A polyphasic taxonomy of Daldinia (Xylariaceae)

Stadler, Marc; Læsøe, Thomas; Fournier, Jacques; Decock, Cony; Schmieschek, Beata; Tichy, Hans-Volker; Peršoh, Derek

Published in:
Studies in Mycology

DOI:
10.3114/sim0016

Publication date:
2014

Document Version
Publisher's PDF, also known as Version of record

Citation for published version (APA):
A polyphasic taxonomy of Daldinia (Xylariaceae)1

Marc Stadler*, Thomas Lasserre2, Jacques Fournier3, Cory Decock4, Beata Schmieszek5, Hans-Volker Tichy6, Derek Peršoh7,8

1Helmholtz Centre for Infection Research, Dept. Microbial Drugs, Infloffenstrasse 7, D-38124 Braunschweig, Germany; 2University of Copenhagen, Department of Biology/Natural History Museum of Denmark, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark; 3Las Muros, F-09420, Rimont, France; 4Mycthèque du Monastère de Lourains (MUCL, BCCM®); Earth and Life Institute - Microbiology (ELM), Université catholique de Louvain, Croix du Sud 2 bte 17.05.06.B-1346, Louvain-la-Neuve, Belgium; 5LUPA ITL GmbH, Dr.-Helm-Str. 6, D-24107 Kiel, Germany; 6Bayer Pharma AG, Product Supply, API - Supply Center Eberfeld Quality Unit - OCB-Mikrobiologie 1, 42096 Wuppertal, Germany; 7University of Bayreuth, Dept. Mycology, Universitätstrasse 30, D-95540 Bayreuth, Germany; 8Present address: Ruhr-Universität Bochum, AG Geobotanik, Universitätstrasse 150, D-44780 Bochum, Germany

*Correspondence: Marc Stadler, marc.stadler@helmholtz-hzi.de

Abstract: For a monograph based on a polythetic concept, several thousands of herbarium specimens, and several hundreds of freshly collected and cultured specimens of Daldinia and allied Xylariaceae, originating from around the world, were studied for morphological traits, including by SEM, and chemically by HPLC profiles using UV-visible and mass spectrometric detection. Emphasis was given to tropical material, and importantly, ancient specimens, including as many types as possible, were tracked and studied to review earlier taxonomic concepts. An apophyta of D. eschscholtzii was selected as representative of the monothecate type that is most widely distributed in the tropics. Six new species of Daldinia from the tropics and the southern Hemisphere are described. Daldinia asphalatum is resurrected, and D. nemorosa is resurrected, and Daldinia asphalatum, D. caldariorum, and D. starbaeckii are proposed, and many new synonymies in Daldinia are conserved against earlier synonyms. The species concept is based mainly on morphological and chemotaxonomic evidence. In the rDNA based phylogenetic tree, 5.8S/ITS nrDNA including numerous representatives of all hitherto described taxa for which cultures are extant, was found basically in agreement with the above mentioned segregation of the genus, based on phenotypic characteristics. Some unnamed but aberrant specimens were not found in good condition and are therefore not formally described as new species. However, they are illustrated in detail in a hope that this will facilitate the discovery of fresh material in future. A preliminary molecular phylogeny based on 5.8S/ITS ndDNA including representatives of all hitherto described taxa for which cultures are extant, was found basically in agreement with the above mentioned segregation of the genus, based on morphological and chemotaxonomic evidence. The rDNA based phylogenetic tree, Daldinia appears clearly distinct from members of the genera Annuclathypoxylon and Hypoxylon; nevertheless, representatives of small genera of predominantly tropical origin (Ennotasema, Phylacia, Ruwenzoria, Rhopalostroma, Thamnomyces) appear to have evolved from daldinioid ancestors and are nested inside the Daldinia clade. Interestingly, these findings correlate with chemotaxonomic characters to a great extent, especially regarding the distribution of marker metabolites in their mycelial cultures. Hence, the current study revealed for the first time that fungal secondary metabolite profiles can have taxonomic value beyond the species rank and even coincide with phylogenetic data.

Keywords: Ascomycota, biodiversity, chemotaxonomy, systematics, Xylariaceae.

Taxonomic novelties: Daldinia andraea sp. nov., D. australis sp. nov., D. hauskechtii sp. nov., D. nehrmi sp. nov., D. starbaecki sp. nov., D. theisseni sp. nov., D. cauchosa comb. nov., D. nemorosa comb. nov.


INTRODUCTION

This paper addresses two major topics: i) a taxonomic revision of the genus Daldinia Ces. & De Not. 1863, and ii) a reassessment of its intergeneric affinities. Recent evidence suggests the need to redefine the genus and its boundaries with related Xylariaceae. Therefore, both the taxonomic history of Daldinia, as well as recent work on the affinities between the Xylariaceae with nodulisporium-like anamorphs are reviewed below, in order to provide the context for this monograph. In addition, some facts about the biology and ecology of Daldinia are summarised. All accepted species of Daldinia are listed in Table 1.

Taxonomic history of Daldinia

The genus Daldinia was erected by the Italian mycologists, Cesati & De Notaris (1863) in honour of the Swiss monk, Agostino Daldini, to separate pyrenomycetes with conspicuous stromata and horizontally zonate stromatal interior from the internally azonate, predominantly effused-pulvinate forms of Hypoxylon. The type species, D. concentrica (basionym Sphaeria concentrica) as well as the genus, are now conserved against earlier synonyms. The conspicuous, persistent stromata develop on woody plants and may at times occur in masses. Therefore, they can hardly be overlooked as easily as other xylariaceous fungi. Hence, humankind possibly knew them since the early stages of civilisation.

The first historical record of a Daldinia sp. dates back to the British botanist Ray (1868), who described a “Fungus fraxineus, niger, durus, orbiculatus “ (Fries 1823). The Tyrolian physician and naturalist, Giovanni Antonio Scopoli, who maintained close contact to Linneaus, proposed the first binomial of what is regarded a Daldinia today i.e., Valsa tuberosa Scop. (Scopoli 1772). In the 18th and 19th century, many pyrenomycetes were eventually

Dedicated to Dr Hartmund Wollweber, Wuppertal, Germany, who has been instrumental in helping us in the initial stage of our studies of Daldinia.
Table 1. List of taxa in *Daldinia* that are accepted in the present study, with authorities, year of publication, and corresponding MycoBank Acc. Nos. Details can be found on the MycoBank and Index Fungorum websites. Taxa newly erected in this study are printed in **bold**.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>MycoBank No.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Daldinia albofibrosa</em> M. Stadler, M. Baumgartner &amp; Wollw. 2001 (p. 57)</td>
<td>MB474115</td>
</tr>
<tr>
<td><em>Daldinia albozonata</em> Lloyd 1919 (p. 59)</td>
<td>MB141379</td>
</tr>
<tr>
<td><strong>Daldinia andina</strong> Læssøe, J. Fourn. &amp; M. Stadler 2014 (p. 33)</td>
<td>MB800022</td>
</tr>
<tr>
<td><em>Daldinia asphalatum</em> (Link ex Fr.) Sacc. 1882 (p. 106)</td>
<td>MB247095</td>
</tr>
<tr>
<td><em>Daldinia australis</em> J. Fourn. &amp; M. Stadler 2014 (p. 78)</td>
<td>MB563696</td>
</tr>
<tr>
<td><em>Daldinia bakeri</em> Lloyd 1919 (p. 88)</td>
<td>MB246639</td>
</tr>
<tr>
<td><em>Daldinia bambusicola</em> Y.M. Ju, J.D. Rogers &amp; F. San Martin 1997 (p. 60)</td>
<td>MB436494</td>
</tr>
<tr>
<td><em>Daldinia barkalovi</em> Lar.N. Vassiljeva &amp; M. Stadler 2008 (p. 110)</td>
<td>MB511595</td>
</tr>
<tr>
<td><em>Daldinia brachysperma</em> F. San Martín, Y.M. Ju &amp; J.D. Rogers 1997 (p. 60)</td>
<td>MB436495</td>
</tr>
<tr>
<td><strong>Daldinia cahuchucosa</strong> (Whalley &amp; Watling) M. Stadler &amp; Læssøe 2014 (p. 90)</td>
<td>MB807746</td>
</tr>
<tr>
<td><em>Daldinia caldariorum</em> Henn. 1898 (p. 61)</td>
<td>MB247207</td>
</tr>
<tr>
<td><em>Daldinia carpinicola</em> Lar.N. Vassiljeva &amp; M. Stadler 2008 (p. 111)</td>
<td>MB511594</td>
</tr>
<tr>
<td><em>Daldinia childiae</em> J.D. Rogers &amp; Y.M. Ju 1999 (p. 74)</td>
<td>MB460536</td>
</tr>
<tr>
<td><em>Daldinia clavata</em> Henn. 1902 (p. 65)</td>
<td>MB247027</td>
</tr>
<tr>
<td><em>Daldinia concentrica</em> (Bolton) Ces. &amp; De Not. 1863 (p. 28)</td>
<td>MB146158</td>
</tr>
<tr>
<td><em>Daldinia cuprea</em> Starbäck 1901 (p. 67)</td>
<td>MB146524</td>
</tr>
<tr>
<td><em>Daldinia decipiens</em> Wollw. &amp; M. Stadler 2001 (p. 111)</td>
<td>MB474112</td>
</tr>
<tr>
<td><em>Daldinia dennisii</em> var. <em>dennisii</em> 2004 (p. 35)</td>
<td>MB482296</td>
</tr>
<tr>
<td><em>Daldinia dennisii</em> var. <em>microspora</em> Wollw. &amp; M. Stadler 2004 (p. 35)</td>
<td>MB488679</td>
</tr>
<tr>
<td><em>Daldinia eschscholtzii</em> (Ehrenb.) Rehm 1904 (p. 49)</td>
<td>MB146911</td>
</tr>
<tr>
<td><em>Daldinia gelatinoides</em> Lar.N. Vassiljeva 1998 (p. 92)</td>
<td>MB450312</td>
</tr>
<tr>
<td><em>Daldinia gelatinosa</em> Y.M. Ju, J.D. Rogers &amp; F. San Martin 1997 (p. 113)</td>
<td>MB436496</td>
</tr>
<tr>
<td><em>Daldinia govorovae</em> Lar.N. Vassiljeva &amp; M. Stadler 2008 (p. 115)</td>
<td>MB511596</td>
</tr>
<tr>
<td><em>Daldinia graminis</em> Dargan &amp; K.S. Thind 1985 (p. 121)</td>
<td>MB128584</td>
</tr>
<tr>
<td><em>Daldinia grandis</em> Child 1932 (p. 93)</td>
<td>MB239743</td>
</tr>
<tr>
<td><strong>Daldinia hausknechtii</strong> J. Fourn. &amp; M. Stadler 2014 (p. 95)</td>
<td>MB488678</td>
</tr>
<tr>
<td><em>Daldinia illoydi</em> Y.M. Ju, J.D. Rogers &amp; F. San Martin 1997 (p. 116)</td>
<td>MB436497</td>
</tr>
<tr>
<td><em>Daldinia loculata</em> (Lév.) Sacc. 1882 (p. 97)</td>
<td>MB239483</td>
</tr>
<tr>
<td><em>Daldinia loculataoides</em> Wollw. &amp; M. Stadler 2004 (p. 99)</td>
<td>MB488678</td>
</tr>
<tr>
<td><em>Daldinia macaronesica</em> M. Stadler, Wollw. &amp; J.M. Castro 2004 (p. 38)</td>
<td>MB488619</td>
</tr>
<tr>
<td><em>Daldinia macrospora</em> F. San Martin, Y.M. Ju &amp; J.D. Rogers 1997 (p. 118)</td>
<td>MB436498</td>
</tr>
<tr>
<td><em>Daldinia martini</em> M. Stadler, Venturella &amp; Wollw. 2004 (p. 38)</td>
<td>MB489539</td>
</tr>
<tr>
<td><em>Daldinia mexicana</em> F. San Martin, Y.M. Ju &amp; J.D. Rogers 1997 (p. 119)</td>
<td>MB436499</td>
</tr>
<tr>
<td><strong>Daldinia nemorosa</strong> (M. L. Davey) M. Stadler, J. Fourn. &amp; Læssøe 2014 (p. 100)</td>
<td>MB800145</td>
</tr>
<tr>
<td><em>Daldinia novae-zelandiae</em> Wollw. &amp; M. Stadler 2004 (p. 101)</td>
<td>MB522267</td>
</tr>
<tr>
<td><em>Daldinia palmenis</em> M. Stadler, Wollw. &amp; Tichy 2004 (p. 40)</td>
<td>MB488618</td>
</tr>
<tr>
<td><em>Daldinia petriniae</em> Y.M. Ju, J.D. Rogers &amp; F. San Martin 1997 (p. 103)</td>
<td>MB436500</td>
</tr>
<tr>
<td><em>Daldinia placentiformis</em> (Berk. &amp; M.A. Curtis) Theiss. 1909 (p. 125)</td>
<td>MB438125</td>
</tr>
<tr>
<td><em>Daldinia pyrenaica</em> M. Stadler &amp; Wollw. 2001 (p. 80)</td>
<td>MB474113</td>
</tr>
<tr>
<td><em>Daldinia raimundi</em> M. Stadler, Venturella &amp; Wollw. 2004 (p. 40)</td>
<td>MB489537</td>
</tr>
<tr>
<td><strong>Daldinia rehmi</strong> Læssøe, M. Stadler &amp; J. Fourn. 2014 (p. 69)</td>
<td>MB512370</td>
</tr>
<tr>
<td><em>Daldinia sacchari</em> Dargan &amp; K.S. Thind 1985 (p. 123)</td>
<td>MB128585</td>
</tr>
<tr>
<td><em>Daldinia singularis</em> Y.M. Ju, Lar.N. Vassiljeva &amp; J.D. Rogers 1999 (p. 120)</td>
<td>MB460421</td>
</tr>
<tr>
<td><strong>Daldinia starbaeckii</strong> M. Stadler &amp; Læssøe 2014 (p. 69)</td>
<td>MB512385</td>
</tr>
<tr>
<td><em>Daldinia steiglichii</em> M. Stadler, M. Baumgartner &amp; Wollw. 2001 (p. 82)</td>
<td>MB474114</td>
</tr>
<tr>
<td><strong>Daldinia theissenii</strong> Læssøe, J. Fourn. &amp; M. Stadler 2014 (p. 73)</td>
<td>MB564867</td>
</tr>
<tr>
<td><em>Daldinia vanderguchtae</em> M. Stadler, Wollw. &amp; Briegert 2004 (p. 42)</td>
<td>MB491383</td>
</tr>
<tr>
<td><em>Daldinia vernicosa</em> Ces. &amp; De Not. 1863 (p. 84)</td>
<td>MB249419</td>
</tr>
</tbody>
</table>
accommodated in the genus *Sphaeria*, in which Bolton (1789) erected *Sphaeria concentrica*, based on material from England. *Sphaeria* was reorganised by Persoon (1801), who included *Sphaeria concentrica* in sect. *Peripheriae*. Fries (1823), on the other hand, listed this species in tribe *Pulviniatae*, subgenus *Hypoxylon*, and it was included accordingly in the genus *Hypoxylon* by Greville (1828) as *Hypoxylon concentricum* (Bolton: Fr.) Grev.

When Fries (1849) reorganised the genus *Hypoxylon* Bull., *Sphaeria concentrica* (= *Hypoxylon concentricum*) remained in *Pulviniatae*. Meanwhile, Véellvé (1845) had created tribe *Concentricae* in *Sphaeria* to include, among others, the new species, *S. loculata* and *S. cingulata*, which were later assigned to *Daldinia* by Saccardo (1882). The latter author accepted *Daldinia* as a genus, and, although some authors preferred to continue to refer to it as *Hypoxylon* (cf. Læssøe 1994), the name has been in general use ever since. During the late 19th and early 20th century, *Daldinia* was included in numerous general studies of *Xylariaceae* and other pyrenomycetes. Several additional species of *Daldinia* were erected, in particular by Hennings (1988, 1901, 1902) and Lloyd (1919, 1924). Sometimes, aberrant stromatal morphology as exemplified by the holotype of *D. fissa* and discussed here under *D. vernicosa* gave rise to erection of new taxa, but the common feature of these new species was the internally zonate stroma, as defined by Cesati & De Notaris (1863).

The first attempt to broaden the concept of *Daldinia* by including *hypoxylloid* taxa that lack the conspicuously zonate stromatal interior goes back to Theissen (1909). Arguing that *Hypoxylon placentiforme* had reduced concentric zones, while being otherwise similarly to typical *Daldinia*, he transferred this species to the latter genus as *D. placentiformis*. However, this procedure was not followed by other mycologists who treated *Xylariaceae* in the 20th century.

The first “world monograph” of *Daldinia* by Marion Child (1932) resulted from her PhD thesis at the Missouri Botanical Garden. She compared freshly collected material from Central and Eastern USA to numerous herbarium specimens from around the world and recognised 13 species. At first glimpse, her work may appear visionary, because she described anamorphic characters and even segregated species, based on physiological traits. On the other hand, in retrospective one cannot fail to note that her monograph caused a lot of confusion. For instance, she analysed the ascospore size ranges, which she deemed important in her taxonomic concept, using a complicated statistical evaluation that was, however, highly problematic (see for example our Notes on *D. eschscholtzii* in the taxonomic part) and has to our knowledge never been confirmed by any other mycologist.

Furthermore, she inadvertently confused the characteristics of several species, as revealed from retrospective studies on type material. Child (1932) erected three new species: *D. occidentalis* Child (as “occidentale”), *D. simulans* and *D. grandis* (as “grande”). The first two species were shown to be later synonyms of other taxa (Ju et al. 1997), and the type specimen she designated for *D. grandis* appears to be lost. Most mycologists who provided local or general monographs in the second half of the 20th century relied on the descriptions provided by Child (1932), but did apparently not study the original specimens to validate her species concepts. Therefore, the treatments of *Daldinia* (Dennis (Central Africa, 1963)), Martin (1969, global, but with emphasis on Africa and America), Third & Dargan (1978, India), Petrini & Müller (1986, Europe) and Van der Gucht (1994 and 1995, Papua New Guinea), have all referred to species sensu Child (1932) that correspond to different taxa herein.

Descriptions of conidial states of *Daldinia* spp. were provided early on by Tulasne & Tulasne (1863) and Molliard (1904), but their significance in the taxonomy of the *Xylariaceae* was only recognised after the 1960s. Anamorphic data from certain *Daldinia* species made it easier to interpret the affinities between taxa showing a similar teleomorphic morphology, and holomorphic species concepts could thus also be employed in the genus *Daldinia* (Greenhalgh & Chessers 1968, Martin 1969, Petrini & Müller 1986, Van der Gucht 1994).

The second monograph of *Daldinia* by Ju et al. (1997) certainly helped to settle some of the problems associated with Child’s ill-defined concepts. Accurate and workable descriptions of *D. bakeri*, *D. caldarianorum*, and *D. loculata* were provided; most of the type specimens were examined and related to recently collected specimens, which were cultured and studied for anamorphic traits. Most of the material studied in fresh state by Ju et al. (1997) originated from the home countries of the authors (namely Mexico, Taiwan, and USA), whereas relatively few specimens from other regions, including Europe, were included.

Only two years later, Rogers et al. (1999) revised the concept of the type species, based on an original Bolton specimen that disagreed with the concepts of *D. concentrica* sensu Child (1932) and Ju et al. (1997), who had regarded this taxon to be almost cosmopolitan and frequent in the USA. Rogers et al. (1999) selected an epitype for *D. concentrica*, based on material from the UK, and the species matching this concept has so far not been recorded from outside Europe. The cosmopolitan species reported as “*D. concentrica*” is now known as *D. childiae*. However, it should be noted that specimens referable to various species were listed sub “*D. concentrica*” by Child (1932). While neither Ju et al. (1997) nor Rogers et al. (1999) revised a significant portion of the material listed in Child’s monograph, an additional species and data on anamorphic states of some *Daldinia* species were described by Ju et al. (1999).

Aside from morphological traits, complementary techniques have proven valuable for characterisation and segregation of certain *Xylariaceae* taxa. In *Daldinia* and *Hypoxylon* (Ju & Rogers 1996, Ju et al. 1997), the current taxonomic classification relies in part on the occurrence of stromatal pigments, i.e., a character relating to secondary metabolism. Such pigments are determined by using 10 % KOH to extract the outermost part of the stromata, and by comparison of resulting colours with a colour chart (Rayner 1970). Such stromatal pigment colours are species consistent, at least when several specimens of a given species are compared in the same developmental stage. Moreover, they relate to the presence of specific secondary metabolites, which are consistently found in certain species or species groups. These compounds are often present in extraordinarily high concentrations in the stromata of *Daldinia* and allied taxa, remain extremely stable in the stromata, and often exert significant biological activities (Stadler & Hellwig 2005, Stadler & Fournier 2006, Stadler et al. 2006, 2007). They can be detected easily in the stromata, using non-invasive analytical techniques based on HPLC, which, if combined by a reference library search based on UV/Vis and ESI mass spectra (Bitzer et al. 2007), may allow for the unambiguous detection of certain metabolites in the nanogram range. Such HPLC profiles are particularly informative in those cases where similar stromatal pigment colours are due to the presence of entirely different chemical matters, or if secondary metabolites that proved to be taxonomically significant are not pigments but only show absorption in the ultraviolet spectral range. A selection of these compounds that occur in *Daldinia* is presented in Fig. 1.

In the past years, the taxonomic work has been supported by intensive collaboration with analytical chemists, and so far over 100 secondary metabolites, the majority of which proved new to science, were identified during our studies from *Daldinia* spp. and related
This helped to assess the specificity of the distribution of certain compounds and even to draw conclusions on their putative biosynthetic pathways. The true value of the chemotaxonomic data matrix was only revealed as molecular phylogenies became available from comparisons of DNA sequence data.

The first valuable contribution to the taxonomy of *Daldinia* including molecular data was by Johannesson et al. (2000), who studied the genus in Northern Europe and Eastern Russia and provided a preliminary phylogeny based on ITS nDNA for a number of well-characterised specimens. Similar work was published by Stadler et al. (2011), who outlined the distribution of secondary metabolites from stromata of *Daldinia*.
a (2001b). However, PCR-based techniques could hardly be applied to old herbarium specimens, and even the stromata of relatively fresh material are often not suitable for PCR, possibly because the secondary metabolites act as PCR inhibitors (M.S., H.G. Wetzstein & H.V.T., unpubl. data). For molecular studies, as well as for evaluation of characters related to the anamorph, it appears indispensable to obtain cultures from fresh material. On the other hand, HPLC profiling proved suitable even for characterisation of material that had been collected in the 19th century (Stadler et al. 2001b).

Consequently, a polythetic approach, relying on morphological studies and HPLC profiling in conjunction with PCR fingerprinting and scanning electron microscopy (SEM) (Stadler et al. 2001c, d, 2002) supported the status of D. chilliae, revealed that D. concentrica sensu Rogers et al. (1999) and D. eschscholtzii contain similar secondary metabolites in theirstromata, and confirmed previous results by Van der Gucht (1993, 1994) on their anamorphic and ultrastructural characteristics. Stadler et al. (2004a) described five additional “cryptic” species from the Canary Islands, the Channel Islands, and Sicily. These taxa differ from D. concentrica and from one another only when teleomorphic, anamorphic and ultrastructural traits are combined. Molecular studies including D. eschscholtzii and D. concentrica suggest that ITS nrDNA sequences are sufficiently distinct to assume a long, divergent evolution, albeit both species have apparently maintained various similar morphological and chemical traits (Triebel et al. 2005, Bitzer et al. 2008). Stadler et al. (2004d) found neither D. concentrica nor D. eschscholtzii among a selection of ca. 80 specimens from Australia and New Zealand. Instead, they reported the two varieties of D. dennisi from Australia and New Zealand to be counterparts of D. eschscholtzii and D. concentrica in the Southern Hemisphere. Several further species were described by Stadler et al. (2001c, d) and Vasilyeva & Stadler (2008). Consequently, the number of accepted taxa in Daldinia has substantially increased, while the concept of the type species has changed considerably, and more than 50 % of the taxa described by Ju et al. (1997) still needed to be re-evaluated. Even after this monograph was published, there have been relatively few studies, including those by Hladki (2004) and Hladki & Romero (2006, 2009) on Xylariaceae from Argentina, and our own cited papers, in which the modern concept of Daldinia has been fully adopted.

A pilot study by Stadler et al. (2002) revealed the utility of SEM for discrimination of Daldinia spp. This technique had until then only been scarcely used for characterisation of Daldinia (Beckett 1976, Van der Gucht 1993, 1994), but was now employed to characterise the ascospores of all types and some other critical specimens.

The above, recent studies were mainly carried out on material from temperate and subtropical climates. Tropical species of Daldinia needed further study as relatively few recently collected specimens have been available. Rogers (2000) has argued convincingly that the Xylariaceae probably evolved in warmer climates. The apparent diversity of Daldinia in temperate regions prompted us to conduct an intensive study on their tropical relatives. Since SEM and HPLC profiling were likely to provide additional diagnostic evidence, it appeared feasible to work on ancient and depauperate specimens and link them to material whose anamorphic morphology and molecular phylogeny could be evaluated. Recording chemotaxonomic and molecular data, however, afforded the availability of fresh material. Hence, a large number of other “historical”, as well as recently collected materials from all over the world, and in particular from warmer climates, were included, and it took over ten years before the data matrix for the present monograph finally became available.

Ecology and physiology

Except for some species of the genera Biscogniauxia, Rosellinia, and Entoleuca (see overview by Edwards et al. 2003), most of the stromatic Xylariaceae, including all hyphoxylloid taxa to which Daldinia is believed to be related, have been traditionally regarded as saprobes that cause white rot on dead angiospermous (or, exceptionally, gymnospermous) wood. Especially, the genus Daldinia was until recently regarded as “plurivorous”, or no reliable data had been available regarding the apparent host specificity of thestromata. In addition, it was thought that Daldinia spp. would colonise the wood of their host plants rather early, assuming that the propagules arrive from the exterior environment, later to be replaced by the “more competitive” wood-rotting basidiomycetes (cf. Boddy et al. 1987, Whalley 1996). However, by now it is well-established that the “early colonisation” of burnt (or freshly felled) woody substrates relates to the endophytic lifestyle of the respective fungi (Johannesson et al. 2001, Guildot et al. 2003, Nugent 2004). They are actually present in the host tissue in apparently dormant stages, presumably for a very long time without causing any symptoms of disease. Some species preferentially form their stromata only once the host is damaged or stressed and have therefore been considered “rare”, when in fact they might be rather ubiquitous.

Petri & Petri (1985) studied xylariaceous endophytes of seed plants and reported how to recognise anamorphic Daldinia spp. by the presence of characteristic stromatic structures. Nevertheless, information on their life cycle and highly interesting ecology has only recently been provided, based on the availability of specific molecular methods, which were in turn based on reference DNA sequences that were derived from well-characterised specimens.

Daldinia is a very good example to demonstrate that a stable taxonomic concept constitutes an important prerequisite to attain a better understanding of fungal ecology. In our opinion, broad species concepts will often disguise the associations with other organisms, while concise identification methods will provide a better understanding of the interactions of the fungi in their ecosystems. Traditionally, host species were often reported along with new records of Xylariaceae and other stromatic pyrenomycetes, as such reports were often made by botanists and plant pathologists. Even if the stromata of Daldinia are found on dead wood, the host plants can often be recognised, e.g., by examination of the bark and the internal structure of the wood. Still, the taxonomic part will show that most previous assessments of apparent host specificity in the genus are quite unreliable because the respective fungi have often been identified using broad, outdated species concepts. Reliable host affinities have therefore been elaborated only after holomorphic species concepts were established. For instance, Petri & Müller (1986) have already established the affinities of what they regarded as D. occidentalis, for Alnus (= D. petriniae). In addition, D. bambusicola, D. graminis and D. sacchari have so far only been found on monocots.

Ju et al. (1997) discussed the ecology of Daldinia in a classical context and cited several papers that dealt with the ability of “D. concentrica” (s.l.) to destroy wood. The reports they cited on apparent host-specificity have to be taken with caution, considering that our extensive revisions revealed that less than five percent of the specimens in large US herbaria were correctly identified, according to the current taxonomy, and almost none of them had been revised, following the monograph by Ju et al. (1997).

Daldinia spp. have been characterised as “early colonisers”, owing to the fact that their stromata often appear immediately after
their woody host plants have been stressed or damaged, e.g., by fire or lightning. For instance, Rhoads (1918) characterised *D. vernicosa* (probably identical to this species in the current sense) as “pyroxylophilous” fungus, and many specimens of other *Daldinia* spp. we have examined over the past years were also found on burnt substrates, or occasionally, on tree trunks that had very recently been felled. In any case, it is pretty well known that *Daldinia* spp. may persist on woody substrates for rather long periods of time. Depending on the climatic condition, scarce to luxuriant production of their stromata can be observed in temperate climate zones over several vegetation periods, whereby the substrate is slowly being decayed. Except for *D. concentrica* and some allied species, most species of the genus that appear in temperate to subtropical climates produce their stromata in early summer and the ascospores become mature in autumn. From continuous observations of the stromata on such sites over many years, we have been able to confirm the statement by Ju et al. (1997) based on artificial cultures in the laboratory that the concentric zones of *Daldinia* are not regions of abortive perithecia as postulated by Bayliss-Elliot (1920): the stromata are not perennial, despite immature as well as overmature stromata left over from the past season can sometimes still be found in the next spring.

Regardless of the life cycle of stromatal production, the decay of the wood and the production of anamorphic structures that further colonise the substrate will always continue as long as humidity and temperatures are favourable for the physiological activities of the fungi. Some studies on the capabilities of *Daldinia* to degrade wood of different host plants have been published fairly recently (Johannesson et al. 2002, Shary et al. 2007), and even some of the respective enzymes have been characterised (Lee 2000, Karnchanatat et al. 2007, Ng et al. 2010).

*Daldinia* is not a parasitic genus. There are relatively few records of *Daldinia* spp. collected from living trees, and from our own experience we suspect that most of those were derived from damaged hosts that had partly become senescent. For example, we have studied *D. concentrica* growing on a standing tree trunk of *Fraxinus* in the Neandertal for over 15 years. The stromata appeared in 1994 immediately after the tree had been hit by lightning and was seriously damaged, but remained restricted to the dead branch. Stromata have appeared in abundance in every spring since then, and continued to grow in April of 2013, while the host tree is still alive and has fully recovered in other parts.

The same substrate may even be co-inhabited by more than one *Daldinia* species, which may produce stromata on the same tree branch, immediately after the host has been damaged by fire. Whalley & Watling (1980) noted the frequent occurrence of *D. vernicosa* on burnt *Ulex*. Wollweber & Stadler (2001) found their collections actually comprised stromata of both *D. caldariorum* and *D. vernicosa*. In one of these collections from the same site the stromata of both species were intermingled. Their teleomorphs have an extremely similar morphology, with overlapping ascospore sizes. Bitzer et al. (2008) could prove conclusively, using HPLC profiling and molecular data, that the culture ATCC 36660, isolated by Whalley & Watling (1980) from the mixed collection of *Ulex*-inhabiting stromata, was obtained from the *D. caldariorum*, rather than the *D. vernicosa*, element.

These examples show that, similar to other groups of fungi whose taxonomy has changed drastically in the past decades, there is no way around revising thousands of herbarium specimens, if significant data relating to their apparent host specificity, chorology and biogeography shall be obtained in retrospective. The current monograph is largely based on such revisionary work. We have examined up to several hundred specimens of some common species, but additional work is clearly needed. With regard to apparent host specificity, some tendencies have become evident, which have been outlined in detail in the taxonomic part.

For instance, neither *D. chilidiae* nor *D. vernicosa* appear to have any apparent host specificity. *Daldinia concentrica* (*Fraxinus*) and *D. loculata* (*Betula*), are rather constantly associated with certain genera of host plants, but may at times also appear on other woody substrates (e.g., both were frequently found on *Salicaceae* as well). The apparently endemic *D. macaronesica* was mostly found on the lauraceous and likewise endemic *Ocotea foetens*, but occasionally colonised other lauraceous plants that are typical for the Macaronesian Islands. However, another taxon that is regarded as highly host specific, namely *D. lloydii* (normally restricted to *Betula*) has at least once been found on the gymnospermous *Pinus*.

The “plurivorous” *D. eschscholtzii* (likewise recorded here from *Pinus*) and *D. chilidiae* (*fide* label of a BPI specimen on *Cryptomeria* in India) also occasionally colonise gymnosperms. Such data on aberrant hosts appear all the more plausible, considering the life cycle of these fungi.

Ju et al. (1997) reflected the view of other mycologists in stating that “*Daldinia* spp. are probably weak facultative parasites that continue to decay the wood following decline and death of their hosts”. This view may be adequate from the standpoint of a plant pathologist, but recent studies relying on molecular data point towards a more complicated situation. Guidot et al. (2003) have postulated a rather complicated life cycle for *D. loculata*, using modern methods of population genetics. By genotyping the mycelium growing in the wood and the sexual ascospores in a geographically isolated burnt forest site in southern Sweden, they concluded that wind-dispersed ascospores, as well as conidia transferred by pyrophilous insects are essential vectors for the realisation of the sexual cycle of this fungus.

Some of these insect vectors were identified by Šrůtka et al. (2007), who reported anamorphic *D. decipiens* and an anamorphic xylariaceous fungus they referred to as *Entonaema cinnabarum* to be associated with woodwasp nests (genus *Xyphidia*). This paper and the subsequent study by Pažoutová et al. (2010) demonstrated that the apparent host specificity of certain *Daldinia* species is due in part to their association with insects that are likewise host specific. Pažoutová et al. (2013) have concurrently described a new woodwasp-associated species of *Daldinia*, *D. hawksworthii*, while the current monograph was already in press. This species, of which no sexual stage has so far been encountered, is not included here. The report of *E. cinnabarum* by Šrůtka et al. (2007) was later found to be due to the fact that the stromata of the *Entonaema* specimen from which the reference DNA sequence was obtained by Triebel et al. (2005) had actually been colonised by *D. chilidiae*, whose stromata were found in abundance on the same collection site (J.F. & M.S., unpublished observations). Several *Daldinia* species have been isolated in our laboratory from stromata of other *Xylariaceae*, and especially *D. eschscholtzii* has caused problems in the past because its anamorphic stage infested old and overmature stromata of other members of its own family. It remains unclear whether these observations relate to a mycophilic lifestyle, but in any case they illustrate the ubiquitous occurrence. Nugent (2004) also found the anamorphs of *Daldinia* spp. to be quite common in areas where sexual stromata occurred. The occurrence of the conidial stages of *Daldinia* in those areas where the stromata can be found is certainly, at least to some extent, due to the fact that these fungi have developed a way to produce ascospores very efficiently, even in periods of drought. The ascospores are numerous and fairly persistent, and under favourable conditions, they germinate and produce mycelium rather rapidly. The
cultures of all *Daldinia* spp. so far examined are able to grow on a broad range of substrates and utilise a broad range of nutrients. They grow much faster than the species of most other *Xylariaceae* genera. Hence, they may easily colonise a broad range of host plants, as well as woody and other substrates in the natural environments as well.

Ju et al. (1997) have attributed the internal concentric zones, which are highly gelatinous in many species, as a means of water storage, which evolved in adaptation to a xerophilic lifestyle. They cited earlier work by Inglod (1946, 1954, 1965), who established that stromata of *D. concentrica* are able to produce ascospores in the natural environment over periods of several months. Laboratory experiments using the detached stromata revealed that water stored in the stromata is used to aid in spore production and discharge. Ju et al. (1997) also argued convincingly that the nocturnal ascospore discharge observed for *Daldinia* (Inglod & Cox 1955), and the ability of the ascospores to germinate almost immediately under favourable conditions are additional adaptations of these fungi to a xerophilic lifestyle. Furthermore, they attributed that the waxy to carbonaceous crust encasing the stroma might retard evaporation from the interior. According to our observations, *Daldinia* spp. are encountered in humid habitats, such as tropical and subtropical rainforests, at least as often as in arid areas. However, this apparent contradiction was explained by Rogers (2000), who stated that these fungi might have originally evolved in dry areas but have meanwhile found refuge in the rainforests.

According to our own observations, even a tropical rain forest can be extremely dry at a local scale or during a particular season. Moreover, in tropical as well as temperate climate zones, *Daldinia* spp. tend to produce stromata above ground level and often in big tree fall areas where the sun has free access. Other *Xylariaceae* genera, including various Nemania spp. and even some taxa in *Hypoxylon*, however, seem to avoid such habitats, and their stromata often occur in damp places inside the forest where they are not exposed to sunlight and drought at all. Some species, such as *D. eschscholtzii* and *D. petriniae*, seem to occur more often on dead, fairly decayed woody substrates, whereas *D. loculata* and *D. vernicosa* are mostly found on freshly felled wood or on damaged, still living trees. Even though this phenomenon deserves to be studied further by using traditional methods of field work in conjunction with molecular data, we conclude that various evolutionary lineages of *Xylariaceae* seem to have adapted different lifestyles in relation to their plant hosts, which clearly constitutes one of the main determinative factors for the diversity of this family.

Another fact not mentioned by Ju et al. (1997), namely the extreme persistence of the thick-walled ascospores of *Daldinia*, has become evident repeatedly in our successful attempts to culture herbarium specimens that had been collected several years previously. Cultures were obtained from various specimens after several years of collection, as exemplified by a specimen of *D. novae-zelandiae* from the Chatham Islands that we cultured again in 2003 from the original PDD material (cf. Stadler et al. 2001d). Ju et al. (1997) had reported an identical culture from this specimen (as *D. grandis*), and we could still germinate the ascospores when we obtained the material 11 years after collection.

Boddy et al. (1985) observed that cultures of *D. concentrica* were more tolerant of low water potentials than some wood destroying basidiomycetes. According to our own observations, vegetative stages of other *Daldinia* spp. are also rather resistant to drought, which might in part be due to their ability to form the characteristic stromatic structures illustrated by Petrini & Müller (1986) and Van der Gucht (1994). In cultures of what is here regarded as *D. andina*, Stadler et al. (2004c as *D. grandis*, figs 33–38) no regular conidiophores were found. Instead, thick walled, incrusted hyphae were observed (Stadler et al. 2004d), which sometimes released globose to obovoid conidia-like structures after constriction of terminal parts or by budding at lateral parts, which possibly may serve as propagules. Some further papers dealing with ecological aspects of the *Xylariaceae* in general have been summarised by Whalley (1996), Rogers (2000) and Stadler (2011) and are therefore not treated here in detail.

**Chemotaxonomy, molecular phylogeny and generic affinities in the Xylariaceae**

There has never been any doubt about the close affinities of *Daldinia* with *Hypoxylon sensu lato*, in which it has been included by many taxonomists (Lassoe 1994). Nevertheless, Ju et al. (1997) maintained it separately from *Hypoxylon*. They stated that the concentric zones in *Daldinia* developed as special anatomic features in the course of its xerophilic lifestyle, and that biological features should be strongly considered when delimiting generic boundaries in *Xylariaceae*. In addition, they mentioned various other genera that also appear related to *Hypoxylon* and *Daldinia*, sharing, e.g., nodulisporium-like anamorphs and the presence of stromatal pigments.

Furthermore, Whalley & Edwards (1995) already found that the typical secondary metabolites in cultures of *Daldinia* are quite different from those of *Hypoxylon* (and other genera in the *Xylariaceae* that had meanwhile been removed from *Hypoxylon sensu Miller 1961*). In retrospect, it can be stated that their chemotaxonomic work predicted genetic relationships that were meanwhile established on the basis of anamorph-teleomorph connections and largely confirmed by methods of molecular phylogeny. Stadler et al. (2001a, b) confirmed and refined the results of Whalley & Edwards (1995), based on a HPLC-based study on cultures of several *Daldinia* spp., but even found several otherwise rare secondary metabolites in the stromata of *Daldinia* (examples see Fig. 1). Some of them also occur in particular *Hypoxylon* spp., and it was shown that *Hypoxylon* can be segregated into chemotypes comprising species groups, based on the occurrence of these compounds (Mühlbauer et al. 2002, Stadler et al. 2004c, Hellwig et al. 2005). *Hypoxylon* sect. *Annulata sensu Ju & Rogers* (1996) was found to differ from sect. *Hypoxylon* with regard to its stromatal pigments (Quang et al. 2005). Indeed, molecular data based on α-actin and β-tubulin genes were in accordance with morphological and certain chemotaxonomic traits, which resulted in the erection of the genus *Annulohypoxylon* (Hsieh et al. 2005).

