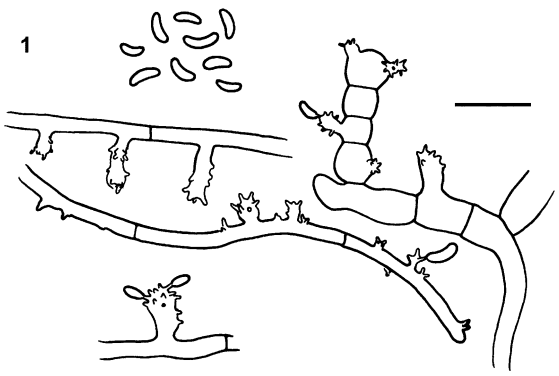


Figure 1. *Cerinosterus*-like anamorph of *Cerinomyces crustulinus* in culture. Conidiophores and conidia. Scale bar: 10 μm.

to the Dacrymycetales. Massee (1890) proposed the genus *Dacryopsis* in order to accommodate species similar to *Dacrymyces* but being accompanied by a *Tubercularia* s.l. anamorph with pleurogenous, one-celled conidia. The nature of this associated anamorph was hitherto not clarified and *Dacryopsis* was considered as a synonym of *Ditiola* (McNabb 1966). *Dacrymycella aurantiaca* D.A. Reid forming orange, gelatinous sporodochia with one-celled conidia was considered as having affinities to the Dacrymycetales based on morphology (Reid 1969). This connection, however, has not yet been confirmed.

In the high mountains of southwestern China, we found gelatinous sporomata with a bright yellow rim. Consistency and colour of these sporomata were reminiscent of species of the Dacrymycetales and Tremellales. Microscopic investigations, however, revealed that the sporomata were asexual and produced septate, branched conidia. These and further findings suggested the description of a new genus and a new species for this fungus and its connection with the Dacrymycetales.

Materials and methods

Conidiomata of the new anamorphic fungus were found on dead twigs of *Rhododendron* sp. still attached to the plants in a forest dominated by species of *Abies* Mill. and *Rhododendron* L., Laojunshan, 3400–3800 m, Jianchuan, Yunnan, China, 26.–28.VII.2001, R. Kirschner et al. 868, 920, and 944 (deposited at the herbarium of the Kunming Institute of Botany, Academia Sinica, China, KUN F45015, KUN F45016, and KUN F45014, respectively), and on rotten bark or wood without bark in a forest dominated by species of *Abies* and *Rhododendron*, Daxueshan, 4060 m, Xiangcheng, Sichuan, China, 24.VII.1998, Z.L. Yang 2421 (KUN F32002). The fungus was not cultivated. For light microscopy, material was mounted in 5–10% KOH with or without staining with 1% aqueous phloxine. Measurements of 30 conidia are given as extreme values in brackets and means ± SD.

To investigate the ultrastructure of the hyphal septa of the anamorphic fungus, TEM was conducted as described in Kirschner et al. (2001a).

A basidioma of *Cerinomyces crustulinus* (Bourdot and Galzin) G.W. Martin was collected on a rotting branch of *Pinus luchuensis* Mayr lying on the ground in Peitou, Taipei, Taiwan, 17.VII.1999, R. Kirschner 542 (deposited at the herbarium of the National Museum of Natural Science Taichung, Taiwan, TNM). A basidioma of *Colacogloea peniophorae* (Bourdot and Galzin) Oberw., R. Bauer and Bandoni was collected on rotting wood of *Pinus sylvestris* L., Morgenstelle, Tübingen, Baden-Württemberg, Germany, 05.VI.1998, R. Kirschner 370 (deposited at the herbarium of the Senckenberg Institute Frankfurt, Germany, FR). In order to obtain cultures arising from germinating basidiospores discharged from the basidioma, a portion of the basidioma was fixed beneath a lid of a Petri dish containing 2% malt extract agar. A culture of *Ce. crustulinus* was deposited in the culture collection of the Botanical Institute, University of Tübingen, Germany; a culture of *Co. peniophorae* was not preserved.

For isolation, amplification, and sequencing of nuclear DNA cultures of *Ce. crustulinus* and *Co. peniophorae* were used as described in Kirschner et al. (2001b). Herbarium material of the anamorphic fungus (R. Kirschner et al. 944) was used for isolating DNA using the PeqLab E.Z.N.A.® Fungal DNA kit, and for PCR as mentioned above. PCR products were purified using the PeqLab E.Z.N.A.® Cycle-Pure kit. Sequencing of dsDNA was done by SRD (Oberursel, Germany). An alignment was produced with MEGALIGN of the Lasergene package (DNASTAR, Inc. 1997) using partial DNA sequences of the gene coding for the nuclear large RNA subunit deposited in GenBank (accession numbers listed in Table 1).