In the same study, *H. placentiformes* was transferred back to *Daldinia*, even though the stromata of *D. placentiformis* do not show conspicuous concentric zones. The molecular data based on α-actin and β-tubulin sequences reported by Hsieh et al. (2005) clearly revealed affinities of this species to *Daldinia*. Recently, these phylogenetic relationships were confirmed based on chemotaxonomic and ITS rDNA sequence data (Bitzer et al. 2008). Several polyphasic studies using chemotaxonomic, morphological, and molecular data were meanwhile undertaken to verify the affinities of the cleistocarpous genera of the *Xylariaceae*. A comparison of *Phylacia* and *Pyrenomyxa* (syn. *Pulveria Malloch & Rogerson*) clarified that the former is closely related to *Daldinia*, while the latter is probably derived from the *H. rubiginosum* complex (Stadler et al. 2004b, Hellwig et al. 2005, Stadler et al. 2005, Bitzer et al. 2008). Affinities between the genera *Daldinia, Entonaema*, and *Rhopalostroma* were also established by chemotaxonomic
The concept of Entonaema, as conceived by Möller (1901), comprised two species that have developed in convergence in two major lineages of Xylariaceae. While the type species, *E. liquescens*, appears closely related to *Daldinia*, *E. mesentericum* (syn. *E. pallidum* G.W. Martin) is now included in *Xylaria* (Stadler et al. 2008a). *Rhopalostroma* and *Thamnomyces* Ehrenb. are also closely linked to *Daldinia* by chemotaxonomic evidence (Stadler et al. 2004b). The affinities of *Thamnomyces* (Stadler et al. 2010a) and *Rhopalostroma* (Stadler et al. 2010c) to *Daldinia* were recently also confirmed by a comparison of molecular and further chemotaxonomic data. Interestingly, the phylogeny inferred from ITS nrDNA data presented in the aforementioned studies revealed *Daldinia* to be split in two major clades, one being more closely related to *Phylacia*, *Rhopalostroma* and *Thamnomyces*, and another showing closer affinities with *Entonaema* and *Ruwenzoria* (Stadler et al. 2010b), another recently recognised genus with aberrant morphological features that preclude its inclusion in *Hypoxylon* and *Daldinia*. The genus *Rostrohypoxylon* (Fournier et al. 2010a) is another representative of the hypoxyloid Xylariaceae that could not be accommodated in the current generic concept, and seems to have evolved from within *Annulohypoxylon*, as judged from the outcome of a preliminary phylogenetic study (Tang et al. 2009, where the type material was still treated as “Xylariaceae sp. JF 06-04”). As demonstrated in Fig. 2, those taxa that were found most closely related to *Daldinia* have in common the production of various metabolites in culture, which were so far not found in *Hypoxylon* and allies. Notably, they seem to be derived from at least four

Fig. 2. Secondary metabolites from cultures of *Daldinia* and related Xylariaceae. Distribution: 10–13: Ubiquitous in *Daldinia* and immediate allies (*Entonaema*, *Phylacia*, *Rhopalostroma*, *Ruwenzoria* and *Thamnomyces*). 15: Green pigment of *Hypoxylon fragiforme*, also present in various cultures of *Daldinia* and in other *Hypoxylon* species. That release greenish pigments into the agar when fermented on solid media. 16–18: Not yet found in *Daldinia*, even after chromatographic separation of the crude extracts by HPLC, but present in most species of *Hypoxylon*, *Annulohypoxylon*, *Pyrenomyxa* and other hypoxyloid genera so far examined as major metabolites. 14: Ubiquitous in all the aforementioned genera, often as major metabolites.

8-methoxy-1-naphthol (10) \( R = CH_3 \); 1, 8-naphthol (10a) \( R = H \)

5-hydroxy-2-methylchromone (11)

5-hydroxy-2-methylchroman-4-one (11a)

2,6-Dihydroxyacetophenone (11b)

eutypinol methyl ether (14)

eutypine methyl ether (14a)

1-(2,6-Dihydroxyphenyl)-butan-1-one (12)

Ab-5046-B (13)

isosclerone (12) \( R = H \)

3-hydroxyisosclerone (13) \( R = OH \)

Hypoxyxyleone (15)

mellein (16) \( R = H \)

5-methylmellein (16a) \( R = CH_3 \)

ramulosin (17)

Isochracein (18)
different polyketide synthase gene clusters that are not expressed in Hypoxylon and allies (cf., discussion in Stadler et al. 2010a). On the other hand, the characteristic dihydroisocoumarin derivatives of the melilite type have so far not been encountered in “daldinoid” taxa. They are, however, also found in other taxa of Xylariaceae with nodulisporium-like anamorphs, such as Biscogniauxia, Camiella, Lopadostoma, and Obolarina, which have been discussed in the literature to be closely allied to, or to constitute ancestral groups of, Hypoxylon (cf. Bitzer et al. 2008). The conclusion by Lessae (1994), that Daldinia at that time constituted an “ingroup” within Hypoxylon, remains intact. However, the drastic changes in secondary metabolism that has evidently occurred in Daldinia and allies, along with some morphological features that are discussed elsewhere herein, points toward their being more evolutionarily derived.

It remains unclear whether and which of these secondary metabolites may be responsible for the various uses of Daldinia in ethnomycology. Traditional uses of Daldinia in folk medicine and folklore have been reported for many countries, including Cameroon (Kinge et al. 2011), Malaysia (Chang & Lee 2004), Nigeria (Osowenwe et al. 2010), Mexico (Guzman 2008, who even cited Daldinia “fissa” as an edible mushroom), and India (Tripathi & Basu 2010). Whereas the exact purpose of use of the fungus remains widely obscure in the above references, which are mostly dedicated to inventories of various fungi in the ethnomycology of the respective countries, there are a few reports that actually include biological characterisation studies. For instance, Benie et al. (2008a, b) found oestrogen-like effects in an extract of Daldinia “concentrica”, whereas Quang et al. (2006) demonstrated that the daldinals from D. chilidae are inhibitors of nitric oxide production in RAW 264.7 cells, thereby exhibiting antioxidative potential. Nagasawa et al. (2000) found that cytochalasins from D. eschscholtzii (as D. vernicosa, cf. Stadler et al. 2001a) are strong inducers of apoptosis in cancer cells. Cytochalasins in general are classified as cytotoxic mycotoxins. The fungus referred to as “Daldinia concentrica” in many tropical countries is very likely the ubiquitous pantropical D. eschscholtzii. As discussed in the taxonomic part, this species accumulates cytochalasins in its stroma, hence special care should be taken with consumption and administration of the respective African and Asian folk drugs.

The above studies have created a matrix on which we hoped to be able to interpret intergeneric affinities more easily, and we think that the time has come to update the status of Daldinia at the infrageneric level. In any case, it became necessary to further emend the classical concept of Daldinia, based on the presence of concentric zones in the stroma, in view of the recently obtained chemotaxonomic and molecular data.

There are additional reports on secondary metabolites of Daldinia spp., e.g. by Lee et al. (2002), Qin & Liu (2004a, b), Qin et al. (2006a, b) and Wang & Liu (2004) from Korea and China, respectively. Some of the chemical structures of these molecules are depicted in Fig. 3. However, these papers refer to the source of their metabolites as “D. concentrica”, despite the fact that the type species of Daldinia has still not been found in Asia. Even though some of these compounds have been reported to possess rather interesting chemical structures and even biological activities, the taxonomy of the producer organisms should be revised. The same holds true for the culture named “D. concentrica” by Shao et al. (2008), from which the authors reported some “induced” compounds, which they unfortunately named daldinins A, B, and C despite these trivial names were then already in use for entirely different metabolites (cf. Hashimoto et al. 1994b, Hashimoto & Asakawa 1998). Qin et al. (2008) have later published further “induced” botryane terpenoids from cultures of “D. concentrica”, which surprisingly belong to a class of compounds that was hitherto only found in unrelated ascomycetes, such as Botrytis and Hymenoscyphus sensu lato. Some of these confusions may have arisen from the unfortunate fact that it has become common practice to “identify” fungal specimens by mere comparison of ITS nrDNA (cf. results on D. concentrica vs. D. steglichii in the phylogenetic part below).

Before they can be seriously considered in a chemotaxonomic context, such results as those provided by Qin et al. (2008) and Shao et al. (2008) will need a careful re-examination, since nobody, including ourselves, has hitherto found any sesquiterpenes or compounds of the “induced daldinin” type in Daldinia. On the other hand, the genus is known to be extremely diverse with respect to its secondary metabolism, and the discovery of many unprecedented compounds can still be expected.

In this context, it should be mentioned that since reliable molecular data on the most common Daldinia spp. have become available, reports on new chemical compounds have been increasingly associated with rather sound molecular identification methods. Albeit no details on the morphology of the respective producer organisms did accompany the respective publication of chemical data, the compounds reported were chemically rather similar to the known metabolites of Daldinia, and high degrees of homology of 99 % of the nrDNA sequence data to those of well-characterised reference specimens, would suggest that at least the species group has been correctly identified. This concerns, e.g., a report by Nadeau et al. (2010) on polyketides from a soil-derived isolate of D. loculata, as well as concurrent reports on D. eschscholtzii from quite unusual habitats. Zhang et al. (2008, 2011) reported a culture of the latter species to be associated with a mantis insect, and isolated highly interesting immunosuppressive compounds from this strain.

Even the molecular biology of the biosynthesis of these unique compounds has now been elucidated (Fang et al. 2012). On the other hand, Tarman et al. (2012) reported helicoascoside derivatives from another strain of D. eschscholtzii derived from a marine alga. As inferred from their chemical structures, the aforementioned compounds could well be derived from the ubiquitous dihydroxyanaphthalene melanin biosynthesis that is omnipresent in Daldinia and allied genera. The latter examples also show that studies on the secondary metabolites of fungi from hitherto unexplored habitats may even contribute to our knowledge on the ecology of the respective organisms. Likewise, the similarity of the chemical structures of compounds reported by Igarashi et al. (1993), Kozlovsky et al. (2003) and Dai et al. (2006, 2009) from endophytic species of Nodulisporium to those found from teleomorphic Xylariaceae in the course of our own work suggest that the producer organisms probably constitute anamorphic states of Daldinia or its allies. In one case (Dai et al. 2006), even coupling products of naphthalenes and chromones, i.e. the prevailing metabolites in cultures of all Daldinia spp., were encountered along with the corresponding monomers.

On the other hand, some of the confusions of Asian Daldinia spp. with “D. concentrica” might relate to the fact that the Asian D. steglichii has identical ITS nrDNA sequences to the European type species, as shown later in the molecular phylogeny section. Unfortunately, it has become customary especially in applied mycology to “identify” specimens that yield new secondary metabolites or are used in biotechnology, by ITS nrDNA sequences alone.

In other cases, the same compounds were reported by us or by other research groups concurrently in Daldinia, after their preparative isolation and structure elucidation by NMR and
HR-MS. When in doubt, such preparative work should always be preferable over analytical studies, even if HPLC-MS and authentic standards are available. However, as preparative HPLC systems are even less frequently available in mycological laboratories than analytical HPLC systems, collaboration with chemists are essential to accomplish such tasks.

Although the biogenesis of the characteristic metabolites in stromata and cultures of *Daldinia* has never been studied using methods of molecular biology, or even incorporation of labelled precursors, it is possible to assess conceivable origins for all the most important compound classes so far identified from analogous studies on other Ascomycota. These origins are here briefly described to explain their significance; further information can be found in earlier studies (Bitzer et al. 2008, Stadler et al. 2010a, c) and in the review by Stadler (2011).

- BNT (1) and other naphthalenes and naphthoquinones (2–5) are polyketides derived from 1,8 DHN biosynthesis. Daldinones and perylene quinones (2–5) are conceivably derived by oxidation from a BNT (1)-like carbon skeleton, implying that their biogenesis could be mediated by the same polyketide synthase complex. The conversion of BNT (1) to perylene quinones (2) could be mediated by specific enzymes...
that are only present in certain *Daldinia* spp. of the *D. petriniae* complex, which have olivaceous stromatal pigments. In those species that show purple pigments in their young stromata, this enzyme becomes active as the stromata become mature, yielding compound 2 and this resulting in greenish stromatal pigments.

- Accordingly, the naphtoquinone hypoxylon (5) is derived from a different precursor, which has so far not been isolated from any xylariaceous fungus. Species containing hypoxylon, however, must possess an active PKS domain that is not functional in species that contain only BNT.
- Daldinins and daldinals (6–7) are additional polyketides, whose biogenesis is mediated by further, specific PKS complexes; in case of the daldinals this polyketide is even linked to various fatty acids. The specific co-occurrence of daldinals and daldinins in *D. childiae* and allies is striking in the genus, even though these compounds have also been occasionally found in certain species of *Hypoxylon*, in particular the *H. fuscum* complex (Stadler et al. 2008b, Stadler 2011).
- Cytochalasins (8), which have mostly been found in *D. eschsholtzii* and other tropical species, are of mixed PKS/NRPS origin.
- Concentricals (9) are, unlike all other chemotaxonomic marker compounds, terpenoids derived from the acetate-mevanolate pathway and, like the cytochalasins, are only encountered in *D. concentrica* and *D. eschsholtzii* and their respective allies.
- Species like *D. loculata* and *D. vernicosa* do not contain any of the above mentioned compounds aside from the ubiquitous BNT; they generally appear poor in stromatal secondary metabolites.

**Cultural characteristics of *Daldinia* spp. (Figs 4–8)**

Cultures of *Daldinia* spp. are characterised by certain macromorphological features that can sometimes facilitate recognition of the species or species group. However, these features may also be highly dependent on the culture medium and the age of the cultures. In Figs 4–8, images of representative cultures of most species that are treated herein have been compiled, mostly according to the respective species groups as defined in the taxonomic part. Some isolates were photographed at different developmental stages, or on different culture media. In those cases where production of immature stromata was observed, enlarged images are shown.

While previous reports on cultures and anamorphs of *Daldinia* mainly relied on one or a few representatives, the current study is based on several hundreds of isolates, and the majority of accepted species has now been cultured, often repeatedly. Details on individual species are given in the taxonomic part. However, some general aspects that appear characteristic of the genus and its relatives, and certain species groups, are summarised below. We have also included some practical observations that may facilitate the study of these fungi and their handling in the laboratory.

In accordance with chemotaxonomic and molecular data, cultures derived from the genera *Entonaea* (cf. Stadler et al. 2009a), *Rhopalostroma*, *Ruwenzoria*, *Phylacia*, and *Thamnomycetes* can hardly be discriminated from *Daldinia* with respect to their growth characteristics in culture. They appear rather different from the cultures of the related genera, *Annulohypoxylon* and *Hypoxylon*. A species that was formerly included in the latter genus, *H. placentiforme*, has now been transferred to *Daldinia* (as *D. placentiformis*), based on molecular data (Hsieh et al. 2005) and this procedure also appears justified from a comparison of phenotype-based characteristics, because its characteristic secondary metabolite profiles (cf. Bitzer et al. 2008) and cultural morphology are reminiscent of the *D. eschscholtzii* complex, rather than of a *Hypoxylon*.

All *Daldinia* species so far examined initially show fairly rapid growth, colonising the agar from the inoculum point at the centre by non-differentiated, whitish hyphae. These hyphae soon form a fleshy, azonate mycelium and become greenish in patches (cf. *D. clavata* in Fig. 5J and *D. lloydii* in Fig. 8C), finally turning Mouse Gray (118). These patches indicate the melanisation of hyphae and often give rise to the characteristic stromatic structures that are rather typical of *Daldinia* and related genera, but do not normally develop into conidiophores. Sometimes the stromatic structures develop as the mycelial mat becomes concentrically zonate. As the stromatic structures become fully differentiated, the surface of the cultures turns blackish, and the entire mycelium is often converted to such highly melanised material. At this stage of development, radial mycelial growth appears to slow down, even though the mycelium of all species so far examined will finally reach the edge of the agar plates. Sharland & Rayner (1986) have reported the radial extension of *D. concentrica* from Britain at 20 °C on malt agar to be in the range of 5–8 mm/d. Those growth rates were basically confirmed in our studies, which were generally undertaken at 23 °C. At 27 °C, some cultures of *D. caldarium* and *D. eschscholtzii* even grow faster, attaining radial growth rates of over 1 cm/d (M. Stadler et al., unpubl. data).

The natural function of the stromatic structures might be to help the fungus to survive periods of drought in the natural environment, similar to the chlamydospores that are produced by various filamentous fungi. It has in our experience sometimes (but not always) been possible to revive the cultures from dried agar plates by placing some of these stromatic structures into liquid culture media. In other instances, especially on YMG medium, which best supports secondary metabolite production, it was not even possible to revive the cultures despite that the vegetative hyphae were still apparently intact. The compounds that are overproduced in cultures of *Daldinia* have antibiotic activities, hence the cultures might poison themselves in later developmental stages. It is therefore advisable to carry out cryo-preservation (in liquid nitrogen or at -80 °C) and other measures for permanent preservation with relatively young mycelia that have not yet commenced to produce secondary metabolites. The onset of secondary metabolite production can often be observed by the release of Dull Green (70) to Citrine (13) pigments into the culture medium, even if many secondary metabolites that have so far been found from cultures of *Daldinia* do not constitute pigments themselves.

Another peculiar feature that is very characteristic of all *Daldinia* species and the above mentioned allies is the production of volatiles which have a rather characteristic odour. The volatiles have not been identified but might be chemically related to the ubiquitous chromone (13) and other small molecules of polyketide origin that are also ubiquitous in these fungi. The odour has been noted by several mycologists who have studied *Daldinia* in the past. Webber & Gibbs (1989) described it as "fruity", and associated this production of volatiles with the ability of *Daldinia* cultures to attract certain beetles. Panisset (1929) called it "sickly sweet", and Van der Gucht (1994) referred to it as "ether-like, with a sweet component". In any case, this characteristic odour unmistakably points toward *Daldinia* and allies. It will even reveal the identity of endophytes isolated from plant tissues, or mycophilic daldinoid
Xylariaceae that we have frequently obtained from stromata and perithecial contents of other Xylariaceae genera (see Notes to *D. eschscholtzii*). Notably, the same odour also occurs in all genuine cultures of *Entonaema, Phylacia, Rhopalostroma, Ruwenzioria* and *Thamnomyces*, which we have so far obtained.

Some species, especially of the *D. concentrica* and the *D. eschscholtzii* groups, produce their conidiogenous structures rather soon, after less than one week of incubation. In such cultures, the conidiogenous structures become scattered throughout the colony, but normally first arise from regions close to the inoculation point in the centre. The conidiogenous regions can often be discriminated from the regions where the above mentioned stromatic structures are produced by their pigmentation. In most species of *Daldinia*, they attain olivaceous brown colours, ranging from Buff (45) to Honey (64), Hazel (88), and Olivaceous Buff (89) to Vinaceous Buff (86). Species of the *D. petriniae* group (cf. Fig. 8A, D) often have rather pale conidiogenous structures ranging from Pale Luteous (11) to Ochraceous (42). Only in certain species of the *D. eschscholtzii* group they tend to be darker, appearing Mouse Gray (118) or Smoke Gray (105), initially with olivaceous tones, but later appearing blackish when occurring in masses. Then, they are difficult to discriminate from the melanised vegetative mycelium. After some time the conidia germinate to form a secondary mycelium that covers the surface of the cultures (cf. Fig. 4B for *D. concentrica*). At this stage it is very difficult to find anamorphic structures.

Some other species, especially those of the *D. chilidiae* group, produce their conidiophores only after prolonged incubation periods, and in general they become more abundant in the

---

**Fig. 5.** Macromorphology of cultures of *Daldinia* spp. (*D. eschscholtzii* group) on 9 cm OA plates (except G on YMG agar) after 2 (A, C, D–J) or 4 (B, E, F) wk of incubation. A. *D. eschscholtzii* MUCL47186 (P.R. China). B. *D. starbaecki* MUCL 45436 ex-type (French Guiana). C. E. *D. caldariorum* CBS 113043 (Ecuador). F. *D. theissenii* CBS 113043 ex-type (Ecuador). I. J. *D. clavata* MUCL 47436 (Gabon). I: OA; J: YMG. In some cases, areas of production of immature stromata (S) are indicated by arrows.
Fig. 6. Macromorphology of cultures of Daldinia spp. (D. childiae group) on 9 cm OA plates after 2 (D, F) or 4 (A–C, E) wk of incubation. A. B. D. childiae. A. MUCL 51679 (USA). B. CBS 116993 (Germany). C. D. australis. ex-type CBS 116732 (New Zealand). D. D. pyrenaica ex-type MUCL 43507 (Spain). E. D. cf. pyrenaica MUCL 51701 ex AS2506 (Ukraine). F. D. steglichii CBS 119994 (La Réunion). In E, production of immature stromata (S) is indicated by an arrow.

Fig. 7. Macromorphology of cultures of Daldinia spp. (D. vernicosa/loculata group) on 9 cm OA plates (except A on YMG agar) after 2 wk of incubation. A. D. vernicosa MUCL 52671 (Germany). B. D. gelatinoides MUCL 46173 (Russia). C. D. loculata MUCL 51688 (Sweden). D. D. novae-zelandiae ICMP 18259 ex PDD 82745 (New Zealand). E. D. cf. grandis IMCP 18266 ex PDD 90478 (New Zealand). F. D. loculatoides CBS 113279 ex-type (UK).
periphery of the colonies, often indicated by formation of tuft-like hyphal aggregations. In some other cases, conidiogenous structures are almost exclusively observed on stromatal primordia, which may either arise from the centre or from the periphery of the cultures. As shown for D. andina (Fig. 7E vs. Fig. 7F) OA is not always the optimal medium for induction of stromata, and different media such as YMG have sometimes led to a higher differentiation of the cultures. Cultures of certain species such as the apparently rare D. gelatinosa (Fig. 8E, F) always seem to readily produce stromata. We have constantly observed them in all cultures obtained, but only a few of our numerous cultures of D. eschscholtzii, and only one of the cultures of the D. childiae complex (MUCL 51701, see Fig. 7E) produced stromata on agar. The ability of Daldinia spp. to produce stromata in culture may get lost during frequent subculture onto new media.

The stromata produced on OA and YMG plates remain immature in most cases, even though they are often covered with conidioiophores. Whereas Ju et al. (1997, 1999) have reported some species of Daldinia to be able to form the teleomorph in culture, this has mostly not been possible in our own studies, except for D. caldariorum. This might have been due to the fact that our cultures contained insufficient amounts of nutrients to support differentiation of stromata. As an alternative, incubation of the cultures on Fernbach flasks or Erlenmeyer flasks containing larger amounts of nutrients, cellulose or even wood chips made from the original substrate, seems to favour stromatal production in general. Employing such a methodology it may be feasible to obtain the teleomorph from a larger number of cultures, as exemplified by the isolates that were obtained from endophytic strains of D. eschscholtzii in the laboratory of A.J.S. Whalley (here referred to as Ww 3771-3773) and showed exactly the same characteristics as teleomorph-derived material when studied by us.

Anamorphic structures (Figs 9–15)

We agree with Ju & Rogers (1996) that the anamorphic structures of Daldinia can be generally referred to as Nodulisporium, which is a synapomorphy that may soon be considered specific for a new family of the Xylariales. The current “innovations” in fungal nomenclature will inadvertently lead to the abandonment of many teleomorphic genus names, as older anamorphic names like Aspergillus and Trichoderma are now about to take preference over the well established corresponding teleomorph names. However, this will in all likelihood not so much concern the Xylariaeae, whose stromatic core genera have all been named for a long time for the teleomorphs, Stadler et al. (2013). In addition, their current classification has been based on holomorphic morphology for several decades, which has in retrospective turned out to be a wise decision because a 1 Fungus = 1 Name (1F1N) concept has already been realised. Nevertheless, anamorphs of Daldinia have been referred to various genera in the past, depending on the complexity of their nodulisporium-like conidial stages. Realising that these forms are merely due to different degrees of complexity of homologous conidiogenous structures, Ju & Rogers (1996) have proposed a rather sound classification system in their monograph of Hypoxylon, which is maintained here. This system does not use the generic names such as “Nodulisporium”,

Fig. 8. Macromorphology of cultures of Daldinia spp. (D. petriniae group and D. cf. nemorosa) on 9 cm YMG (A, C, D) or OA (B, E, F) plates after 2 (C, D) or 4 (A, B, E, F) wk of incubation. A, B. D. petriniae MUCL 51850 (Switzerland). C. D. lloydii CBS 113483 (Germany), showing the characteristic habit of young, undifferentiated cultures of Daldinia. D. D. decipiens MUCL 51690 (Germany). E, F. D. cf. nemorosa UAMH 9035 (Canada), F showing close up of stromata that arise at the margins of colonies after 2–3 wk. In E, production of immature stromata (S) is indicated by an arrow.
Stadler et al. but describes the different stages of complexity that can occur in conidiophores of the Xylariaceae as “nodulisporium-like” and so forth. Interestingly, a similar system has recently been proposed by Hawksworth et al. (2011) to replace the classical dual nomenclature, which should not be used anymore for pleomorphic fungal taxa. In this sense, Ju & Rogers (1996) could be considered as the inventors of “modern” ascomycete nomenclature. In any case, we have adapted the anamorph classification system of Ju & Rogers (1996). The most important types of anamorphic structures are briefly explained in the following paragraphs.

The most simple, unbranched forms are referred to as sporothrix-like branching patterns, which are often characterised by rather short, stout conidiophores and relatively large apical conidiogenous cells. Occasionally, such sporothrix-like conidiophores may have a single terminal bifurcation, leading to the presence of two apical conidiogenous cells.

There are other cases where the conidiophores are repeatedly branched, usually with intercalary conidiogenous cells from whose bases another conidiogenous hypha will arise, resulting in rather complex structures of up to 300 µm length, but with a maximum of two terminal conidiogenous cells. This type has been called virgariella-like conidiophore by Ju & Rogers (1996) and is typically found in certain species such as D. novae-zelandiae. By far the most common type of conidiophore in Daldinia, however, is the nodulisporium-like branching pattern, which results in groups of two to four conidiogenous cells at the apex of conidiophores, intercalary conidiogenous cells being the exception rather than the rule. The nodulisporium-like conidiophores are often not found in a single level. In some

Fig. 9. Photomicrographs of anamorphic structures of the Daldinia concentrica complex from OA culture, 1000×, showing nodulisporium-like conidiophores if not indicated otherwise. A. C. D. concentrica. A. Regular conidiophore of MUCL 51689 ex Ww 2357 (France). B. C. Aberrant sporothrix-like conidiophores of KC 1693 ex K(M)98806 (B) and KC 1688 ex K(M)91667 (C, both from UK). D. D. raimundi, from ex-type culture CBS 113038. E. F. D. macaronesica STMA11005/MUCL 53751 (La Gomera). G. H. D. dennisii var. dennisii, ex-type culture CBS 114741 (Australia). G. With young conidiogenous cells. H. With mature conidiogenous cells. I. J. D. dennisii var. microspora CBS 116733 ex PDD 76657 (New Zealand). K. D. palmensis, from ex-type culture CBS 113039 (La Palma). L. D. vanderguchtiae, ex-type culture CBS 113036 (Jersey). Scale bars. A–L = 10 µm.

2Ju & Rogers (1996) and many authors who had adopted this concept still used the genus names capitalised and in italics, but we refer to them here in the non-italic, non-capitalised form, according to the 1F1N concept.
cases, the conidiophores are composed of a main axis, and sometimes one or more major branches, which terminate in 2–4 conidiogenous cells arising in whorls. This is referred to as a periconiella-like branching pattern. Such conidiophores, which can also arise from synnemata, are relatively uncommon in *Daldinia* (except in *D. albofibrosa*, *D. bambusicola*, *D. steglichii* and *D. vernicosa*), but far more commonly encountered in *Hypoxylon* and *Annulohypoxylon*.

*Daldinia petriniae* and immediate allies have in common that their conidiophores normally produce conidia from percurrently...
proliferating conidiogenous cells, whereas most other taxa in *Daldinia* have a holoblastic conidiogenesis, producing sympodulospores. Even though it is not clear whether the conidiogenesis in these species is actually holoblastic or enteroblastic, as no ultrastructural studies on the topic have so far been conducted, the annellides in the conidiogenous region are striking features of the *D. petriniae* complex. Annellidic conidiophores have also been observed in *Annellosporium*, a recently described anamorphic genus, which is here considered as a synonym of *Daldinia* (see taxonomic part and Davey 2010), and in *D. palmensis* (Stadler et al. 2004a).

In this study, several *Nodulisporium* spp. could be assigned to members of the genus *Daldinia*, since a comparison of morphological, molecular and chemotaxonomic data with cultures derived from well-studied teleomorphs leave no doubt as to their identity. However, this was only accomplished because the HPLC profiles left no doubt that they belong to *Daldinia* and allies, rather than to *Hypoxylon* or *Anulohypoxylon*, and type strains were extant that could be studied for their molecular phylogeny. In all likelihood, there are also numerous species of anamorphic daldinoid and hypoxyloid Xylariaceae, which, not unlike other Ascomycota, have abandoned the production of the telemorph altogether. In addition, from the morphological descriptions of the known *Nodulisporium* spp. that have been published in the past before it became customary to deposit living cultures of ex-type strains in public collections and DNA sequence data available, it is impossible to determine whether they correspond to a certain telemorph genus or species. Therefore, it will in all likelihood never be possible to do without the anamorph genus *Nodulisporium*, no matter how hard certain mycologists are now trying to raise a classification system that can do without dual nomenclature for pleomorphic fungi.

The conidiogenous cells of *Daldinia* spp. are generally cylindrical, hyaline, smooth or finely roughened, and bear one to several apical poroid conidial secession scars that indicate former points of conidiogenesis. The conidia are also mostly hyaline, smooth, ellipsoid to almost globose, often with flattened base indicating former point of attachment to the conidiogenous cells.
MATERIALS AND METHODS


Specimens examined

All specimens examined are listed in the taxonomic part. Public herbaria and culture collections are cited according to Index Herbariorum\(^3\) and fungal names according to “Index Fungorum”\(^4\).

Fig. 14. Photomicrographs of anamorphic structures of the *Daldinia vernicosa/loculata* complex (from OA culture, phase contrast, 1000×). A. *D. loculata*. Nodulisporium-like conidiophore of MUCL 51688 (Sweden). B, C. *D. vernicosa*. nodulisporium-like (B) and sporothrix-like (C) conidiophores of KC1525 ex K(M) 24541. D. Nodulisporium-like conidiophore of *D. cf. nemorosa* UAMH9035 (Canada), showing annellidic conidiogenesis. E. Nodulisporium-like conidiophore of *D. loculatoides* CBS 113729 ex-type (Scotland), showing holoblastic conidiogenesis. F, G. Virgariella-like conidiophore (F) and conidiogenous cell (G) of *D. novae-zelandiae* CBS 114739 ex PDD 61834 (Chatham Islands, New Zealand). Scale bars A, B = 25 µm; C–G = 10 µm.
A polyphasic taxonomy of *Daldinia* (*Xylariaceae*)

(when appropriate the sanctioning author, however, is included here in contrast to this database).

**Morphological studies**

The methodology used for morphological examination of specimens and cultures was done in analogy to Stadler et al. (2004a). Briefly, dimensions of perithecia were determined using a dissecting microscope at 50–100× magnification. Microscopic

---

*Morphological studies*

The methodology used for morphological examination of specimens and cultures was done in analogy to Stadler et al. (2004a). Briefly, dimensions of perithecia were determined using a dissecting microscope at 50–100× magnification. Microscopic

---

features were determined using water mounts (brightfield or phase contrast microscopy at 1000× or 1200×), or using the reagents described in Stadler et al. (2004b) for studies of ascal structures: 1 % SDS served in case of old herbarium material to rehydrate perithecial contents and dissociate ascospores and asci. Perispore dehiscence was tested with 10 % KOH by adding 10 % KOH to water mounts preferably to direct observation in KOH to avoid some false negative reactions; further comments on this technique and illustrations are provided in the Notes to D. grandis and D. singularis where it proved effective. The ascal apical apparatus was examined in Melzer’s reagent. Ascospores and conidial sizes mostly relied on at least 10 and up to 25 measurements, unless fewer ascospores were observed (old and immature specimens) and are given as the most frequent values and the extreme values in parentheses. Regarding the large number of specimens studied, the averages were only calculated for some representatives of the D. eschscholtzii complex, while other data are given as in Ju et al. (1997) and all other publications on the genus cited since then. Dimensions given for perithecia, asci, ascal apical apparatus, conidiophores, and conidigenous cells are at least based on five individual measurements.

The KOH-extractable pigments are obtained by placing a fragment of stroma including the outer crust in a drop of 10 % KOH and observed against a white background. They may be readily released in much less than one minute but in some cases a longer incubation over several minutes may be necessary (in D. eschscholtzii for example). In case no colour reaction is featured in the plates, it is because no reaction was observed in the specimens used for illustrations, mostly old or weathered specimens.

Most specimens were cultured from material withdrawn under sterile conditions from perithecia in a similar manner as described by Ju et al. (2004), and therefore are presumably multiple spore isolates. Some single ascospore isolates were also studied for comparison. Surviving cultures are deposited in public collections; some of them are also preserved in the culture collection of InterMed Discovery GmbH, under liquid N₂. The classification of branching patterns and anamorph types follows Ju & Rogers (1996). SEM and corresponding data processing was done as described in Stadler et al. (2002). In contrast to previous taxonomic papers that were published after the monograph by Ju et al. (1997), the morphological descriptions were somewhat modified and simplified. For instance, width and length of the apical apparatus (which is no longer referred to as a “ring”), perithecial mounds are here referred to as “outlines”; ostioles are referred to as papillate, slightly papillate (equivalent to “punctiform” in previous papers), umbilicate, discoid or inconspicuous (equivalent to “obsolete” in previous papers). Perithecia are strictly speaking not “tubular” in Daldinia, but have a narrowed base and are therefore characterised as lanceolate, except for the few cases where they rather appeared obvoid. Stromatal dimensions are given as length × width × height and perithecial dimensions as height × width.

What we, herein, call the stromatal pruina is the thin powdery layer responsible for the brownish colour of stromata, which lies just above the crust composed of coloured granules. When this pruina is progressively worn off at maturity the stromatal surface becomes blackish and often shiny. In contrast, the stromatal “coating” is a thick, felt, usually pale brown-coloured tissue occurring on immature stromata and largely composed of anamorphic tissues. It usually vanishes during early states but can be persistent in some species like D. lloydii.

Based on the examination of hundreds of herbarium specimens, we found that the morphological study of Daldinia is too often hampered by the bad condition of the material, especially the perithecial contents, even though the stromata were in mature condition when collected. This is due to the high level of moisture inside the fresh stromata that prevents a quick air drying. Instead huge quantities of ascospores are released as asci dissolve in the perithecia and important microscopic characters disappear. The ascospores remaining in perithecia often germinate, losing their perispore and/or the whole interior becomes mouldy. Slow air-drying of entire stromata is likewise very favourable to the development of insects larvae that frequently occur in stromata of Daldinia at immature or mature state and can completely destroy an invaluable collection. The use of driers without caution most often involves drastic shrinkage of the stromata and “cooks” the perithecial contents such that ascal structures are badly damaged. A good option is to section at least one fresh stroma into slices 5–10 mm thick that will be easily air dried before asci disintegrate and ascospores released. Other stromata, especially the bigger ones, should be divided into halves and gently dried to keep their shape as intact as possible. Deep freezing of dried stromata over at least 2–3 d is highly recommended to avoid further development of insects during storage. The use of chemicals and insecticides should be avoided because this may result in false colour reactions of stromata with KOH. The best way to preserve the stromata in a fairly good condition is to freeze-dry them as soon as possible after collection as was done with many specimens from Germany and Central Europe prior to their deposit in the WUP/KR herbaria.

Chemotaxonomic evaluation (Figs 16–19)

Stromatal pigments were determined from tissue taken from the crust containing the waxy granules immediately beneath the stromatal surface and evaluated as described in Ju et al. (1997) and Wollweber & Stadler (2001). The colours were noted after about 1 min of incubation on a slide but left for another 5–10 min to check for colour changes, and the colour codes were determined after comparison with a colour chart (Rayner 1970).

Preparation of samples for HPLC profiling was carried out using the sensitive, non-invasive method as described in Stadler et al. (2004b) and Hellwig et al. (2005). Cultures of all Daldinia spp. were propagated in shake flasks and extracted with ethyl acetate as described in Stadler et al. (2001a), and their extracts were also analysed using the same HPLC method as in case of the stromatal material. HPLC was carried out using two different gradient systems and readouts, both of which are described in detail in the above references. Agilent (Waldbronn, Germany) HP1100 HPLC instruments were either coupled to a diode array detector (DAD) to obtain spectra and chromatograms in the UV-visible range (HPLC-UV/Vis), or to a Micromass (Manchester, UK) mass spectrometer to simultaneously obtain mass spectra in the positive and negative electrospray (ESI) mode (Hellwig et al. 2005). With specimens collected after 2006, the alternative HPLC-MS methodology described by Bitzer et al. (2007) and Laesøe et al. (2010) was employed.

The chromatograms (see representative data in Figs 16–19) only show the HPLC-UV traces at 210 nm, since most of the peaks corresponding to characteristic secondary metabolites were fairly detectable at this wavelength. In some cases, the corresponding HPLC-UV and HPLC-MS spectra are shown as well. Since two different gradient systems and stationary phases were employed and standards of numerous (known and yet unidentified) pure secondary metabolites were available for comparison, the
Identification was based on two datasets of spectra and retention times and allowed for unambiguous identification of known compounds in most cases. Spectral and chromatographic data of yet unknown components were saved in a HPLC library that may allow for their future identification, or for similarity analyses that are not based on their chemical structures.

Molecular phylogeny

The preliminary molecular phylogeny of *DalDinia* presented here is exclusively based on ITS rDNA gene sequence data. We wish to emphasise that several species (and in case of the sugarcane-associated species, possibly entire lineages) of the genus have not yet been characterised by molecular phylogenetic methodologies. Nevertheless, the present study is the first ever published for the entire *Xylariales* where a significant number of the most common morphospecies as well as representatives of various rare and new species have been studied for molecular phylogenetic affinities. The current taxonomic treatment based on phenotype-derived traits should help to find the teleomorphic stages of the missing taxa and allow for a further refinement of the phylogenetic affinities.

Taxon selection. During alignment of the sequence data of ca. 600 representative *Xylariales* (retrieved from GenBank, own unpublished data and sequences published first here), we noted that the resolution of the phylogenetic tree was highly dependent on the taxon selection, which greatly influenced the percentage of reliably alignable data. Finally, most taxa of xylarioid *Xylariaceae* (i.e., genera with geniculosporium-like anamorphs like *Xylaria*, *Kretzschmaria*, *Nemania*, and *Rosellinia*; cf. Fournier et al. 2011) were omitted, since their ITS regions sequences were found to contain too many DNA portions that could not be aligned with certainty. The tree was rooted with *Calceomyces lacunosus*, and *Graphostroma platystoma* and *Biscogniauxia nummularia* were included as additional outgroup taxa. These fungi all show morphological characters that are regarded as basal in the *Xylariaceae* (e.g. bipartite stromata erumpent from the host) or show an ascospore morphology reminiscent of the *Diatrypaceae*, but have in common with *DalDinia* and allies their nodulisporium-like anamorph. Whereas *Calceomyces* and *Graphostroma* show aberrant ascospore morphologies, *Biscogniauxia* has the typical xylariaceous ascospore morphology. Aside from representatives of all *DalDinia* taxa of which cultures are available, twenty additional strains representing taxa from different subgroups of the genera *Annulohypoxylon* and *Hypoxylon* and some genera that have been believed to related to them (*Pyrenomyxa*, *Thuemenella*) were included for comparison. DNA sequence data of several *Hypoxylon* species, as well as of *Graphostroma platystoma*, are reported and published here for the first time. In the case of *DalDinia*, several strains of the more common taxa such as *D. concentrica*, *D. loculata* and *D. vernicosa* from different geographic regions and host plants were selected. A list of all specimens studied is given in the Results Section (Molecular Phylogeny chapter). This list also includes sequence data retrieved from GenBank and the respective references. Special care was given not to retrieve unreliable reference data, where it was not clear whether the material was correctly identified and deposited in a public domain collection.

Phylogenetic reconstruction. Double-stranded sequences of the ITS region (ITS1, 5.8S rRNA gene, and ITS2) were obtained and further processed as outlined earlier (Triebel et al. 2005). The final alignment included 158 sequences, throughout which 381 positions
Fig. 17. Representative HPLC profiles (210 nm) of some specimens of the *Daldinia eschscholtzii* group and DAD spectra of characteristic metabolites. Most of these specimens contain cytochalasins (e.g., 9) in large amounts (see DAD spectra above left) and only traces of BNT (1), but some specimens like Ww 3591 (DAD spectra above right) preferentially contain concentricol A (8) and larger amounts of BNT, along with smaller quantities of cytochalasins. Daldinone B (4) was only found as prominent metabolite in *D. starbaeckii*. The numbers in this legend in **bold** refer to Fig. 1 of this issue.
were alignable with certainty (positions 33–62, 99–101, 105–132, 143–368, 386–437, and 443–461 according to AY616683, derived from D. concentrica). The most likely molecular-phylogenetic tree was reconstructed using RAxML v. 7.0.3 (Stamatakis 2006), as implemented in ARB (Ludwig et al. 2004). The program was also used to test the robustness of the tree topology by calculating 500 bootstrap replicates. Default parameters and the GTRCAT model of nucleotide substitution were applied for both analyses, with all free model parameters having been estimated by RAxML.

**TAXONOMIC PART**


Kingdom Fungi, Division Ascomycota, Subdivision Pezizomycotina, Class Sordariomycetes, subclass Xylario-
mycetidae, Order Xylariales, Family Xylariaceae.


**Lectotypus** [fide Greuter et al. 2000]: *P. concentricum* (Bolton: Fr.) S.F. Gray [≡ *Sphaeria concentrica* Bolton: Fr.]