Table 1. GenBank accession numbers of species used in the phylogenetic analyses.

Species	Voucher specimen[a]	GenBank accession no.[b]
Amanita citrina (Schaeff.) Pers.		AF041547
Auricularia auricula-judae (Fr.) J. Schröt.		AF291289
Calocera cornea (Batsch) Fr.		AF291302
Cerinomyces crustulinus (Bourdot and Galzin) G.W. Martin	R. Kirschner 542 (TNM)	AY600248
Colacogloea peniophorae (Bourdot and Galzin) Oberw., R. Bauer and Bandoni	R. Kirschner 370 (FR)	AY604566
Cuniculitrema polymorpha R. Kirschner and J.P. Samp.		AY032662
Dacrymyces stillatus Nees		AF291309
Dacrymyces variisporus McNabb		AF291310
Dacryomitra pusilla Tul. and C. Tul.		AF291311
Dacryopinax spathularia (Schwein.) G.W. Martin		AF291312
Dacryoscyphus chrysochilus R. Kirschner and Zhu L. Yang	R. Kirschner et al. 944 (KUN)	AY604567
Ditiola haasii Oberw.		AF291314
Ditiola peziziformis (Lév.) D.A. Reid		AF291330
Exidia saccharina Fr.		AF291323
Guepiniopsis buccina (Pers.) L.L. Kenn.		AF291332
Polyporus varius (Pers.) Fr.		AF291356
Tremella flava Chee J. Chen		AF042238

[a]FR, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; KUN, Kunming Institute of Botany, Yunnan; TNM, National Museum of Natural Sciences, Taichung, Taiwan.
[b]AF041547, AF042238, and AY032662 were from Hopple and Vilgalys (1999), Chen (1998), and Kirschner et al. (2001b), respectively; data with accession number 'AF29' initial were from Weiß and Oberwinkler (2001); the other numbers were obtained in this study.

The PHYLIP package, version 3.5 c (Felsenstein 1993) was used to perform a neighbour-joining analysis (Kimura two-parameter distances, transition/transversion ratio 2.0), followed by a bootstrap analysis with 1000 replicates. PAUP 4.0b10 (Swofford 2003) was used for maximum parsimony analysis with heuristic search, TBR branch swapping with the 'MulTree' option in effect, deepest descent option not in effect, gaps treated as missing, also combined with bootstrapping with 500 replicates with the same parameters. *Co. peniophorae* was chosen as outgroup. Besides Dacrymycetales and Auriculariales (with continuous parenthesomes), other important basidiomycetous groups with perforate parenthesomes (*Amanita* Pers., *Polyporus* Fr.), with cupulate parenthesomes (*Cuniculitrema* J.P. Sampaio and R. Kirschner), and simple pored Urediniomycetes (*Colacogloea* Oberw. and Bandoni) are represented.

Results

Dacryoscyphus R. Kirschner and Zhu L. Yang, gen. nov.

Genus hyphomycetum. Conidiomata cupulata, gelatinosa, stipite laterali minuto, hyalina vel colorata. Cellulae conidiogenae in parte apicali aggregatae, terminales vel intercalares, monoblasticae. Conidia applanata, septata, ex cellula basali et brachiis composita, hyalina vel pallide colorata.

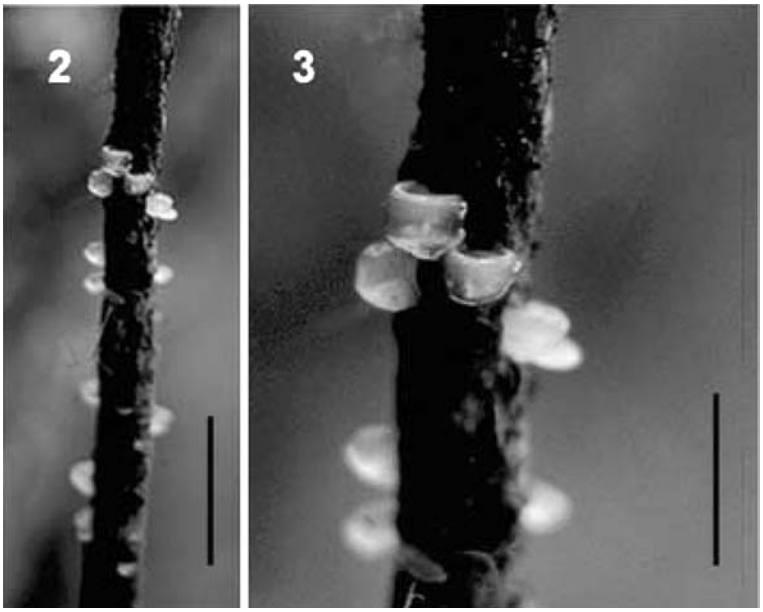
Typus generis: *Dacryoscyphus chrysochilus* R. Kirschner and Zhu L. Yang, in opero ipso descriptus.

Etymology: Greek, latinized, Dacryo- from dacryon-tear, referring to the dacrymycetaceous relationship, scyphus from scyphos-cup.

Conidiomata cupulate, gelatinous, attached to the substratum with a minute lateral stipe, hyaline or coloured. Conidiogenous cells aggregated in the upper surface of the conidiomata, terminal or intercalary, monoblastic. Conidia plane, septate, composed of a basal cell carrying branches, hyaline or pale.

Dacryoscyphus chrysochilus R. Kirschner and Zhu L. Yang, sp. nov. (Figures 2–5)

Conidiomata cupulata, gelatinosa, stipite laterali minuto, usque 0.5 mm longo et 1 mm diameter, cupulae 2–5 mm lata, 1.5–3 mm longa, 1.5–3 mm alta, hyalina pro parte majore, superficie partis superioris concava margine lunata aurata. Hyphae hyalinae, tenuitunicatae, laeves, septis sine fibulis,



Figures 2 and 3. Dacryoscyphus chrysochilus. Photographs of conidiomata in the natural orientation on dead twigs in the field (R. Kirschner et al. 920, paratypus). Scale bar: (2) 20 mm (3) 10 mm.

1–3 μm diameter. Conidiophora irregulariter aggregata in margine lunata, irregulariter ramosa. Conidia laevia, applanata, a cellulis conidiogenis lateralibus vel terminalibus monoblasticis oriunda, ex cellula basali 5–7(–8) × 2–5.5 μm et 2–4 brachiis 1–6-septatis (18–)24–34 × 4–6 μm composita, appendicibus terminalibus divergentibus 3–20 × 1 μm, omnino (30–)34–40(–42) μm longa.

Holotypus: China, Yunnan Prov.: Jianchuan, Laojunshan, 3800 m, in a forest dominated by species of *Abies* and *Rhododendron*, on dead twigs of *Rhododendron* sp. still attached to the plant, 28.VII.2001, R. Kirschner et al. 944 (KUN F45014).

Paratypi: China, Sichuan Prov.: Xiangcheng, Daxueshan, 4060 m, in a forest dominated by species of *Abies* and *Rhododendron*, on rotten bark or wood without bark, 24.VII.1998, Z.L. Yang 2421 (KUN F32002), Yunnan Prov.: Jianchuan, Laojunshan, 3400–3800 m, in a forest dominated by species of *Abies* and *Rhododendron*, on dead twigs of *Rhododendron* sp. still attached to the plants, 26.VII.2001, R. Kirschner et al. 868 (FR, KUN F45015), 27.VII.2001, R. Kirschner et al. 920 (KUN F45016).

Etymology: Greek, latinized, chryso- from chrysos – golden, chilus from cheilos – lip, *D. chrysochilus* – 'golden-lipped tear-cup'.

Conidiomata gelatinous when wet, cupulate, laterally attached to the substratum with a short stalk up to 0.5 mm long, 1 mm in diameter and composed of dense hyphae (Figures 2–4a). Root-like structures extending from the stalk into the substratum not found. Upper surface of the conidiomata slightly concave, in many cases wider than long when seen from above, cupulae 2–5 mm wide, 1.5–3 mm long and 1.5–3 mm thick with a semicircular or crescent-shaped golden yellow rim where conidia are produced, lower part hyaline or whitish, composed of gelatinized, loosely interwoven hyphae (Figure 4b). Conidiomata forming an inconspicuous, thin, pale yellow layer when dry. Hyphae uniform throughout the conidioma, hyaline, thin-walled, smooth, unclamped, 1–3 μm diameter. Conidiophores irregularly arranged in the yellow rim, irregularly branched (Figure 4c). Conidium production monoblastic, lateral or terminal. First a clavate cell separates from the conidiophore. This cell is divided by a transversal septum resulting in a basal cell becoming the stalk cell of the mature conidium, 5–7(–8) μm long and 2–3 μm wide at the base, 4–5.5 μm wide at the apex, and an apical cell becoming the main arm of the conidium by additional growth and