**Lectotypus** [fide Greuter et al. 2000]: *Sphaeria concentrica* Bolton: Fr.


---

Fig. 18. Representative HPLC profiles (210 nm) of stromatal methanol extracts of some specimens of the Daldinia chilidae group and DAD spectra of characteristic metabolites. The profile of *D. chilidae* is also characteristic of *D. australis* and *D. pyrenaica*. *Daldinia* cf. *childiae* from P.R. China and *D. steglichii* differ in containing no detectable amounts or only minor quantities of daldinol (1a) and daladin C (6), respectively. All species of this complex are characterised by daladinal A (7) being by far the most prominent stromatal metabolite. Compounds with spectral characteristics reminiscent of daladin A2 (6a) and two apparently specific, rather hydrophilic compounds C1 and C2, which are apparently specific for this species complex, were also often present in the extracts of these fungi. The numbers in this legend in bold refer to Fig. 1 of this issue.
Stadler et al.

Typus: *H. concentrica* (Bolton: Fr.) Klotzsch [= *Sphaeria concentrica* Bolton: Fr.]


Typus: *V. cahuchucosus* Whalley & Watling


**Typus: Anelllosporium nemorosum** M.L. Davey

= *Daldinia nemorosa* (M. L. Davey), M. Stadler, J. Fourn. & Læssøe, comb. nov. [Mycobank MB800145]


---

**Fig. 19.** Representative HPLC profiles (210 nm) of stromatal methanol extracts of the holotype specimens of four species of the *Daldinia petriniae* group and DAD spectra of characteristic metabolites. All profiles, except for that of *D. lloydii* reveal mainly BNT (1) and compounds with similar DAD spectra (depicted above left), which are presumably binaphthyl derivatives, resulting in purple pigments in KOH. *Daldinia lloydii*, however, mainly contains oxidised binaphthalenes like the perylene quinone (2, see DAD spectra above right), which are responsible for the greenish olivaceous pigments of this species in KOH. BNT (1) is a conceivable biogenetic precursor of (2), even on the stromatal surface, which in part explains the fact that different colours are sometimes observed in young vs. mature specimens of this complex. The major difference in the HPLC profiles of the members of the *D. petriniae* complex as compared to other species groups in *Daldinia* with purple pigments in KOH (e.g. *D. fissa*, *D. loculata*) appears to be the greater variety of binaphthalenes in the former, and that conversions of BNT (1) to perylene quinones (2) and related compounds is often observed. The numbers in this legend in **bold** refer to Fig. 1 of this issue.
Emended generic description:
Teleomorph: Stromata conspicuous, spherical, depressed-spherical, placentiform, peellite, turbinate, clavate, or cylindrical, sessile, subsessile to stipitate, solitary to aggregated, outline smooth or with inoscillations to conspicuous perithecial outlines. Surface coloured, often brown or purple in youngstromata, which are often covered with a thin, olivaceous or reddish brown pruina, but darkened and dull or blackened and varnished in age; dark waxy granules forming a thin continuous crust appear immediately beneath the surface pruina, with or without KOH-extractable pigments; tissue between perithecia pithy to woody; tissue below perithecial layer appearing essentially homogeneous, or, more frequently, composed of alternating differently coloured zones. If alternate concentric zones present, darker zones are dark brown or grey brown, pithy to woody, lighter zones being white, gray, or brown, pithy, woody, or gelatinous, persistent or disintegrating, sometimes completely absent in mature specimens and replaced by a hollow cavity or not developing dark zones and therefore appearing white and azonate. Perithecia obvoid to lanceolate. Ostioles inconspicuous, umbilicate, discoid/annulate, slightly papillate, discoid papillate or papillate. Asci eight-spored, cylindrical, often very long-stipitate, with ascosporae arranged uniseriately or, rarely, partly biseriately, with apical apparatus ± discoid, amyloid, rarely inamyloid. Ascosporae brown to dark brown, unicellular in both mature and immature states, inequilaterally ellipsoidal or nearly equilateral, with narrowly or broadly rounded ends, with straight or slightly sigmoid germ slit usually spore length, on more convex or, infrequently, less convex side; perispore dehiscent or indehiscent in 10% KOH, smooth or transversally striate; epispore smooth. Anamorph when produced on stromata, on the substrate, or in artificial culture, Nodulisporium with different branching patterns as defined in Ju & Rogers (1996), with holoblastic or annellidic conidiogenesis.

Secondary metabolites (cf. Figs 1 and 2): BNT (1) always present in stromata and 1-methoxy-8-naphthol and 2-hydroxy-5-methylchromone (12, 13), Ab-5046-A (13) and Ab-5046-B (14) always produced on solid and liquid media, such as yeast-malt glucose medium. Eutypin methyl ether (11) and eutypine methyl ether (12) also present in some species, but meleine and 5-methylmeliein (1, 2) not detectable.

Species concept and species descriptions

For practical reasons, the genus is divided in various groups within which we regard the species to be closely related to one another, based on our morphological, chemotaxonomic and molecular studies: Group A: D. concentrica group; B: D. eschscholtzii group; C: D. chilidae group; D: D. vernicosas/loculata group; E: D. petriniae group and F: sugarcane-associated taxa. For each group the representative species is described and illustrated first, followed by related species ranked in alphabetical order. The major characteristics to recognise these groups are:

- Type of conidiogenesis of the anamorphic stages (annellidic, vs. regular holoblastic)
- Anatomy of the stromatal interior

Some salient morphological and chemotaxonomic features that help to distinguish these groups are listed in Table 2. Within these complexes, it may be difficult to recognise particular species, especially if only stromatal material is available and no molecular data and anamorphic studies are carried out. Characters that are regarded primarily as relevant to segregate species (and are used in addition to those mentioned further above, delineating species groups) are:

- Ascospore size and germ slit morphology
- Dimensions of ascopore apical apparatus
- Branching pattern of the conidiophores according to Ju & Rogers (1996)
- Morphology of ostioles and perithecial outlines
- Anatomy of the internal concentric zones of the stromata (in particular ratio of lighter to darker zones)
- Ornamentation of the ascospore perispore by SEM
- Dimensions of conidiophores and conidia
- Stromatal habit (size, shape etc.) is treated as a subordinate character, also in the key, as this may be highly variable in certain species
- Shape of asci did not appear to be a good discriminating character since it is consistently cylindrical. The same applies to paraphyses that are often apparently absent and lack distinctive features

Chemotaxonomic data are strikingly well in agreement with morphological traits, and aside from KOH-extractable pigments, some other compounds like concentrical A (8) which can only be detected by HPLC-DAD and HPLC-MS have proved to be good chemotaxonomic markers. Nevertheless, the secondary metabolites of the stromata themselves are not used as species discriminators; the key for identification presented here is only based on morphological and anatomical traits.

Based on these data, the taxonomic part was organised into six chapters, five of which deal with species groups that we regard as related to one another from a comparison of phenotype-derived features. The sixth chapter comprises descriptions of species with yet unknown affinities, as well as several preliminary descriptions of some single specimens that are obviously representatives of undescribed taxa but do not appear to be suited well to serve as type material. With few exceptions, the molecular phylogeny based on ITS nrDNA data largely supports this concept, and in one case (D. andina) the molecular data even gave hints where to place the respective fungus.

Molecular data (of the ITS rRNA and α-actin and β-tubulin DNA sequences) have also been generated for several species (Kuhnert et al. (2014), Bitzer et al. 2008, Hsieh et al. 2005, Triebel et al. 2005). However, as discussed above, they are not available for a significant number of specimens in most taxa. Moreover, several Daldinia spp. from the tropics have still not even been cultured. Even though the major groups of species are supported by the available phylogenies, molecular data are not considered strongly in the current species concept. Nevertheless, such affinities as inferred from molecular phylogenies have been mentioned in the “Notes” to the respective species groups and species, whenever this was deemed appropriate.
Table 2. Salient characters of the major groups of Daldinia.

<table>
<thead>
<tr>
<th>Group</th>
<th>Perispore dehiscence (KOH)</th>
<th>Predominant stromatal metabolites</th>
<th>Ascospore ornamentation (SEM)</th>
<th>Ascospore shape</th>
<th>Conidiogenesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. concentrica group</td>
<td>+</td>
<td>BNT, concentricols</td>
<td>Species specific (smooth or striate)</td>
<td>Inequilateral; narrowly rounded ends</td>
<td>Mostly holoblastic</td>
</tr>
<tr>
<td>D. eschachtzii group</td>
<td>+/-</td>
<td>BNT, cytochalasins</td>
<td>Species specific (smooth or striate)</td>
<td>Inequilateral; mostly narrowly rounded ends</td>
<td>Holoblastic</td>
</tr>
<tr>
<td>D. graminis/D. sacchari</td>
<td>-</td>
<td>BNT, cytochalasins</td>
<td>Conspicuously striate</td>
<td>Inequilateral; narrowly rounded ends</td>
<td>Unknown</td>
</tr>
<tr>
<td>D. childiae group</td>
<td></td>
<td>BNT, daldinal, daldinalins</td>
<td>Conspicuously striate</td>
<td>Inequilateral; narrowly rounded ends</td>
<td>Holoblastic</td>
</tr>
<tr>
<td>D. vernicosa/loculata group</td>
<td>-</td>
<td>BNT</td>
<td>Smooth</td>
<td>Equilateral to inequilateral; broadly rounded ends</td>
<td>Holoblastic</td>
</tr>
<tr>
<td>D. petriniae group</td>
<td>+</td>
<td>BNT, perylene quinones</td>
<td>Conspicuously striate</td>
<td>Inequilateral; narrowly rounded ends</td>
<td>Anellidic</td>
</tr>
</tbody>
</table>

Data on geographic distribution and apparent host specificity of the stromata are probably incomplete for most species.

**Group A: The Daldinia concentrica group (Figs 20–27)**

The *D. concentrica* group comprises the type species and several related taxa that are typically distributed in mild temperate and subtropical climates of western and southern Europe; some related taxa occur in tropical Africa and in the Southern Hemisphere. They have so far not been found in the Americas and the temperate regions of Asia, despite diligent search. All previous records of “*D. concentrica*” from Asia and America obviously need to be revised.

Their stromata are typically semiglobose to depressed-hemispherical and non-stipitate and may be up to 9 cm across. They feature rather compact, alternating internal blackish or grey and brown concentric zones, and the entostroma does not tend to disintegrate into gelatinous tissue as much as in other species groups, even though stromata of some collections of *D. dennisii* do become loculate with age. Their ascospores are ellipsoid-inequilateral with narrowly rounded ends and have a perispore dehiscence in KOH. SEM of ascospores has been used as a valuable discriminative character in this species complex (Stadler et al. 2002, 2004a, d), confirming earlier results by Van der Gucht (1993) on the utility of such features for species discrimination in *Daldinia*. Additional parameters that can be used to discriminate the less well-known members of this species complex from the European type species, are the size of the ascal apical apparatus, the asci and ascospores, the ratio of width of darker vs. lighter internal concentric zones and the microscopic details of the anamorphs. Their stromatal pigments in KOH are weakly purplish even in immature (SUN).

A synopsis of discriminative characters is provided in Tables 3 and 4. Most species in this group have been described in detail fairly recently (Stadler et al. 2002, 2004a, d), and only one additional species is erected here. The illustrations in the taxonomic part will focus on those aspects that have not been depicted in the preceding papers, where for example, anamorphic structures and SEM characteristics of ascospores have been illustrated extensively, but details of the stromatal morphology and ascal structures as seen by light microscopy were not illustrated at all. New evidence is also presented on the ascospore germ slit morphology of certain species, and a synoptic table is presented to allow for better discrimination. Furthermore, some new evidence on the biogeography and chorology is provided, as are preliminary descriptions of apparently undescribed taxa from the Southern Hemisphere and tropical Africa. We hope that these data will help in locating additional records of these fungi, to allow for their complete characterisation.


**Etymology:** Named for the internal concentric zones of its stromata, which actually gave rise to the erection of the genus.


A POLYPHASIC TAXONOMY OF Daldinia (Xylariaceae)

Table 3. Major discriminative characters of the species in the D. concentrica group. CC: Conidiogenous cells; CON: Conidia; H: holoblastic (or E: annellidic) conidiogenesis; TS: transverse striation. N, V, S, referring to the most frequently observed branching pattern, i.e. nodulisporium-, virgariella- or sporothrix-like, respectively, as defined in Ju & Rogers 1996).

<table>
<thead>
<tr>
<th>Species (Daldinia)</th>
<th>Ascospore size (µm)</th>
<th>Ascospore ornamentation (SEM)</th>
<th>Ascal apical apparatus (µm)</th>
<th>Conidiogenous structures (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>andina</td>
<td>17.5–21.5 × 7–10</td>
<td>Smooth</td>
<td>0.8–1.2 × 3.5–4</td>
<td>Not produced in culture</td>
</tr>
<tr>
<td>concentrica</td>
<td>13–17.5(–18) × (5.5–)6–7.5</td>
<td>Almost smooth</td>
<td>0.5–1 × 3–3.5</td>
<td>CC:10–25 × 3–4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(&lt; 10.000×)</td>
<td>CON: (5.5–)6.5–8(–9) × 3.5–4.5</td>
<td>(H; N)</td>
</tr>
<tr>
<td>dennisii var. dennisii</td>
<td>(13–)16–18(–19) × 6–8(–9)</td>
<td>Smooth</td>
<td>0.75–1 × 4–4.5</td>
<td>CC: 12–21 × 3–4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(&lt; 10.000×)</td>
<td>CON: (6.5–)7–9.5 × 4–5</td>
<td>(H; N)</td>
</tr>
<tr>
<td>dennisii var. microspora</td>
<td>12–15 × 6–8</td>
<td>Smooth</td>
<td>0.5–0.75 × 3.5–4</td>
<td>CC: 12–21 × 3–4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(&lt; 10.000×)</td>
<td>CON: (6.5–)7–9.5 × 4–5</td>
<td>(H; N)</td>
</tr>
<tr>
<td>macaronesica</td>
<td>13–16(–18) × 5–7(–8)</td>
<td>Almost smooth</td>
<td>0.5 × 4–4.5</td>
<td>CC: (9–)12–15 × 3–5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(&lt; 10.000×)</td>
<td>CON: (7.5–)8–9.5(–10) × (3.5–)4–5(–6)</td>
<td>(H; N)</td>
</tr>
<tr>
<td>martinii</td>
<td>14–17(–21) × 6–8(–9)</td>
<td>TS (5.000×)</td>
<td>0.5 × 4</td>
<td>CC: 10–12(–14) × 3–3.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(&lt; 10.000×)</td>
<td>CON: 6.5–8(–8.5) × 2.5–3.5</td>
<td>(H; S, V, N)</td>
</tr>
<tr>
<td>palmensis</td>
<td>(10–)11–13(–14) × 5.5–6.5(–7.5)</td>
<td>TS (2.500×)</td>
<td>Unknown</td>
<td>CC: 12–15 × 3–5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(&lt; 10.000×)</td>
<td>CON: 4–6 × 2–2.5 (–3)</td>
<td>(E/H; S, N)</td>
</tr>
<tr>
<td>raimundi</td>
<td>12–14(–15) × (5–)6–7</td>
<td>TS (5.000×)</td>
<td>0.8 × 3–3.4</td>
<td>CC: 12–20 × 3–4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(&lt; 10.000×)</td>
<td>CON: 7.5–8.5(9.5) × 4–4.5</td>
<td>(H)</td>
</tr>
<tr>
<td>vanderguchtiae</td>
<td>10–14 × 5–7(–8)</td>
<td>Smooth</td>
<td>Unknown</td>
<td>CC: 11–23 × 2.5–3 CON: 7.5–10 × 3.5–5</td>
</tr>
<tr>
<td></td>
<td>(20.000×)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4. Characters relating to stromatal anatomy that may help to discriminate the species of the D. concentrica group, but should only be used in conjunction with micromorphological data.

<table>
<thead>
<tr>
<th>Species (Daldinia)</th>
<th>Ratio of the width of the darker/lighter zones</th>
<th>Osteoles</th>
<th>Perithecia (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>andina</td>
<td>1:0.5–2</td>
<td>Umbilicate</td>
<td>1.5–1.8 × 0.3–0.5</td>
</tr>
<tr>
<td>concentrica</td>
<td>1:2–3</td>
<td>Slightly papillate</td>
<td>1–2.2 × 0.3–0.6</td>
</tr>
<tr>
<td>dennisii</td>
<td>1:4–10</td>
<td>Slightly papillate to papillate</td>
<td>0.8–1.5 × 0.4–0.8</td>
</tr>
<tr>
<td>macaronesica</td>
<td>1:2–5</td>
<td>Slightly papillate</td>
<td>1.2–1.5 × 0.3–0.4</td>
</tr>
<tr>
<td>martinii</td>
<td>1:3–6</td>
<td>Slightly papillate</td>
<td>1–1.5 × 0.3–0.4</td>
</tr>
<tr>
<td>palmensis</td>
<td>1:2–3</td>
<td>Papillate, sometimes porate</td>
<td>0.5–1.5 × 0.2–0.5</td>
</tr>
<tr>
<td>raimundi</td>
<td>1:4–6</td>
<td>Slightly papillate</td>
<td>0.5–1.5 × 0.2–0.5</td>
</tr>
<tr>
<td>vanderguchtiae</td>
<td>1:1.5–2.5</td>
<td>Umbilicate</td>
<td>1.2–1.6 × 0.4–0.5</td>
</tr>
<tr>
<td>MUCL 51268 (Africa)</td>
<td>1:4–10</td>
<td>Papillate, with low rim</td>
<td>1.3–1.7 × 0.35–0.5</td>
</tr>
</tbody>
</table>

≡ Sphaeria fraxinea Sibth., Fl. Oxon.: 401. 1794.  

Selected illustrations: Whalley & Watling (1980), figs 1, 2 (teleomorph and SEM of anamorph); Petruni & Müller (1986); Abb. 40 (anamorph); Van der Gucht (1994), Plates 25 (teleomorph) and 26 (anamorph); Rogers et al. (1999), figs 1–3 (stromata). Wollweber & Stadler (2001); Abb. 5.1–5.4 (teleomorph); Stadler et al. (2002), fig. 1 (SEM of ascospores).
Known distribution/host preference of stromata: Western, central and southern Europe, reaching Denmark in the north; apparently rare in regions with predominantly continental climates, stromata most frequently occurring on *Fraxinus* and, to a lesser extent, *Betulaceae, Fagaceae* and *Salicaceae*. Although the predominant host, *Fraxinus excelsior*, is common in Norway and Sweden there are apparently yet no confirmed records of the species from there.
Teleomorph: Stromata hemispherical to depressed-spherical, widely attached to the substrate, very rarely stipitate, smooth or with inconspicuous perithecial outlines, 2–9 × 2–9 × 1.2–4 cm; surface even or frequently cracked into a fine network, Brown Vinaceous (84), Chestnut (40), or Sepia (63), blackened and somewhat varnished in age; dull reddish brown granules immediately beneath the surface, with KOH-extractable pigments Livid Purple (81) or Dark Purple (36), often rather dilute, especially in fully mature to overmature specimens; tissue between perithecia greyish brown to brown, pithy to woody; tissue below the perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2–0.7 mm thick, lighter zones brown, pithy to woody, persistent, 0.5–1 mm thick. Perithecia lanceolate, 1–2.2 × 0.3–0.6 mm. Ostioles slightly papillate. Asci 210–290 × 8–14 µm, p. sp. 70–100 µm, stipes 110–180 µm, with amyloid, discoid apical apparatus 0.75–1 × 3–3.5 µm. Ascospores brown to dark brown,
ellipsoid-inequilateral with narrowly rounded ends, 13–17.5–(18) × (5.5–)6–7.5 µm, with straight to slightly sigmoid germ slit spore ellipsoid-inequilateral with narrowly rounded ends, 13–17.5(–18) µm, 12095).

Stadler et al. (2001a,b) demonstrated that this fungus is widely distributed, especially in those regions of Western Europe that are under the mild influence of the Atlantic, and that it prefers Fraxinus as host. This was further confirmed by Johannesson et al. (1999), Johannesson et al. (2005). Ceredigion: Lampeter, Falcaldene, Fern Cottage, on dead branches of Prunus serrula, 1 April 2001, M. Rotheroe (KU 84463, culture KC 1687).

Notes: This study and other data provided by Petriù & Müller (1986), Van der Gucht (1994), Rogers et al. (1999), Johannesson et al. (2000) and Stadler et al. (2001a,b) demonstrated that this fungus is widely distributed, especially in those regions of Western Europe that are under the mild influence of the Atlantic, and that it prefers Fraxinus as host. This was further confirmed in this study (see above specimen list), especially with material

*The majority of specimens listed here from Kew were correctly identified by B.M. Spooner and their taxonomy was only confirmed in this study.
from Belgium in BR. Rogers et al. (1999) also reported that *Daldinia* (sensu stricto) is by far the most predominant *Daldinia* sp. in Britain, and the collections they studied from the AJSW herbarium were mostly derived from *Fraxinus*. Among the materials studied for anamorphic structures, only the cultures KC 1693 ex K(M)98806 and KC 1688 ex K(M)91667 differed from the typical form in lacking a nodulisporium–like anamorph on OA, but mostly produced reduced sporothrix–like conidiophores (Fig. 9B, C). Nonetheless, their teleomorphic anamorph on OA, but mostly produced reduced sporothrix–like cultures KC 1693 ex K(M)98806 and KC 1688 ex K(M)91667.

Among *Fraxinus* herbarium were mostly derived from *Daldinia* specimens deposited in German herbaria, despite extensive, D. concentrica last decennia but still without luck. Only immature stromata of this species in southeast Europe and the Mediterranean. The *Fraxinus* reported as the host plant. These cases was here reported from herein. Typical stromata of *Daldinia* are here reported from the herbarium at PAD. Some of his specimens are listed elsewhere of various taxa of obviously included from Northern, Central and Eastern Europe.

2000, Wollweber et al. Previous work (Johannesson Notaris (1863), indeed, corresponds with *Daldinia* CWU revealed that at least one of the records of Cesati & De Notaris, 1863), D. concentrica as preferred host plant for the stromata is therefore to end up in the collections than standard material. The dominance of *Daldinia* sensu stricto from the specimen list above. Interestingly, we even failed to find this species among old specimens deposited in German herbaria, despite extensive, dilligent search (cf. Wollweber & Stadler 2001). All records of *D. concentrica* that were made prior to 1980 correspond with *D. loculata*, *D. petriniae* or other taxa, and the recent records from Mecklenburg-Vorpommern were made in regions that had been monitored intensively by field mycologists for quite a long time. We conclude that this fungus is spreading from the mild climates of the Atlantic Western Europe further northwest.

Notably, it can be misleading to rely entirely on herbarium specimens when host preference is considered. Odd substrates of an otherwise common species (UK situation) are much more likely to end up in the collections than standard material. The dominance of *Fraxinus* as preferred host plant for the stromata is therefore probably even more pronounced than it already becomes evident from the specimen list above.


**Diagnosis:** A *Daldinia grandis* differt ascosporibus regulariter ellipsoideo-inconspicuous. *Daldinia* sensu stricto (Xylariaceae) holotype, ex-type culture CBS 116024, GenBank Acc. No. AM749918).

**Etymology:** For the Andean region of South America.

**Known distribution:** Only known from two collections in Ecuador.

**Teleomorph (holotype):** *Stromata* peltate to turbinate, most often almost flat-topped with a slightly revolute margin and a stout and high stipe, with inconspicuous perithecial outlines, 1.8–4 × 0.8–3.7 × 1.1–4.2 cm; surface Brown Vinaceous (84) to Fuscous (103), deeply wrinkled, dull reddish brown granules immediately beneath surface, with dense KOH-extractable pigments Violet (32) to Livid Purple (81); tissue between perithecia blackish brown, woody; tissue below the perithecial layer very hard-textured and compact, composed of weakly contrasted alternating zones, darker zones blackish, woody, 0.35–0.7 mm thick, lighter zones dark gray, woody, somewhat gelatinous when rehydrated, 0.7–0.8 mm thick. Perithecia lanceolate, 1.5–1.8 × 0.3–0.5 mm. Ostioles umbilicate, inconspicuous. Asci fragmentary, p. sp. 130–150 × 12–13.5 µm, stipes not measured, with amyloid, discoid apical apparatus 0.8–1.2 × 3.5–4 µm. Ascospores dark brown, ellipsoid-inequilateral mostly with narrowly rounded ends, at times slightly crescentic, lacking bevelled ends, 17.5–21.5 × 7–10 µm, with straight germ slit score length on convex side; perispore dehiscent in 10 % KOH, smooth by LM; epispore smooth by LM.

**Additional specimen examined:** Ecuador, Loja Prov., near Loja, ca. 15 km on road towards Vilcabamba, on dicot. trunk across stream in disturbed bamboo dominated wet mountain forest, 2 Aug. 1987, T. Læssøe AAU 59449 (C, culture CBS 114736).

**Stromatal secondary metabolites:** BNT (1) and other binaphthalene derivatives prevailing.

**Cultures:** See Stadler et al. (2004d) as *D. grandis*. Anamorph not produced in culture.

**Notes:** The holotype collection was first assigned to *D. grandis* due to its fairly large stromata and large ascospores, but a closer examination and comparison with the paratype of *D. grandis* showed they markedly differ in stromatal shape and the reaction of the perispore to KOH. While in *D. grandis* the perispores are indehiscent, which was confirmed by observation of several other relevant collections of this taxon, the perispores of the present material from Ecuador are clearly dehiscent and fairly thick. Moreover, ascospores of *D. andina* are more inequilateral and more regular in shape than those of *D. grandis* and never exhibit bevelled ends as in *D. grandis* and related taxa. The stromata of *D. andina* appear distinctive in this collection in being flat-topped, highly stipitate and very hard-textured with a blackish faintly zonate interior but these characters are different in *AAU 59449*, illustrating how some morphological characters may vary with environmental conditions and state of development. The specimen *AAU 59449* showed an identical HPLC profile, the same morphology of cultures and ascospores and an identical ITS sequence. However, it deviates from the holotype in having a sessile stroma with surface faintly roughened by slightly papillate ostioles, a soft-textured fibrous interior and paler brown ascospores with perispore readily dehiscent in SDS. Presumably, these deviating characters are due to the slightly overmature state of the stroma.

The frequent presence of somewhat equilatral ascospores with broadly rounded ends and dehiscent perispore being the
main character that members of the vernicosa-foculata group have in common, it appears impossible to assign this new species to this group, but the combination of characters we observed sets it apart from any of the groups we circumscribed herein. In our studies of Daldinia spp. from high altitudes in the tropics, we have often come across apparently rare and undescribed taxa, which might have evolved in the course of geographic isolation. It is important to state here that in absence of characteristic features linking it to any other group, D. andina is tentatively placed in the concentrica group based on molecular results.

*Etymology:* Named for the British mycologist, R.W.G. Dennis.

**Typus:** Australia, New South Wales, West Pennant Hills, Cumberland, S.F., *Pittosporum undulatum*, 30 Jul. 2001, P. O’Hara ex herb. J.A. Simpson 142.01, Ww 3954 (DAR 76506 holotype; M isotype; ex-type culture CBS 114741).

Additional specimens examined: Australia, Lord Howe Island, Middle Beach, toward Vaildon Guest House, on dead stump, 13 Sep. 1963, A.C. & H.M. Beaucheloe 170 (K[M] 61442); New South Wales, West Pennant Hills, Cumberland State Forest, Eleocarpus reticulatus, 31 Jul. 2001, J.A. Simpson 143.01, Ww 3953 (DAR 76505, culture CBS 114742), New Zealand, Bay of Plenty, near Ruaatuhara, Tarapounamu, Beilschmiedia tawa, 3 Dec. 2006, B.C. Paulus et al. AOD 1 as *D. childiae* (PDD 93635, culture ICMP 18262); Mid Canterbury, Christchurch, wood, J. Mitchell, Lloyd herb No 11795, det. M. Child (1932) as *D. grandis* (BPI 717052); South Canterbury, Geraldine, Talbot Reserve, fallen wood, 14 May 2000, P.R. Johnston & R.E. Beever (PDD 71607); South Island, Bank’s Peninsula, 1874, S. Berggren (UPS); Wellington, Lake Papetonga, Myoporum laetum, Oct. 1930, G.H. Cunningham (BPI 594617).

*Notes:* This species was typified, based on material from Australia, but it seems to be widely distributed in New Zealand as well. We assume that a great percentage of specimens previously reported as *D. concentrica* from this geographic region will turn out to correspond to *D. dennisii* var. *dennisii*, once a critical revision of the material has been carried out. We agree with *Ju et al.* (1997) that the type of *H. simile* is rather depauperate. They had tentatively referred it to *“D. concentrica“* (*i.e.* *D. chidiae sensu* Rogers *et al.* 1999). However, we found that the HPLC profile of the type material did not reveal typical daldinin and daldinal derivatives as usually encountered in *D. chidiae* (see Studler *et al.* 2001a; cf. figs 1, 6, 7). Only traces of BNT (1) were detected, and the ectostroma yielded a faint purplish colour in KOH. Since the morphology and size range of the few spores observed agreed with that of *D. dennisii* var. *dennisii* (*i.e.* 14–17 × 7–8 μm with broadly to narrowly rounded ends and dehiscent perispore), we regard *H. simile* as a probable synonym of the latter name. Anamorphic and chemical characters are the same as in var. *microspora* as discussed below.


*Etymology:* Refers to the smaller ascospores as compared to the typical variety.


**Holotypus:** Australia, Graemere, O’ Shenesy (PAD).

Additional specimens examined: *Federal States of Micronesia*, Caroline Islands, Yap, north of Parafi, on dead, burnt logs, 27 Feb. 1948, C.C.Y. Wong 549 (NY); same label, rev. J.H. Miller as *D. bakeri* (BPI 594956); same label, det. J.D. Rogers as *D. eschscholtzii* (FH 79488). *French Polynesia*, Tahiti, Tatau,
on dead coconut (Cocos nucifera), May 1922, H.E. Parks ex Lloyd herb. 12394 (BPI 715026; see Child 1932 as D. eschscholtzii). New Zealand, Auckland, Tiritiri-Matangi Island, Wattle Trail, Acacia, 9 Dec. 2001, C. Deeley (PDD 74610); Tiritiri-Matangi Island, cf. Acacia, 27 Oct. 2000, P.R. Johnston (PDD 71921); Waiheke Island, Whakanewha Regional Park, wood, 21 Nov. 2002, P. White PW 91 (PDD 76657, culture CBS 116733, ICMP 15776); Christchurch, wood, J.

---

**Fig. 23.** Teleomorphic characteristics of Daladnia dennisii var. dennisii (Ww 3953; A–F), D. dennisii var. microspora (PDD 81346; G–M) and Daladnia sp. (PDD 87953; N–P). A, G. Stromatal habit. B, C, H, I, N. Stroma in longitudinal section showing internal concentric zones and perithecial layer. B, I, N (inserted). Stromatal pigments in 10 % KOH. J. Stromatal surface with ostioles. D, K, P. Ascospores in SDS. E. Ascospores in KOH, showing dehiscing perispore. F, M. Ascospores by SEM (10.000×). O. Anamorphic structure in 1 % SDS. Scale bars A, B, G, H, N = 1 cm; J = 5 mm; C, I = 1mm; D, E, K, L, O, P = 10 µm; F, M = 5 µm.
A polyphasic taxonomy of Daldinia (Xylariaceae)

Notes: Unlike the typical variety, D. dennisii var. microspora is here shown to have a wider geographic distribution than reported by Studer et al. (2004d). It is not restricted to Australia and New Zealand but proved to be more widely distributed in the Southern Hemisphere, including, e.g., some Pacific islands and even South Africa. One of the specimens from that country (Ww 3982) was cultured, and its anamorph showed only minor differences to that of D. dennisii var. dennisii [conidiogenous cells 14–21 × 2.5–3.5 µm and conidia 7–9.5 µm vs. 2.5–3–6 µm in Ww 3982 vs. 14–18 × 3–3.5 µm vs. (6.5–)7–9.5 × 4–5 µm in D. dennisii var. dennisii]. The exsiccate "de Thümen Ww 3892", same locality, Beilschmiedia tawa, 15 Oct. 2003, P.R. Johnston, immature (PDD 83499); same locality, Beilschmiedia tawa, 15 Apr. 2004, P.R. Johnston (PDD 81345); Te Urewera, Ruarahuna, just before Te Waiti, Beilschmiedia tawa, 14 Oct. 2003, P.R. Johnston (PDD 81346); same locality, 4 Dec. 2006, B.C. Paulus & P.R. Johnston BCP 4326 (PDD 92220, culture ICMP 16284); near Ruarahuna, Te Waiti, 17 May 2006, B.C. Paulus & P.R. Johnston BCP 3718 (PDD 92967, culture ICMP 18261); Marlborough, Marlborough Sounds, 21 Jan. 1988, R.E. Beever Reb 794 (PDD 55100); Mid Canterbury, Governor's Bay, Forest & Bird Arboretum, Nov. 2002, P. White PW 92 (PDD 76710, culture CBS 116734, ICMP 15775); Northland, Poor Knights Island, Tawihiti Rahi, The Bluffs, Nestegis apetale, 22 Apr. 1991, R.E. Beever Reb 1139 (PDD 59178); Wellington, Wairarapa, 15 Aug. 1919, G.H. Cunningham (BPI 594616); Wellington, Myersine salicina, 28 Aug. 1977, T. Aldridge ex herb. G. Stevenson GS 330 (PDD 90481).

Republic of South Africa, Western Cape, Tsitsikamma, near "Big Tree", on cf. Podocarpus in Podocarpus forest, 16 Feb. 2000, V. Kummer, Ww 3982 (KR, culture CBS 114485, MUC 45011); Somerset East, near the Cape of Good Hope, on dead trunks, 1875–1876, MacOwan & Tuck, de Thümen, Mycothea universalis No. 698 as D. concentrica (B–7 00009631, FH 220992, M–0079882; 2 packets in NY); near Cape of Good Hope ("Kapland"), no date, Ecklon & Zegher (B70 000958).

Solomon Islands, inland from Empress Augusta Bay, west side of Bougainville, 6 May 1944, C.T. Rogerson (131) 3372 (NY); same locality, C.T. Rogerson (147) 3370 (NY, duplicate in CUP 34309, n.v.).

Some studies examined were generally found in agreement with D. dennisii var. microspora with respect to their stromatal morphology, but showed deviations in their microscopic characters and their pigment profiles, respectively. Their characteristics are here:

a) Two specimens from Pacific islands [Tonga, Vava’u, Cocos nucifera, 19 Feb. 1977, R.A. Maddison (PDD 39800). French Polynesia, Society Islands, Tahiti, West coast, Paea, 8 Dec. 1978, R.W.G. Dennis (K(M) 130239; similar to PDD 39800, wood deposited with the specimen probably a palm species), presumably both derived from palms, appeared morphologically similar to D. dennisii var. microspora. However, they differed in having Olivoaceous (48) pigments in KOH, owing to the presence of daldinone A (3), which was found prevailing in their stromata besides small amounts of BNT (1). Cytochalasins and concentricols (8) were not detected in their HPLC profiles. The only other Daldinia species with concentric zones that contains such large amounts of daldinone A (3), is D. albofibrosa, even though D. placentiformis, as well as some species of Annulohypoxylon and Hypoxylon also contain daldinone A (3) as major stromatal metabolite (cf. Hellwig et al. 2005, Quang et al. 2005; where Annulohypoxylon was still referred to as "Hypoxylon sect. Annullata."). However, none of the above specimens from the Pacific would serve as type material, and no anamorph was seen on the stromata of the depauperate, unculturable materials. Therefore, no new name for the palmicolous Daldinia is provided as yet, but we report its characteristics in the hope that it might be recognised soon in this geographic region in the living state. Interestingly, Child (1932) also reported D. eschscholtzii from coconut in Polynesia, which could relate to the current specimens as well. Since these specimens were lacking the chemotaxonomic marker, concentricol A (8), it even remains unclear whether they belong to the D. concentrica group; however they also bear little resemblance to the species known from monocots.

b) Another specimen collected in New Zealand: South Canterbury, Geraldine, Talbot Reserve, 29 Jan. 2006, P.R. Johnston (PDD 87953, cultures ICMP 18265, isolated by MS and ICMP 16408, isolated by the collector, n.v.) featured large stroma up to 60 mm diam, with compact interior (Fig. 23N) reminiscent of a member of the D. concentrica group, and purplish pigments in KOH. Its ascospores (Fig. 23P) measure 12.5–16(–17.5) 6–7 µm, and are rather variable in size, sometimes twisited. The anamorph in culture and on stroma (Fig. 23O) revealed short and broad conidiogenous cells, 12–15 × 3.5–4 µm, with conidiogenous structures sporothrix-like or virgariella-like, and ellipsoid conidia (6–6.5 × 3.5 µm) with a broadly truncate base. This fungus appears to be intermediate with respect to the discriminative characters of the teleomorph and can, therefore, not be assigned to one of the known varieties of D. dennisii. In addition, it clearly shows deviations with respect to its anamorphic morphology and might eventually be recognised as a separate taxon. The ITS nrDNA data (see below), however, are not significantly different from those of other taxa in this group.

**Etymology:** For its area of distribution.

**Types:** Spain, Canary Islands, Tenerife Prov., Isla de La Palma, Cubo de La Galiga, on wood and bark of a trunk of *Ocotea foetens*, Jun. 2002, J.M. Castro, *WW 4196* (M-holotype; KR (previously WUP) isotype).

**Selected illustrations:** Stadler et al. (2004a), figs 1 (stromata), 6, 7 (ascospores by SEM), 16–18 (anamorph).

**Known distribution/host preference of stromata:** Macaronesian Islands (Canary Islands, Madeira, Azores), frequently on *Ocotea foetens* and other endemic Lauraceae.

**Teleomorph:** Stromata semiglobose to depressed-spherical, 4.5–8 × 2.5–6 × 1.5–3.5 cm; stromatal surface reddish brown in young stromata, blackening with age, almost smooth, brown, with inconspicuous perithecial outlines; ectostroma easily detachable in aged specimens, not cracked into a fine network in any of the specimens examined; with dull reddish brown granules immediately beneath the surface and with KOH-extractable pigments Vinaceous Purple (101); tissue between perithecia of alternating zones, darker zones dark greyish brown, pithy to woody, 0.2–0.6 mm thick, lighter zones white or cream to light brown, somewhat gelatinous when fresh but very hard when dry, becoming pithy to woody, or loculate with age, 0.4–0.8 mm thick, 0.1–0.3 mm thick, lighter zones white or cream to light brown, somewhat gelatinous when fresh but very hard when dry, becoming pithy to woody, or loculate with age, 0.4–0.8 mm thick (Ratio darker/lighter zones 1:2–5).

**Asci:** 16–18 (anamorph).**

**Notes:** *Daldinia macaronesica* appears closely related to *D. concentrica*, from which it mainly differs in its ascospore morphology, and in the dimensions of its nodulisporium-like conidiophores (Stadler et al. 2004a; Table 3). This fungus was hitherto only found on the Macaronesian Islands, where its stromata are mostly associated with endemic Lauraceae. It is here for the first time reported from the Azores, Gran Canaria and La Gomera on similar hosts.

**Daldinia martini** M. Stadler, Venturella & Wollw., Mycol. Res. 108(3): 263. 2004. Fig. 24H–M.

**Etymology:** For the American mycologist P.W.D. Martin.


**Selected illustrations:** Stadler et al. (2004a), figs 2 (stromata), 8, 9 (ascospores by SEM), 19–22 (anamorph).

**Known distribution/host preference of stromata:** So far identified from southern Europe, northern Africa and northern India, no apparent host specificity.

**Teleomorph:** Stromata up to 5 × 3.5 × 2.5 cm, semiglobose, sessile or subsessile; surface at first vinaceous brown, blackening with age and frequently cracked into a fine network, with inconspicuous perithecial outlines; with dull reddish brown granules immediately beneath surface and with KOH-extractable pigments dilute, Livid Purple (81) or Vinaceous Purple (101); tissue between perithecia brown, pithy to woody and below the perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2–0.6 mm thick, lighter zones light brown, gelatinous when fresh but very hard when dry, becoming pithy to woody, persistent, 0.4–1.6 mm thick. (ratio lighter/darker zones: 3–6:1). *Perithecia* lanceolate, 1.2–1.5 × 0.3–0.4 mm. Ostioles slightly papillate. Asci 230–310 × 10–15 μm, p. sp. 90–120 μm, stipes 130–200 μm, with amyloid, discoid apical apparatus 0.5 × 4–4.5 μm. Ascospores dark brown, ellipsoid-equilateral or ellipsoid-inequilateral, with narrowly rounded ends, 13–16 (18) × 5–7 (8) μm, with straight or slightly sigmoid germ slit, silt spore length or nearly spore length on convex side of inequilateral spores; perispore dehiscent in 10% KOH; appearing smooth by LM, faint transverse ridge-like ornamentations by SEM only becoming visible at 10 000× magnification (Stadler et al. 2004a).

**Cultures and anamorph:** Colonies on OA reaching the edge of 9 cm Petri dish in 6 d, whitish, felt, azonate, with diffuse margins, becoming Smoke Gray (105); reverse Dull Green (70); sporulating regions scattered over entire surface of colony, Smoke Gray (105). Conidiogenous structure nodulisporium-like; conidiophores mononematous, stout, di- or trichotomously branched, sometimes with additional branches arising from the first level of conidiogenous regions, hyaline, finely to coarsely roughened, up to 80–100 × 3–4 μm, with two to three conidiogenous cells arising from each terminus. Conidiogenous cells cylindrical, hyaline, smooth or finely roughened, (9–)12–15 × 3–5 μm. Conidia produced holoblastically in sympodial sequence, hyaline, smooth to finely roughened, dacyroid to ellipsoid, mostly with flattened base, (7.5–)8–9.5 (10) × (3.5–)4–5 (6) μm.

slit spore length on convex side; perispore dehiscent in 10 % KOH, appearing smooth by LM, faint transverse striations on perispore becoming visible by SEM at 5,000× magnification.

*Cultures and anamorph:* Colonies on OA reaching the edge of 9 cm Petri dish in 6–7 d, whitish, felty, azonate, with diffuse margins, becoming Smoke Gray; reverse initially Dull Green (70), blackening with age; sporulating regions at first appearing at the margins, later scattered over entire surface of colony, Smoke Gray (105). *Conidiogenous structures* highly variable, ranging from sporothrix-, virgariella- or the more complex nodulisporium-like type; nodulisporium-like conidiophores mononematous, di- or trichotomously branched, sometimes with additional branches arising from the first level of conidiogenous regions, hyaline, finely to coarsely roughened, 100–150 × 3–4 µm, with two to four conidiogenous cells arising from each terminus; virgariella-like conidiophores dichotomously branched, with one or two conidiogenous cells arising from each terminus, same size; sporothrix-like conidiophores up to 80 µm long, unbranched, usually with a single, terminal conidiogenous cell. *Conidiogenous

---

Fig. 24. Teleomorphic characteristics of *Daldis panamanica* (holotype; A–G) and *D. martinhoi* (IF-10016; H–M). A, H. Stromatal habit. B, C, I. Stroma in longitudinal section showing internal concentric zones and perithecial layer. D, J (inserted). Stromatal pigments in 10 % KOH. E, K. Ascospores in SDS. F, L. Ascospores in KOH, showing dehiscing perispore. G, M. Ascospores by SEM (10,000×). Scale bars A, B, H, I = 1 cm; D = 5 mm; C, J = 1 mm; E, F, K, L = 10 µm; M = 5 µm; G = 2 µm.
cells in all these stages similar, cylindrical, hyaline, smooth or finely roughened, 10–12–(14) × 3–3.5 µm; conidia produced holoblastically in sympodial sequence, hyaline, smooth to finely roughened, dacryst to ellipsoid, mostly with flattened base, 6.5–8–(8.5) × 2.5–3.5 µm.


Notes: This species appears closely related to D. concentrica, from which it mainly differs in having larger ascospores with more conspicuous ornamentation by SEM, and in its anamorphic morphology, with a greater variability of conidiophore branching types (Table 3; Stadler et al. 2004a). The collections listed from Algeria, Ceuta and India were morphologically similar but their determination is based on teleomorphic characters only and they were not in a particularly good shape when studied by us. Curiously, Child (1932) listed the Algerian specimen as D. eschschoitzii, despite its ascospores being significantly larger than allowed in her species description. Daldinia macaronica is the only unnamed taxa from tropical Africa described at the end of this chapter, are further examples of members of the D. concentrica group that occur on this continent.


Etymology: For the Canarian Island (San Miguel de) La Palma.


Selected illustrations: Stadler et al. (2004a), figs 3 (stromata), 12 (ascospores by SEM), 23–26 (anamorph).

Known distribution/host preference of stromata: Monotypic, from Laurus on the Canary Islands.

Teleomorph: Stromata semiglobose, sessile, 1–2 × 1–2 × 1–1.5 cm, stromatal surface at first reddish brown to vinaceous brown, blackening with age, with inconspicuous perithecial outlines; with dull reddish brown granules immediately beneath surface and with KOH-extractable pigments dilute Vinaceous Purple (101); tissue between perithecia brown and below the perithecial layer composed of alternating zones darker zones vinaceous brown, pithy to woody, 0.2–0.4 mm thick, lighter zones white to cream, gelatinous in fresh stage and very hard when dry, becoming pithy to woody, persistent, 0.3–0.6 mm thick (Ratio darker/lighter:zones 1:2–5). Perithecia lanceolate, 0.5–1.5 × 0.2–0.5 mm. Ostioles slightly papillate to porate and surrounded by a low rim in places, most likely due to the overmature state. Asci not observed. Ascospores brown, ellipsoid–inequilatorial with broadly to narrowly rounded ends, (10–)11–13–(14) × 5.5–6.5(–7.5) µm; germ slit straight or slightly sigmoid, spore length or slightly less than spore length, located on the more convex side of the inequilateral spores; perispore dehiscent in 10 % KOH, smooth; appearing smooth by LM, but showing conspicuous transverse striations by SEM (2.500–5.000×)

Cultures and anamorph: Colonies on OA reaching the edge of 9 cm Petri dish in 9 d, whitish, felty, azonate, with diffuse margins, becoming Smoke Gray (105) with slight olivaceous tone; reverse Citrine (13) or remaining uncoloured; sporulating regions scattered over entire surface of colony, Smoke Gray (105). Conidiogenous structure of the sporothrix- or, more frequently nodulisporium-like. Conidiophores unbranched (sporothrix-like) or di- or trichotomously branched (nodulisporium-like), sometimes with additional branches arising from the first level of conidigenous regions, hyaline to yellowish, finely to coarsely roughened, 55–100 × 3–4 µm, with two to three conidigenous cells arising from each terminus; aged conidiophores and hyphal strands tending to develop characteristic thick-walled swollen hyphal cells, somewhat reminiscent of arthroconidia, but no disintegration observed. Conidiogenous cells cylindrical, hyaline, finely roughened, 12–15 × 3–5 µm. Conidia mostly produced holoblastically in sympodial sequence, or, less frequently, produced from percurrently proliferating conidigenous cells, hyaline, smooth to finely roughened, ellipsoidal, with flattened base, 6.5–7 × 4.5–5 µm. Conidiophores on stromata sporothrix-like only, slightly smaller. Conidia 4–6 × 2–2.5 (–3) µm.

Notes: This species differs from D. concentrica and D. macaronica in having smaller ascospores bearing a conspicuously striate perispore by SEM, and from D. dennisi var. microspora, D. eschschoitzii, D. raimundi and other taxa with similar ascospore morphology, in producing a different anamorph in culture. It is the only species within this group of which annellidic conidiogenesis has so far been observed. This would suggest affinities to the D. petriniae group, but HPLC profiles and morphological traits of the teleomorph clearly point toward it being more closely related to D. concentrica (Stadler et al. 2004a). We have meanwhile studied numerous specimens from various Macaronesian islands, but a second record of this species still remains to be encountered. The frequent Daldinia species of the laurisilva is D. macaronica.


Etymology: For the Italian botanist, Francesco Maria Raimondo.


Selected illustrations: Stadler et al. (2004a), figs 4 (stromata), 13 (ascospores by SEM), 27–28 (anamorph).

Known distribution/host preference of stromata: Southwestern Europe and Mediterranean, on Quercus ilex and related species.

40
**Teleomorph:** Stromata subglobose, sessile, 3–4 × 3–4 × 2–3 cm; surface purplish brown in young stromata, later often becoming shiny, dark brown and finally blackening, with inconspicuous perithecial outlines; tissue between perithecia brown, pithy to woody and below the perithecial layer composed of alternating zones, darker zones dark vinaceous brown, pithy to woody, 0.1–0.25 mm thick, lighter zones white to greyish brown, slightly gelatinous when fresh but becoming very hard when dry, becoming pithy to woody, persistent, 0.8–1.5 mm thick (Ratio lighter/darker zones ca. 4–6:1). Stromatal pigments in KOH dilute, Greyish Lavender (98), Vinaceous Grey (116) or Purplish Grey (128). Perithecia lanceolate, 0.5–1.5 × 0.2–0.5 mm. Ostioles slightly papillate. Ascii 205–225 × 8–9 µm, p. sp. 80–85 µm, stipes 120–150 µm, with amyloid, discoid apical apparatus 0.8 × 3–3.4 µm. Ascospores brown, slender, ellipsoid-inequilateral, mostly with narrowly rounded ends, 12–14(–15) × (5–)6–7 µm; germ slit straight, spore length or slightly less than spore length, located on the more convex side of the spore; perispore dehiscent in 10 % KOH, smooth by LM, showing conspicuous transverse striations by SEM, clearly visible at 5.000× magnification.

**Cultures and anamorph:** Colonies on OA reaching the edge of 9 cm Petri dish in 7–10 d, whitish, felty, azonate, with diffuse margins, becoming Smoke Gray (105) with olivaceous tones; reverse Dull Green (70); sporulating regions scattered over entire surface of colony, Smoke Gray (105). Conidiogenous structures

---

**Fig. 25.** Teleomorphic characteristics of *Daldinia palmensis* (Holotype Ww3518: A–F) and *D. raimundii* (JF-08099 (France): G–L). A, G. Stromatal habit. B, H. J. Stroma in longitudinal section showing internal concentric zones and perithecial layer. C, I. Stromatal surface. I. (inserted): Stromatal pigments in 10 % KOH. D, K. Ascospores in SDS. E, L. Ascospores in KOH, showing dehiscing perispore. F. Ascospores by SEM (10,000×). Scale bars A, B, G, H = 1 cm; J = 2 mm; C, I = 1 mm; D, E, K, L = 10 µm; F = 2 µm.
nudulisporium-like. *Conidiophores* mononematous or sometimes synnematous, di- or trichotomously branched, sometimes with additional branches arising from the first level of conidiogenous regions, hyaline to yellowish, finely to coarsely roughened, 100–150 × 3–4 µm, with two to three conidiogenous cells arising from each terminus; conidiogenous cells cylindrical, hyaline, finely roughened, 12–20 × 3–4 µm. *Conidia* produced holoblastically in sympodial sequence, hyaline, smooth to finely roughened, dacryoid or, less frequently, ellipsoid with flattened base, 7.8–8.5 × 4–4.5 µm.


**Notes:** *Daldinia raimundi*, first described from Sicily, has now been encountered in France, where it may have followed its typical host (*Q. ilex*), and on the island of Cyprus, suggesting that the species may be more frequently found in warmer climates of Europe and the Mediterranean. We have found numerous additional specimens in the holm oak forests of the Ile de Ré during forays in 2006 and 2008, of which only some representatives, which were cultured and deposited in public collections, are listed here. Its characteristic features are ascospores slightly smaller than in *D. concentrica*, lack of the characteristic cracked surface in mature specimens as pointed out for the latter species by Rogers et al. (1999), and a slightly different anamorph (Stadler et al. 2004a). However, the most striking difference between these two species is the more conspicuous ornamentation on the ascospore perispore of *D. raimundi* by SEM. We have meanwhile found that the ascospores may attain 1 µm longer in average than in the type material, based on studies of additional specimens. The first material found from Sicily showed ascospores that were almost like those of *D. eschscholtzii* (Stadler et al. 2004a). Recent results suggest that the host specificity and geographic distribution of *D. concentrica* is in fact overlapping, and so are the ascospore sizes in both species.


**Etymology:** For the Belgian mycologist, Katleen Van der Gucht.


**Selected illustrations (all from holotype):** Stadler et al. (2002), fig. 3, as *Daldinia* sp. Ww 3378 (ascospores by SEM); Stadler et al. (2004a), figs 5 (stromata), 14 (ascospores by SEM), 29–32 (anamorph).

**Known distribution/host preference of stromata:** Great Britain, so far recorded from *Aceraceae*, *Fagaceae* and *Rosaceae*.

**Teleomorph:** Stromata semiglobose to depressed-spherical, 2.5–4.5 × 2–4 × 1.5–3.5 cm. Stromatal surface smooth, without visible perithecial outlines, brown, blackening and becoming varnished with age. Dull reddish brown granules immediately beneath surface, with KOH-extractable pigments dilute Livid Purple (81) or Vinaceous Purple (101), almost without pigment in mature specimens. Tissue between perithecia brown, pithy to woody; tissue below the perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.1–0.5 mm thick, lighter zones light brown, gelatinous and very hard when dry, becoming pithy to woody, persistent, 0.4–1 mm thick (ratio lighter/darker zones: 1.5–2–5 : 1). *Perithecia* lanceolate, 1.2–1.6 × 0.4–0.5 mm. *Ostioles* umbilicate. *Asci* not observed. Ascospores brown to dark brown, unicellular, ellipsoid-inequalular or, less frequently, ellipsoid-equilateral, with narrowly or, less frequently, broadly rounded ends, 10–14 × 5–7 (–8) µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, appearing smooth by both LM and SEM (up to 12.000×).

**Cultures and anamorph:** Colonies on OA reaching the edge of a 9 cm Petri dish in 8–9 d, whitish, felty, azonate, with diffuse margins, becoming grey with olivaceous tone; reverse at first Citrine (13), blackening with age. Sporulating regions scattered over entire surfaces of colony, Smoke Gray (105). Conidiogenous structure variable, mostly virgariella-like, rarely approaching nudulisporium-like. *Conidiophores* of the virgariella-like type always strictly dichotomously branched, resulting in two dominant main axes. Sometimes additional branches arising from the first level of conidiogenous regions and terminating in a second level of conidiogenous regions; but no intercalary production of conidia observed. *Conidiophores* 120–200 µm long and 3–3.5 µm diam, hyaline, finely to coarsely roughened, with one or two conidiogenous cells arising from each terminus. *Conidiogenous cells* cylindrical, hyaline, finely roughened, 11–23 × 2.5–3 µm, with apical scars. *Conidia* produced holoblastically in sympodial sequence, hyaline, smooth to finely roughened, ellipsoid, with flattened base, 7.5–10 × 3.5–5 µm; conidia on stromata slightly smaller; (4–)5–8 × (3.5–)4–5 µm.


**Notes:** This species differs from *D. concentrica* by having smaller ascospores, which are smooth by SEM even at higher magnifications (Stadler et al. 2004a), it does not come as a great surprise to encounter this fungus in England as well (see additional specimens). In addition, its anamorph features smaller conidia and conidiophores, and the stromata have so far not been found on *Fraxinus* or *Salicaceae*. In contrast to *D. eschscholtzii*, the stromata contain concentricols (8) and lack cytochalasins (9) as major metabolites, and the ascospores lack the characteristic coil-like ornamentation by SEM (Fig. 26F). Molecular data (see Results section on molecular phylogeny) also revealed that it is related more closely to *D. concentrica* than to *D. eschscholtzii*.

**New records of the Daldinia concentrica group from Africa**

In our search for further members of the *D. concentrica* group, we came across some interesting materials from tropical Africa. Their characteristics did not match any of the above described species, and they may eventually be shown to correspond to additional species of this complex, once additional, living material becomes available. Interestingly, they were all found at rather high elevations where the climate is not typically tropical. Possibly, these African specimens constitute further segregates
of the *D. concentrica* group, which are derived from once world-wide occurring populations but now restricted to mountainous regions in tropical Africa.

a) A specimen from the Democratic Republic of the Congo, North Kivu, Mt. Rwenzori, area of the WWF-ICCN Kalonge altitude chalet, about 00°33,961' N – 29°81,795' E, between 2138–2400 m alt., mountain tropical forest, 3–5 Feb. 2008, C. Decock, STMA 08019 (culture and specimen in MUCL 51268) is reminiscent of *D. concentrica*. Its characteristics are reported below (Figs 4E, 27A–G): Stromata semiglobose to depressed spherical, 4–5.5 × 2.8–3.5 cm, widely attached to the substrate; surface dull Brown Vinaceous (84), even, consisting of a thin crust 60–80 µm thick of dull red brown granules yielding Livid Violet (79) pigments in 10 % KOH. Interior loosely fibrous, grey brown, composed of alternating light and darker zones, lighter layers 1.3–2 mm thick, lacunose, darker layers 0.3–0.5 mm thick, more compact. Ostioles papillate, slightly raised with a low rim, 70–80 µm diam. *Perithecia* lanceolate, 1.3–1.7 × 0.35–0.5 mm. Asci not seen. *Ascospores* 12.5–15.5 × 6–6.8 µm, ellipsoid-inequalateral with narrowly rounded ends, brown, smooth, with a straight germ slit on the more convex side, spore length to often much shorter; perispore dehiscent in 10 % KOH and at times even in water, thin and fragile, smooth.

Fig. 26. Teleomorphic characteristics of *D. vanderguchtiae*. A–F: Holotype Ww 2378 (UK), G–L, K(M) 156281 (UK). A, G, H. Stromatal habit. B. J. Stroma in longitudinal section showing internal concentric zones and perithecial layer. C, I. Stromatal surface. I. (inserted): Stromatal pigments in 10 % KOH. D, K. Ascospores in SDS. E, L. Ascospores in KOH, showing dehiscing perispore. F. Ascospore by SEM (10,000×). Scale bars A, B, G, H, J = 1 cm; C = 1 mm; I = 0.5 mm; D, E, K, L = 10 µm; F = 2 µm.
Fig. 27. Teleomorphic characteristics of *Daldinia* sp. A–G. STMA 08019 (Congo). H–N. *Daldinia* sp. (Rammeloo 7094, H–M. Rammeloo 7147) (Malawi). A, H. Stromatal habit. B, D, I, J. Stroma in longitudinal section showing internal concentric zones and perithecial layer. C, K. Stromatal surface with ostioles and stromatal pigments in 10 % KOH (inserted). E, L. Ascospores in SDS. F, G, M. Ascospores in KOH, showing dehiscing perispore and germ slit. N. Ascospore by SEM (10,000×). Scale bars A, B, H, I = 1 cm; C, D, J, K = 1 mm; E, F, G, L, M = 10 µm; N = 2 µm.
b) Another specimen from Ethiopia: Shewa Prov., Oromoa, Ginchi, Jul. 2003, C. Decock, STMA 03W20 (culture and specimen in MUCL 45434) was immature, with only a few ascospores in the same size range as the above described specimen STMA09019 and its stromata were generally in agreement with it. The cultures produced a nodulisporium-like anamorph, which was actually reminiscent of D. concentrica, except for the conidigenous cells (15–25 × 3.5 µm vs. 10–25 × 3–4 µm in D. concentrica) and conidia (7–10 × 4–5 µm vs. 6.5–8 × 3.5–4.5 µm) being slightly larger. Furthermore, the Ethiopian culture (albeit not the culture of MUCL 51268) readily produced immature stromata on OA (Fig. 4F).

c) Three specimens all collected in Malawi, Mt. Mulanje, near Linje stream, mountain rain forest with Widdringtonia whytei, Nov. 1981, J. Rammeloo 7094 (BR–Myco 003525,60); same locality, 5 Nov. 1981, J. Rammeloo 7147 (BR–Myco 033526,61); same locality, 11 Nov. 1981, J. Rammeloo 7337 (BR–Myco 032700,11), also resemble D. concentrica, showing the following characteristics (Figs 4E, 27H–N):

Stromata semiglobose, 1–3 × 1–2.5 cm, widely attached to the substrate to substipitate; surface without conspicuous perithecial outlines, covered with a reddish-brown pruina, blackened and varnished with age, frequently cracked into a fine network, with dull reddish brown granules immediately beneath surface, with KOH-extractable pigments Livid Purple (81); tissue between perithecia brown, pithy to woody; tissue below the perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.1–0.2 mm thick, lighter zones light brown, persistent, 0.3–1.1 mm thick, 3–6 times thicker than the darker ones. Perithecia lanceolate, densely crowded, 0.9–1.2 × 0.35–0.6 mm. Ostioles slightly papillate. Asci fragmentary, p. sp. 72–93 × 10–14 µm, with amyloid, discoid apical apparatus, 0.5–0.75 × 2.75–3.25 µm. Ascospores dark brown, unicellular, ellipsoid, slightly inequilateral to equilateral with broadly to narrowly rounded ends, (13–)16–18 × (6–)7–8(–9) µm, with straight germ slit spore length on more convex side of the spore; perispore dehiscent in 10 % KOH; showing conspicuous transverse striations by SEM (12.000x).

These specimens resemble most closely D. concentrica, aside from their ascospore morphology and ultrastructure. They are not assigned here to any species of the D. concentrica group because their anamorphic characteristics are as yet unknown.

Group B: The Daldinia eschscholtzii group (Figs 28–41)

The D. eschscholtzii group almost exclusively comprises species from tropical regions, and some of the species are pantropical in their distribution. Only D. caldariorum has made it to Europe. Other species are apparently endemic to the neotropics or to fearerastern Asia. It is being treated here extensively, considering that it constitutes one of the most important groups of tropical Xylariaceae. Molecular phylogenetic data helped to define this group, suggesting that it constitutes a sister group to the other Daldinia species. Furthermore, it has a similar secondary metabolism in culture compared to genera such as Phylacia, Rhopalostroma, Ruwenzoria and Thamnomycetes (cf. Stadler et al. 20010a, b) and to D. placentiformis (see molecular phylogenies in Bitzer et al. 2008, Hsieh et al. 2005, and the current study). The stromatal morphology within this group is quite variable, ranging in shape from placentiform, turbinate to stipitate, while truly semiglobose, sessile stromata are only exceptionally encountered. Several species contain large amounts of cytochalasins in their stromata, which co-occur with BNT and other naphthalenes. They mostly reveal purple colours in KOH, or, especially in old stromata lacking the pruina, their ectostroma may even lack KOH-extractable pigments. Their anamorphs are nodulisporium- or virgilliella-like (rarely approaching periconiella-like with synnematous conidiophores) and show an exclusively holoblastic conidiogenesis.

The core species, D. eschscholtzii, is certainly among the most frequently reported pyrenomycetes of the tropics. It was first described as Sphaeria eschscholtzii Ehrenb.7 from the Philippines. The original illustration by Ehrenberg (1820, reproduced here as Fig. 28) shows placentiform stromata with conspicuous internal zones (the lighter zones up to ca. 2–3 times wider than the darker ones), tubular perithecia arranged in a dense layer, whose ostioles are at the same level as (or somewhat lower than) the stromatal surface, and conidiophores and conidia whose actual size and shape can hardly be determined. As pointed out by Lloyd (1919) and Dennis (1963), the depicted specimen was probably not mature. Apparently, it had just developed perithecia. Neither asci nor ascospores were described by Ehrenberg (1820). The corresponding specimen is no longer extant, hence this illustration must serve as type. Fries (1823) listed it as “Sphaeria concentrica Bolton: Fr. var. eschscholzii Ehrenb.: Fr.”. Owing to the prominent concentric zones of the entostroma, it was later transferred to Daldinia by Saccardo (1882), who emphasised the “oblong” perithecia and the “copper–coloured” stromatal surface as main differences to typical D. concentrica. However, Saccardo also stated that the material on which he based his description was from Brazil, rather than the Philippines. Subsequently, the Swedish mycologist Starbäck (1901) studied material from the Regnell Expedition to Brazil and for the first time described ascospores in connection with this name. Not much later, the German mycologist Heinrich Rehm (1904) described material from Texas as “D. eschscholzii (Ehrenb.) Rehm”, and subsequently reported a specimen from Samoa (Rehm 1907), “to agree with the material from Texas”. The same author also erected D. luzonensis Rehm (Rehm 1913) from the Philippines, but subsequently (Rehm 1914a, b), he listed material from the same country as “D. eschscholzii Ehrenb. : Rehm”. Apparently, Rehm recognised differences between D. eschscholzii and D. luzonensis, albeit he only commented in the description of D. luzonensis (translating from German) that its stromatal habit was “reminiscent of Hypoxylon placentiforme, but it nevertheless constitutes a true Daldinia”. He further remarked that the specimen “appeared related to the D. concentrica group, but differed from it by having smaller ascospores and by lacking visible ostiola” (cf. Rehm 1913).

Rehm’s mentioning the “D. concentrica group” relates to the fact that D. concentrica and D. eschscholtzii have always been considered to be “sister taxa” that primarily differ in ascospore size (and in the more tropical distribution of the latter). However, a comparison of literature data reveals that previous species concepts strongly disagree with one another, and that various taxa have been involved. For instance, Theissen (1909) included both of the Daldinia taxa described by Starbäck (1901) in “D. concentrica var. microspora (Starbäck) Theiss.”, since he found that they had

---

7Ehrenberg and many others authors used the name “eschscholzii”, which is an orthographic error that was only recently corrected in Index Fungorum and MycoBank to “eschscholtzii”.
smaller ascospores than “D. concentrica” (for which he did not cite a particular specimen but only referred to Brazilian material studied earlier by Möller 1901). In contrast, Miller (1930) even doubted whether D. eschscholtzii deserved to be treated at varietal rank, for he found “ascospores of Rehm’s type” (not naming a particular specimen, but probably referring to the Texas Material) to be of similar size as those of “typical D. concentrica”.

Upon re-examination of the above mentioned material reported by Rehm, we confirmed that their size ranges never agreed with the 12–15 × 5–7 µm for D. eschscholtzii given by Miller (1930), but rather with Theissen (1909) and Starbäck (1901). On the other hand, Miller (1942) gave an ascospore size range of 8–14 × 3–6 µm for D. eschscholtzii (vs. 12–17 × 6–9 µm in D. concentrica). In his later work, Miller may have followed Child (1932), who had meanwhile prepared her monograph of Daldinia. She cited at least 100 specimens from around the world as D. eschscholtzii, and regarded D. luzonensis as a synonym. She mainly distinguished D. concentrica from D. eschscholtzii, based on ascospore size and morphology of perithelial outlines and ostiola. Moreover, she recognised four subgroups within D. eschscholtzii, differing in their average ascospore sizes, albeit this data is rather puzzling: While reporting an overall average size of 11.2 × 4.8 µm, three of her subgroups had larger average dimensions (Table 5), which is mathematically impossible. Unfortunately, Child (1932) did not state which of her subgroups contained the authentic and type specimens reported earlier by Rehm and Starbäck. Nonetheless, her interpretation of D. eschscholtzii continued to find application for decades. Albeit Dennis (1963) did not even accept this fungus as a species, he widely referred to the description in Child’s monograph. Child (1932) had cited all specimens previously studied by Starbäck and Rehm (Table 5), but out of those, only the type of D. luzonensis was located and studied by Ju et al. (1997) and Stadler et al. (2004a). We now were able to examine Starbäck’s materials from Brazil (showing smaller ascospores), but the Rehm specimens from the Philippines, Texas, and Western Samoa were all in agreement with one another. The only exception was “Evaristo 1562” (S), cited by Rehm (1914b) as “juvenile D. eschscholtzii” and later so listed by Child (1932), which turned out to be an immature specimen reminiscent of D. placentiformis with green pigments in KOH and azonate stromatal interior.

The above observations on the heterogeneity of previous reports on D. eschscholtzii prompted us to conduct a comprehensive study on the specimens from around the world that had previously been identified as D. eschscholtzii. In accordance with previous studies (Stadler et al. 2004a) we decided on the following procedure: i) link the ancient types to recently collected material by a combination of light microscopic studies and HPLC fingerprinting; ii) culture as many specimens as possible and compare their anamorphic structures; iii) compare ascospores of representatives by SEM.

The results are summarised, and the importance of these criteria for taxonomic purposes as inferred from these studies is explained below.

Secondary metabolites, stromatal pigments and HPLC profiles: HPLC–based extrolite profiles were conclusive in most cases (see chemical structures in Fig. 1, HPLC profiles in Fig. 17 and Table 5 for a summary of data on the D. eschscholtzii group). We confirmed that this group of Daldinia spp. in general is characterised by containing relatively small amounts of BNT (1). This binaphthalene derivative usually co–occurred with (or was overlaid by) particular UV–inactive compounds in varying concentrations. These chemotaxonomic markers, i.e., concentricols (2, 3), and cytochalasins (e.g. 4, 5) were identified by comparison with standards isolated by Hashimoto & Asakawa (1998), Stadler et al. (2001c), and Quang et al. (2002a, b). BNT (1) is omnipresent in Daldinia (Stadler et al. 2001c), but was hardly detectable in several specimens of D. eschscholtzii sensu stricto, by HPLC–DAD, in which case the sensitive HPLC–MS technique served for its identification. Specimens containing little BNT often did not show apparent stromatal pigments in KOH, in agreement with Stadler et al. (2001a, b). Concentricols were often only detected tentatively, overlaid by signals that were obviously caused by cytochalasins.

There are indications that the specimens listed further below sub D. eschscholtzii can be divided into two chemotypes according


Table 5. Ascospore size ranges reported for Daldinia eschscholtzii and its synonyms in the literature. * Material not re–examined in this study. – ** Only some representative specimens were located by us. – # as D. concentrica var. microspora, based on Starbäck’s material.

<table>
<thead>
<tr>
<th>Author(s)</th>
<th>Size ranges (µm)</th>
<th>Origin of material/Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Starbäck (1901)</td>
<td>10–12.5 × 5–6</td>
<td>Brazil</td>
</tr>
<tr>
<td>Rehm (1904)</td>
<td>10–12 × 5</td>
<td>USA, Texas</td>
</tr>
<tr>
<td>Rehm (1907)</td>
<td>10–12 × 5–7</td>
<td>Western Samoa</td>
</tr>
<tr>
<td>Theissen (1909)</td>
<td>8–11.5 × 4–5</td>
<td>Brazil</td>
</tr>
<tr>
<td>Rehm (1913)</td>
<td>10 × 4–5</td>
<td>D. luzonensis, first description</td>
</tr>
<tr>
<td>Miller (1930)</td>
<td>12–15 × 5–7</td>
<td>“Rehm’s material” of D. eschscholtzii (from Texas 1904 ?), and D. luzonensis (1913a)</td>
</tr>
<tr>
<td>Child (1932)</td>
<td>(6)–(11.2)–(14.4) × 4.8(–6.4)</td>
<td>Various specimens from around the world in tropical and subtropical climates, also including material from Europe (France, Germany (!))**</td>
</tr>
</tbody>
</table>

Mean value = 11.2 × 4.8

Four subtypes recognised with
a) mean value = 11.2 × 4.8
b) mean value = 11.2 × 6.4
c) mean value = 12.8 × 6.4
d) mean value = 12.8 × 4.8

Miller (1942) 8–15 × 3–6 South Africa*
Dennis (1963) (11–)12 × 14(–15) × 5–6(–7) Western and Central Africa
Dennis (1974) 11–13 × 5–6 Papua New Guinea (Asia, for comparison)
Martin (1969) 12–13 × 5.5–7 South Africa, USA, Costa Rica*
Thind & Dargan (1978) 12–16(–17.5) × 5.5–8.5 India*
Rogers et al. (1987) 10.3–11.8 × 5.5–9 Indonesia (Sulawesi) as D. cf. eschscholtzii
San Martin (1992) 10–14 × 5–6.5(–7) Mexico**
Van der Gucht (1994) (11–)12–13.4(–14.5) × 5.5–6.5 (M = 12.6 × 5.7) Papua New Guinea, (Africa, for comparison)

Correspondence of materials examined to the defined subtypes not stated

Telemorphic morphology: From previous treatments (Table 5), size and morphology of ascospores appeared to be among the most important diagnostic characters that may allow for further segregation of D. eschscholtzii and allies, and this was confirmed by our overview. When the ascospore characteristics of all examined materials (Table 6) were compiled, two major groups were recognised, corresponding well with the specimens studied previously by Starbäck (1901) and Rehm (1913), respectively. Interestingly, all materials that we confirmed to belong to the D. eschscholtzii group from the Saccardo herbarium (PAD) were reminiscent of the “Rehm” type, even though at least one of them was collected from Brazil. Aside from ascospore morphology, several morphological traits that can find application in the segregation of other groups of Daldinia spp. (Ju et al. 1997) appeared quite variable and difficult to apply to D. eschscholtzii and its ilk. Stromatal size and anatomy, as well as the colours of internal zones sometimes may vary even within a single collection of specimens within the D. eschscholtzii group, while being more homogeneous in D. concentrica and immediate allies. A higher size ratio of darker/lighter zones than 1:3 indicates a taxon different from D. eschscholtzii, especially if accompanied by other morphological traits. Asci could usually not be observed in old specimens, while in recently collected material they were found in agreement with Ju et al. (1997). The same holds true for other morphological traits such as shape and size of ostiola and perithecia.


Etymology: Named by Ehrenberg (1820) in honour of the German–Baltic botanist, zoologist, physician and naturalist, Johann Friedrich von Eschscholtz (1793–1831), who joined Chamisso in his famous expedition to the Pacific.

≡ Sphaeria eschscholtzii Ehrenb., Fung. Chamisso Coll., pl. 18, fig. 8. 1820.
≡ Sphaeria concentrica var. eschscholtzii (Ehrenb.: Fr.) Fr. 1823.

Lectotypus (selected here): Philippines, Luzon Island (latitude 14.5°N), near the base of trunks, specimen not extant; fig. VIII in Ehrenberg (1820).
### Table 6. Ascospore sizes and HPLC characteristics of representative specimens of *D. eschscholtzii* and allies (including those that are described further below as *D. rehmii* and *D. starbaeckii*, and as aberrant forms of *D. eschscholtzii*). Materials were sorted according to geographic origin. For chemotypes 1 and 2, which differ in their pattern of cytochalasins, see chromatograms in Fig. 17. Further metabolites have also been pointed out if deviating from either of the main types. Chemical structures see Fig. 1.

<table>
<thead>
<tr>
<th>Herbarium Code</th>
<th>Country</th>
<th>Ascospore size (µm)</th>
<th>Chemotype</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Africa: Most frequent morphochemotype</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR–Myc 129691,89, BR–Myc 130322,61, BR–Myc 112811,00, BR–Myc 130340,69, BR–Myc 130322,61</td>
<td>Benin</td>
<td>(10–)11–14 × 5.5–6.5(–7)</td>
<td>2</td>
</tr>
<tr>
<td>JHP 00194 (C), Guissou No. 34 (C)</td>
<td>Burkina Faso</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B70 0009593, M-0079884, Ww 4059, LB-01-157 (M)</td>
<td>Cameroon</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR–Myc 033509,44</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 130372, K(M) 130373, K(M) 131680, K(M) 131681</td>
<td>Ghana</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 130374, K(M) 130375</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 130245, K(M) 131682, K(M) 131683, Maguire (NY)</td>
<td>Kenya</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R 4281 (L)</td>
<td>Rwanda</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B70 0009594, S-F 43703</td>
<td>São Tomé e Príncipe</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR–Myc 003529,64</td>
<td>Senegal</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 130371, K(M) 131688</td>
<td>Sierra Leone</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 131685A &amp; B</td>
<td>Sudan</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 130379, K(M) 130380, K(M) 130381</td>
<td>Tanzania</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BPI 594955</td>
<td>Uganda</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR–Myc 129040,17, J. Rammeloo 423, 424, 428 (GENT)</td>
<td>Uganda</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR–Myc 033518,53</td>
<td>D.R. Congo</td>
<td>(8–)9–10(–11) × 4–5(–5.5)</td>
<td>2 (+ daldinone B (3) and other binaphthyls)</td>
</tr>
<tr>
<td>B70 0009592 (Holst)</td>
<td>D.R. Congo</td>
<td>8–10 × 4–4.5(–5)</td>
<td>1</td>
</tr>
<tr>
<td>K(M) 130378, K(M) 130377</td>
<td>Tanzania</td>
<td>10–12 × 5–6</td>
<td>2</td>
</tr>
<tr>
<td>BR–Myc 129040,17, J. Rammeloo 423, 424, 428 (GENT)</td>
<td>Tanzania</td>
<td>(10–)11–13 × 5–6(–7)</td>
<td>2 (containing BNT (1) and additional binaphthyls)</td>
</tr>
<tr>
<td><strong>Africa: Deviating collections</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rammeloo 470 (Ww 3774 &amp; Ww 3775, GENT)</td>
<td>D.R. Congo</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 130378, K(M) 130377</td>
<td>Uganda</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR–Myc 129040,17, J. Rammeloo 423, 424, 428 (GENT)</td>
<td>D.R. Congo</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR–Myc 033518,53</td>
<td>D.R. Congo</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B70 0009592 (Holst)</td>
<td>Tanzania</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 130378, K(M) 130377</td>
<td>Uganda</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Americas: Most frequent morphochemotypes</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S-F 43785</td>
<td>Argentina</td>
<td>(10–)11–13 (–13.5) × 5–6.5</td>
<td>2</td>
</tr>
<tr>
<td>BPI 594804, BPI 594759, Bononi 16, Bononi 132 and 320 (NY), Rodrigues 215, 190, and 1163 (NY), K(M) 130240, L 0275625</td>
<td>Brazil</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 91626</td>
<td>Cayman Islands</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ww 3846, Ww 3852, STMA 04019, STMA 04020</td>
<td>Cuba</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TL 9833</td>
<td>Ecuador</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Guzmán 16304 (NY), Guzmán 10169 (NY), Guzmán 10319 (NY), Guzmán 10152 (NY), Guzmán 15557 (NY), Guzmán 15559/15571 (NY), Pérez–Silva (NY), Mojica 7 (NY), M. Eckel (K), A. Welden 4001 (NY), SM 23, 422A, 1035 (JDR)</td>
<td>Mexico</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BPI 594808</td>
<td>Nicaragua</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BPI 594808</td>
<td>Panama</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Welden 7988 (NY)</td>
<td>Peru</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. Lassæe P–013, P–153 P–288 (C)</td>
<td>Saint Lucia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 25381</td>
<td>Surinam</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR–Myc 093359,45, L 0275626, L 0275627, NY 460110, Welden 2351 (NY)</td>
<td>USA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S-F 43788 (Rehm 1904)</td>
<td>USA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 130241, K(M) 131691, Ww 3960 (C)</td>
<td>Bolivia</td>
<td>(10–)11–13(–14) × 5–6.5</td>
<td>1</td>
</tr>
<tr>
<td>S-F 38150, S–F38151, S–F38152, Samuels 751 (NY)</td>
<td>Brazil</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S-F 43784</td>
<td>Brazil</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Underwood &amp; Earle 738 (NY), Ww 3847, Ww 3850, Ww 3853 (K), Ww 3591, Ww 3592 (MUCL)</td>
<td>Cuba</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orr No. 943 (NY), Ww 3943</td>
<td>Ecuador</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Le Gallo (NY)</td>
<td>Guadeloupe</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
**A Polyphasic Taxonomy of Daldinia (Xylariaceae)**

Table 6. (Continued).

<table>
<thead>
<tr>
<th>Herb Code/Continent/Species</th>
<th>Country</th>
<th>Ascospore size (µm)</th>
<th>Chemotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>BPI 594811</td>
<td>Honduras</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 130242, S-F 43795</td>
<td>Venezuela</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Americas: Deviating collections**

<table>
<thead>
<tr>
<th></th>
<th>Country</th>
<th>Ascospore size (µm)</th>
<th>Chemotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>S-F 38151 and S-F 38152, Samuels 751 (NY).</td>
<td>Brazil</td>
<td>(9–)10–12 × 5–6</td>
<td>2 + daldinone B (3)</td>
</tr>
<tr>
<td>JFM 340 (KR), TL 9703 (C)</td>
<td>Ecuador</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MUCL 45436 (D. starbaeckii, holotype)</td>
<td>French Guiana</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CL–0882 (KR)</td>
<td>Martinique</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stj 106 Stj 187, Stj 191, F.J. Beaver 777 and 811 (NY)</td>
<td>US Virgin Islands (St. John)</td>
<td>12–15 × 5.5–7</td>
<td>2</td>
</tr>
<tr>
<td>K(M) 103863</td>
<td>Venezuela</td>
<td></td>
<td></td>
</tr>
<tr>
<td>INPA 78-470 ex NY (D. rehmii, holotype)</td>
<td>Brazil</td>
<td>9.5–10.5 (–11) × 4.5–5.5</td>
<td>1</td>
</tr>
<tr>
<td>AAU 59501</td>
<td>Ecuador</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Asia/Australia/Oceania: Most frequent morphochemotype**

<table>
<thead>
<tr>
<th></th>
<th>Country</th>
<th>Ascospore size (µm)</th>
<th>Chemotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ww 3959, Ww 3551</td>
<td>Japan</td>
<td>(10.5–)11–13(–14) × (5–) 6–6.5</td>
<td>1</td>
</tr>
<tr>
<td>M-0079863, TL5156, TL6173, Ww 4174 - Ww 4181 and Ww 4183 (ex AJSW)</td>
<td>Malaysia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 131699</td>
<td>Bangla Desh</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M–0079877, M–0079878</td>
<td>Pakistan</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR–Myc 093358,44, BR–Myc 079661,01, BPI 594812, Ww 3781, Ww 4089 (B)</td>
<td>Indonesia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BPI 594760</td>
<td>P.R. China</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S-F 38156, BPI 594768, Saccardo 1817 (PAD), BPI 71066, BPI 71062, S-F 38156, S-F 43786, C. J. Baker 5488 (PAD), S-F 43789, S-F 43790, S-F 43791, S-F 43791, Saccardo &quot;Laguna&quot; (PAD)</td>
<td>Philippines</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ww 4166 (M), Ww 4171 - Ww 4173 (ASJW), Demoulin 5405 (NY)</td>
<td>Thailand</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 131694, Ww 4365 (K)</td>
<td>Sri Lanka</td>
<td></td>
<td></td>
</tr>
<tr>
<td>YMJ 264, BPI 594688</td>
<td>Taiwan</td>
<td></td>
<td></td>
</tr>
<tr>
<td>STMA 07012 (KR)</td>
<td>Vietnam</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 24537, K(M) 24521, Ww 4182/AJSW</td>
<td>Australia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 24568, K(M) 91622, Ww 3779</td>
<td>New Guinea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>K(M) 130238, Ww 3563</td>
<td>Caroline Islands</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BPI 594936, BPI 594761, M-0079881</td>
<td>W. Samoa</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PDD34954, PDD45927</td>
<td>Solomon Islands</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PDD38258</td>
<td>Tahiti</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Asia/Australia/Oceania: Deviating collections**

<table>
<thead>
<tr>
<th></th>
<th>Country</th>
<th>Ascospore size (µm)</th>
<th>Chemotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>G.J. Samuels 2357a, 1939, 2035, 2052, 2230, (NY), L 0275624</td>
<td>Indonesia</td>
<td>(9.5–)10–12 × 5–6</td>
<td>1</td>
</tr>
<tr>
<td>M–0079879</td>
<td>P.R. China</td>
<td>9.5–12 × 4–5.5</td>
<td>2</td>
</tr>
</tbody>
</table>

**Epitype** (selected here): MBT177380; *Philippines*, La Laguna Prov., Luzon Island, Mt. Makiling Peak, 1 Apr. 2001, T.H. Quimio & M.M. Baldovino (K(M) 136899 ex CALP 1126; GenBank Acc. No. of DNA sequence: HE590893).