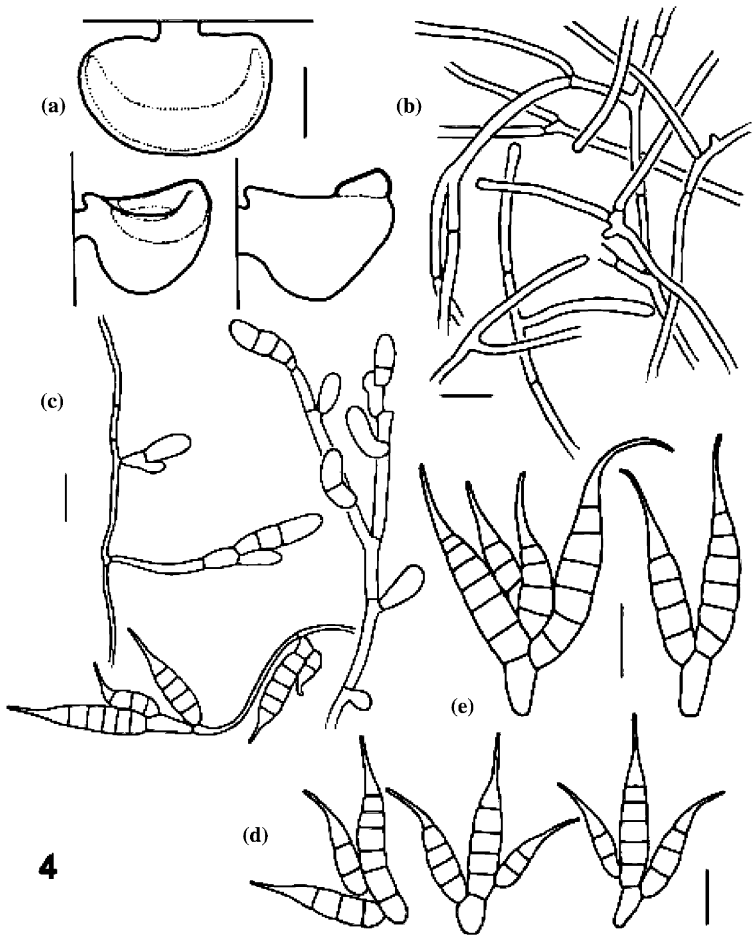


Figure 4. *Dacryoscyphus chrysochilus*. Drawings of characteristics of the holotype. (a) Habit sketches of conidiomata, the upper one seen from above, the lower left from the side, the lower right in a median section, with the yellow area indicated by a dotted line. Scale bar: 2 mm. (b) Hyphal structure in the centre of the conidioma. Scale bar: 10 μm. (c) Conidiophores with developing conidia. Scale bar: 10 μm. (d) Conidia with three arms. Scale bar: 10 μm. (e) Conidia with two arms (right) and four arms (left). Scale bar: 10 μm.

septation. The second arm develops from an outgrowth of the basal cell, additional 1–2 arms usually arise from the first and second basal cells of the main arm. Arms divergent or appressed to each other at the base and distally divergent, obclavate, with 1–6 transversal septa, (18–)24–34 μm long (including appendage) and 4–6 μm wide at the broadest part, with a terminal, straight or slightly curved filamentous appendage 3–20 $\times$ 1 μm. Mature conidia hyaline when seen singly with the light microscope, but in mass forming a yellow zone in the conidioma, smooth, in most cases composed of a stalk cell and 2–4 (mostly 3) arms arranged in a plane, total length of the conidia (30–)34–40(–42) μm (Figures 4d and e).

As seen by TEM, the hyphal septa are perforated by dolipores with continuous parenthesomes (Figure 5).

In the neighbour-joining analysis (Figure 6), the new taxon is placed within a group formed by the genera *Calocera* (Fr.) Fr., *Cerinomyces*, *Dacrymyces*, *Dacryomitra* Tul. and C. Tul., *Dacryopinax* G.W. Martin, *Ditiola*, and *Guepiniopsis* Pat., with a support of 90%. *D. chrysochilus* belongs to a group of fungi which is distinct from the cluster formed by *Ditiola haasii* and *Ditiola peziziformis*. However, the position within this core clade of Dacrymycetales is not resolved. The same topologies were obtained with the maximum parsimony analysis (not shown), but with lower bootstrap values and without clustering the *Ditiola* species in a single clade.

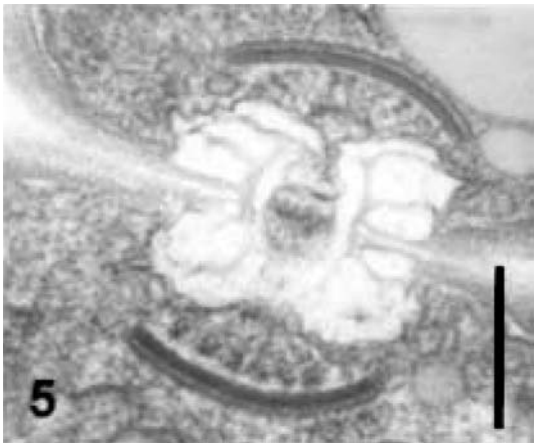


Figure 5. *Dacryoscyphus chrysochilus*. Median section through a dolipore of a hyphal septum with continuous parenthesomes seen with TEM. Scale bar: 0.25 μm.

Discussion

The gelatinous consistency, the bright yellow pigmentation of parts of the conidiomata, and the presence of dolipores with continuous parenthesomes in the hyphal septa suggest a phylogenetic affinity of the new taxon *D. chrysochilus* to the Dacrymycetales. A gelatinous consistency and carotenoids are known in basidiomata of species of *Calocera* and *Dacrymyces* (Dacrymycetales) as well as of *Tremella* Pers. (Tremellales) and cannot be used to separate these orders (Valadon 1976; Gill and Steglich 1987). The presence of carotenoids is merely assumed to be present in the new taxon because of the bright yellow pigmentation, but has not yet been proven. Parenthesomes of the dolipores, however, differ in members of the Dacrymycetales and Tremellales (Wells 1994). In species of the Dacrymycetales, parenthesomes are continuous, whereas they are not continuous in species of the Tremellales. However, continuous parenthesomes are also present in members of a few other orders of the Basidiomycota.

The grouping of the new taxon among the taxa used as representatives of the Dacrymycetales is supported by the molecular phylogenetic analysis (Figure 6). The topology of these taxa is similar to that found by Weiß and Oberwinkler (2001). On the generic level, a particularly close relationship of the newly described anamorph to a certain teleomorph is not supported. The anamorph appears, however, not to be closely related to the species of *Ditiola* used in the analysis.

The conidia are similar to branched cortical or marginal hairs described from basidiomata of several members of the Dacrymycetales, e.g. species of *Dacrymyces*, *Dacryopinax*, and *Guepiniopsis* (McNabb 1965a, b, 1973). Hairs are considered as potential phylogenetic markers for supraspecific taxa by Oberwinkler (1994). Both authors of the present contribution independently from each other found conidiomata with conidia in two different provinces of China. There were no sporomata morphologically intermediate between *D. chrysochilus* and mature basidiomata of species of Dacrymycetales, e.g. of *Dacrymyces* sp. and *Guepiniopsis* sp., also found in the same areas (R. Kirschner, Z.L. Yang, personal observations). The conidia might, nevertheless, be homologous to these hairs, and conidiomata might be able to turn into basidiomata at a later stage of development.

The conidia of *D. chrysochilus* differ from the sympodially produced one-celled conidia and from the arthroconidia hitherto known in members of the Dacrymycetales as well as from the one-celled conidia of species assumed as anamorphs with affinities to the Dacrymycetales by some authors. Whereas the *Cerinosterus*-like anamorphs are mostly known from culture and do not produce conidiomata, *Dacrymycella aurantiaca* is known from the field. In this species, one-celled conidia are produced from denticles of conidiogenous cells within orange, gelatinous, pustulate conidiomata (Reid 1969). These characteristics and the morphology of hyphal endings at the sterile surface of the conidiomata indicate a relationship to the Dacrymycetales (Reid 1969), but this hypothesis should be confirmed by additional studies.