Selected illustrations: *Ju et al.* (1997), figs 9, 30–32, 73; *Van der Gucht* (1994), figs 10c, d and 11a–c. *Stadler et al.* (2002), figs 1, 2; *Stadler et al.* (2004a), fig. 15.

Known distribution/host preference of stromata: Widespread in warmer climates with clear preference for the tropics; frequent in Africa, America and Asia, but also recorded from Northern and Western Australia and New Guinea. Apparently absent in Europe, but present in subtropical climates of southern Japan and southern USA and very common all over the Caribbean. Without apparent host specificity. Stromata have been found on dead wood of numerous dicotyledonous agricultural plants and native trees, often in sunny, exposed positions. There is one confirmed record on a gymnosperm and one on a monocot (palm).

Teleomorph: Stromata turbinate to placentiform, only exceptionally depressed-hemispherical in large luxuriant stromata, sessile to subsitipitate, 1–7 × 1–4.5 cm, surface without conspicuous perithecial outlines; Brown Vinaceous (84), Dark Brick (60), Greyish Sepia (106), or Vinaceous Grey (116) in young stromata, but blackened and varnished in age; dull reddish brown granules immediately beneath surface, with KOH-extractable pigments dilute, Livid Purple (81), Dark Livid (80), or Vinaceous Purple (101) in fresh and young stromata, usually appearing after several minutes of incubation, but
frequently without apparent stromatal pigments in mature and old herbarium specimens; tissue between perithecia brown, pithy to woody; tissue below the perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2–0.5 mm thick, lighter zones grey or greyish brown, gelatinous and very hard when dry, becoming pithy to woody, persistent, 0.4–1 mm thick (Ratio of darker/lighter zones 1:1–3). Perithecia lanceolate 0.9–1.8 × 0.3–0.6 mm. Ostioles inconspicuous or, rarely, slightly papillate. Asci
Stromatal metabolites: BNT (in young stromata) and cytocalasins (often in abundance); concentricrils detected tentatively in some specimens.

Cultures and anamorph: Colonies on OA reaching the edge of the 9 cm Petri dish in 5–8 d, initially whitish, felly, azonate, with diffuse margins, becoming Smoke Grey (105) with slightly olivaceous margins, becoming Smoke Grey (105) with slight olivaceous turning Dull Green (70), due to production of pigments tentatively identified as hypoxylxylerone (15) derivatives. Characteristic thick-walled stromatic structures always formed besides conidiophores in old cultures. Stromata in culture occasionally produced, pulvinate, Brown Vinaceous (84), remaining sterile; stromatal structures always formed besides conidiophores identified as hypoxylxylerone (5.000×); epispore smooth.

Additional specimens examined: Angola, Louanda, Mar. 1918, J. Gossweiler, Lloyd 4895 (NH, OUA); South Ouest province, F.C. de Mouhoun, 9669 (NY); same locality, Instituto de Botanica, 5 Nov. 1969, D.M. Rodriguez et al. (CA, OUA); near Bonda, Dec. 1908, C.F. Baker in herb. F.S. Earle (NY).

160–210 × 7–10 µm, p. sp. 70–90 µm, stipes 90–120 µm, with amyloid, discoid apical ring, 0.5–0.75 × 2.5–3 µm. Ascospores dark brown, unicellular, ellipsoid–inequilateral, with narrowly rounded ends, (10–11)–13–14 × 5–6.5 µm, with straight germ slit spore length on convex side; perispor dehiscent in 10 % KOH smooth by L.M, but showing conspicuous transverse striations by SEM (5,000×); epispore smooth.

Maniconi, Estrada de Estanhoo km 40, on dead trunk, 16 Apr. 1985, K. Rodrigues 190 (NY); Paria Grande, Inv. Botanico-Ecologico del Territorio Federal Amazonas, 23 Apr. 1978, G.E. Iturriaga 31360 (NY); from Boat Vista to Venezuela border, 2 km after Boca do Mata, Carapeha, on dead trunk, 10 Dec. 1977, G. Samuels et al. 751 (NY); Belem, Pará, dead wood, 31 Jul. 1997, A.F. Vital 1393 (L 027526); same locality, A.F. Vital 1565 (BPI 94241); same locality, 16 Feb. 1955, A.F. Vital in herb. P. Martinelli (IM); see Martin 1909 (NY); on decorticated trunk, on fallen log in forest, 2 Jan. 1987, K. Rodrigues et al. 1163 (NY); same locality, Instituto de Botanica, 6 Nov. 1969, D.M. Dirr 188 (K(M) 131690); Burkina Faso, Ouagadougou, in park, 24 Aug. 2002, J.H. Petersen ‘H’00194 (C, OUA, culture CBS 117470); Ouagadougou University grounds, 7 Jun. 1999, Gissouss 34 (OUA); South West Province, F.C. de Mouhoun, 440m, forest near highway Oronda-Banfora, Jul. 2009, S. Gahr, STMA 01622 (OUC, culture MUCUL 52675). Cameroon, South Province, Bippid, wind in rain forest, no date, G. Zanker 1360a (M–O070884); South West Province, Limp, on dead stump in Botanic Garden, 2 Nov. 2001, L. Beenken & T. Frank 2122 (M, culture CBS 113699); same locality, Motre on putrefied trunk, 1 Oct. 2001, L. Beenken K01159 (KR, culture CBS 117735); exact locality unknown, label reading “Bundim” (probably meaning Bipinti), Regio Kamerounensis, Apr. 1891, J.R. Jungner (B70 000953); near Criaumbina, on dead wood, 1 Oct. 1929, H. Kreisel et al. (Kr.); near Schouam village, 12º50'E., 3º21'N, 640 m, 28 Jun. 1997, P.P. Daniels et al. (IMI).

Colonies 13234 (NY); Territory of Roraima, Vic. of Auaris, on burnt logs in plantations, Jul. 1974, O. Fidalgo et al. (NY);
Stadler et al.

Haut-Katanga, Keyboge, Base de Mukuwe, “on small termite hill” (?), 24 Feb. 1947. D. Soyer 244 (B–MYC 03315.6; see Dennis 1963); District Forestier Central, Kisangani (Stanleyville), Feb. 1926, Ghesquiere 328, (K(M) 130243); Iamumu, 1 Feb. 1956, H. Vandenbroucke 9295 (B–MYC 03353.61); Kasai, Kakenge, Entandrophragma cylindrom, no date, Deschamps 22 (B–MYC 033522.57 – immature); Kisantu, 20 May 1956, H. Vandenbroucke 9166 (B–MYC 033539.48 – immature); same locality, 1906, H. Vandenbroucke (B–MYC 033510.45 – immature); Kisantu, 2 Aug. 1956, H. Vandenbroucke 9190 (B–MYC 033505.49); Kisantu, 26 Aug. 1956, F. Rehorey 610 (K(M) 130374); Kinshasa, E. Schulz 102, 6 Feb. 1997 (K(M) 130375); Kinshasa, J. Gillet (B–MYC 033509.44; see Dennis 1963); same locality, 25 Jan. 1907, H. Vandenbroucke (B–MYC 033504.39 – immature); same locality, 2001, J. Gillet, det Saccardo as D. concentrica var. eschscholtzii, ex herb. Saccardo (PAD); Kivu, Panzi, Oct. 1947, Goossens–Fontana (see Dennis 1963).


San Martín 1992).


San Martín 1992).

San Martín 1992).

San Martín 1992).
A POLYPHASIC TAXONOMY OF Daldinia (Xylariaceae)

Table 7. Anamorphic characteristics of *Daldinia eschscholtzii* and related species. CC: Conidiogenous cells; CON: Conidia. If not stated otherwise, the anamorphic branching pattern is nodulisporium-like *sensu* Ju & Rogers (1996) with holoblastic conidiogenous cells, normally located at the termini of conidiophores.

<table>
<thead>
<tr>
<th>Species and origin of material</th>
<th>Conidiogenous structures (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>D. albofibrosa</strong>&lt;br&gt;Papua New Guinea (MUCL 38738 ex-type); Malaysia (CBS 117737)</td>
<td>CC: 10–16 × 2–2.5&lt;br&gt;CON: 4–6 × 2–3 (av. 5.1 × 2.4)</td>
</tr>
<tr>
<td><strong>D. bambusicola</strong>&lt;br&gt;(data given in Ju et al. 1997 confirmed by us):&lt;br&gt;Thailand (CBS 122872 ex-type)</td>
<td>Nodulisporium-like to periconiella-like branching pattern</td>
</tr>
<tr>
<td><strong>D. caldariorum</strong>&lt;br&gt;(current study):&lt;br&gt;Cuba (MUCL 47595); France (MUCL 49217); R. South Africa (MUCL 47715); Taiwan: (BCRC34042); UK (KC1523, ATCC 36660)</td>
<td>CC: 10–17 × 2.5–3.5&lt;br&gt;CON: 3.5–4.5 × 2.5–3 (av. 4.2 × 2.7)</td>
</tr>
<tr>
<td><strong>D. caldariorum</strong> (Ju et al. 1997):&lt;br&gt;Mexico (CBS 122874)</td>
<td>Periconiella-like branching pattern predominant</td>
</tr>
<tr>
<td><strong>D. cf. caldariorum</strong>&lt;br&gt;Ecuador (CBS 113045)</td>
<td>CC: 10–20 × 2.3–5</td>
</tr>
<tr>
<td><strong>D. cf. eschscholtzii</strong>&lt;br&gt;Benin (MUCL 45434, MUCL 45435); Burkina Faso (CBS 117470); Cameroon (CBS 113969, CBS 117735)</td>
<td>CON: 4.5–6.5(–7) × 2.5–4.5</td>
</tr>
<tr>
<td><strong>D. cf. eschscholtzii</strong>&lt;br&gt;Malaysia (CBS 116036)</td>
<td>CC: 6–12 × 2.5–3</td>
</tr>
<tr>
<td><strong>D. cf. eschscholtzii</strong>&lt;br&gt;Malaysia (CBS 116040, CBS 116041)</td>
<td>CON: 4.5–5(–5.5) × 1.5–2(–2.5) (av. 4.9 × 2.1); conidiophores rather small, 50–70 × 2–2.5 µm</td>
</tr>
<tr>
<td><strong>D. eschscholtzii sensu stricto</strong>&lt;br&gt;(in agreement with Ju et al. 1997):&lt;br&gt;Australia (CBS 116032); Cuba (e.g., MUCL 41777, MUCL 41778, MUCL 46087, MUCL 47596); Ecuador (CBS 116025); Malaysia (CBS 116037, CBS 11603-34 CBS 116038-41); Martinique (CBS 121676, MUCL 51832-51841) Mexico: KC1698, MUCL 47106; Panama (MUCL 47598); P.R. China (MUCL 47144, MUCL 47166, MUCL 47965); Peru (CBS 113042); Saint Lucia: (KC 1616); Seychelles (CBS 119994); Sri Lanka (CBS 113466); Taiwan (BCRC 34047); Thailand (CBS 113047, CBS 116031, CBS 122877); USA (CBS 122876); Vietnam (MUCL 49359)</td>
<td>CC: 8–22 × 2.5–3&lt;br&gt;CON: 4.5–6.5 × 2–3 (av. 5.2 × 2.8)</td>
</tr>
<tr>
<td><strong>D. starbaeckii</strong>&lt;br&gt;Cayman Islands (KC 1692); Ecuador (MUCL 45438, CBS 116026); French Guyana (MUCL 45436); Martinique (MUCL 52986)</td>
<td>CC: 16–22 × 2.5–3.5&lt;br&gt;CON: 5–8 × 3–4.5 (av. 6.8 × 4.0)</td>
</tr>
<tr>
<td><strong>D. theissenii</strong>&lt;br&gt;(= <em>D. clavata sensu.</em> Ju et al. 1997)&lt;br&gt;Argentina (CBS 113044); Peru (CBS 113043 ex-type); a culture from Mexico reported by Ju et al. (1997) as <em>D. clavata</em> was also studied earlier on (Stadler et al. 2001a, b) but is not extant anymore.</td>
<td>Virgariella-like branching pattern predominant&lt;br&gt;CC: 8–22 × 2.5–3 µm&lt;br&gt;CON: 4.5–6.5 × 2–3 (av. 5.2 × 2.8)</td>
</tr>
</tbody>
</table>

**Notes:** From the aforementioned studies we conclude that *D. eschscholtzii* as epitypified above is conspecific with *D. luzonensis* and omnipresent in tropical and subtropical countries. It does not correspond to *D. concentrica var. eschscholtzii sensu* Starbäck (1901) and *D. eschscholtzii sensu* Rehm (1904), here treated under *D. starbaeckii* (cf. Tables 7, 8). The conidiogenous structures agree well with the description of *D. eschscholtzii* by Ju et al. (1997), based on cultures from Martinique, Texas, and Thailand, which were also studied by Stadler et al. (2001a, b) and Hsieh et al. (2005). This fungus appears to be particularly frequent in Southern and Eastern Asia, but it also occurs in warmer climates of the Americas and in Central Africa. Aside from the type of *D. luzonensis*, and Rehm’s verified materials of *D. eschscholtzii*, several further specimens from the Philippines (including some that had been determined earlier as *D. bakeri* or *D. concentrica*) also correspond with *D. eschscholtzii*. Apparently, Teodoro (1937) in his Philippine checklist uncritically compiled all earlier names and this has caused some confusion (Dennis 1963). Our results corroborate this statement. Aside from one specimen each of *D. steglichii* and *D. caldariorum* (see elsewhere herein), all speci-mens studied from Luzon Island (the type locality of *D. eschscholtzii*), and most specimens from other regions in the Philippines agreed with *D. eschscholtzii* and the type of *D. luzonensis* and other specimens reported on by Rehm (1907, 1914a, b). One of them is selected as epitype of *D. eschscholtzii* and is illustrated here in Fig. 29H. Interestingly, all these Asian specimens produce a similar HPLC profile, exemplified as “chemotype 1” in Fig. 17. As suspected by Ju & Rogers (1999), we found that the specimen reported by Sawada (1959) as *D. concentrica* from Taiwan also belongs here.

Most materials from Africa agreed well with the epitype with respect to their teleomorphic morphology, aside from having slightly larger ascospores (Table 5). HPLC profiling, however,
Table 8. Comparison of *D. eschscholtzii*, *D. clavata*, and morphologically similar species of tropical occurrence.

<table>
<thead>
<tr>
<th>Species (DalDinia)</th>
<th>Known occurrence</th>
<th>Typical stromatal shape</th>
<th>Ascospore Size [µm]; perispore by SEM (5.000×)*</th>
<th>Ascal apical apparatus [µm]</th>
<th>Pigments in KOH; characteristic stromatal secondary metabolites</th>
</tr>
</thead>
<tbody>
<tr>
<td>albofibrosa</td>
<td>New Guinea</td>
<td>Subglobose to turbinate</td>
<td>(8–)9–10.5 × 4–4.5; CTS</td>
<td>0.5–0.75 × 2–2.5</td>
<td>Greenish olivaceous; BNT(1) and daldineone A (3) predominant</td>
</tr>
<tr>
<td>albozonata</td>
<td>Africa</td>
<td>Turbine</td>
<td>(6.5–)7–9(–9.5) × 3–4; CTS</td>
<td>not seen</td>
<td>Very faint purple; BNT (traces) and cytochalasins (9) in large amounts</td>
</tr>
<tr>
<td>bambusicola</td>
<td>Thailand</td>
<td>Semiglobosa</td>
<td>8.5–11 × 4–5; CTS</td>
<td>0.3 × 2</td>
<td>Faint purple; BNT and cytochalasins in small amounts</td>
</tr>
<tr>
<td>brachysperma</td>
<td>Mexico</td>
<td>Turbine to peltate</td>
<td>6.5–7.5 × 3–4; CTS</td>
<td>0.2 × 1.5</td>
<td>Very faint purple; BNT (traces) and cytochalasins in large amounts</td>
</tr>
<tr>
<td>caldarium</td>
<td>Cosmopolitan, even on Fabaceae in Europe</td>
<td>Turbine to depressed-spherical</td>
<td>8–11(–12) × 4–6.5; S</td>
<td>0.5–0.75 × 2</td>
<td>Intense purple; BNT (large amounts), cytochalasins also often detected</td>
</tr>
<tr>
<td>clavata</td>
<td>Africa, South America</td>
<td>Cylindrical to subclavate</td>
<td>8–11.5 × (3.5–) 4–5.5; CTS</td>
<td>0.5 × 2.5–3</td>
<td>None or faint purple; BNT (often only in traces) but no cytochalasins detected</td>
</tr>
<tr>
<td>cuprea</td>
<td>Africa, South America</td>
<td>Cylindrical to subclavate</td>
<td>10–11.5(–12.5) × 4.5–5.5(–6); CTS</td>
<td>0.5 × 2–2.5</td>
<td>Greyish-olivaceous; BNT and unknown specific pigments that are probably parylene quinones (2) or naphthoquinones (5)</td>
</tr>
<tr>
<td>eschscholtzii</td>
<td>Pantropical</td>
<td>Turbine to placentiform</td>
<td>(10–)11–13(–14) × 5–6.5; CTS</td>
<td>0.5–0.75 × 2.5–3</td>
<td>Absent or weakly purple; small amounts of BNT, major components: cytochalasins, and concentrals (8) or unidentified UV-inactive compounds</td>
</tr>
<tr>
<td>rehmi</td>
<td>America (Asia)</td>
<td>Irregularly hemispherical to turbinate</td>
<td>9.5–10.5(–11) × 4.5–5.5; Type specimen not yet checked by SEM</td>
<td>0.5–0.75 × 2–2.5</td>
<td>Purple; BNT as major component, concentricol A also tentatively detected</td>
</tr>
<tr>
<td>starbaecki</td>
<td>America</td>
<td>Turbine to placentiform</td>
<td>(9–)10–12 (–13) × 5–6(–6.5); CTS</td>
<td>0.5–0.75 × 2.5–3</td>
<td>Yellowish to olivaceous; BNT, daldineone B (4) and cytochalasins</td>
</tr>
<tr>
<td>theissenii</td>
<td>South America</td>
<td>Clavate-cylindrical</td>
<td>(8–)9–12(–13) × 5–6; S</td>
<td>0.5 × 2.5</td>
<td>Purple; BNT detected in fairly large quantities but no cytochalasins were noted</td>
</tr>
</tbody>
</table>

* CTS: Conspicuous transverse striations; S = essentially smooth.

revealed them to belong to chemotype 2. Interestingly, anamorphic structures of African material were slightly more robust than those observed in specimens originating from the Americas and Asia (Table 6). However, deviations in anamorphic features were also seen in some specimens belonging to chemotype 1. For instance, cultures of *AJSW 914–93* and *AJSW/Ww 4174* showed a more robust anamorph, reminiscent of the cultures from African material mentioned above. In contrast, a culture derived from *AJSW 637/Ww 4183* produced rather diminutive conidiogenous structures (Table 7), although some specimens showing the typical features were collected in roughly the same geographic region. Whalley et al. (2002) reported *D. eschscholtzii* to be “common in the Kuala Selangor National Park of Malaysia”, but only studied their teleomorphs. It should be interesting to collect and culture further materials (stromata as well as endophytes) to establish correlations between these variations in anamorphic morphology, host specificity, chemical and molecular characteristics. For the time being, we refrain from erecting new taxa for them, since the teleomorphs are hardly distinguishable from the typical form.

Deviations in ascospore sizes were also noted among specimen groups derived from local populations. For example, some specimens from Venezuela and the US Virgin Islands resembled *D. eschscholtzii*, but they had larger asci (180–210 µm total length, p. sp. 80–90 × 8–10 µm, stipe 100–130 µm, with amyloid apical apparatus 0.75 × 2.5–3 µm) and ascospores (12–15 × 5.5–7 µm). Their HPLC profiles resembled those of *D. eschscholtzii* in revealing cytochalasins in abundance, rather than concentrals as in the *D. concentra* group. The culture from Venezuela did not produce the anamorph, which may already be an indication that it is different from *D. eschscholtzii*, considering that cultures of the latter species usually show prolific conidiogenesis.


12St. John (= St. Jan) was a Danish protectorate at that time.
Another somewhat aberrant specimen from Mexico, Mazatlan, Dec. 1961, P. Martin 910 (NY, see Martin 1969 as “D. occidentale Child”) has the following characteristics (Fig. 30): Stromata depressed-spherical, subsessile to shortly stipitate, 1.2–2 cm diam; surface even, Dark Brick (60) turning black and shiny when overmature, finely cracked; dull orange brown granules immediately beneath surface, with Vinaceous Grey (116) KOH-extractable pigments; tissue between perithecia grayish brown, pithy to woody; tissue below the perithecial layer composed of alternating weakly contrasted zones, darker zones brown, pithy to woody, 0.1–0.3 mm thick, lighter zones grayish brown, pithy to woody, persistent, up to 1 mm thick. Perithecia lanceolate, 1 × 0.15–0.2 mm. Ostioles papillate. Asci not seen. Ascospores brown to dark brown, ellipsoid-inunequilateral, with narrowly rounded ends, 12–14.5 × 6–6.5 µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, smooth by LM; epispore smooth.

As in the above material from Venezuela and US Virgin Islands, this collection from Mexico (which may have been determined by Martin as “D. occidentalis”, i.e. D. loculata in the current sense, because of the papillate ostioles) possesses ascospores averaging slightly larger than those of typical D. eschscholtzii as encountered in the Neotropics. In addition, the Mexican material differs in having clearly papillate ostioles. Although their HPLC profiles are similar to that of D. eschscholtzii, the pigments in KOH appear slightly darker. As the stromata of these collection were either immature or overmature and because of the absence of cultural and anamorphic data, a final decision about their taxonomic status must wait until living, fully mature material becomes available.

We also confirm that the specimens from Sulawesi, Indonesia, reported by Rogers et al. (1987) as “D. cf. eschscholtzii” show smaller ascospores in average than the other specimens studied from the Indopacific region. Nonetheless, their HPLC profiles and other morphological characters did not deviate much from other Asian collections of D. eschscholtzii. Since none of them could be cultured, there is insufficient evidence as yet to erect a new taxon.


Specimens from Tanzania, Usambara Mountains, Kinuba Valley, Jul. 1893, C. Holst (B70 0009592, B70 0009596, B70 0009600; 3 packets) deviate in having smaller ascospores, and in their HPLC profiles reveal BNT and additional binaphthyls, which probably account for their faintly olivaceous pigments in KOH. The material was rather depauperate, and no intact asci were seen.

Aside from the above described deviations that in part may reflect local endemism, the consistency of the morphological and chemical characters that we regard as crucial for classification of D. eschscholtzii and allies was also confirmed by studies on stromata derived from artificial culturing of some endophytic Nodulisporium spp. from Thailand provided by A.J.S. Whalley (Ww 4171-Ww 4173). Those showed the typical morphological and chemical characteristics of D. eschscholtzii. Their ascospores were cultured again from the artificial stromata and showed the typical anamorph. Results by Triebel et al. (2005) already indicated that

---

1All specimens were cited as D. cf. eschscholtzii in Rogers et al. (1987).

Fig. 30. Teleomorphic characteristics of Daldinia sp. (cf. eschscholtzii) Martin 910 (Mexico). A, B. Stromatal habit. C, D. Stoma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). F. Ascospores in SDS. G. Ascospores in KOH, showing dehiscing perispore. Scale bars A–C = 5 mm; D, E = 1 mm; F, G = 10 µm.
two Nodulisporium endophytes from Thailand, originally reported on by Polishook et al. (2001), correspond to D. eschscholtzii or a close relative, because they have highly similar ITS nrDNA sequences. Daldinia eschscholtzii and other Xylariaceae (Whalley 1996, 2004) are frequently isolated as endophytes in the tropics. In future, it may become feasible to link other endophytic Xylariaceae to teleomorphic Daldinia spp. in a similar manner.

A culture (MUCL 3630 = IMI 91073), referred to as Nodulisporium gregarium by Meyer (1959) was studied by Bitzer et al. (2008) and reported to have a daldinia-like HPLC profile. Indeed, its morphological characters are in full agreement with the typical form of D. eschscholtzii in the current sense, and so are its ITS nrDNA sequences (see Results on molecular phylogeny). Interestingly, this strain was isolated from Morus alba in Changa Manga, Pakistan by S. Ahmad, and we have encountered several specimens of D. eschscholtzii in public collections that were derived from the same substrate and region by the same collector. It remains unclear whether the original strain studied and deposited by Meyer was originally derived from stromata or from the substrate. In any case, Meyer (1959) made the formal recombination of Stachylidium gregarium (originating from Cuba) in Nodulisporium, but does not appear to have studied original Cuban material of this name. Interestingly, the type strain of N. gregarium was studied by Deighton (1985), who confirmed that its conidigenous structures are highly similar to those of the typical anamorph of D. eschscholtzii described herein. Creating a straightforward synonymy between Nodulisporium gregarium and D. eschscholtzii may appear practical at first glance. However, as we have observed very similar anamorphic features in other species of this complex (see D. theissenii and the comparison in Table 7), which differ markedly in their teleomorphic morphology as well as in their chemical profiles, we refrain from doing so in the current monograph. As the molecular phylogenetic data available (see results on molecular phylogeny) do not yet allow for a clear-cut separation of D. eschscholtzii and related species and it is not clear whether DNA extraction from the type specimens of these fungi will succeed, we feel unable to provide a final solution for the typification of this fungus at this time.


Etymology: Refers to the characteristic broad, white, fibrous zones of the entostroma.


Notes: This species was until recently only known from New Guinea, from where it was reported as D. albozonata by Van der Gucht (1994, 1995), who also described the anamorph and recorded SEM characteristics of the ascospores. Our previous studies (Stadler et al. 2001c) generally agreed with these results but revealed that D. albofibrosa shows morphological deviations in respect to D. albozonata and D. clavata. In addition, the fungus from New Guinea strongly differs in having greenish brown KOH-extractable pigments, which were attributed by Stadler et al. (2001c) to the presence of daldinin C (6). When morphologically similar material from Thailand and Malaysia (Borneo) became available, this was first regarded as a different taxon, since the anamorphic

---

14 Okane et al. (2008) cited a specimen collected from Thailand, Khao Sok National Park (culture BCC 21041, GenBank Acc. No. of LSU DNA sequence AB376806) under the provisional name ‘D. sabahense’, which is in fact D. albofibrosa. The specimen was studied by us but is not cited here for lack of collection details.
characters slightly deviated and daldinone A (3) was detected as major metabolites. However, the HPLC analyses of the stromatal extracts of the above mentioned specimens from New Guinea were repeated, revealing the presence of daldinone A as well. Therefore, the material from Malaysia and Thailand (see footnote) was also found to be conspecific with *D. albofibrosa*, but the latter species is no longer regarded as a member of the *D. childiae* group.

Molecular data (see Results on molecular phylogeny) also suggest that *D. albofibrosa* is more closely related to the *D. eschscholtzii* group. Unfortunately, the “working” name “*Daldinia sabahense* ined.” that we used for the Malaysian specimens before the synonymy with *D. albofibrosa* became evident, has already found access to the literature and Internet databases, even though it was never validly published. For instance, Okane *et al.* (2008) have used it in their study on xylariaceous endophytes in Thailand.

*Daldinia albozonata* Lloyd, Mycol. Writ. 5: 822 (1919). Fig. 32.

**Etymology:** For the broad, white lighter concentric zones.

**Holotypus:** Cameroon, Bipindi, wood, W. Zenker, Lloyd herb. 12375 (BPI 716969).

---

**Fig. 31.** Teleomorphic characteristics of *Daldinia albozonata*. Holotype (Papua New Guinea). A. Stromatal habit. B, D, E. Stroma in longitudinal section showing hollow interior, internal concentric zones and perithecial layer. C. Stromatal surface with ostioles, and stromatal pigments in 10% KOH inserted. E. Ascospores in SDS. F. Ascospores in KOH, showing dehiscing perispore. G. Ascospores by SEM (5,000×). Scale bars A–D = 1 mm; E, F = 10 µm; G = 5 µm.
A polyphasic taxonomy of Dalinia \textit{(Xylariaceae)}

Selected illustrations (all from holotype): Lloyd (1919), fig. 1456 (stromata); Child (1932), Plate 27, fig. 3 (ascospores), Plate 31, fig. 3 (perithecia).

Known distribution/host preference of stromata: Tropical Africa; host affinities unknown.

Teleomorph: This fungus differs from typical \textit{D. clavata} in having smaller ascospores in average, (6.5–)7–9(–9.5) × 3–4 µm, and in having more turbinate to cylindrical, rather than clavate stromata. It differs from \textit{D. albofibrosa} in having weakly greyish purple stromatal pigments in KOH.

Cultures and anamorph: Unknown.

Stromatal metabolites: BNT and cytochalasins.

Additional specimens examined: Angola, 1921, Servicios de Agricultura Dept. 288, det. R.W.G. Dennis as \textit{D. albozonata} (K(M) 120968). Cameroon, Bipindi, W. Zenker ex herb. Petrak as \textit{D. albozonata} (M-0079687, probably part of type).

Notes: Ju et al. (1997) treated this name as a synonym of \textit{D. clavata}. However, we prefer to accept it \textit{ad interim} until freshly collected culturable material from Africa becomes available. Even though the ascospore sizes are slightly overlapping, their range appears to be rather constant in the individual specimens of both taxa. The type material from Cameroon and the specimen from Angola have significantly smaller ascospores than other taxa in \textit{Daldinia} aside from \textit{D. brachysperma}. Their stromatal habit also differs from that of typical \textit{D. clavata}. In fact, it has already been pointed out by Lloyd (1919, see also his fig. 1456), that they are almost peltate, with a very narrow constricted stipe-like base, while the stromata of \textit{D. clavata} (cf. Lloyd 1919) are mostly larger, clavate-cylindrical with a broad base. This also agrees with Child (1932) and San Martín (1992), both of whom also noted the smaller ascospores of the type specimen in comparison to typical \textit{D. clavata}. The ascospores of both species have narrowly rounded ends and show conspicuous transverse striations by SEM.
**Daldinia bambusicola** Y.M. Ju, J.D. Rogers & F. San Martin, Mycotaxon 61: 253. 1997. Fig. 33.

**Etymology:** For the host plants.


*Selected illustrations* (all from holotype): Ju et al. (1997), figs 2 (ascospores), 21–23 (stromata) and 74 (anamorph).

**Known distribution/host preference of stromata:** From nature so far only known from bamboo in Thailand with a record from USA treated as a likely introduction.


*Teleomorph, cultures and anamorph:* as described by Ju et al. (1997).

**Stromatal metabolites:** BNT (1) as predominant stromatal pigment and cytochalasins (9) in relatively small quantities.

*Notes:* See Ju et al. (1997) for a detailed description of the teleomorph and (periconiella-like) anamorph and Stadler et al. (2001a) for HPLC profiles. Based on the examination of the holotype, this species is morphologically mainly characterised by a soft and fragile, white interior lacking zonation and small ascospores. The isotype specimen revealed BNT and cytochalasins (Fig. 17), and the ascospores showed conspicuous transverse striations by SEM (Fig. 34G). Both features have not been reported previously and suggest close affinities of this fungus to the *D. eschscholtzii* group.

This species is said to be specifically associated with bamboo and presumably originates from Southeastern Asia. It resembles *D. caldariorum,* from which it mainly differs in its ascospore characteristics, and also seems to share characters with other members of the *D. eschscholtzii* group including the dehiscent ascospore perispore and the occurrence of cytochalasins in the stromata. Interestingly, the species clusters very close to *D. caldariorum* in the molecular phylogenetic study of Hsieh et al. (2005), based on a comparison of its β-tubulin and α-actin DNA sequences, as well as in our own phylogenetic tree based on nrDNA data (Figs 73/74). In contrast to other species that are specifically associated with monocotyledonous plants, we have included it in the *D. eschscholtzii* group because of the affinities to *D. caldariorum.*

**Daldinia brachysperma** F. San Martin, Y.M. Ju, & J.D. Rogers, Mycotaxon 61: 255. 1997. Fig. 34.

**Etymology:** For the short ascospores.

*Types:* **Mexico,** Quintana Roo State, Othón P. Blanco municipality, Ejido La Unión, 8 Jul.1986, San Martin 1376B (ITCV, holotype, n.v.; WSP 69653, isotype).

*Selected illustrations* (from holotype): Ju et al. (1997), figs 3 (ascospores) and 24, 25 (stromata).

**Known distribution/host preference of stromata:** Only known from Mexican type, host unknown.

**Teleomorph:** Stromata peltate, slightly wrinkled, nodulose, 0.7–0.8 × 0.5 cm; surface Brown Vinaceous (84); dull reddish brown granules immediately beneath surface, without apparent KOH-extractable pigments; tissue between perithecia grayish brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.1 mm thick, lighter zones white to grayish brown or yellow, pithy to woody, persistent, up to 0.5 mm thick. (Ratio darker/lighter zones: 1–5:1). *Perithecium* obvoid to slightly lanceolate, 0.8 × 0.3 mm. Ostioles slightly papillate, inconspicuous. *Asci* fragmentary, p. sp. ca. 65–74 × 6–8 µm, with amyloid, discoid apical apparatus 0.2 × 1.5 µm, length of stipes not determinable. Ascospores brown to dark brown, ellipsoid-inequilateral, with narrowly rounded to almost acute ends, 6.5–7.5 × 3–4 µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, smooth by LM, but revealing conspicuous ornamentations by SEM (visible at 2,500–5,000×); epispore smooth.

**Cultures and anamorph:** Unknown.

**Stromatal metabolites:** BNT and cytochalasins.

*Notes:* This poorly known species (first described by San Martin 1992 as *D. albozonata* affinis,) differs from all other taxa of the genus primarily in having peltate stromata and rather small ascospores (Ju et al. 1997). Its anamorph is not known. From its stromatal morphology and anatomy it appears related to *D. albozonata, D. clavata* and *D. caldariorum.* The HPLC profile of the isotype specimen revealed BNT and cytochalasins (Fig. 17), and the ascospores showed conspicuous transverse striations by SEM (Fig. 34G). Both features have not been reported previously and suggest close affinities of this fungus to the *D. eschscholtzii* group.


**Etymology:** Probably for the collection site of the type material (a greenhouse).

*Lectotypus* (selected by Ju et al. 1997): **Germany,** Berlin, fern house in Botanic Garden, Nov. 1885 (S–F38115A – tiny aberrant specimens with abnormal morphology; mixed with specimens of *D. childiae,* the latter designated S–F38115B).


The holotype specimen was still extant in B and studied by Child (1932), but was obviously destroyed by fire during WW II.)
A Polyphasic Taxonomy of DalDinia (Xylariaceae)


Typus: New Caledonia, Tendéa, wood, Bernier (FH-holotype; BPI 716961 ex Lloyd herb. 12374 - isotype).

= Daldinia hibiscus (Henn.) Lloyd, Mycol. Writings 6: 901. 1919.
≡ Hypoxylon hibisci Henn., Hedwigia 47: 259. 1908.


Typus: Argentina, La Plata, wood, 28 Nov. 1906, C. Spegazzini (LPS 159 - holotype).


Typus: India, Ficus carica, W. Gollan (holotype previously housed in B, but not located there in 2007 - was obviously destroyed by fire during WW II).


Typus: French Equatorial Africa, on Hevea brasiliensis (n.v., not located in PC).


Typus: (fide Saccardo 1882): East Africa, on wood, (n.v., not located in PC).


Fig. 33. Teleomorphic characteristics of DalDinia bambusicola. Holotype, WSP 69652 (Thailand). A, B, D. Stromatal habit. C. Part of stroma in longitudinal section showing perithecial layer. E. Stromatal surface showing the ostioles (inserted: Stromatal pigments in 10 % KOH). F. Ascospores in SDS. G–I. Ascospores in KOH, showing dehiscing perispore and germ slit. Scale bars A, B, D = 1 cm; C-E = 1 mm; F–I = 10 µm.
Stadler et al.

Fig. 34. Teleomorphic characteristics of Daldinia brachysperma (isotype, Mexico). A. Stromatal habit. B, C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Ascospores in SDS. F. Ascospores in KOH, showing dehiscing perispore. G. Ascospores by SEM (10.000×). Scale bars A–D = 1 mm; E, F = 10 μm; G = 2 μm.


Selected illustrations: Whalley & Watling (1980) as D. vernicosa, fig. 5 (anamorph); Ju et al. (1997), figs 4 (ascospores), 26 (atypically small stroma of lectotype) and 70 (anamorph); Wollweber & Stadler (2001), Abb. 6 (stromata). Images in Child (1932) are explicitly excluded.

Known distribution/host preference of stromata: Widespread in warm-temperate to tropical climates; with preference for burnt Ulex in Europe.

Teleomorph: Stromata turbinate to depressed-spherical, sessile or with short, stout stipe, smooth, sometimes with major wrinkles, 0.4–2 × 0.3–1.5 cm; surface Brown Vinaceous (84) or Grayish Sepia (106), blackened and varnished in age; dull reddish brown granules immediately beneath surface, with KOH-extractable pigments Livid Purple (81), Dark Livid (80), Vinaceous Purple (101), old specimens often with dilute or lacking KOH-extractable pigments; tissue between perithecia whitish to gray, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.1–0.3 mm thick, lighter zones whitish, gray, or brown, pithy to woody, mostly persistent, but sometimes larger stromata are gelatinous when fresh and become loculate with age, 0.3–1 mm thick.
A polyphasic taxonomy of *Dalldinia* (*Xylariaceae*)

Fig. 35. Teleomorphic characteristics of *Dalldinia caldariorum* (A–G: JF-07045, Ulex, France; H: K(M) 47140, Ulex, UK). A–C. Stromatal habit (C: Inserted: Stromatal pigments in 10 % KOH). D, E. Stroma in longitudinal section showing internal concentric zones, locules and perithecial layer. F. Ascospores in KOH. G. Ascospores in SDS, showing germ slits. H. Ascospore by SEM (10.000×). Scale bars A = 1 cm; B–E = 1 mm; F, G = 10 µm; H = 2 µm.

(Ratio darker/lighter zones 1:2–8). Perithecia obovoid, 0.5–0.8 × 0.2–0.5 mm. Ostioles inconspicuous or slightly papillate. Ascii 130–155 × 6–7 µm, p. sp. 60–75 µm, stipes 60–80 µm, with amyloid, discoid apical apparatus 0.5–0.75 × 2 µm. Ascospores brown, ellipsoid, slightly inequilateral to equilateral, with broadly to, less frequently, narrowly rounded ends, 8–11(–12) × 4–5.5 µm, with straight germ slit spore length usually on less convex side; perispore indehiscent in 10 % KOH; smooth by LM and SEM (15.000×).

Stromatal metabolites: BNT and other binaphthalenes, occasionally also cytochalasins in minor quantities, especially in young stromata.

Cultures and anamorph: Colonies on OA reaching the edge of 9 cm Petri dish in 6–8 d, whitish, felty, azonate, with diffuse margins, becoming fusicoculose; reverse uncoloured. Sporulating regions preferentially at edge of colony, Hazel (88). Conidiogenous structures nodulisporium-like. *Conidiophores* dit- or trichotomously branched, sometimes with additional branches arising from the first level of conidiogenous regions, hyaline to yellowish, coarsely roughened, up to 240 µm high and 2.5–3 µm diam, with two to three conidiogenous cells arising from each terminus. *Conidiogenous cells* cylindrical, hyaline, roughened, 10–20 × 2–3.5 µm. *Conidium* produced holoblastically in sympodial sequence, hyaline, smooth, ellipsoid, with flattened base, 4.5–6.5(–7) × 2.5–4.5 µm.

European material from burnt Ulex in the UK (see Whalley & Watling 1980 as D. vernicosa p.p.; Stadler & Wollweber 2001, where D. vernicosa is referred to as D. fissa) and other parts of the world is highly similar to tropical specimens with regard to teleomorphic and anamorphic morphology. The notable difference between the culture ATCC 36660 originating from the work by Whalley & Watling (1980) and the Mexican strain CBS 122874, which we examined for comparison, was the ability of the latter to form stromata on OA, as described by Ju et al. (1997). However, the dimensions of their conidiogenous structures, HPLC profiles, and ITS nrDNA sequences of the American and European cultures (i.e., data for CBS 122874 vs. published data in Bitzer et al. 2008) agreed well with one another. It was hitherto thought that D. caldariorum has close affinities to D. vernicosa, with which it may even co-occur on the same host plant (Wollweber & Stadler 2001). However, recent molecular data provided by Hsieh et al. (2005) and Bitzer et al. (2008) on different gene portions show that the phylogenetic distance between D. caldariorum and D. vernicosa as assessed by a comparison of ITS sequences, as well as α-actin and β-tubulin genes, is unexpectedly high. In fact, D. caldariorum appears more closely related to the D. eschscholtzii group in molecular phylogenies. ITS sequences and secondary metabolite profiles even revealed affinities to the cleistothecial tropical genera Phylacia and Rhopalosorla, and also to Thammomyces. On the other hand, the morphologically similar D. vernicosa showed closer affinities to other temperate Daldinia species. The prominent white internal concentric zones of these species and their similar ascospore morphology could therefore have arisen convergently, which is also corroborated by the fact that the anamorph of D. vernicosa is fairly different from that of D. caldariorum. The former features highly variable conidiophores, while the latter is similar to D. eschscholtzii in possessing conidiophores of the nodulisporium-type with relatively small conidia.