Anamorphic taxa with soft or gelatinous conidiomata were previously described as species of *Dacrymyces* and subsequently assigned to other genera: e.g. *Agyriella nitida* (Lib.) Sacc., *Ditangium cerasi* (Tul.) Cost. and L. Duf. (anamorph of *Craterocolla cerasi* (Tul.) Bref.), *Hainesia lythri* (Desm.) Höhn., *Linodochium hyalinum* (Lib.) Höhn., and *Pseudocenangium succineum* (Sprée) Dyko and B. Sutton (McNabb 1973; Dyko and Sutton 1979). These species, however produce unbranched conidia.

The conidia of *D. chrysochilus* might be described as cheiroid or chiroid, or as digitate,

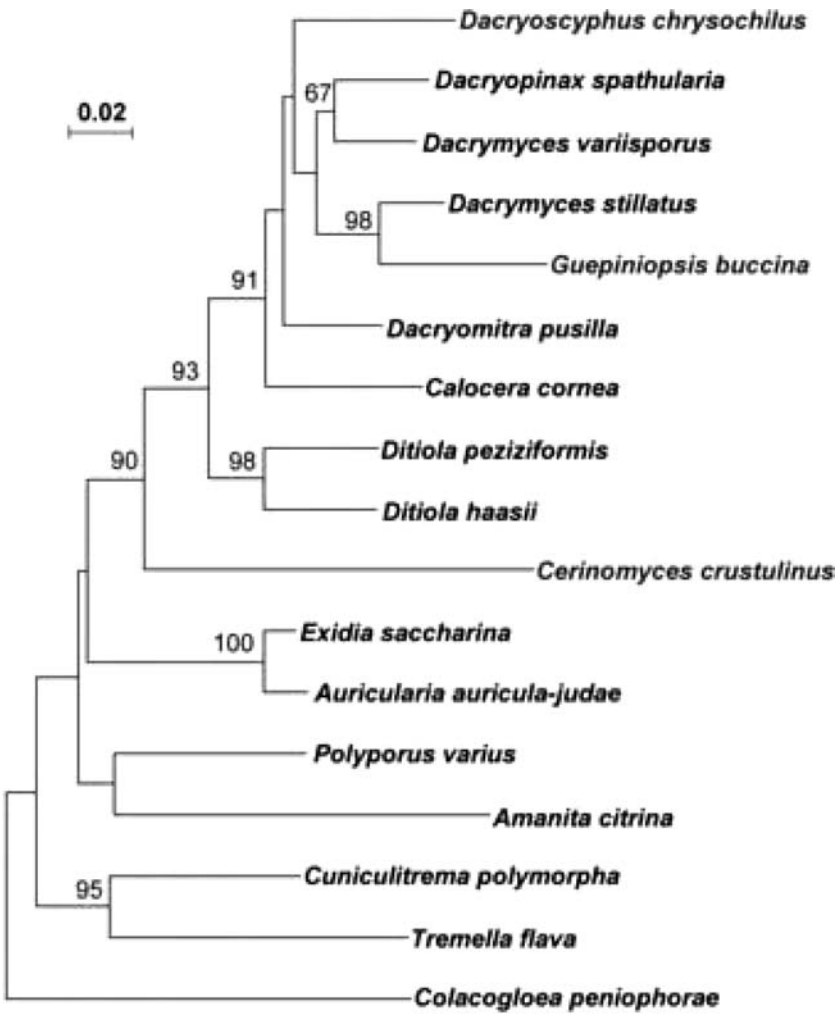


Figure 6. Phylogenetic hypothesis derived from neighbour-joining analysis of partial nuclear large subunit ribosomal RNA gene sequences of *D. chrysochilus* and other species of Basidiomycota. The topology is rooted with *Co. peniophorae*. Bootstrap values are given as numbers (in percentages) on branches based on 1000 replicates. Branch lengths are scaled in terms of expected numbers of nucleotide differences per site.

because they are formed like hands with fingers in some cases appressed together at the base. A key to chirosporous genera was proposed by Ho et al. (2000), but does not include a genus like *Dacryoscyphus*. As a more general term, 'staurospores' (branched conidia), can be applied to the morphology of the conidia of *D. chrysochilus*.

Cruciger lignatilis R. Kirschner and Oberw. and *Digitodochium rhodoleucum* Tubaki and Kubono are terrestrial hyphomycetes that produce staurospores in light-coloured sporodochia on woody branches in nature (Tubaki and Kubono 1989; Kirschner and Oberwinkler 1999), but differ by non-cupulate conidiomata and non-cheiroid conidial structure.