Tropical collections of D. caldariorum are hard to tell from D. clava (the only distinguishing teleomorphic microscopic features being the indistinct isoperidium and position of the germ slit). Possibly, the origin of this species is in the tropics, and it may eventually have invaded Europe from there, perhaps in association with the notorious invasive weed, Ulex europaeus, which has colonised many parts of the world as it is extremely well adapted to coastal and other disturbed environments. We did not obtain mature stromata on OA, as described for the Mexican culture (CBS 122874) by Ju et al. (1997). Only MUCL 47715 from South Africa occasionally developed stromatal primordia at the edge of the colonies, but those were only covered with the conidiophores. In addition, CBS 122874 has the smallest dimensions of conidiophores and conidia of all cultures we studied, hence the data given in the species description deviate from those in Ju et al. (1997). Interestingly, cultures of D. caldariorum were recently reported to deviate from other Daldinia spp. by producing eutypinol derivatives aside from other common metabolites (Bitzer et al. 2008). In the same study, a culture from “soil and plant debris” originating from Democratic Republic of the Congo (“Zaire”; MUCL 3531, IMI 62333, referred to as Nodulisporium africanum Smith by Meyer 1955) showed a similar HPLC profile to D. caldariorum. We have meanwhile found that this strain also closely resembles the latter species with respect to the dimensions of its conidiogenous structures, even though it did not produce stromata on OA. However, this culture does not constitute the type strain of N. africanum, which was apparently not deposited by Smith (1951). In the absence of living cultures, it might prove very difficult to reassign all the anamorphic Nodulisporium spp. that have been described over the past centuries and decades to an accepted teleomorphic species. After all, various other genera of the Xylariaceae that appear rather distantly related to one another have highly similar morphological structures of their conidiophores.
**Daldinia clavata** Henn., Hedwigia 41: 14. 1902. Figs 5j, I, 36.

**Etymology:** For the stromatal shape.


**Holotypus**: **Brazil**, Matto Grosso, Guia, ad trunkum mucidum in “capoeira” varustata, 13 May 1894, G. Malme 595 (S-F40196).


**Holotypus**: **Argentina**, Misiones, Puerto Pampa, Jan. 1901, E. Kermes (LPS 160).

≡ *Daldinia barbata* Rick, Broteria 5: 50. 1906.


**Selected illustrations**: Child (1932), Plate 27, fig. 2 (ascospores of type of *D. clavata*), Plate 30, fig. 6 (stromata of type of *D. argentinensis*); and Plate 33, fig. 5 (perithecium of type of *D. vericosica* var. microspora).

**Known distribution/host preference of stromata**: Tropical Africa and the Americas, rarely found in subtropical regions. Host plants are largely unknown, but apparently it grows on dicots.

**Teleomorph:** Stromata cylindrical to somewhat clavate, unbranched or sometimes branched, subsessile or with stout stipe usually bearing constricted rings, solitary to infrequently aggregated, smooth or with inconspicuous to conspicuous perithecial outlines, 1.35–1.5 cm, the stipe up to 2.5 cm long × 0.5–1.5 cm diam; surface Brown Vincasce (84) to Sepia (63), blackened and vanished in age; dull reddish brown granules immediately beneath surface, with KOH-extractable pigments Dark Livid (80), Vinaceous Gray (116), or without apparent KOH-extractable pigments in old overmature specimens; tissue between perithecia whitish, grayish, or brown, pithy to woody; tissue below perithecial layer composed of alternating zones, usually extending into the stipe; darker zones dark brown, pithy to woody, 0.2–0.4 mm thick, lighter zones white to light grayish brown, pithy, becoming fibrous and loculate, 0.7–2.2 mm thick (Ratio darker/lighter zones 1:3–6). *Perithecia* obovoid, 0.61–1.03–0.5 mm. *Ostioles* slightly papillate, inconspicuous. Ascii 155–195 × 6.5–7.5 µm, p. sp. 60–80 µm, stipes 95–130 µm, with amyloid, discoid apical apparatus 0.5 × 2.5–3.5 µm. Ascospores brown to dark brown, ellipsoid-inequalitarian, with narrowly rounded ends, 8–11.5 × (3.5–4–5.5 µm, with straight germ slit sori length on convex side; epispore dehiscent in 10 % KOH; smooth by LM but showing conspicuous transverse striations by SEM (2.500–5.000×); epispore smooth.

**Cultures:** Colonies on OA reaching the edge of 9 cm Petri dish in 8–10 d, at first whitish, felter, azonate, with diffuse margins, becoming zonate with alternate whitish and Mouse Gray (119), to Greenish Grey (110), layers, the latter consisting of inflated, melanised hyphae. Aged cultures later becoming covered with Olivaceous Buff (89) mycelial layer. Reverse remaining uncolored or turning faint Hazeld (88) on OA. Cultures on YMG agar showing a similar habit, but releasing more of the pigment in to the agar and finally turning Umber (9) to Sepia (63). No stromata and no conidigenous structures observed on either OA or YMG agar.

**Stromatal metabolites**: BNT and other binaphthalenes, no cytochalasins detected even in immature stromata.


Notes: The erection of this species was based on material collected by Möller (1901) from southeastern Brazil. The concept of Ju et al. (1997) comprises specimens from the African and American tropics with clavate to cylindrical stromata (albeit they added in their “Notes” that the stromata of the type of *D. albozonata* are “turbinate to clavate”), inconspicuous perithecial outlines, KOH-extractable stromatal pigments purple or lacking, rather broad, white, broad internal concentric zones, and ascospores 8–11.5 × (3.5–)4–5.5 µm. The types of *D. albozonata*, *D. barbata*, *D. clavata*, and *D. vericosica* var. microspora have been studied for comparison, including HPLC (Fig. 17) and SEM analyses. Only the types of *D. barbata*, *D. vericosica* var. microspora, and other specimens listed above completely agreed with that of *D. clavata* when their stromatal anatomy, ascospore morphology, ascosporal ultrastructure, and HPLC profiles were compared. The type of *D. albozonata* differed in having significantly smaller ascospores, and in apparently containing cytochalasins, similar to those 1997.

1997.
found in *D. eschscholtzii*. In contrast, only BNT was found in all specimens listed here as *D. clavata*. Although the HPLC results on the old type specimens should be confirmed based on fresh material, we regard the lack of cytochalasins as significant, and follow Child (1932), who treated *D. clavata* and *D. albozonata* as separate, albeit closely related species that can be distinguished based on stromatal and ascospore morphology.

The African and American *Dalpinia* spp. with clavate to cylindrical stromata can currently be discriminated best by the aid of SEM and/or by studies on their anamorphic structures (even though *D. clavata* also seems to be unique in having obvoid, rather than tubular perithecia, and a close morphological examination of the stromatal features can also aid in their discrimination). Some even show affinities to *D. caldariorum*, from which *D. clavata* mainly differs in its stromatal habit and its ascospore morphology (differences in perispore, position of the germ slit). Unfortunately, material of *D. sp* and allies is not easily available since these fungi appear to be much rarer than, e.g., *D. eschscholtzii*, and fresh collections were therefore not encountered during our recent forays in the tropics. While all other specimens treated above show purple or no stromatal pigments at all in KOH, the morphologically similar can be much rarer than, e.g., *D. eschscholtzii*, and/or by studies on their anamorphic structures (even though *D. clavata* is here listed as *D. eschscholtzii* var. *microspora* (selected here): MBT177383; Paraguay, Parauari, Cerro Negro, 8 Aug. 1893, G.A. Malme (S-F11857 - holotype *fide* Ju et al. 1997 but an identical element (isolateotype) is stored in S as S-F11856).


Selected illustrations: Starbäck (1901), fig. 2 (stromata, type); Child (1932, correspondence of material not always stated), Plate 27, fig. 1 (ascospores), Plate 28, fig. 6 (stromatal surface), Plate 30, fig. 7 (stromata of type of *D. argentinensis*) and Plate 31, fig. 4 (perithecia); Ju et al. (1997), figs 8 (ascospores) and 36, 37 (stromata).

Known distribution/host preference of stromata: South America and Africa; host affinities unknown.

Teleomorph: Stromata usually cylindrical to subclavate, subsessile or with stout stipe usually bearing constricted rings, rarely peltate, without conspicuous perithecial outlines, 1–2 × up to 5.5 cm, the stipe up to 2 × 0.7–1.3 cm; surface Fuscous (103), blackened and varnished in age; dull reddish brown granules immediately beneath surface, with KOH-extractable pigments variable, ranging from Mouse Gray (119), Greenish Grey (110), Greyish Sepia (106) or Brown Vinaceous (84); tissue between perithecia grayish or brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2–0.3 mm thick, lighter zones white, pithy, becoming fibrous and loosening, 2–3 mm thick (Ratio darker/lighter zones 1.8–12). Perithecia obovoid, 0.6–0.8 × 0.4–0.6 mm. Ostioles slightly papillate. Asc–fragmentary, p. sp. 65–80 µm, with amyloid, discoid apical apparatus, 0.5 × 2.5 µm. Ascospores brown to dark brown, ellipsoid-inferiometric, with narrowly rounded ends, 10–11.5(–12.5) × 4.5–5.5(–6) µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, smooth by LM, but showing conspicuous transverse striations by SEM (5,000×); epispore smooth.

Cultures and anamorph: Unknown.

Stromatal metabolites: BNT and unknown compounds that are perylene quinones or naphthaquinones as inferred from HPLC-DAD/MS data.


Notes: As stated by Ju et al. (1997) this species mainly differs from *D. clavata* in having slightly larger ascospores, different pigments and more prominent perithecial outlines. We studied the “holotype”, now designated lectotype, in S, and the LPS type of *D. granulosa* (*fide* Ju et al. 1997). We agree with their conclusion, but wish to emphasise that the perithecial outlines are not that prominent (this may appear so because the ostioles are quite conspicuous on the light coloured background of the stromatal surface; also cf. our results on *D. lloydii*). In addition, the lighter internal zones of *D. cuprea* are 8–12 times wider than the darker ones, whereas this ratio is much smaller in *D. clavata* and morphologically similar species. Ascospores of the type specimen of *D. cuprea* showed conspicuous transverse striations by SEM (Fig. 37G). We found the stromatal pigments in KOH quite variable, differing from Mouse Gray (119) as stated by Ju et al. (1997), greenish grey or brown vinaceous tones, depending on the concentrations and incubation times. Accordingly, the HPLC profile revealed BNT (1) and a series of apparently specific, unknown secondary metabolites,
which are probably perylene quinones (2). As a main difference to
D. cuprea, D. clavata and other relatives always contained BNT (1)
as prevailing component and showed purple or no apparent pigments
in KOH, while the greenish pigments of D. albofibrosa are due to
the presence of daladione A (3). The latter species also does not
show the characteristic cylindrical stromatal habit, and its stromata
are stouter and smaller. Despite the rejection of a previous record
by Dennis (1963, see here sub D. clavata from D.R. Congo), we,
evertheless, confirm that D. cuprea occurs in tropical Africa.

Daldinia rehmii Læssøe, M. Stadler & J. Fourn., sp. nov.
MycoBank MB512370. Figs 5D, E, 38.

Etymology: Named for the German mycologist, Heinrich Rehm.

A Daldinia eschoscholtzii differt in ascosporae minorae, 9.5–10.5(-11) × 4.5–5.5
µm vel granulis violaceis obscura in KOH dissolutis.

Holotypus: Brazil, Roraima, Boa Vista-Venezuela road, 2 km
Dumont INPA 78-470 (NY).

Known distribution/host preference of stromata: Tropical South
America; hosts unknown dicots.

Teleomorph: Stromata irregularly hemispherical to turbinate with a
short stout stipe, somewhat shrivelled, with margins strongly revolute,
1–2.1 × 0.8–1.4 cm, surface Brown Vinaceous (84), blackening in
places, smooth to finely reticulate, often cerebriform due to shrivelling,
with reddish brown granules immediately beneath surface, with
KOH extractable pigments dense Livid Violet (79); tissue between
perithecia blackish to grey brown, woody, tissue beneath perithecial
layer composed of alternating concentric zones, woody, darker
zones blackish brown, 0.3–0.4 mm thick, lighter zones brownish grey,
persistent, 0.3–0.5 mm thick (Ratio of darker/lighter zones 1:1–1.5).
Perithecia lanceolate, 1.5–1.7 × 0.25–0.35 mm, densely crowded. Ostiolar inconspicuous, non-papillate. Asci fragmentary, cylindrical, probably very long-stipitate, p. sp. 70–83 × 6.5–7 μm, with amyloid, discoid apical apparatus 0.5–0.75 × 2–2.5 μm. Ascospores brown, ellipsoid-inegalitarian with narrowly to broadly rounded ends, 9.5–10.5(–11) × 4.5–5.5 μm, with straight dorsal germ slit spore length, perispore dehiscent in 10 % KOH, smooth by LM; epispore smooth.

Cultures and anamorph: Unknown.

Stromatal metabolites: relatively large amounts of BNT, concentricol A and further binaphtyls as major components, cytochalasins and daldinone B as major component. Additional specimens examined: Ecuador, Cotopaxi, 1 km south of Mana, 00° 56' S, 79° 14' W, alt. 175 m, dead hardwood in cacao plantation, 10 Jun. 1985, T. Læssøe AAU 59501 (C).

Notes: This fungus differs from D. eschscholtzii in having shrivelling stromata with revolute margins and well-defined stipes, a more woody internal tissue, much darker pigments in KOH in relation to a different HPLC profile, more tubular perithecia and smaller ascospores. Specimen AAU 59501 is tentatively referred to D. rehmi because of strong morphological resemblance and similar HPLC profiles, but deviates by slightly larger ascospores 10–11(–12) × 5.5–6.5 μm.


Etymology: Named for the Swedish mycologist Karl Starbäck.

A Daldinia eschscholtzii var. concentrica in having shrivelling stromata with revolute margins and well-defined stipes, a more woody internal tissue, much darker pigments in KOH in relation to a different HPLC profile, more tubular perithecia and smaller ascospores. Specimen AAU 59501 is tentatively referred to D. rehmi because of strong morphological resemblance and similar HPLC profiles, but deviates by slightly larger ascospores 10–11(–12) × 5.5–6.5 μm.


Known distribution/host preference of stromata: The Americas mainly in the Neotropics; probably also in Central Africa; on unknown dicot hosts.

Teleomorphic and anamorph: This species differs from D. eschscholtzii in having smaller ascospores, ellipsoid–inegalitarian with broadly to narrowly rounded rounded ends, (9)–10–12(–13) × 5–6(–6.5) μm, in having relatively dense yellowish-olivaceous, rather than weak purple stromatal pigments in KOH, and in producing virgariella-like conidiogenous structures rather than nodulisporium-like as usually found in D. eschscholtzii. Conidiophores up to 100 × 2.5–3 μm (shorter than in D. eschscholtzii), dichotomously branched, with one or two terminal conidiogenous cells. Conidiogenous cells cylindrical, 16–24 × 2.5–3.5 μm; conidia ellipsoid, sometimes with flattened base, 5–9 × (2.5)–3–4.5 μm (larger than in D. eschscholtzii). Stromatal metabolites: relatively large amounts of BNT, cytochalasins and dalldinone B as major component.


Notes: This species was encountered in central, western and northern South America and the Caribbean, where it co–occurs with D. eschscholtzii. The collection reported by Rehm (1904) from Texas is also listed here, but notably, the ascospores we studied by SEM and LM were often not intact and many of them had already lost their perispore. The few sporas found in a SEM preparation appeared smooth unlike typical D. starbaeckii, but this observation remains to be confirmed by studies on fresh material. It could constitute a yet different taxon. The Brazilian specimens reported by Starbäck (1901) as D. concentrica var. eschscholtzii correspond well with this species with respect to teleomorphic features and their HPLC profile. The ascospores of D. starbaeckii are smaller in average than those of D. eschscholtzii, and the stromata release yellowish-olivaceous pigments in KOH. It differs from D. eschscholtzii and D. rehmi in that dalldinone B (4) is always clearly detectable in crude extracts, while containing relatively small amounts of cytochalasins and concentricols. This feature most probably also accounts for the deviating pigment colours as compared to D. eschscholtzii. Dalldinone B (4) was originally obtained from D. concentrica as a minor component only after preparative extraction of stromata and separation by HPLC (Quang et al. 2002a, b). The compound is only detectable by the highly sensitive HPLC–MS techniques in the crude stromatal extract of D. concentrica and is apparently absent in most specimens examined of D. eschscholtzii. Notably, the anamorphic structures in the cultures of D. starbaeckii showed a certain degree of variability. While the ex–type culture mostly produced a typical virgariella–like anamorph, the conidiophores in some of the materials from the Caribbean appear to grade into the more complex nodulisporium–like branching pattern. The specimens cited above as D. eschscholtzii from Martinique appear related but still had larger ascospores, and the Hazel (88) KOH-extractable pigments observed in some of them were not attributed to the presence of dalldinone B (4) according to HPLC–MS. In addition, the cultures showed nodulisporium-like conidiophores, reminiscent of the other materials studied of D. eschscholtzii. The anamorph of D. starbaeckii differs from that of D. eschscholtzii by the former having only one or two apical conidiogenous cells on the conidiophores. In addition, the conidiogenous structures and conidia of D. starbaeckii are more robust (Table 3).

Some further specimens from tropical Africa (Fig. 40) may also belong here, as they have significantly smaller ascospores than found in typical D. eschscholtzii. Their KOH–extractable
pigments are weakly purple, overlaid with a shade of Hazel (88), and HPLC reveals minor amounts of daldinone B (4) aside from BNT (1) and cytochalasins (9). Two specimens from Uganda in K also showed similar characteristics as those from the Congo region. Among those, K(M) 130376 has broader internal zones (almost as in the D. clavata group) but the stromata are turbinate to placentiform. They differ from D. rehmii and D. caldariorum in their HPLC profile and in their stromatal

Fig. 38. Teleomorphic characteristics of Daldinia rehmii (A–J: Holotype, Brazil) and D. cf. rehmii (J–M: AAU 59501, Ecuador). A, B. Stromatal habit (J: Inserted: Stromatal pigments in 10 % KOH). C, D, K. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface (inserted: Stromatal pigments in 10 % KOH). F, G. L. Ascospores in SDS, showing germ slits. H. Ascus top in Melzer’s reagent showing apical apparatus. I, M. Ascospores in KOH, showing dehiscing perispore. Scale bars J, K = 1 cm; A–C = 5 mm; D, E = 1 mm; F–I, L, M = 10 µm.
morphology and anatomy. In addition to daladinone B (4), further peaks corresponding to unknown compounds (possibly lipophilic binaphthalenes as judged from their similar HPLC-UV and HPLC-MS characteristics) were also observed in their stromatal extracts.

The only specimens found in rather good condition (D.R. Congo, District Forestier Central, Irangi, Kivu, on Polyscias fulva, May 1972, J. Rammeloo 470/JRZ (divided into two packets by H. Wollweber & M.S. with specimens showing slightly deviating HPLC profiles and stromatal pigments (GENT; designated Ww 3774/Ww 3775) are described below in detail.

The stromata separated as Ww 3775 (Fig. 40A–G) are turbinate to irregularly peltate (larger stromata shrivelled), without visible perithecial outlines, centrally to laterally stipitate with stipes up to 20 × 10–22 mm, less often nearly sessile, 3.2–5.4 × 2–3.5 cm; surface Dark Vinaceous (82), blackening and becoming shiny where the outer pruina is worn off; dull orange brown granules immediately beneath surface, with dilute Isabelline (65) KOH-extractable pigments; tissue between perithecia grey brown, pithy; tissue below perithecial layer composed of alternating zones, darker zones brown, pithy to woody, 0.35–0.45 mm thick, lighter zones brownish gray, pithy to woody, solid, rarely loculate in places, 0.4–0.65 mm thick. Perithecia lanceolate, 1.5–1.8 × 0.4 mm. Ostioles slightly papillate, 80–100 µm diam. Asci not seen. Ascospores dark brown, ellipsoid, slightly inequilateral with broadly to narrowly rounded ends, 9.5–11 × 5–6 µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, smooth to very faintly striate by LM; epispore smooth. The other part of this collection (Ww 3774) (Fig. 40H–N) is composed of smaller stromata, not exceeding 30 mm diam, hard-textured, stipitate, cerebriform, apparently shrivelled upon drying. Interior is darker and layers less contrasted but likewise somewhat loculate, especially in upper parts. Perithecia are a little broader and shorter. Ascospores are somewhat darker and slightly larger (10–12.5 ×
5.5–6 µm). These specimens fit well the concept of D. starbaeckii; however cultures should be obtained and studied before their status can finally be decided upon.

Additional specimens examined (of D. cf. starbaeckii from Africa): D.R. Congo, District Forestier Central, km 51 on road to Bengamisa, 12 Nov 1939, J. Louis 16312 (BR–Myc 129040,17; see Dennis 1963 and Van der Gucht 1994 as D. eschscholtzii); Equateur, Eala, Jun. 1907, L. Pyneaert 1584 (BR–Myc 033516,51; see Dennis 1963); same locality, Aug. 1930, P. Staner 415 (BR–Myc 033517,52; see Dennis 1963); Lohulo, Kabambere, Parc National Albert, 11 Sep. 1954, G.F. de Witte 11250 (BR–Myc 033518,53; see Dennis 1963); Uganda, Kopaya, on stump, Apr. 1915, R. Duemmer 1442 (K(M) 130377); Mabira Forest, 1915, T.D. Maitland 23 (K(M) 130376).

**Daldinia theissenii** Læssøe, J. Fourn. & M. Stadler, sp. nov. MycoBank MB564867. Figs 5H, 10K–M, 41.

**Etymology**: Named for the German mycologist, Friedrich Theissen.

A Daldinia clavata differt in ascosporibus levis per SEM (5000× magnitudine) et perithecia lanceolata.

**Holotypus**: Peru, Dept. Huanuco, Tingo Maria, Parque National Tingo Maria at Cuevas de los Lechuzas, in shadowy clearing, on very rotten, dicot. trunk in association with Xylaria cf. multiplex, 7 Jul. 1987, T. Læssøe P-210 (C; ex-type culture CBS 113043, MUCL 44608).
**Polyphasic Taxonomy of Daldinia (Xylariaceae)**

**Misapplied name:** *D. clavata* sensu Ju et al. (1997) p.p.

**Known distribution/host preference of stromata:** Only known from South America, host affinities unknown.

**Teleomorph and anamorph:** This taxon differs from typical *D. clavata* primarily in having slightly larger ascospores, which are ellipsoid-inequilateral with broadly to less frequently narrowly rounded ends, (8–)9–12(–13) × 5–6 µm, with perispore dehiscent in 10 % KOH (showing a similar morphology as those of the latter by LM but with conspicuous transverse striations by SEM and lanceolate perithecia vs. obovoid ones in *D. clavata*). It also differs by the presence of a nodulisporium-like anamorph similar to that of *D. eschscholtzii*, while *D. clavata* does not produce the anamorph in culture. Cultures and anamorphic structures were described by Ju et al. (1997) as *D. clavata*, and also resemble the description given here for *D. eschscholtzii*.

**Stromatal metabolites:** BNT in traces and cytochalasins in abundance.

**Additional specimen examined:** Argentina, Iguazú, dead angiosperm wood, Mar. 1995, H. Dörfelt (KR, culture CBS 113044, MUCL 44609, see Stadler et al. 2001a,b as *D. clavata* Ww 3728; GenBank Acc. No. of DNA sequence AM749932).

Further corresponding culture: Mexico, Tamaulipas state, Gómez Farias town, Mar.1988, Flores 2 & San Martin 1024 (ICTV, culture BCRC34045, CBS 122875; GenBank Acc. Nos AY951695 and AY951693; see Ju et al. 1997, Stadler et al. 2001a and Hsieh et al. 2005 as *D. clavata*; voucher YMJ 106 in the latter study).

**Notes:** Daldinia clavata and *D. theissenii* have very similar teleomorphic characters. The stromata of the latter are more variable, e.g., some stromata of *D. theissenii* may attain a rather flattened top or an almost lense-shaped habit (Fig. 41A, B). The new species, however, contains large amounts of cytochalasins especially in young stromata, which are lacking in *D. clavata*. Instead, stromata of the latter species contain larger amounts of binaphthyls in fresh and young specimens. In addition its ascospores are smooth by SEM, and it readily produces the anamorph in culture.

We have not studied the corresponding teleomorph of a cultured specimen from Mexico referred to by Ju et al. (1997) as *D. clavata* to compare its ascospores by SEM. However, the culture of Ww 3728 showed the same morphology and specific PCR fingerprints as the above Mexican material (Stadler et al. 2001b), and the ascospores of Ww 3728 were smooth by SEM (Stadler et al. 2002). The anamorph of *D. theissenii* (i.e., *D. clavata* sensu Ju et al. 1997, as proven by Stadler et al. 2001b), strongly resembles that of *D. eschscholtzii* described in detail above. Like the cultures of the latter species, those of *D. theissenii* readily produce conidiophores after less than one week of incubation, and even tend to produce immature stromata on OA after 2–3 wk. The only culture we have obtained from a specimen that showed the typical teleomorphic characteristics of *D. clavata*, however, failed to produce the anamorph. We conclude that Ju et al. (1997) have described a culture of what we regard as *D. theissenii*. The conidiogenous structures of this fungus are similar to those of *D. eschscholtzii*, despite *D. theissenii* is easily segregated from the latter species by comparison of ascospore morphology and stromatal anatomy. Out of the *D. eschscholtzii* group as understood here, it appears most closely related to *D. starbaeckii*, which differs from it in having smaller ascospores, and more robust anamorph grading into virgariella-like, and in its stromatal pigments.

---

**Fig. 41.** Teleomorphic characteristics of Daldinia theissenii. Holotype (Peru) A. Stromatal habit. B, C. Stroma in longitudinal section showing internal concentric zones and perithecial layer. D. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). E. Ascospores in SDS. F. Ascal tops in Melzer’s reagent showing apical apparatus. G. Ascospores in KOH, showing dehiscing perispore. H. Ascospores by SEM (10.000×). Scale bars A, B = 5 mm; C, D = 1 mm; E–G = 10 µm; H = 5 µm.
The *Daldinia chilidae* group comprises species that have yellowish brown stromatal pigments, owing to the presence of daldinins (7) and daldinals (8). They are frequently clustered and darker concentric zones are often apparent above the stromatal surface, particularly in young stromata. The ascospores of this group are narrowly inequilaterally ellipsoid with dehiscent zones. In most cases, ostioles are slightly papillate, often discoid.

**Table 9.** Major discriminative characters of the species in the *D. chilidae* group. CC: Conidiogenous cells; CON: Conidia. N, V, S, P, referring to the most frequently observed branching pattern, i.e. nodulisporium-, virgariella-, or sporothrix-like, respectively, as defined in Ju & Rogers (1996).

<table>
<thead>
<tr>
<th>Species</th>
<th>Ascospore size (µm)</th>
<th>Ascal apical apparatus (µm)</th>
<th>Stromatal pigments (KOH)</th>
<th>Ratio darker/lighter concentric zones</th>
<th>Anamorphic structures (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>australis</em></td>
<td>13.5–18–(19) × 7–8.5</td>
<td>0.8–1 × 3.5–4</td>
<td>Cinnamon (62) to Fulvous (43)</td>
<td>1–2:1</td>
<td>CC: 10–21 × 3–4.5</td>
</tr>
<tr>
<td><em>childiae</em></td>
<td>12–16(–17) × 5.5–7.5</td>
<td>0.5 × 3</td>
<td>Mostly Umber (9) or Cinnamon (62)</td>
<td>1:1–2</td>
<td>CC: 10–25 × 3–4</td>
</tr>
<tr>
<td><em>pyrenaica</em></td>
<td>13–17(–20) × 6.5–8(–9)</td>
<td>1.5 × 4</td>
<td>Fulvous (43), Apricot (42), Umber (9), or Honey (64)</td>
<td>1:1–2</td>
<td>CC: 10–25 × 2.5–3</td>
</tr>
<tr>
<td><em>stiglichii</em></td>
<td>(13–)14–15.5(–17.5) × 7–8</td>
<td>0.8–1 × 3–3.5</td>
<td>Sepia (63), Umber (9), Fuscous Black (104)</td>
<td>1:1–2</td>
<td>CC: 12–20 × 2.5–3.5</td>
</tr>
</tbody>
</table>

**Group C: The Daldinia chilidae group (Figs 42–46)**

The *D. chilidae* group comprises species that have yellowish brown stromatal pigments, owing to the presence of daldinins (7) and daldinals (8). They can be discriminated by the morphological features compiled in Table 9. Oxidised naphthalenes and perylene quinones, as well as cytochalasins and concentricol, are apparently lacking. Their stromata are often substipitate to turbinate and very rarely truly sessile and hemispherical. They feature compact, light brown to dark brown internal concentric zones, quite often turning loculate with age, alternating with dark brown darker internal concentric zones. In most cases, ostioles are slightly papillate, often discoid. The ascospores are narrowly inequilaterally ellipsoid with dehiscent zones. In most cases, ostioles are slightly papillate, often discoid.

The anamorphs exclusively show a holoblastic conidiogenesis and stromatic structures are always produced in culture. This species has been found in central Europe, and our results indicate that it is absent in southeastern Canada. In Europe, it appears to be frequent only in warmer climates; especially frequent in USA. Widely distributed, with preference for warmer climates; especially frequent in USA. Without apparent host preference and even recorded on a conifer (*Cryptomeria*).
inequilateral, with narrowly rounded ends, 12–16–17 × 5.5–7.5 µm, with straight germ slit sori length on convex side; perispora dehiscent in 10% KOH, by SM but showing conspicuous transverse striae by (2.500–5.000) µm; epispore smooth.

**Cultures and anamorphs:** Colonies on OA reaching the edge of 9 cm in 10% KOH, smooth by LM but showing conspicuous transverse striae by (2.500–5.000) µm.

Conidiogenesis in cultures from the first level of conidiogenous regions, hyaline to yellowish, finely dusted, up to 240 × 3–3.5 µm, di- or trichotomously branched, sometimes with additional branches arising from the first level of conidiogenous regions, hyaline to yellowish, finely roughened, with 2–3 conidiogenous cells arising from each terminus.

Conidiogenous cells cylindrical, hyaline, finely roughened, 10–25 × 3–4 µm. Conidiogenesis in cultures often ceases after several consecutive transfers to new culture media, and in some cultures, no conidiogenous structures appeared.


N. **Acer campestre** (label reading "Russia"); Caucasus, Abkhazia, Gagri, 30 Oct. 1968, J. M. Sim in Lloyd herb. (STMA 10037); Karlsruhe City, Naturkundemuseum, on wood stem of A. campestre, 6 Oct. 2006, A. Akulov (CWU-Veshenskaya, Semenovskaya beam, 48°14'N, 134°58'E, unburnt log, 12 Oct. 1945, E.G. Simmons (NY, 2 packets); same data, fallen trunk of A. campestre, 26 May 1903, Prof. P. Voss in herb. Saccardo (PAD).
A POLYPHASIC TAXONOMY OF DALDINIA (XYLARIACEAE)


Further, authentic cultures (corresponding stromata not studied, but rDNA data and morphology in accordance with the above specimens): Japan, exact locality unknown. J. Abe (ATCC 73618), USA, New York State, Frost Valley YMCA, Perimeter trail, Fagus sp., W. Unterreiner (MUCIL 41709).

Notes: This fungus has undoubtedly been confused and lumped with the European D. concentrica for several decades. This certainly relates to the fact that it is by far the most frequent species of the genus in several countries including the USA and its stromata have been found on many different woody angiospermous host plants. Aside from Ju et al. (1997) and Child (1932), even Saccardo (1882) and many other mycologists who monographed Daldinia in the 20th century, did, indeed, include D. childiae in their concept of D. concentrica, as demonstrated by the above list of specimens. Based on HFLC data and morphological studies we exclude Hypoxylon simile from the list of synonyms of D. childiae (see D. dennisii) as well as D. concentrica f. confluens (which is here regarded as possible synonym of D. petriniae), and we also found that the type specimen of D. concentrica var. minuta corresponds to D. caldariorum. Daldinia chilidiae is, indeed, cosmopolitan and even seems to be more widely distributed in Europe than hitherto thought. For instance, it is here also recorded from Denmark, Germany and Latvia. Daldinia chilidiae definitely prefers warmer temperate climates, but is not restricted to those and appears to be more frequent at higher altitudes than e.g. D. eschscholtzii in the tropics, as exemplified by the material from Ecuador. Notably, the synonymy of D. concentrica sensu Child (1932) with D. chilidiae is not quite straightforward. Upon revision of numerous specimens listed in her monograph, we found that her concept of D. concentrica included some typical D. concentrica sensu stricto. (and sensu Rogers et al. 1999) from Fraxinus in Europe, as well as at least six other species in the current sense. The most frequent occurrence was with D. eschscholtzii.

Applying the concept of Child (1932) to European material, Petrin & Müller (1986) accordingly reported a “D. (cf.) eschscholtzii” from France (actually collected from the same region as the type of
**D. childiae**, Dept. Pyr. Atlantiques, where this fungus is extremely frequent), and gave a detailed description of the teleomorph, anamorph, and cultures (see their Abb. 41). Although not mentioned by Rogers et al. (1999), this proved identical with *D. childiae* (Stadler et al. 2001a). *Daldinia concentrica sensu* Petriň & Müller (1986) also agrees with the descriptions by Van der Gucht (1994) and Rogers et al. (1999). Hence, they were the first to describe the most important differences in the morphology of *D. childiae* and *D. concentrica*. The concept of *D. concentrica* as understood by Martin (1969) also did not fully correspond to *D. childiae*. Although this fungus was represented, e.g., by some specimens from California, some other specimens identified by him as *D. concentrica*, are listed elsewhere herein (e.g., *D. petrińea*). One collection, he identified as *D. eschscholtzii* from Louisiana, actually agrees with *D. childiae*. Unfortunately, none of the specimens from which he deposited cultures has so far been relocated. It is therefore difficult to reconstruct the correspondence of his anamorphic description to any of the currently accepted taxa. His description of the anamorph seems to deviate from our data on both *D. concentrica* and *D. childiae*. The *D. childiae* cultures from France reported by Rogers et al. (1999) were recently deposited with CBS, but the ex-type strain has lost its characteristic morphological features. Nevertheless, there are many more or less authentic cultures of this species, including a paratype strain, derived from material collected in Tartas that still shows the typical anamorphic structures. Strain CBS 159.31, deposited by Child as “*D. concentrica*”, is, likewise, degenerate and did not show any distinct morphological characters to prove its identity. It did not even produce the characteristic compounds (8-methoxy-1-naphthol etc.; cf. Fig. 2) in culture.

**Deviating material in the *Daldinia childiae* group**

As with other apparently frequent and ubiquitous taxa in the genus, there are indications that yet undescribed taxa still exist in the *D. childiae* group. For instance, a specimen from P.R. China (Fig. 43): Yunnan, Chu Xiong, Zi Xí Shan Nature Reserve, 2500 m asl, 25°01.178’ N, 101°24.245’ E; *Prunus* sp., 17 Sep. 2008, C. Decock CH-08-539 (MUCL 51694, incl. culture) deviates from typical *D. childiae* in having sessile, depressed-spherical stromata and slightly larger ascospores (14.5–17 × 6.8–8.5 µm), featuring a straight germ slit, 2/3 to less frequently nearly spore length on the most convex side. Its anamorphic characteristics and HPLC profile were the same as in *D. childiae* from other localities. As the spore size ranges largely overlap and in absence of other differential characters, the germ slit length alone does not allow for the creation of a new taxon.


**Etymology:** For the distribution in the Southern Hemisphere.

A *D. childiae* differt ascosporibus maiorae 13.5–19 × 7–8.5 µm usque at status anamorphosis Virgariellam similis.

Differs from typical *D. childiae* in having larger ascospores, 13.5–19 × 7–8.5 µm, and in producing a virgariella-like anamorph.

**Holotypos:** New Zealand, Nelson, Snowdens Bush, Podocarpaceae wood, 11 May 2004, P. Catcheside et al. (PDD 81102; *ex-type culture* CBS 116732, ICMP 15559).

**Teleomorph:** Stromata hemispherical, depressed-spherical to turbinate, sessile or with short, stout stipe, even to cerebriform, 1.4–3 × 1.2–2.2 cm; surface Brown Vinaceous (84); dull orange brown granules immediately beneath surface, with KOH-extractable pigments Cinnamon (62) to Fulvous (43); tissue between perithecia dark grey, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.4–1 mm thick, lighter zones brownish grey, pithy to woody, 0.5–0.7 mm thick, frequently loculate (Ratio of darker/lighter zones 1:1–2). Perithecia lanceolate, 0.8–1 × 0.3–0.4 mm. Ostiolo papillato-discol. Asci 190–260 × 12–13 µm, p. sp. 90–110 µm, stipes 90–160 µm, with amyloid, discoid apical apparatus 0.8–1 × 3.5–4 µm. Ascospores brown to dark brown, ellipsoid-inerugulat, with narrowly rounded ends, 13.5–18(–19) × 7–8.5 µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, smooth by LM but showing conspicuous transverse striations by SEM (2.500–5.000×); epispore smooth.


**Notes:** Whereas all specimens listed above under *D. childiae*, regardless of their geographic provenance, showed the same ascospore size range and those that we were able to culture had an anamorph with a nodulisporium-like branching pattern similar to that described by Rogers et al. (1999), deviations were observed in some specimens from the Southern Hemisphere and the Hawaiian Islands. These specimens have larger ascospores, while otherwise being more or less in agreement with *D. childiae* from the Northern Hemisphere and the Tropics. The anamorph approached a virgariella-like branching pattern (Fig. 44H) and the more complex nodulisporium-like type was not observed. Therefore, a new taxon is erected to accommodate them. *Daldinia pyrenaica* has more slender ascospores and yet a different anamorph.

Another specimen from Australia: Queensland, Bunya Mountains, on bark, 28 Mar. 2009, D. Remy 090326G ex herb JF (KR, culture STMA09063, MUCL 53761) featured subtostipitate, semiglobose, somewhat flattened stromata, with an outer crust apparently bipartite in places, composed of a thin layer of red brown granules above a thick layer of yellow granules, yielding Dark Brick (60) pigments in 10 % KOH. Its HPLC profile and micromorphological characteristics are in agreement with *D. australis*, but as the anamorph was not seen in the cultures, we refrain from assigning it to *D. australis* with certainty.


**Etymology:** Refers to the Pyrenean region, where this fungus was first found.

A polyphasic taxonomy of *DalDinia* (Xylariaceae)

Selected illustrations: Petrini & Müller (1986), as *D. loculata*, fig. 42 (ascospores and anamorph); Stadler *et al.* (2001c - of holotype), figs 1–4 (stromata), 8–10 (anamorph) and 15 (ascospores by SEM). Wollweber & Stadler (2001 – holotype). Abb. 5 (stromata); Stadler *et al.* (2002 - holotype), fig. 8 (ascospores by SEM).

**Known distribution/host preference of stromata:** Europe; often on *Quercus* and *Salicaceae*.

**Teleomorph:** Stromata subclavate, turbinate to subglobose, subsessile or with short stipe, with inconspicuous perithecial outlines (which may, however, appear prominent owing to the contrast between the colours of the ostioles and the surface in specimens bearing the anamorph), 1–2.5 × 1–1.5 × 1.5–2.5 cm, surface reddish brown to Vinaceous Brown (84), blackening with age, with KOH extractable pigments Fulvous (43), Apricot (42), Umber (9), or Honey (64), tissue between perithecia pithy to woody, tissue below perithecial layer composed of alternating concentric zones, zonation extending into the stipe, darker zones dark brown, pithy to woody, 0.2–0.5 mm thick, lighter zones fuscos, pithy to woody, persistent, 0.2–0.7 mm thick (Ratio of darker/lighter zones 1:1–2). Perithecia lanceolate to obovoid 0.5–1.5 × 0.2–0.5 mm. Ostioles papillate-discoid. Aci 220–285 × 10–15 µm, p. sp. 90–95 µm, stipe 130–195 µm, with discoid, amyloid apical apparatus 1.5 × 4 µm. Ascospores brown, ellipsoid-inequalilateral with narrowly rounded ends, 13–17(–20) × 6.5–8(–9) µm, germ slit straight, on
the more convex side of the ascospore, perispore dehiscent in 10 % KOH, smooth by LM, but faint transversal striations become visible by SEM (5.000×), epispore smooth.

Cultures and anamorph: Colonies on OA reaching the edge of a 9 cm petri dish in 5–8 d, at first whitish, felty, zonate, with diffuse margins, becoming greenish brown when sporulating, reverse yellow-greenish, blackening with age. Sporulating regions scattered over entire surface of colony. **Conidiophores** reaching a maximum height of 200 µm, dichotomously or (sometimes) trichotomously branched, smooth or finely roughened, 2–2.5 µm diam, with 1–3 conidiogenous cells arising from each terminus, showing a nodulisporium-like or, less frequently, a sporothrix-like branching pattern. **Conidiogenous cells** terminal or intercalary, cylindrical, hyaline, smooth, 10–25 × 2.5–3 µm. **Conidia** produced holoblastically from sympodially proliferating conidiogenous cells, hyaline, ovoid to dacrystoid, smooth or finely roughened, 6.5–7(–8) × 4–5 µm. Anamorph on stromata similar, but only sporothrix-like conidiophores and slightly smaller conidia observed.

Notes: This species is also reported here from Germany and Ukraine. Further specimens from Northern Spain in MA were also found to correspond with *D. pyrenaica*. It shows a HPLC profile similar to that of *D. childiae*, from which it differs in having larger ascospores and in its anamorphic morphology (Stadler et al. 2001c). Recently, it was reported to be one of the most frequent *Daldinia* spp. in the vicinity of Kharkov, Ukraine (see Akulov & Stadler 2008 for preliminary results). These findings were rather surprising, but they suggest that this species might be unearthed more frequently in Central and Southeast Europe in the near future. The determinations rest on teleomorphic characters, and we were able to observe an anamorph in only one of the cultures (CBS 117736,

**Etymology:** Named for the German chemist Wolfgang Steglich.

**Holotypus:** *India*, West Bengal, Chattar Chombz, 30. Aug. 1966, K.S. Thind 7239 as *D. bakeri* (K(M) 78833).

**Selected illustrations:** Van der Gucht (1995) as “Daldinia cf. grande”, figs 10E, F (stromata) and 11G, H (anamorph); Stadler et al. (2001c, holotype), figs 5 (stromata), 12 (anamorph) and 19 (ascospores by SEM).

**Known distribution/host preference of stromata:** Tropical and subtropical regions of South and East Asia and Australasia; several of the specimens so far identified were collected from *Quercus*.

**Teleomorph:** *Stromata* subglobose, subsessile or with stout stipe, 1–2.5 × 0.7–1.7 cm, with inconspicuous perithecial outlines but often wrinkled, surface reddish brown, blackened in age, with red brown granules immediately beneath the surface, with KOH extractable pigments *Sepia* (63), *Umber* (9), or *Fuscous Black* (104), tissue between perithecia pithy, brown, tissue below perithecial layer composed of alternating concentric zones, more persistent zones dark brown, pithy to gelatinous, loculate in aged specimens, 0.3–0.7 mm broad (Ratio of darker/persistent zones fibrous, greyish brown, pithy to gelatinous, more persistent zones dark brown, pithy, 0.3–0.7 mm thick, less persistent zones fibrous, greyish brown, pithy to gelatinous, loculate in aged specimens, 0.3–0.7 mm broad (Ratio of darker/lighter zones 1:1–2). *Perithecia* lanceolate, 0.8–1.2 × 0.2–0.3 mm. *Ostioles* inconspicuous, slightly papillate to papillate-discoid. *Asci* 220–325 × 10–11 µm, p. sp. 80–105 µm, stipe 130–220 µm, with amyloid discoid apical apparatus, 0.8–1 × 3–3.5 µm. *Ascospores* brown, unicellular, ellipsoid-equilateral (shape reminding of a Rugby ball) or slightly inequilateral with narrowly cylindrical, smooth, 12–20 × 2.5–3.5 µm. *Conidia* produced holoblastically from symmetrically proliferating conidiogenous cells, hyaline, obvoid, smooth or finely roughened, (5.5–)6–7.5(–8) × 3.5–4.5(–5) µm.


**La Réunion.** Saint Paul, Bois de Sans-souci, 1400 m, hardly decayed branch of *Acacia heterophylla*, 23 Mar. 2011, A. Hausknecht, Re 89/11 (KR 0029401, WU); same data, Re 95a/11 (KR 0029401, WU), *cultures* MUCU 53886.

**Notes:** *Daldinia steglichii* shows a HPLC profile similar to that of *D. chilidae*, but differs from the latter species in not containing daldinol (1a). Its ascospores are slightly longer and wider, and it differs from all other *Daldinia* spp., except *D. albofibrosa* and *D. bambusicola*, in producing a periconiella-like anamorph in culture. It has so far been recorded from India and Papua New Guinea by *Van der Gucht* (1994) as “*D*. cf. *grandis*” and Stadler et al. (2001c), and here the Philippines and La Réunion are added. The holotype was originally identified as *D. bakeri* by Dargan & Thind (1984), but it is not clear whether the remainder of the specimens cited by these authors actually corresponds with *D. steglichii* as well. The above cited specimen in *CALP* was not cultured, and it has ascospores 13–17(–18) × (6.5–)7–8.5 µm, which is slightly larger than in the type material. Because of the relatively few specimens available as of now, the status of these fungi and their affinities to other members of the *D. chilidae* group should be verified when suitable material becomes available, based on further culturing experiments.

This species is peculiar in that the two kinds of alternating concentric zones can hardly be differentiated into darker and lighter ones. In contrast, persistent layers alternating with gelatinous to fibrous layers of similar thickness that both become loculate with age are observed in fully mature stromata. With age, the gelatinous layers become fibrous and much paler, which makes the internal anatomy difficult to use as a differential character, unless stromata are compared at the same stage of maturity. Interestingly, both cultures obtained from material in La Réunion and New Guinea showed ITS nrDNA sequences quite similar to those of *D. concentrica* and allies, whereas their teleomorphic morphological features and especially their secondary metabolite profiles are very characteristic of the *D. chilidae* group; endophytes or environmental sequences of this species might therefore soon be misidentified as belonging to *D. concentrica* by “molecular taxonomists” if only ITS *nrDNA* is considered.

**Group D:** The *Daldinia vernicosa – Daldinia loculata* group (Figs 47–56)

This species group is characterised by having ellipsoid-inequilateral to almost cylindrical ascospores, mostly with broadly rounded ends and perispores indehiscent in KOH. Species can be distinguished based on stromatal morphology and anatomy, ascospore size, and anamorphic characters (cf. Table 10). Aside from the omnipresent BNT (1) and other yet unidentified binaphthalenes, whose
presence results in purple pigments in KOH, the stromata of this species group do not contain any additional pigments or other unique secondary metabolites. Cytochalasins are also lacking. The most frequently recorded members of this group, i.e., *D. vernicosa* (previously referred to as *D. fissa* by Ju et al. 1997) and *D. loculata*, differ in their stromatal morphology and in their anamorphic structures. However, both have often been recorded from burnt or otherwise damaged substrates, above all from *Betulaceae* in the Northern Hemisphere. They were sometimes considered “primary colonisers” but accumulating evidence suggests that they are actually classical endophytes that may inhabit their host plant for a long time and produce stromata only if their host is under severe stress or recently dead.

As in other groups of the genus, a striking bipolar distribution was noted regarding the biogeography of the Northern vs. the Southern Hemisphere species. Records from the tropics are relatively rare, mostly derived from higher altitudes, and those species that occur in lowland tropical regions, definitely, need further study.


*Etymology:* For the varnished nature of the mature stromata.


**Holotypus:** USA, North Carolina, Salem, Syn. 1175 (PH).


≡ *Daldinia fissa* Lloyd, Mycol. Writ. 7: 1313. 1922.
Table 10. Major discriminative characters of the species in the D. vernicosa/loculata group. CC: Conidiogenous cells; CON: Conidia; N,V, S, referring to the most frequently observed branching pattern, i.e. nodulisporium-, virgariella-, or sporothrix-like, respectively, as defined in Ju & Rogers 1996.

<table>
<thead>
<tr>
<th>Species (Daldinia)</th>
<th>Ascospore size (µm)</th>
<th>Ascal apical apparatus (µm)</th>
<th>Stromatal pigments (KOH)</th>
<th>Ratio darker/lighter concentric zones / Significant stromatal features</th>
<th>Anamorphic structures (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>bakeri</td>
<td>14.5–16 × 8–8.5</td>
<td>0.5–0.75 × 3–3.5</td>
<td>Purple or absent</td>
<td>1:5–40 Lighter zones greyish white</td>
<td>Unknown</td>
</tr>
<tr>
<td>cahuchucosa</td>
<td>13–17(–18) × 7.5–9(–10)</td>
<td>0.5–0.75 × 3–5.4</td>
<td>Purple</td>
<td>Only faint zonation in otherwise homogeneous context</td>
<td>Unknown</td>
</tr>
<tr>
<td>gelatinoides</td>
<td>(11–)12–13(–14) × 6–8</td>
<td>0.5–0.75 × 3</td>
<td>Purple or absent</td>
<td>STR entirely hollow at maturity</td>
<td>CC: 10–21 × 3–4.5 CON: 7.5–9.5(–11) × 4.5–6.5 (S, V)</td>
</tr>
<tr>
<td>grandis</td>
<td>(14–)17–22(–25) × 7–10(–11), highly irregular</td>
<td>1–1.5 × 4.5–5</td>
<td>Purple</td>
<td>Lighter zones light brown</td>
<td>Not produced in culture</td>
</tr>
<tr>
<td>hausknchtii</td>
<td>13–16 × 7–8, regular</td>
<td>Unknown</td>
<td>Purple, purple</td>
<td>Lighter zones greyish white</td>
<td>CON: 6.5–7–9.5 × 2–4.5 (V)</td>
</tr>
<tr>
<td>novae–zelandiae</td>
<td>(14–)16–23 × 8–13(–14), highly regular, ovoid</td>
<td>0.75–1 × 3.5–4.5</td>
<td>Dense purple</td>
<td>Lighter zones light brown</td>
<td>CC: 10–22 × 2–3.</td>
</tr>
<tr>
<td>loculata</td>
<td>11–14(–15) × 6–8</td>
<td>0.75–1 × 3–3.5</td>
<td>Dense purple</td>
<td>Lighter zones light brown</td>
<td>CON: 6–7.5 × 4.5–5 (N)</td>
</tr>
<tr>
<td>loculatooides</td>
<td>15–19(–21) × 7–9(–10)</td>
<td>0.75–1 × 4–4.5</td>
<td>Dense purple</td>
<td>Lighter zone light brown</td>
<td>CC: 12–16 × 3–3.5(–4) CON: 4.5–7.5 × 3–5.5 (S)</td>
</tr>
</tbody>
</table>

Holotypus: USA, Ohio, Toledo, W.R. Lowater ex Lloyd herb. 12382 (BPI 716013).

Selected illustrations: Schaeffer (1774), Tafel 329 as Lycoperdon atrum, reproduced as Abb. 9 in Wollweber & Stadler (2001), as D. fissa, stromatal habit; Martin (1969), Plate IV, figs 6 (asci) and 10 (ascospore) and 11 (stromata) and Plate VI, fig. 4 (anamorph); Ju et al. (1997), figs 1 (ascospore) and 40–43 (stromata of D. fissa type material), Ju et al. (1999), fig. 12 (anamorphic structure).

Known distribution/host preference of stromata: Widely distributed in temperate and subtropical climates of the Northern Hemisphere, but only rarely identified from tropical countries (and if so, always reported from high altitudes). No remarkable apparent host specificity, but stromata frequently found on Betulaceae and on fire-damaged woody hosts in general.

Teleomorph: Stromata turbinate or peltate, usually stipitate, surface smooth or rarely wrinkled (in specimens that have been rapidly dried), without or with faintly visible perithecial outlines, 0.5–5 × 0.5–5 cm (but mostly only up to 2.5 cm high); surface Brown Vinaceous (84), blackened and characteristically varnished in age; dull reddish brown granules immediately beneath surface, with KOH-extractable pigments Dark Livid (80) or Livid Violet (79); tissue between perithecia grayish brown to dark grey, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.1–0.2 mm thick, lighter zones white, gelatinous, disintegrating and becoming loculate when dry, 0.6–1.3 mm thick (Ratio darker/lighter zones: 1.5–10). Perithecia obovoid to lanceolate, 0.8–1.5 × 0.3–0.5 mm. Ostioles slightly papillate. Ascii 120–160 µm × 9–11 µm, p. sp. 65–75 µm, stipe 55–85 µm, with amyloid, discoid apical apparatus 0.5 × 3–3.5 µm. Ascospores dark brown to blackish brown, ellipsoid, slightly inequilateral to equilateral, with broadly to narrowly rounded ends, 11.5–14.5(–15) × 6.5–8(–9) µm, with straight germ slit spore length on more convex side when inequilateral; perispore indesincent in 10 % KOH; perispore/epispore smooth by LM and SEM (10.000×).

Stromatal secondary metabolites: BNT (1) and other binaphthalene derivatives prevailing.

Cultures and anamorph: Colonies on OA reaching the edge of 9 cm Petri dish in 5–6 d, at first whitish, floccose, azonate, with diffuse margins, becoming Greenish Olivaceous (90) at places; reverse remaining uncolored. Stromata, see Ju et al. (1999), only occasionally observed in freshly isolated cultures. Sporulating regions usually first observed at edge of colony after 7–9 d, later spread all over the colony. Buff (45) to Vinaceous Buff (86). Conidiogenous structure variable, ranging from sporothrix-like, nodulisporium-like to periconiella-like branching patterns. Conidiophores mostly arising from aerial hyphae on a slender, sometimes highly reduced main axis, 1.5–2 µm, mononematous, unbranched or di- or trichotomously branched, sometimes with KOH-extractable pigments Dark Livid (80) or Livid Violet (79); tissue between perithecia grayish brown to dark grey, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.1–0.2 mm thick, lighter zones white, gelatinous, disintegrating and becoming loculate when dry, 0.6–1.3 mm thick (Ratio darker/lighter zones: 1.5–10). Perithecia obovoid to lanceolate, 0.8–1.5 × 0.3–0.5 mm. Ostioles slightly papillate. Ascii 120–160 µm × 9–11 µm, p. sp. 65–75 µm, stipe 55–85 µm, with amyloid, discoid apical apparatus 0.5 × 3–3.5 µm. Ascospores dark brown to blackish brown, ellipsoid, slightly inequilateral to equilateral, with broadly to narrowly rounded ends, 11.5–14.5(–15) × 6.5–8(–9) µm, with straight germ slit spore length on more convex side when inequilateral; perispore indesincent in 10 % KOH; perispore/epispore smooth by LM and SEM (10.000×).
additional branches arising from the first level of conidiogenous regions, hyaline, smooth to finely roughened, with 1–4 conidiogenous cells arising from each terminus. Conidiogenous cells cylindrical, hyaline, finely roughened, 8–23 × 3–4.5 μm. Conidia produced holoblastically in sympodial sequence, hyaline, smooth, subglobose to ellipsoid, with flattened base, 6.5–9(–11) × 4.5–6 μm. Anamorph on young stromata largely resembling that observed in the cultures.

Additional specimens examined: Austria, Lower Austria, Vienna, Lobau, Mühleiten: L 5, 23 Jul. 1982, A. Hausknecht (WU-Myk. 2143); Maissau, Grübern, Robinia pseudoacacia, 9 Aug. 1985, J. Hogl (WU-Myk. 4765; see Cetto 1993); Kronau, alter Donauarm, Fraxinus, 9 Sep. 1990, W. Zöhrer (WU-Myk. 9099); near Laxenburg,
Annotated with the following:

*Bitzer, 1997* & *Lucchini, 1997*
*Martin, 1969*
*Wk, 2005*
*Whalley & Watling, 1980*
*Whalley, 1980*
*Wulf, 1996*
*Wulf, 1997*
*Wulf, 1998*
*Wulf, 1999*
*Wulf, 2000*
*Anonemus, 1989*
*Martin, 1989*
*Wulf, 2000*
*Wulf, 2002*
*Wulf, 2003*
*Wulf, 2004*
*Wulf, 2005*
*Wulf, 2006*
rationale was that Lloyd’s name was the oldest available, since the basionym of *D. vernicosa*, *Sphaeria vernicosa* Schwein., a later homonym of *S. vernicosa* for published. Here we, based on advice from Paul Kirk, treat the *S. vernicosa* for published. Here we, based on advice from Paul Kirk, treat the *D. vernicosa* Schaeffer (1774) cited an earlier valid name, *Cesati & De Notaris* (1863), and conspecificity with *D. concentrica* regarded as a synonym of *D. vernicosa*, a fungus originally described by Schaeffer *Lycoperdon atrum* Schwein. in order to save this long established name. Wollweber specimens reported by Ju *et al.* (1997), Stadler *et al.* (2001a) and Stadler et al. (2002) as *D. fissa*. Some of the gregarious, rather large stromata are almost entirely hollow, but all of them show at least remnants of the characteristic broad, white internal zones. It can still not be excluded that *D. fissa* will eventually be regarded as separate taxon, once additional material of this aberrant “*D. vernicosa-like*” fungus have become available from USA. *Daldinia simulans* is another synonym, featuring smaller compact stromata (cf. Ju *et al.* 1997), which are, however, indistinguishable from those of *D. vernicosa* with respect to their micromorphological characters. A culture deposited by Marion Child at CBS did not produce conidiophores, albeit the typical metabolites were detected in YMG cultures, and the ITS rRNA gene sequence data (see molecular phylogeny below) showed 99 % similarity with those derived from *D. fissa sensu* Hsieh et al. (2005) and Ju et al. (1997, 1999).

Vasilyeva (1998) elevated “*D. concentrica var. obovolta*” to species level but the combination proved to be superfluous and invalid (cf. Vasilyeva & Stadler 2008). For unknown reasons Ju *et al.* (1997) listed *D. concentrica var. obovolta* as an oblate synonym of *D. fissa*. To our knowledge this name remains untypified.

Our description of the anamorph of *D. vernicosa* is based on Ju *et al.* (1999), who actually studied a culture made from the specimen that is here selected as epitype, and is also in agreement with Martin (1969). The latter author described the anamorph of this fungus (as *D. vernicosa*), and found a similar morphology and slightly larger conidiogenous structures than in our cultures derived from other specimens collected in Germany. In contrast to most other species treated here, his concept appears to be congruent with ours.

Despite this species appears to be widely distributed, not many cultures have been studied and deposited in public collections as yet. It could certainly be an ideal model organism for molecular ecology or biogeography. However, it remains to be seen whether cryptic species can be further distinguished in this apparently heterogeneous complex, based on anamorphic studies and molecular data. For apparent heterogeneity of *D. vernicosa* and its ilk, see further in “Notes to *D. gelatinoides*”.

**Daldinia bakeri** Lloyd, Synopsis of some genera of the large Pyrenomycetes: 25. 1919. Fig. 49.

**Etymology:** Named after the collector of the type specimen.

**Holotypus:** Australia, New South Wales, Sydney, 1901, R.T. Baker in Lloyd herb. 12377 (BPI 716970).

Selected illustrations: Ju *et al.* (1997), figs 1 (ascospores) and 18–20 (stromata); Stadler *et al.* (2004a), figs 10, 11 (ascospores by SEM), all illustrated from type specimen.

**Known distribution/host preference of stromata:** Temperate Southern Hemisphere; (specimens from tropical countries listed below will need to be reassessed as fresh material becomes available); known from a couple of unrelated hosts.

**Teleomorph:** Stromata irregularly pulvinate to almost semiglobose, with inconspicuous perithecial outlines, 4–5.5 × 4–5 × 2–4 cm; surface blackish but with a reddish brown tone, varnished in age; with dull reddish brown granules immediately beneath surface, with KOH-extractable pigments Dark Livid (80) in fresh material, dilute Isabelleine (65) in the type specimen, due to artifacts, cf. Stadler *et al.* 2004a1, tissue between perithecia dark brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2–0.3 mm thick, lighter zones whitish, gelatinous, becoming loculate when dry, 1.3–1.8 mm thick (Ratio darker/lighter zones 1:6–8). *Perithecium* lanceolate, 0.8–1.2 × 0.3–0.4 mm. Ostioles slightly papillate. *Asci* tubular, 160–210 × 8–9 µm, p. sp. 70–100 µm, stipe 90–120 µm, with amyloid, discoid apical apparatus 1 × 3.5–4 µm. *Ascospores* dark brown to blackish brown, ellipsoid, slightly inequilateral to equilateral, with broadly to lanceolate, 0.8–1.2 × 0.3–0.4 mm. *Ostioles* slightly papillate. *Asci* tubular, 160–210 × 8–9 µm, p. sp. 70–100 µm, stipe 90–120 µm, with amyloid, discoid apical apparatus 1 × 3.5–4 µm. *Ascospores* dark brown to blackish brown, ellipsoid, slightly inequilateral to equilateral, with broadly to lanceolate, 0.8–1.2 × 0.3–0.4 mm. *Ostioles* slightly papillate. *Asci* tubular, 160–210 × 8–9 µm, p. sp. 70–100 µm, stipe 90–120 µm, with amyloid, discoid apical apparatus 1 × 3.5–4 µm. *Ascospores* dark brown to blackish brown, ellipsoid, slightly inequilateral to equilateral, with broadly to lanceolate, 0.8–1.2 × 0.3–0.4 mm. *Ostioles* slightly papillate. *Asci* tubular, 160–210 × 8–9 µm, p. sp. 70–100 µm, stipe 90–120 µm, with amyloid, discoid apical apparatus 1 × 3.5–4 µm. *Ascospores* dark brown to blackish brown, ellipsoid, slightly inequilateral to equilateral, with broadly to lanceolate, 0.8–1.2 × 0.3–0.4 mm. *Ostioles* slightly papillate. *Asci* tubular, 160–210 × 8–9 µm, p. sp. 70–100 µm, stipe 90–120 µm, with amyloid, discoid apical apparatus 1 × 3.5–4 µm. *Ascospores* dark brown to blackish brown, ellipsoid, slightly inequilateral to equilateral, with broadly to lanceolate, 0.8–1.2 × 0.3–0.4 mm. *Ostioles* slightly papillate. *Asci* tubular, 160–210 × 8–9 µm, p. sp. 70–100 µm, stipe 90–120 µm, with amyloid, discoid apical apparatus 1 × 3.5–4 µm. *Ascospores* dark brown to blackish brown, ellipsoid, slightly inequilateral to equilateral, with broadly to lanceolate, 0.8–1.2 × 0.3–0.4 mm. *Ostioles* slightly papillate. *Asci* tubular, 160–210 × 8–9 µm, p. sp. 70–100 µm, stipe 90–120 µm, with amyloid, discoid apical apparatus 1 × 3.5–4 µm. *Ascospores* dark brown to blackish brown, ellipsoid, slightly inequilateral to equilateral, with broadly to lanceolate, 0.8–1.2 × 0.3–0.4 mm. *Ostioles* slightly papillate.

**Cultures and anamorph:** Unknown.

**Stromatal secondary metabolites:** BNT (1) and other binaphthalene derivatives prevailing.


1 Dilute isabelleine in the type specimen, due to artifacts, cf. Stadler et al. 2004a.

2 The specimen in IM may have been reported by Carroll as “4638” as *D. vernicosa* based on collections the Danish/Thai Flora of Thailand project (and somehow ended up in Martin’s herbarium).
Notes: Also see Ju et al. (1997) for description of the teleomorph and Stadler et al. (2004c) for HPLC profiles and SEM characteristics. This species as understood here has so far only been recorded from Australia and New Zealand. All records cited by Child (1932) except for the holotype, probably correspond to different species, and all subsequent identifications based on Child’s monograph (e.g., Martin 1969, Thind & Dargan 1978, the latter treated here as D. steiglichii) should be revised as well. A specimen that was reported as D. bakeri sensu Child by Dennis (1963) even turned out to be a mixed collection, comprising depauperate stromata of another, yet undescribed tropical Daldinia species of unsettled affinities (dealt with in the incertae sedis part), and stromata representing the recently described new genus and species Ruwenzonia pseudoannulata (Stadler et al. 2010b).

Nevertheless, we have now found specimens that could represent true D. bakeri from America and Asia, too (see specimen descriptions below). The material from Chile (from which the dimensions of the asci were reported for the first time) and Thailand matched exactly the characteristics of the holotype, whereas the specimen from Costa Rica resembles D. vemicosa in having turbinate stromata but differs in having larger ascospores. The anamorph of D. bakeri described by Martin (1969) probably refers to a different species, as already pointed out by Ju et al. (1997). Data on additional fresh collections from warmer climates, best accompanied by studies on their anamorphs and molecular phylogeny will remain necessary to further clarify the status of this taxon and related fungi.

Two further collections of Daldinia species from Africa with possible affinities to D. bakeri are illustrated and discussed below. It can be noted that, although they both show affinities with D. bakeri, they markedly differ from each other.

Senegal, Haute Casamance, southeast of Kolda in mahogany forest, 7 Sep. 1985, A. Fraiture S13 (BR-Myc 033528,63). Fig. 50A–G.

Stromata irregularly hemispherical, 0.5–1.2 × 0.4–0.9 cm, sessile or with a very short narrow stipe, without visible perithecial outlines;
surface Dark Brick (60), smooth, at times slightly uneven due to
shrivelling, with dull red brown granules just beneath surface yielding
dense Livid Purple (81) pigments in 10 % KOH; tissue between
perithecia dark grey, pithy; tissue below perithecial layer composed of
alternating zones, darker zones blackish, pithy, discontinuous,
0.04–0.1 mm thick, lighter zones pure white, pithy, solid, 0.5–2
mm thick (Ratio darker/lighter zones: 1:5–40). Perithecia obvoid,
0.65–0.85 × 0.4–0.6 mm. Ostioles inconspicuous, not papillate.
Asci 230–270 µm, p. sp. 100–130 × 10–11.5 µm, stipe 130–150
µm, without visible apical apparatus, not bluing in Melzer’s reagent.
Ascospores dark brown, ellipsoid-equalitarian with narrowly to
broadly rounded ends, 14.5–16 × 8–8.5 µm, with straight germ slit
spore length on convex side; perispore indehiscent in 10 % KOH;
perispore/epispore smooth by LM.

Stromatal secondary metabolites: BNT (1) in large amounts.

Notes: This specimen features small semiglobose stromata showing
very thin internal black zones and very wide, white concentric
zones that are not gelatinous nor turn loculate. It is considered here to belong to the verrucosa group based on its ellipsoid almost
equilateral ascospores that lack a perispore dehiscent in KOH
and the dense purple, KOH-extractable pigments. We suppose it may have affinities with D. bakeri because of its predominantly
white interior but it deviates from this taxon in having a reddish
brown surface lacking perithecial outlines, obvoid perithecia and
non-papillate ostioles. The absence of an apical apparatus and reaction to iodine are probably distinctive but the type of D. bakeri
unfortunately lacks ascii for comparison. It probably represents
an undescribed taxon but we refrain from describing it as new,
because of the largely immature condition of the stromata and the absence of cultural and anamorphic data.

Tanzania, Southern Highlands, Iringa District, Mufindi
(Lupene Ten East), Kiban, 1859 m, on dead rotten fallen
branch, 6 May 1968, D.N. Pegler T 782, det. R.W.G. Dennis
as D. concentrica var. eschscholtzii (K (M) 130378). Fig.
50H–N.

Teleomorph: Stromata turbinate to irregularly pulvinate with
fertile part lobed and with revolute margins, subsessile to stipitate,
2.3–4 × 1.8–2.3 × 1.6–2.8 cm, with slightly exposed perithecial
outlines; surface Fuscos (103) to dull black, with dull reddish
brown granules immediately beneath surface, without visible KOH-
extractable pigments; tissue between perithecia dark brown, pithy;
tissue below perithecial layer composed of alternating zones,
darker zones blackish, 0.7–1.25 mm thick, gelatinous and strongly
loculate, lighter zones golden brown, 0.5–0.7 mm thick, solid, pithy
to woody. Perithecia lancelolate, 1–1.2 × 0.25–0.3 mm. Ostioles
discoid to slightly papillate. Asci not seen. Ascospores slightly
inequilaterally ellipsoid with narrowly to broadly rounded ends,
at times with one end bevelled, dark brown, 13.5–17 × 7–8.5 µm,
with a straight germ slit spore length; perispore indehiscent in 10 %
KOH; perispore/epispore smooth by LM.

Stromatal secondary metabolites: BNT (1) and other binaphthalene
derivatives prevailing.

Notes: This collection consists of six fragmentary stromata in very
poor condition; only one still containing ascospores and revealing
a fairly intact interior is illustrated here. This Daldinia is similar to
D. bakeri and D. hausknchtii in having a slightly nodulose
surface, an interior turning loculate and ascospores in the same
size range and lacking a dehiscing perispore. However, it strikingly
differs from D. bakeri and most of taxa belonging to the verrucosa-
group in that the internal layers that turn loculate are black while
the paler ones remain solid. This, combined with the geographical
origin and the ascospore morphology recalling that of D. grandis
and D. loculatoïdes by featuring some ascospores with a bevelled
end, suggests it could represent an undescribed taxon. Fresh
material in good condition is required to confirm these preliminary
observations.

Daldinia cahuchuosa (Whalley & Watling) M. Stadler &
Læsåe, comb. nov., MycoBank MB807746.

Etymology: From the Carib Indian word “cahuchu”, “rubbery”.

Basionym: Versiomyces cahuchuocosus Whalley & Watling, Notes

Holotypus: Australia: Queensland, Brisbane, Boobara National
Park, wood of Eucalyptus, R. Watling 10838 (E).

Selected illustrations: Whalley & Watling (1998), fig. 1 (stroma and
ascospores of the type specimen).

Known distribution/host preference of stromata: Monotypic, from
tropical Australia; on Eucalyptus.

Teleomorph: Stroma cerebriform to irregularly pulvinate, subsessile,
3 × 2 × 1.5 cm, surface wrinkled, lacking perithecial
outlines, blackish and somewhat varnished (but said to be reddish
brown when collected fresh), with dull reddish brown granules
immediately beneath surface, with KOH-extractable pigments
Dark Livid (80); tissue between perithecia dark brown, pithy to
woody; tissue below perithecial layer essentially homogeneous,
woody, very hard to cut, black except for the presence of two
whitish to cream coloured peripheral concentric zones (0.2 mm
thick), which are separated by a dark band, immediately beneath
perithecial layer; rubbery, but covered by a vertically zonate,
greyish white striation, radiating out in a fan-like fashion from
the base to the periphery, as also observed in some specimens
of D. lloydii. Ostioles umbilicate to slightly papillate. Perithecia
elongate ellipsoid, 0.8–1 × 0.5–0.7 mm. Asci fragmentary, p.
sp. 90–100 × 8–10 µm, with discoid amyloid apical apparatus
0.5–0.75 × 3–5.4 µm. Ascospores dark brown, ellipsoid, almost
equilateral to slightly inequilateral, with broadly rounded ends,
with straight germ slit spore length, 13–17(–18) × 7.5–9(–10) µm;
perispore indehiscent in 10 % KOH, perispore/epispore smooth by
LM as well as SEM (20.000×).

Stromatal secondary metabolites: BNT (1) and other binaphthalene
derivatives prevailing.

Cultures and anamorph: Unknown.

Notes: Versiomyces cahuchuocosus was already discussed as a
possible synonym of D. verrucosa (as fissa) by Ju et al. (1997),
and we confirm the affinities to the D. verrucosa/D. loculata group.
by chemotaxonomic methodology and SEM data. As stated by Whalley & Watling (1988), there is, indeed, a tendency of the stromata to become horizontally zonate, even though the zones are less conspicuous than in typical Daldinia spp. However, the faint vertical zonation at the base of the stroma somehow recalls D. lloydii, and notably, Wollweber & Stadler (2001) already reported atypical stromata of D. vernicosa (as D. fissa) that lacked the typical, broad white zones and occurred after an exceptionally hot summer at the same collection site where regular stromata had been observed for several years. Since our concept easily allows for inclusion of taxa that do not show a conspicuous zonation of the stromata, and considering that D. gelatinoides, as well as D. placentiformis are accepted, the genus Versiomyces is synonymised with Daldinia.

The closest affinity of D. cahuchucosa is probably with D. bakeri, with which it shares a strikingly similar perithecial and ascospore morphology. However, the ascospores are slightly larger in the former, and the zonation of the stromata is entirely different in these taxa.

**Etymology:** For the gelatinous interior, and for being like *D. gelatiosa* (a species which does not actually appear to be closely related).

**Holotypus:** (fide Vasilyeva 1998) **Russia**, Primorsky Territory, Ussuriski Reservation, on dead stems of *Carpinus cordata*, 10 Aug. 1989, L.N. Vasilyeva (VLA, n.v.).

**Selected illustrations:** This species has not been illustrated previously.

**Known distribution/host preference of stromata:** Far Eastern Russia, Northern China and Japan; from various dicotyledonous angiosperms.

**Teleomorph:** Stromata turbinate or peltate, sub sessile to stipitate, with highly similar characteristics as *D. vernicosa*; however, tissue below perithecial layer is not composed of alternating zones, but consists of a hollow cavity, with remnants of zonate tissue at base of stroma. Perithecia obvoid to lanceolate, 1–1.3 × 0.35–0.5 mm. Ostiolo inconspicuous, slightly papillate. Asci 130–160 µm, p. sp. 80–100 × 7–8 µm, stipe 50–60 µm, with discoid, amyloid apical apparatus, 0.5–0.75 × 3 µm. Ascospores dark brown, ellipsoid, slightly inequilateral to much less frequently equilateral, with broad rounded ends, (11–)12–13(–14) × 6–8 µm, with straight germ slit spore length on more convex side; perispore indescent in 10 % KOH; perispore/epispore smooth.

**Stromatal secondary metabolites:** BNT (1) and other binaphthalene derivatives prevailing.

**Cultures and anamorph:** Similar to those of *D. vernicosa*, except that a periconiella-like branching pattern has not been found, simple, unbranched sporothrix-like conidiophores are prevailing. Conidiophores up to 90 µm long, conidigenous cells 10–21 × 3–4.5 µm. Conidia ellipsoid to elongate-ellipsoid, hyaline, with flattened base, 7.5–9.5(–11) × 4.5–6.5 µm.


**Notes:** As stated in the protologue, this fungus closely resembles *D. vernicosa*. However, its stromata have an *Entonaema*-like habit. They are highly gelatinous, almost entirely hollow inside and filled with liquid when fresh. We did not see the type but studied two conspecific specimens (collected in the same area as the type), which were kindly provided to us by the author. In the type material, concentric zones, if any, are barely visible in very young stromata (L. Vasilyeva, pers. comm.). However, in our material (see Fig. 51G) they may remain present in the lower parts. This is actually reminiscent of some specimens of *D. vernicosa* that become almost entirely hollow when old (see Fig. 48G). The stromatal habit and ascospore size appear to be less variable than in *D. vernicosa*, and we have so far not seen any specimen of the latter species that becomes entirely hollow and does not maintain its concentric zones even in overmature stromata. While the spores of *D. gelatinoides* show the same morphology (ellipsoid-inequilateral to equilateral with broadly rounded ends) as those of *D. vernicosa*, they appear somewhat narrower in relation to their length. The anamorph of the culture CBS 116991 has a very similar morphology to that of *D. vernicosa* reported by Ju et al. (1999). However, we found slightly larger conidia, and no periconiella-like branching types of conidiophores but mainly sporothrix-like types in the cultures of *D. gelatinoides*.

We accept this taxon until further studies on *D. vernicosa* and its immediate relatives have been carried out. There are several good reasons to assume that this species can eventually be subdivided in further taxa: i) three genotypes were found among specimens identified as *D. vernicosa* (as *D. fissa*) in a molecular study (albeit no corroborating morphological evidence was provided) by Johannesson et al. (2000), and the minisatellite PCR profiles even differed in some specimens that were collected from different host plants in the same geographic region in Germany; ii) Child (1929, 1932) demonstrated that her *D. simulans* appeared physiologically distinct from material she regarded as *D. vernicosa* but an original *D. simulans* culture extant at CBS did not produce the anamorph when studied by us; iii) despite the fungus is one of the most frequently reported *Daldinia* species, only a few cultures have so far been obtained and examined for morphological traits.

As recently revealed from our revision of the genus *Entonaema* (Stadler et al. 2008a) *D. gelatinoides* differs from all *Entonaema* spp. so far studied by the presence of BNT in its stromatal extract, whereas the metabolites of *Entonaema sensu stricto* have been shown to correspond to those found in orange–pigmented *Hypoxylon* spp., or they constitute unknown metabolites. In addition, all *Entonaema* spp. so far studied were devoid of BNT. On the other hand, Stadler et al. (2010a) studied the culture of *D. gelatinoides* along with representatives of numerous closely related *Hypoxylon* *Xylariaceae* and found its nrDNA sequence to be highly similar to that of *D. vernicosa*. These findings, of course, also support the present concept, in which *Daldinia* is being redefined by considering characters that do not relate on stromatal morphology and anatomy alone.


**Etymology:** Not explicitly stated by Child (1932), but probably referring to the large stromata.


**Holotypus:** **USA**, Washington, Sequim, J.M. Grant, Lloyd herb. 12378 (BPI 716340).
A polyphasic taxonomy of Daldinia (Xylariaceae)

Selected illustrations: Child (1932), Plate 28, fig. 8 (ascospores, from type) and Plate 30, fig. 8 (stromata of type specimen); Ju et al. (1997), fig. 12 (ascospore) and 49, 50 (stromata); Stadler et al. (2002) fig. 12 (ascospores by SEM); Stadler et al. (2004d), figs 19–21 (ascospores by SEM).

Known distribution/host preference of stromata: Tropical and temperate America; on various dicotyledonous angiosperms.

Teleomorph: Stromata hemispherical, sessile or subsessile, with perithecial outlines clearly visible, 2.5–8 × 2.5–8 × 1.5–5 cm; surface Brown Vinaceous (84), blackened and varnished in age; with dull reddish brown granules immediately beneath surface, with KOH-extractable pigments dense Livid Purple (81) or Dark Livid (80), absent in old herbarium material examined, tissue between perithecia brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.3–0.8 mm thick, lighter zones light brown to brown, becoming pithy to woody, persistent, 0.8–2 mm thick (Ratio darker/lighter zones 1:3–4). Perithecia lanceolate, 0.8–1.5 × 0.3–0.5 mm. Ostioles papillate. Asci 200–270 × 10–13 µm, p. sp. 90–125 µm, stipe 100–155 µm, with amyloid, discoid apical apparatus, 1–1.5 × 4.5–5 µm. Ascospores dark brown, unicellular, ellipsoid to cylindrical, highly variable, inequilateral, slightly inequilateral to equilateral, with broadly to narrowly rounded ends sometimes pinched or bevelled, (14–)17–22(–25) × 7–10(–11) µm, with straight germ slit spore length on more convex side in inequilateral spores; perispore indehiscent in 10 % KOH; perispore/epispore smooth both by LM and SEM (10.000×).

Stromatal secondary metabolites: BNT (1) and other binaphthalene derivatives prevailing.
Cultures and anamorph: Unknown. The culture described by Stadler et al. (2004d) for D. grandis represents D. andina as understood here, and the anamorph described earlier on by Ju et al. (1997) as D. grandis was taken from a specimen that is now regarded as D. novae-zelandiae (cf. Stadler et al. 2004d).


Notes: Daldinia grandis in the current sense has ascospores with non-dehiscing perispores in 10 % KOH, but a rather dubious reaction was observed in the paratype specimen, as illustrated in Fig. 52G. The hyaline membranous material surrounding some clusters of ascospores resembles free perispores that could have been dehiscing naturally prior to the collection of the stromata. As this was revealed by addition of KOH to the slide, this material was presumably stuck to the ascospores before the addition of KOH. However, despite several attempts it has been impossible to observe a true dehiscence of any perispore by addition of KOH to the slide.

As the reaction of perispores to KOH is a key character in Daldinia (and other hypoxylloid Xylariaceae), we propose, to avoid (and other hypoxyloid Daldinia species) perispore by addition of KOH to the slide. However, despite several attempts it has been impossible to observe a true dehiscence of any perispore by addition of KOH to the slide.

As the reaction of perispores to KOH is a key character in Daldinia (and other hypoxylloid Xylariaceae), we propose, to avoid (and other hypoxyloid Daldinia species) perispore by addition of KOH to the slide. However, despite several attempts it has been impossible to observe a true dehiscence of any perispore by addition of KOH to the slide.

Aside from further records from the USA, we meanwhile identified a specimen from Ecuador to be in full agreement with D. grandis as described by Stadler et al. (2004d) with respect to teleomorphic features. The fungus is also present in Costa Rica and has been reported by Ju et al. (1997) from Mexico. Many of the original specimens used by Child are apparently not extant and might even be misplaced. A specimen from San Bernadino, California was cited by Child (1932) as type of D. grandis, but the data are not identical to the above listed material from NY; fide Child the specimen was from the herbarium of the University of Iowa. In a search for the type specimen, we have been kindly provided with all specimens of Daldinia from COLO, but all were identified as different species (see elsewhere in this paper). As the holotype seems to be lost, fig. 8 of Plate 29 in Child (1932), showing the large confluent stromata of the type specimen, featuring conspicuous perithecial outlines, is therefore selected as lectotype.

A specimen from New Zealand, Stewart Island, Weinmannia racemosa, 4 Feb. 1983, I. Collett, det. G. Stevenson GS 83/26 as D. concentrica (PDD 90478; culture ICMP 18266) (Fig. 52M–Q) agrees with D. grandis with respect to stromatal and ascospore morphology, suggesting that D. novae-zelandiae is not the only large-spored member of this species group in New Zealand. The culture did not produce an anamorph. This specimen could therefore represent yet another undescribed species, or it could actually represent the “American” D. grandis. Molecular data (Figs 73, 74) place it in the D. concentrica group. As the fungus described by Stadler et al. (2004d) as D. grandis is here treated as a separate taxon and D. grandis as represented by the current concept therefore remains to be cultured and studied, we hesitate to draw any final conclusions on the disposition of PDD 90478.