The conidial morphology of *D. chrysochilus* is superficially similar to that of some species of 'Ingoldian fungi', like species of *Dendrospora* Ingold, *Flabellospora* Ingold, *Quadricladium* Nawawi and Kuthub., and *Triscelophorus* Ingold (Ingold 1975; Marvanová 1997). Ingoldian fungi are aquatic or terrestrial hyphomycetes sporulating below the water surface and in culture need to be submerged in water to induce sporulation (Ingold 1975; Ando and Tubaki 1984; Mavanová 1997). Most species produce hyaline staurospores with a

three-dimensional arrangement of the conidial arms, e.g. in species of the genera mentioned above. In *Flabellospora* species and many other staurosporous hyphomycetes from water, all conidial arms arise from a single cell of the conidium (Ingold 1975; Santos-Flores and Betancourt-López 1997). In *D. chrysochilus*, however, conidia are yellow in mass, have a two-dimensional arrangement of arms that often arise from different cells of a given conidium. In many aquatic hyphomycetes conidiophores are only known from culture. Culturing might induce abnormal growth or reduction of conidiomata, especially when conventional media are used. Since natural media are used in most studies about fungi from water, conidiomata are known in cultures of species of several genera and are used for defining taxa of aquatic fungi, e.g. in *Fibulotaeniella* Marvanová and Bärlocher, *Filosporella* Nawawi, *Heliscus* Sacc. and Therry, and *Nodulispora* ('*Nodulospora*') Marvanová and Bärlocher (Marvanová 1980, 1997; Marvanová and Bärlocher 1988, 2000). In addition to differing conidial morphology, conidiomata also provide reliable characteristics for separating *D. chrysochilus* from Ingoldian fungi.

Dacryoscyphus can also be excluded from certain staurosporous coelomycetes. Consulting the monograph of coelomycetes with appendaged conidia by Nag Raj (1993), we did not find any similar genus that could fit the characteristics of *Dacryoscyphus*. The coelomycetous genus *Crucellisporiopsis* Nag Raj includes species with superficially similar, gelatinous and yellow conidiomata, but differs in essential microscopic details like the presence of stromata, annellidic conidiogenous cells, and originating of lateral conidial arms from a common basal cell of the conidia, whereas stromata are absent in *D. chrysochilus*, conidiogenous cells are monoblastic, and lateral conidial arms often arise from other conidial arms.

Cupulate conidiomata are produced by certain lichens and named campylidia by lichenologists. In several species of lichens, the campylidia are brightly coloured or produce septate, branched conidia (Vězda 1986). The campylidia, however, are always connected with a lichen thallus which is absent in *D. chrysochilus*. The functions of these conidiogenous structures might nevertheless be similar. In *D. chrysochilus*, the conidiogenous area is exposed in the concave upper surface of the cupulate conidioma which is functional only after soaking with water during rain. Conidia are, therefore, assumed to be dispersed by rain water. Conidia might be successively dispersed by raindrops splashing onto the concave surface or filling and overflowing this shallow cavity.

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References

Ando K. and Tubaki K. 1984. Some undescribed hyphomycetes in the rain drops from intact leaf-surface. Trans. Mycol. Soc. Japan 25: 21–37.

Chen C.-J. 1998. Morphological and molecular studies in the genus *Tremella*. Bibl. Mycol. 174: 1–225.

Dyko B.J. and Sutton B.C. 1979. A revision of *Linodochium*, *Pseudocenangium*, *Septopatella*, and *Siroscyphella*. Can. J. Bot. 57: 370–385.

Felsenstein J. 1993. PHYLIP (Phylogeny Inference Package), version 3.5c. Distributed by the author. Department of Genetics, University of Washington, Seattle.

Gill M. and Steglich W. 1987. Pigments of fungi (Macromycetes). Progr. Chem. Organ. Nat. Prod. 51: 1–317.

Ho W.-H., Hodgkiss I.J. and Hyde K.D. 2000. *Cheiromyces lignicola*, a new chirosporous anamorphic species from Hong Kong. Mycologia 92: 582–588.

de Hoog G.S. 1993. *Sporothrix*-like anamorphs of *Ophiostoma* species and other fungi. In: Wingfield M.J., Seifert K.A. and Webber J.F. (eds), *Ceratocystis* and *Ophiostoma*. APS Press, St. Paul, Minnesota, pp. 53–60.

Hopple J.S. and Vilgalys R. 1999. Phylogenetic relationships in the mushroom genus *Coprinus* and dark-spored allies based on sequence data from the nuclear gene coding for the large ribosomal subunit RNA: divergent domains, outgroups, and monophyly. Mol. Phylogenet. Evol. 13: 1–19.

Ingold C.T. 1975. An Illustrated Guide to Aquatic Hyphomycetes. Freshwater Biological Association Scientific Publication No. 30. pp. 1–96.

Ingold C.T. 1983. Basidiospore germination and conidium development in Dacrymycetales. Trans. Br. Mycol. Soc. 81: 563–571.

Kirschner R. and Oberwinkler F. 1999. A new basidiomycetous anamorph genus with cruciform conidia. Mycoscience 40: 345–348.

Kirschner R., Bauer R. and Oberwinkler F. 2001a. *Colacosiphon*: a new genus described for a mycoparasitic fungus. Mycologia 93: 634–644.

Kirschner R., Sampaio J.P., Gadanho M., Weiß M. and Oberwinkler F. 2001b. *Cuniculitrema polymorpha* (Tremellales, gen. nov. and sp. nov.), a heterobasidiomycete vectored by bark beetles, which is the teleomorph of *Sterigmatosporidium polymorphum*. Antonie van Leeuwenhoek 80: 149–161.

Maekawa N. 1987. A new species of the genus *Cerinomyces*. Can. J. Bot. 65: 583–588.

Marvanová L. 1980. New or noteworthy aquatic hyphomycetes. Trans. Br. Mycol. Soc. 75: 221–231.

Marvanová L. 1997. Freshwater hyphomycetes: a survey with remarks on tropical taxa. In: Janardhanan K.K., Rajendran C., Natarajan K. and Hawksworth D.L. (eds), Tropical Mycology. Science Publishers Inc., Enfield, New Hampshire, pp. 169–226.

Marvanová L. and Bärlocher F. 1988. Hyphomycetes from Canadian streams. I. Basidiomycetous anamorphs. Mycotaxon 32: 339–351.

Marvanová L. and Bärlocher F. 2000. Hyphomycetes from Canadian streams. V. Two new conidial basidiomycetes. Mycotaxon 75: 409–423.

Massee G. 1890. Mycological notes II. J. Mycol. 6: 178–184, plate 7.

McNabb R.F.R. 1965a. Taxonomic studies in the Dacrymycetaceae II. *Calocera* (Fries) Fries. N. Z. J. Bot. 3: 31–58.

McNabb R.F.R. 1965b. Taxonomic studies in the Dacrymycetaceae VI. *Femsjonia* Nees ex Fries. N. Z. J. Bot. 3: 223–228.

McNabb R.F.R. 1966. Taxonomic studies on the Dacrymycetaceae VII. *Ditiola* Fries. N. Z. J. Bot. 4: 546–558.

McNabb R.F.R. 1973. Taxonomic studies in the Dacrymycetaceae VIII. *Dacrymyces* Nees ex Fries. N. Z. J. Bot. 11: 461–524.

Nag Raj T.R. 1993. Coelomycetous Anamorphs with Appendage-Bearing Conidia. Mycologue Publications, Waterloo, Ontario, Canada.

Oberwinkler F. 1994. Genera in monophyletic groups: The Dacrymycetales. Mycol. Helvet. 6: 35–72.

Reid D.A. 1969 [1968]. Spring fungi in Corsica. Revue Mycol. 33: 341–368.

Santos-Flores C.J. and Betancourt-López C. 1997. Aquatic and water-borne hyphomycetes (Deuteromycotina) in streams of Puerto Rico (including records from other neotropical locations). Caribbean J. Sci. Special Publication, 2: 1–166.

Swofford D.L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), version 4. Sinauer Associates, Sunderland, Massachusetts.

Tubaki K. and Kubono T. 1989. *Digitodochium*, a new staurosporous anamorph genus. Sydowia 41: 344–348.

Valadon L.R.G. 1976. Carotenoids as additional taxonomic characters in fungi: a review. Trans. Br. Mycol. Soc. 67: 1–15.

Vězda A. 1986. Neue Gattungen der Familie Lecideaceae s. lat. (Lichenes). Folia Geobot. Phytotax. 21: 199–219.

Weiß M. and Oberwinkler F. 2001. Phylogenetic relationships in Auriculariales and related groups – hypotheses derived from nuclear ribosomal DNA sequences. Mycol. Res. 105: 403–415.

Wells K. 1994. Jelly fungi, then and now! Mycologia 86: 18–48.