Daldinia hausknchteii J. Fourn. & M. Stadler, sp. nov.


Known distribution: So far only known from the type collection in La Réunion; unknown host.

Teleomorph: Stromata hemispherical with a short stout stipe to depressed-spherical and sessile, with slightly exposed perithecial outlines, 1–2.7 × 1–1.5 cm; surface Sepia (63) to Dark Brick (60), blackening where outer pruina is worn off; dull reddish brown granules immediately beneath surface, with KOH-extractable pigments Vinaceous Purple (101); tissue between perithecia grey brown, pithy; tissue below perithecial layer composed of alternating zones, darker zones brown, pithy to woody, 0.2–0.3 mm thick, lighter zones brownish grey, pithy to fibrous, loculate in places, 0.25–0.8 mm thick (Ratio darker/lighter zones: 1:1–2.5). Perithecia lanceolate, 1 × 0.2–0.25 mm. Ostioles umbilicate to slightly papillate. Asci not seen. Ascospores dark brown, ellipsoid-inequilateral with narrowly rounded ends, at times with one end bevelled, highly variable in shape and dimensions, 13–16 × 7–8 µm, with straight germ slit spore length on convex side; perispore indehiscent in 10 % KOH; perispore/epispore smooth by LM.

Stromatal secondary metabolites: BNT (1) and other binaphthalene derivatives prevailing.

Cultures and anamorph: Mycelium covering both OA and YMG agar; in 7–8 d, whitish, feltly, remaining so for a long time. After 2–3 wk, the whitish hyphae become inflated and melanised to some extent, and release small amounts of Citrine (13) pigments into the medium, but no further differentiation and no anamorphic structures are observed even at prolonged incubation times.

Notes: From a morphological view point, identification of stromata with a slightly nodulose surface, violet pigments and relatively large ascospores with perispore not dehiscing in KOH leads to D. hausknchteii, D. bakeri, D. loculata, D. loculatoides or D. grandis. Daldinia hausknchteii differs from D. bakeri by its entostroma (in shades of greyish brown and rather compact vs. white papery with very thin darker zones in D. bakeri) and by its spores that are paler brown, more slender and more variously shaped than those of D. bakeri, often with narrowly rounded ends. The ascospore dimensions are somewhat smaller.
intermediate between those of *D. loculata* and *D. loculatoides*, but the shape is different in being more slender and more irregular, and the stromata lack the typical shiny black surface and yield paler KOH-extractable pigments. The stromatal morphology, especially the entostroma of *D. hausknechtii*, fits *D. grandis* well, as does the variable shape of ascospores, ranging from ellipsoid with broadly or narrowly rounded ends to ellipsoid with one end bevelled or diamond-shaped. The main difference with *D. grandis* is the smaller size of ascospores, at the very lower limit of the range (and geographical origin). The culture did not produce the anamorph; however, a comparison of ITS nrDNA data (Fig. 74) revealed its closest affinities to be with *D. loculata* and *D. loculatoides*, in accordance with the morphological characters of the teleomorph.


**Etymology:** Presumably for the locules that may occur in old stromata (even though this feature is more characteristic of other *Daldinia* spp.).


Holotypus: USA, South Dakota, Black Hills, 1903, H. Schenck (BPI 594265).

Selected illustrations: Wollweber & Stadler (2001), Abb. 11 (stromata); Stadler et al. (2001d), figs 3 (anamorphic structure) and 4D (SEM of ascospores).

Known distribution/host preference of stromata: Circumpolar (Northern Hemisphere) with preference for temperate and, in particular, hemiboreal-boreal climates. Most frequently recorded in Scandinavia and in northern North America. Rarely found in subtropical climates and apparently absent in the tropics. Stromata most frequently occur on Betula, but also on other Betulaceae, Salicaceae (in particular Populus), Fagaceae and Rosaceae. Often found on fire-damaged trees as “primary coloniser” or as a sporulating endophyte.

Teleomorph: Stromata depressed-spherical to hemispherical, sessile or nearly so, solitary, infrequently aggregated or confluent, with inconspicuous to conspicuous perithelial outlines, 2.5–8 × 2.5–8 × 1.5–5.5 cm; surface Brown Vinaceous (84), blackened and sometimes varnished in age; dull reddish brown granules immediately beneath surface, with KOH-extractable pigments Livid Purple (81), Dark Livid (80) or without apparent KOH-extractable pigments in aged specimens; tissue between perithecia brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.3–0.8 mm thick, lighter zones gray, grayish brown to brown, gelatinous when fresh but very hard when dry, becoming pithy to woody, sometimes with locules, persistent, 0.8–2 mm thick (Ratio darker/lighter zones: 1:2–2.5). Perithecia lanceolate, 0.8–1.5 × 0.3–0.5 mm. Ostiolar papillae. Ascii 150–210 × 9–11 µm, p. sp. 65–95 µm, stipe 85–115 µm, with amyloid, discoid apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm, p. sp. 65–95 µm, stipe 85–115 µm, with amyloid, discoid apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm, p. sp. 65–95 µm, stipe 85–115 µm, with amyloid, discoid apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm, p. sp. 65–95 µm, stipe 85–115 µm, with amyloid, discoid apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm, p. sp. 65–95 µm, stipe 85–115 µm, with amyloid, discoid apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm, p. sp. 65–95 µm, stipe 85–115 µm, with amyloid, discoid apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm, p. sp. 65–95 µm, stipe 85–115 µm, with amyloid, discoid apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm. Ascospores dark brown, ellipsoid-equilateral to slightly inequilateral, with broadly rounded apical apparatus, 0.75–1 × 3–3.5 µm.

Notes: This fungus appears to be closely connected to *Betula* throughout the Northern Hemisphere, where it is certainly not uncommon. The record from the Himalaya region in India suggests that it can be found in the entire distributional area of its preferred host. *Daldinia loculata* is also the best studied species of the genus (and perhaps of the *Xylariaceae* in general) with regard to its

---

**Fig. 54.** Telomorphological characteristics of *Daldinia loculata*. Ww 2886 (Germany). A. Stromata habit. B. Stromata in longitudinal section showing internal concentric zones and perithecial layer. E. Ascospores in SDS. F. Ascospores in KOH, showing non-dehiscing perispore. G. Ascospores by SEM (10,000x). H. Stromatal surface (inserted: Stromatal pigments in 10 % KOH). Scale bars A, B, C = 1 cm; D, H = 1 mm; E, F = 10 µm; G = 5 µm.
population genetics. Johannesson et al. (2000) demonstrated rather small differences within subpopulations from Fennoscandinavia and Far Eastern Russia. Likewise, morphological studies on all materials referable to this species listed here or previously (Stadler et al. 2001a, 2004d) revealed that it is rather homogeneous with regard to chemical and morphological traits. Daldinia loculatoïdes appears to be its closest relative, only differing from D. loculata in ascospore size and morphology and in the dimensions of its conidiogenous structures.


**Etymology:** For its similarity to *D. loculata*.

**Holotypus:** UK, Scotland, Alva, Silver Glen, Fagus, exposed trunk, old tree, stroma occurring on burnt wood of hollow trunk and on unburnt parts, 23 Aug 1981, B.J. Coppins 8630, det. as *D. grandis* by Johannesson et al. 2000 (E, ex-type culture CBS 113729, GenBank Acc. No. AF176982).

**Selected illustrations:** Stadler et al. (2004d, all from holotype), figs 3, 4 (stromata), 10–12 (ascospores) and 24, 29, 30 (anamorph).

**Known distribution/host preference of stroma:** Temperate, Northern Hemisphere (America, Europe), apparently rare; preferably on burnt wood of various angiosperm hosts. Not yet recorded from Asia.

**Teleomorph and anamorph:** This species differs from *D. loculata* in having larger ascospores, 15–19(–21) × 7(–9)–10 µm, mostly with broadly rounded ends and often being reminiscent of a Rugby ball, and in having predominantly sporothrix-like conidiophores with smaller conidia (4.5–7.5 × 3–5.5 µm). It differs from *D. grandis* mainly in the more regular ascospores and by having less conspicuous ostioles.

**Stromatal secondary metabolites:** BNT (1) and other binaphthylene derivatives prevailing.


**Notes:** This species has now also been found on *Betula*, and is here recorded for the first time from the Czech Republic, England, and the USA. The culture of PRM 885050 showed the typical anamorphic characteristics that were also seen in the ex-type culture. *Daldinia grandis* was separated from *D. loculatoïdes* mainly by two characters: the deviating morphology of ascospores and cultures (Stadler et al. 2004d). The latter difference is not valid anymore in our current concept, since the specimens whose cultures were studied for comparison of *D. grandis* and *D. loculatoïdes* has been transferred to *A. andina*. This leaves the ascospore morphology (highly variable in *D. grandis* vs. rather homogeneous and often Rugby ball shaped in *D. loculatoïdes*) as major discriminative characters, but *D. loculatoïdes* also has less conspicuous ostioles. Still, a comparison of fresh material corresponding to typical *D. grandis* from southwestern North America should be made available before a final conclusion about the status of these closely related taxa can be reached.

**Tropical relatives of Daldinia loculata and Daldinia loculatoïdes**

Some specimens of tropical origin show affinities to *D. loculata* with ascospores of intermediate size range between those given above for *D. loculatoïdes* and *D. loculata* (i.e., 12–17 × 6.5–9 µm). The ascospores are more strongly inequilateral than those of the above taxa, with perispores indehiscent in KOH. As all these specimens are rather old, and none could be cultured, it does not appear practical to erect a new taxon at this time. They are, however, reported here in order to demonstrate that it could be worthwhile to conduct a diligent search of specimens reminiscent of *D. loculata* in tropical Asia and Africa, in order to find additional undescribed taxa.

Specimens examined of *D. aff. loculatoïdes*:
- Germany, Hamburg, storage facilities of wood–import company “Müller”, on tree trunk (of presumably tropical origin), Oc. 1935, Liese, det. W. Kirschstein as “D. angolensis” (B70 009590).

**Notes on Daldinia nemorosa (syn. Anelllosporium nemorosum)**

The anamorphic genus and species *Anelllosporium nemorosum*, typified by a culture from Canada, Alberta, Edmonton, Valley Zoo, soil from Vulpes velox den in zoo (UAMH), May 2008, M. L. Davey (UAMH, n.v) was described by Davey (2010) based on morphological aberrances and apparently unique ITS rDNA sequences. The description of the culture was reminiscent of *D. petriniae* complex. Despite the author described an anamorph showing annellicid conidiogenesis, the highest degree of homology of the ITS rRNA gene sequence of the ex-type strain was found to be with *D. loculata*. Some cultures in UAMH from Alberta, Canada, which we had studied concurrently, also showed similar characteristics. The conidiophores were more robust than those of the type strain of *A. nemorosum*, and their ITS sequences also deviated slightly. The corresponding stromata were not fully mature. They showed the general characteristics of *D. loculata*, but more closely resembled *D. loculatoïdes*, as some of the few mature ascospores found in UAMH 9036 attained over 17 µm in length. Our attempts to produce the teleomorph in culture only resulted in immature stromata. We refrain from providing an exhaustive description and illustration of these specimens, but are confident that such *Daldinia* specimens from Alberta will eventually be shown to represent the teleomorph of *A. nemorosa* (*D. nemorosa* herein).

Specimens examined (of *D. cf. nemorosa*):
- Canada, Alberta, Calmar, Populus tremuloides, 21 Aug. 1997, S.P. Abbott SA 256, as *D. grandis* (UAMH, culture UAMH 9035 - stromata largely immature); Edmonton, Devon, UABDG (University of Alberta Devonian Botanic Garden), Matus, Jul. 6, 1993, S.A. Abbott SA 695 as *D. grandis* (UAMH 7406A, stromata immature, culture UAMH 7406); same locality, substrate and collector, Aug. 2, 1992, SA 803 (UAMH 7406).

Etymology: For New Zealand, from where the type originates.


Misapplications: D. grandis sensu Child (1932) and sensu Ju et al. (1997) pro parte.

Selected illustrations: Ju et al. (1997), fig. 75 (anamorph, as D. grandis); Stadler et al. (2004c), figs 5, 6 (stromata, including type material) and 13–16 (SEM of ascospores, including type material).

Known distribution/host preference of stromata: New Zealand; on various hosts, including Nothofagus and Myoporum; one record from Quercus in the Philippines.

Teleomorph: This species differs from D. grandis in having white, rather than light brown lighter internal concentric zones, which often become loculate as in D. vernicosa. In addition, it has more regular, equilateral, almost ovoid ascospores, which are as variable in size as those of D. grandis (14–)16–23 × 8–13(–14) µm.

Stromatal secondary metabolites: BNT (1) and other binaphthalene derivatives prevailing.

Cultures and anamorph: This fungus has a virgariella-like anamorph, which was amply described by Ju et al. (1997) sub D. grandis, and by Stadler et al. (2004c). Conidiophores are up to

Fig. 55. Teleomorphic characteristics of Daldinia loculatoides. A–D, G–J. Holotype (UK); E, F. BPI 594973 (Canada). A, B, E. Stromatal habit (A, E: Side view; B: Top view, with stromatal pigments in 10 % KOH inserted). C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface (stromatal pigments in 10 % KOH inserted). G. Ascii in Melzer’s reagent revealing amyloid apical apparatus. H. Ascospores in SDS. I. Ascospores in KOH, showing non-dehiscing perispore. J. Ascospores by SEM (10,000×). Scale bars A, B, D, E = 1 cm; C, F = 1 mm; G–I = 10 µm; J = 2 µm.
150 µm long, the terminal conidiogenous cells measure 10–22 × 2–3.5 µm, the ellipsoid conidia (6.5–)7–9.5 × 2–4.5 µm.


Notes: This species was previously included in the concept of D. grandis by Child (1932) and Ju et al. (1997) based on the rather large ascospores. More recently, a different ascospore morphology was noted, and even its stromatal anatomy shows consistent deviations from D. grandis (Stadler et al. 2004c). Daldinia novae-zelandiae rather appears related to D. bakeri and D. vernicosa and differs from other large–spored members of the genus in producing a virgariella–like anamorph.
Stadler et al. (2004c) reported on the great variability in ascospore size ranges in different collections from New Zealand, which were only slightly overlapping in some cases. They attributed this phenomenon to the presence of a species complex that could eventually be further resolved by using complementary methods. A single New Zealand specimen (PDD 90476) showed higher similarities with *D. grandis* and is treated there as *D. cf. grandis*.

**Group E: The *Daldinia petriniae* group (Figs 57–67)**

The *D. petriniae* group appears to be the most derived group within the genus, considering that it is characterised by various features that are considered as evolutionary advanced in ascomycete and Xylariaceae taxonomy (highly reduced conidiogenous structures, dehiscence perispores; early deliquescent asci in some species). See also the molecular data (Fig. 74). This species group seems to have undergone a close co-evolution with the species of its predominant host family, Betulaceae and other dicotyledonous woody plants. The salient common feature of all species in this complex that have so far been cultured is their annellidic conidiogenesis, *i.e.*, the production of conidia from percurrently proliferating conidiogenous cells, which are often located at the apex of relatively short, unbranched conidiophores. This feature was discovered in *Daldinia* by Petriti & Müller (1986), who reported it for cultures of a *Daldinia* sp. associated with *Alnus in Switzerland, which they referred to as “*D. occidentalis* Child”. Subsequently, it was shown that the former name was misapplied, due to one of the unfortunate confusions that had occurred in the monograph by Child (1932), who had not recognised that her new species was conspecific with the type of *D. loculata* (Ju et al. 1997). They recognised that the latter species (and therefore, also *D. occidentalis*) primarily differs in having almost equilaternal, obovoid ascospores with indescent perispores in KOH. Accordingly, they proposed the new name *D. petriniae* for the Swiss fungus. Their concept of *D. petriniae* comprised a species, which could be easily separated from *D. concentrica* (s. Ju et al. 1997, *i.e.*, *D. chilidiae* in the current context) based on stromatal pigment colours in KOH, even in the absence of anamorphic characteristics. Even *D. concentrica sensu stricto* and all other members of this group listed above (Group A), can be easily separated from all members of the *D. petriniae* group, because their conidiogenous cells produce exclusively (or preferentially, in case of *D. palmensis*) sympoduloconidia. These species have much more complex conidiogenous structures, mostly approaching a nodulisporium-like branching pattern and conidiophores featuring up to four apical conidiogenous cells. In addition, most of them contain concentricolits besides BNT as predominant stromatal metabolites, resulting in more dilute purple pigments in KOH. The type specimen of *D. petriniae* and all other specimens hitherto found on the same host, *Alnus incana*, have relatively small ascospores, and their stromata are never semiglobose and feature prominent perithelial outlines and papillate ostioles.

However, after the introduction of *D. petriniae*, the situation soon became more complicated. Ju et al. (1999) already gave preliminary descriptions of other *Daldinia* spp. with annellidic conidiogenesis, larger ascospores and associations with other species of *Betulaceae* in Europe and Far Eastern Russia. These species are now recognised as *D. decipiens* and *D. carpinciola*, respectively. Stadler et al. (2001a) and Wollweber & Stadler (2001) described material from *Alnus glutinosa* (Europe) and *A. rhombifolia* (USA) with olivaceous stromatal pigments and larger ascospores than the specimens from *A. incana* on which the protologue of *D. petriniae* was based. They, furthermore, reported inconsistencies in the stomatal pigments in KOH, which were attributed to time-dependent colour changes, owing to the presence of apparently unstable compounds that occur especially in the specimens from host plants other than *A. incana* besides the common BNT (1, cf. also Stadler et al. 2001a). Interestingly, the HPLC profiles of specimens recalling *D. petriniae* from *A. glutinosa*, as well as other *Betulaceae* (Carpinus, Corylus, and especially Betula) strongly recalled those of *D. lloydii*, another species described by Ju et al. (1997), based on stromatal pigments and the characteristic stomatal surface.

The situation became even more complicated when further material from Far Eastern Russia was examined and new species introduced (Vasilyeva & Stadler 2008): the teleomorphic morphology of *D. barkalovi* recalled that of *D. lloydii*, except for having purple pigments; *D. govorovae*, a species recalling the Mexican *D. macrospora* except for having significantly smaller ascospores, and similarities of the third species described by Vasilyeva & Stadler (2008) to *D. cudonia sensu* Ju et al. (1997; i.e. *D. asphalatum* herein) had already been noted by Ju et al. (1999). All the above species display an almost exclusively annellidic conidiogenesis and would, thus, appear to be closely related to *D. petriniae*. Interestingly, *Anellosporum*, the only formally described anamorphic xylariaceous taxon with annellidic conidiogenesis does not show affinities to this group, but rather appears related to *D. loculata* as inferred from molecular phylogenetic data (Davey 2010).

A case could be made to create several synonymies or to accept some of the fungi involved at subspecific rank; however, from the outcome of our work on the more common and better studied members of this genus, and its taxonomical history as such, we prefer to keep most of them at species rank. After all, excessive lumping of taxa has created enough confusion in the past in Xylariaceae taxonomy.

The species descriptions below and the synoptic comparison in Table 11 comprise all hitherto known species; illustrations of some recently described taxa have not been regarded necessary but they are keyed out as well. We have also added some taxa here of which no data on anamorphic structures are available, based on chemotaxonomic data or teleomorphic morphology. The anamorphic structures of this species group appear so homogenous that we have only illustrated examples. Only dimensions of the conidiophores vary to some extent. During our examination of fresh material from around the world, we found that the *D. petriniae* group even includes some tropical species, and that some temperate species are associated with non-betulaceous hosts.


**Etymology:** For the Swiss mycologist, Liliane Petriti, who discovered the annellidic conidiogenesis of this species complex.

**Typus:** Switzerland, Graubünden, Ramosch, Resgia, Alnus incana, 29 Aug. 1986, L. & O. Petrini (WSP 69648 - holotype, ZT - isotype).


**Holotypus:** USA, Idaho, Priest River, Alnus, J.R. Weir ex Lloyd herb. 12279 (BPI 716987).
A polyphasic taxonomy of *Daldinia* (Xylariaceae)

**Table 11.** Major discriminative characters of the species in the *D. petriniae* group. CC: Conidiogenous cells; CON: Conidia; STR: Stromata.

<table>
<thead>
<tr>
<th>Species (Daldinia)</th>
<th>Ascospore size [µm]</th>
<th>Ascal apical apparatus (µm)</th>
<th>Stromatal pigments (KOH)</th>
<th>Ratio darker/lighter concentric zones + significant stromatal features</th>
<th>Anamorphic structures (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>asphaltatum</td>
<td>12.5–16.5 (–19.5) × 6–8</td>
<td>0.5–0.75 × 3–3.5</td>
<td>Purple or absent</td>
<td>1:1.5–9</td>
<td>STR: long stipitate, zones extending into the stipe</td>
</tr>
<tr>
<td>barkalovii</td>
<td>12–14 (–15) × 6–7 (–7.5)</td>
<td>0.75–1 × 2.5–3</td>
<td>Purplish-gray</td>
<td>1:1–1.5</td>
<td>STR: turbinated, with characteristic brownish-yellow striate surface stripes (surface not reticulate!)</td>
</tr>
<tr>
<td>carpinicola</td>
<td>(13–)14–16.5 × (6.5)7–8 (–10)</td>
<td>0.5 × 3–3.5</td>
<td>Purplish-gray</td>
<td>1:0.75–2</td>
<td>STR: mostly clavate</td>
</tr>
<tr>
<td>decipiens</td>
<td>(13–)14–18 (–20) × 6.5–10 (–11)</td>
<td>0.5–0.8 × 4.5–6</td>
<td>Purplish-gray</td>
<td>1:0.75–2</td>
<td>STR: mostly semiglobose-substipitate</td>
</tr>
<tr>
<td>gelatinosa</td>
<td>12.5–16 (–17) × 6–8 (–10)</td>
<td>0.5–1 × 3.5–4</td>
<td>Purplish-gray</td>
<td>1:1–4</td>
<td>STR: mostly turbinated</td>
</tr>
<tr>
<td>govorovae</td>
<td>(15–)16–18 (–20) × 8–10</td>
<td>Not seen</td>
<td>Greenish brown</td>
<td>1:1–4</td>
<td>Stromata in OA culture</td>
</tr>
<tr>
<td>lloydii</td>
<td>(11–)12–18 × 6–8 (–9)</td>
<td>0.5–0.75 × 4–5</td>
<td>Olivaceous</td>
<td>1:2–3</td>
<td>STR: hemispherical to pulvinate, basal parts often vertically zonate, surface of young STR reticulate</td>
</tr>
<tr>
<td>macrospora</td>
<td>22.5–30 × 8.5–10.5</td>
<td>1 × 4</td>
<td>None</td>
<td>1:1–5</td>
<td>Unknown</td>
</tr>
<tr>
<td>mexicana</td>
<td>12.5–15.5 × 6.5–7.5</td>
<td>1 × 3.5–4</td>
<td>Weakly isabelline</td>
<td>1:1–2</td>
<td>STR: mostly turbinated</td>
</tr>
<tr>
<td>petriniae</td>
<td>12.5–16.5 (–6)–6.5–7.5</td>
<td>0.75–1 × 3.5–4</td>
<td>Purplish-grey, sometimes isabelline, often with colour changes</td>
<td>1:1–3</td>
<td>STR: initially hemispherical to almost clavate, later often pulvinate or placentiform</td>
</tr>
<tr>
<td>singularis</td>
<td>9–11 × 4.5–5.5</td>
<td>Perispore very easily detached in KOH</td>
<td>Inamylloid, reduced or absent</td>
<td>1:1–1.5</td>
<td>STR: tiny, max 5 mm diam</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Misapplied name:** *Daldinia occidentalis* Child sensu Petrin & Müller (1986).

**Selected illustrations:** Petrin & Müller (1986), fig. 43 as *D. occidentalis* (ascospores, anamorph). Ju et al. (1997, all from type material), figs 17 (ascospores), 59–61 (stromata) and 76 (anamorph). Wollweber & Stadler (2001), Abb. 12 (stromata).

**Known distribution/host preference of stromata:** All over the temperate-boreal Northern Hemisphere; mostly on Betulaceae, typical morpho-chemotype is associated with *Alnus incana*.

**Teleomorph:** Stromata at first hemispherical to almost clavate, often becoming pulvinate or placentiform, sessile or subsessile, with inconspicuous to conspicuous perithecial outlines, 1–5 × 1–5 × 0.9–3.4 cm; surface Dark Brick (60) to Fuscous (103), blackened and varnished in age; with dull reddish brown granules immediately beneath surface and with KOH-extractable pigments initially Livid Purple (81) or Dark Livid (80), often changing to yellowish tones some minutes after incubation and occasionally Olivaceous (48); tissue between perithecia brown, pithy to woody and below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, persistent, 0.5–1.5 mm thick (Ratio darker/lighter zones 1:1–3), *Perithecia* lanceolate 1–1.5 × 0.3–0.4 mm. *Ostioles* papillate. *Asci* 200–230 × 7–11 µm, p. sp. 75–100 µm, stipes 110–140 µm, with discoid, amylloid apical apparatus, 0.75–1 × 3.5–4 µm. Ascospores brown to dark brown, ellipsoid-inequalitarian, with narrowly rounded ends, 12.5–16.5 × (6–)6.5–7.5 µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, smooth by LM but showing faint transverse striations by SEM (5,000×); epispore smooth.
Stromatal secondary metabolites: BNT (1) and other binaphthalene derivatives prevailing only in specimens from Alnus alnobetula (formerly known as A. viridis), A. incana and A. rhombifolia. Stromata from A. glutinosa, Betula and other Betulaceae often contain perylene quinones (2) as prevailing components in addition to BNT (1).

Cultures and anamorph: Colonies on OA reaching the edge of 9 cm Petri dish in 10–12 d, at first whitish, felty, azonate, with diffuse margins, becoming Honey (64) when sporulating, reverse Citrine (13); sporulating regions scattered over entire surface of colony, but with more abundant sporulation on tufts of hyphae at edge of colony, pale Luteous (11). Conidiogenous structure with sporoorthrix-like to nodulisporium-like branching pattern Conidiophores mononematous, unbranched or dichotomously branched.
hyaline, coarsely roughened, up to 240 × 2.5–3 µm, with 1–2 (–3) conidigenous cells arising from each terminus. Conidigenous cells clavate, hyaline, roughened, 10–24 × 3–5 µm. Conidia produced from percurrently proliferating conidigenous cells or, infrequently, from sympodially proliferating conidigenous cells, hyaline, smooth, subglobose to obovoid, usually with an attenuated flattened base, (5.5–)7–9 × (4.5–)5–6 (–7) µm.


flattened base, (5.5–)7–9 × (4.5–)5–6 (–7) µm. branch of still living (“semivivum”) as (PRM 869448); Moravia, Hranice (“Mährisch Weisskirchen”), (UPS). Pohl, Aug. 1998,

Säterön, dead branches of with typical anamorph on stromata and characteristic HPLC profile (UPS); Linköping, Stige, dead trunk of (UPS); Hälsingland, Harmanger, Strömsbruk, fallen

trunk of

Alnus incana

Nordingrån, Halaviksravinen,

, 26 Jul. 1977, S. Olofsson (UPS); Bavaria, Füssing, Innauen,

KR 550/75

Quercus

17971

), 4 Aug. 1956, L.K. Henry (NY); Oregon, Waldport,

Alnus

1963

, 12 Nov. 1975, D. Benkert, Alnus (B70 0009608). Alnus incana

A. Ludwig as (B70 0009613); Fürstenwalde/Spree, NSG Lochnitztal, (M); exact locality unknown,

, Apr. 1978, H. Marschner (WUP); Württemberg, Finland, Alnus incana

as MUCL 49213; GenBank Acc. No. of DNA sequence AF176975). Further cultures of D. petriniae extant in public collections from

Alnus incana

23011

(UPS); same collection data and host, 7

P.R. China

2001); vicinity of Sanjiang, Nature reserve, 3-5 km from Donxing con,

Sweden

Betula

1974, Z. Pouzar as (PRM 886101, culture CBS 116728).

Alnus incana

KR 304/77

, Jul. 1977, G.J. Krieglsteiner (C). Alnus incana

KR 163/94

. ex herb Krieglsteiner (HJ 103

Further cultures of D. petriniae extant in public collections:


Notes: This species, first identified by Petri & Müller (1986) as “D. occidentalis”, was presumed to be closely associated with Alnus. We here report it from a variety of other Betulaceae and even from some non-betulaceous hosts. In our previous study it was also shown to be variable with respect to its HPLC profiles and its KOH-extractable pigments (Wollweber & Stadler 2001, Stadler et al. 2001a). Some of the collections studied contain highly unstable pigments (presumably perylene quinones, which are derived from binaphthalenes by enzymatic oxidation, or might result from BNT under influence of air during storage (cf. Stadler et al. 2010a), which are also found in even higher quantities in D. lloydii. In several specimens of D. petriniae, including the type specimen, such olivaceous pigments were noted after some years of storage, whereas the fresh material had purple pigments, hence the KOH reaction is more complicated and difficult to interpret in this group of Daldinia spp. In some specimens, both pigment colours may even occur in different portions of the same dried stroma, but it remains to be confirmed whether this also holds true for freshly collected material.

However, the type specimen of D. petriniae and other collections from Alnus incana, Alnus abietina, and A. thomsonii show the ascospore dimensions given above, (i.e. up to 16.5 µm long × 7.5 µm wide), and their KOH-extractable pigments are usually purple, owing to the presence of BNT (1). Other specimens

A POLYPHASIC TAXONOMY OF DALDINIA (XYLARIACEAE)
listed above have the same ascospore size range, but they tend to have Olivaceous (49) pigments in KOH, especially when derived from *Alnus glutinosa*, *Betula*, *Carpinus*, or non-betulaceous hosts. The type specimen of *D. concentrica* var. *confluens* also seems to have affinities to this group, as Olivaceous (48) stromatal pigments and ascospores of 12–15 µm length were observed. Nevertheless, it features small aggregated (i.e., ”confluent”) stromata that are not reminiscent of typical *D. petriniae* and could as well correspond to *D. decipiens* or another yet undescribed taxon of this complicated species complex. However, the specimen is rather depauperate, and the only conclusion we could safely draw from its study was that the synonymies of this name with *D. childiae* as proposed by Rogers *et al.* (1999), and with *D. concentrica* by other authors who treated this fungus before them, needed to be corrected.

Some other specimens showing Olivaceous (48) pigments in KOH often have relatively small, turbinate stromata of less than 2 cm height and relatively broad lighter concentric zones. Their ascospores are larger than those in “regular” *D. petriniae*, 13–17(–18) × (6–)6.5–7.5(–8) µm. These specimens appear to grade into *D. lloydii*. The main differences to *D. lloydii* are the stromatal surface structure and the more papillate ostioles (inconspicuous in *D. lloydii*), which does not appear to be a good criterion to segregate two taxa. When the characteristic scales in *D. lloydii* (which occur particularly frequently in young immature specimens) are not as prominent in mature and overmature specimens, it is easily confused with *D. petriniae*. The only culture we obtained from *D. petriniae* appears to be unstable between *D. lloydii*. The type specimen of *D. petriniae* has previously been reported for *H. fuscum* (cf. Petrini *et al.* 1987), where it has so far not been possible to fully resolve the species complex, except for the erection of *H. porphyreum* (Grammo 1999) and *H. fuscoideae* (Fournier *et al.* 2010b). Notably, both of these taxa are easier to recognise based on stromatal pigment colours, a character which appears to be unstable between *D. lloydii* and *D. petriniae*, as well as in the remainder of *H. fuscum* from *Betulaceae*.

**Daldinia asphalatum** (Link) Sacc., Sylloge Fungorum, 1: 394. 1882. Figs 59, 60.

**Etymology:** Not stated explicitly in the protologue. Presumably for the stromatal surface, which recalls asphalt in old, blackish and varnished stromata.

≡ *Sphaeria asphalatum* Link in Fr.: Fr., Linnaea 5: 540. 1830; Fr., SM3, Index: 160. 1831.

% *Lectotypus* (selected here): *Brazil*, exact locality unknown, [Beyrich] (S-F44597, ex herb. Link, in herb. P. Sydow (S).

≡ *Xylaria cundonia* Berk. & M.A. Curtis apud Berk., Grevillea 4: 47. 1875.

≡ *Daldinia cundonia* (Berk. & M.A. Curtis) Lloyd, Mycol. Writings 7: 1255. 1924.

**Holotypus:** USA, South Carolina, Santee Canal, dead tree, M.A. Curtis (K) (120965).


**Holotypus:** *Mexico*, no further information, W.A. Murrill ex Lloyd herb. 12402 (BPI 717012).

% Selected illustrations: Lloyd (1919) fig. 1888 (as *D. murrillii*); Child (1932) Plate 26, figs 3, 4 (ascospores and ascii); Plate 30, fig. 4 (stromata) and Plate 32, figs 1, 2 (perithecia) all as *D. loculata*; Ju *et al.* (1997) figs 7 (ascospores) and 38, 39 (stromata) as *D. cundonia*.

**Known distribution/host preference of stromata:** Tropical and subtropical North and South America, China; without apparent host specificity.

**Teleomorph:** *Stromata* turbinate to clavate, unbranched, with slender stipe bearing constricted rings, smooth, 0.7–1.5 × 0.7–1.5 × 1–2.7 cm including stipe, stipe 0.5–1.5 × 0.15–0.3 cm; surface Brown Vinaceous (84) or Dark Brick (60), blackened and varnished in age; with dull reddish brown granules immediately beneath surface, with KOH-extractable pigments dilute purple (China), dilute Grey Olivaceous (107) (Mexico) or without apparent KOH-extractable pigments (Brazil and USA); tissue between perithecia brown, pithy to woody; tissue below perithecial layer, but up to 3.5 mm thick in stipe (Ratio darker/lighter zones 1:1.5–9).

**Known distribution/host preference of perithecia:** Tropical and subtropical North and South America, China; without apparent host specificity.

**Teleomorph:** *Stromata* turbinate to clavate, unbranched, with slender stipe bearing constricted rings, smooth, 0.7–1.5 × 0.7–1.5 × 1–2.7 cm including stipe, stipe 0.5–1.5 × 0.15–0.3 cm; surface Brown Vinaceous (84) or Dark Brick (60), blackened and varnished in age; with dull reddish brown granules immediately beneath surface, with KOH-extractable pigments dilute purple (China), dilute Grey Olivaceous (107) (Mexico) or without apparent KOH-extractable pigments (Brazil and USA); tissue between perithecia brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2 mm thick, lighter zones greyish brown to brown, pithy to woody, sometimes with locules, persistent, 0.3–1.5 mm thick close to perithecial layer, but up to 3.5 mm thick in stipe (Ratio darker/lighter zones 1:1.5–9). *Perithecia* lanceolate, 1–1.3 × 0.3–0.4 mm. Ostioles inconspicuous to slightly papillate. Asci 200–280 ×
10–12 µm, p. sp. 80–100 µm, stipe 120–180 µm, with amyloid, discoid apical apparatus 0.5–0.75 × 3–3.5 µm. Ascospores brown to dark brown, ellipsoid-inequilateral, with narrowly rounded ends, 12.5–16.5(–19.5) × 6–8 µm, with straight to slightly oblique germ slit spore length on convex side; perispore dehiscent in 10 % KOH, appearing smooth by LM but showing conspicuous transverse striations by SEM (2.500–5.000×); epispore smooth.

**Cultures and anamorph** (observed in material from China): General habit as described below in detail for *D. decipiens*, with almost exclusively annellidic conidiogenesis, featuring sporothrix-like conidiophores, 60–105 × 3.5–4 µm, with conidiogenous cells 14–22 × 4 µm and ellipsoid, hyaline conidia measuring 6–8 × 3.5–5 µm.

**Stromatal secondary metabolites**: BNT (1) and other binaphthalene derivatives prevailing.

Additional specimens examined: **Mexico**, Veracruz, Xalapa, 5,000 ft, Dec. 1909, W.A. & E. L. Murrill 295 (NY); Veracruz, Atlixpan, San Andres, 3 Jul. 1975, F. Ventura 11566 (NY); Esquinol, Jilotepex, 20 Jul. 1972, F. Ventura 5767 (NY); Veracruz, El Esquinol, Jilotepex, 7 Dec. 1970, F. Ventura 2943 (BPI 594610; NY); Xalapa, Lucas Martin, 27 Aug. 1954, E. Perez-Silva 1002 (NY); near Bandera, Cerro La Martinica,
Sphaeria asphalatum was regarded a nomen dubium, since its description lacks modern diagnostic features and the type was not located by various researchers who monographed the Xylariaceae in the past century (Ju & Rogers 1996, Ju et al. 1997). Previous descriptions (e.g. by Saccardo 1882) did not allow for a conclusive placement of this name. The only material that can be traced back to the original collection by Beyrich (comm. Link) was found in Stockholm. Since it complies with the original description and most probably is part of the original material, it qualifies for lectotypification. The clavate, internally zoned stromata and the microscopic characters (Fig. 59A, B) do not leave any doubt as to their correspondence with the later synonym, D. cudonia. Due to an error in the monograph by Child (1932), this fungus was referred to as “D. loculata” until Ju et al. (1997) clarified its status. Since this species has been rather infrequently collected, and probably has been filed as “D. loculata” for decades, we accept D. asphalatum as the valid name rather than...
A polyphasic taxonomy of *DalDinia* (Xylariaceae)

attempting to conserve *D. cudonia*. Link (in Fries 1830) described the stromata as “globosa different, crusta atra nitida discrete obducta, intus fuliginoso-atra obsolete zonata, perithecia linearius series bi-sinuous.” There is also a long note stating it clearly being different from *D. concentrica* and many further differentiating characters are mentioned including the ostioles as “minima, punctiformia” and stroma as “obsolete zonatum” (etc.). The deformations (as compared to “D. concentrica”) may relate to the presence of stipes, while the other characters described by Saccardo can still be easily assessed in the lectotype. The presumption that this fungus is “probably related to H. sclerophaeum” (Miller 1961) might relate to his studies of a Montagne specimen in PC, which clearly corresponds to *Hypoxylon placentiforme sensu* Ju & Rogers 1996, or on a misinterpretation of Saccardo’s description. Among the material referred to by Ju et al. (1997) as *D. cudonia*, or by Child (1932) as *D. loculata*, which we studied for comparison, only BPI 715095 from Japan has non-stipitate, hollow stromata and smaller ascosporas, and is treated here as *D. gelatinoides*. We, therefore, agree with Ju et al. (1997) that this fungus is mainly distributed in southern North America but it could easily be widespread in the almost unsampled northeastern South America. Interestingly, it is very frequent in some Mexican provinces, but remains to be found again in South America, as far as we are aware. Ascosporas were not found in the type of *D. murrillii* but they were present in another collection by Murrill from the same country (BPI 716969) in the Lloyd herbarium that may have been used by Lloyd to make the description. The stromatal morphology of this species is so strikingly unique that it is certainly one of the most easily recognizable *Daldinia* species. The HPLC profile and SEM characteristics are reported here for the first time. HPLC showed BNT (1) as major detectable component, but the compound was usually present only in traces, and all the old specimens yielded either a rather weak greenish pigmentation or no pigments at all in KOH (the latter is due to the presence of perylene-quinones according to HPLC profiling). The ascospore size range was in agreement with material from America. The ascospores show conspicuous, transverse striaions by SEM (Fig. 59F).

Two recently collected specimens from Northern China (Fig. 60L, N-Q) matched those of *D. asphalatum*, aside from their stromatal stipes being less prominent and their asci and ascal apical apparatus being somewhat smaller and by having purple pigments in KOH. Their cultures and anamorphic structures showed sporothrix-like conidiophores with anellidic conidiogenesis, confirming their affinities to the *D. petriniae* group. However, their identity with *D. asphalatum* remain to be fully established by culturing American material. Notably, Ju et al. (1999) already postulated affinities of morphologically similar temperate *Daldinia* spp. to “D. cudonia”, which are treated here as “D. carpincola” and *D. decipiens*.


**Etyymology:** For the collector of the holotype specimen.

**Holotypus:** Russia, Sakhalin Island, vicinity of Voskresenovka, on dead branches of *Alnus*, 1 Aug. 2003, V. Barkalov (VLA - CBS 116999).

**Selected illustrations:** Vassiljeva & Stadler (2008), figs 5 (stromata) and 6A, B (anamorph).

**Known distribution/host preference of stromata:** Far Eastern Russia; from *Alnus* – only known from the type.

For a detailed description of teleomorphic and anamorphic characters see Vassiljeva & Stadler (2008); for major differences to known species see notes below.

**Stromatal secondary metabolites:** BNT (1) and other binaphthalenes prevailing.

**Notes:** *Daldinia barkalovii* resembles *D. lloydii*, from which it differs in having smaller ascosporas, 12–14(–15) × 6–7(–7.5) μm, in its wrinkled stromatal surface showing wavy stripes of coffee or ochre colour (rather than a reticulate network), and in having Vinaceous Grey (101) pigments in KOH. The internal concentric zones (not reported in detail in the protologue) are dark brown, 0.1–0.2 mm thick and light brown to whitish, 0.1–0.8 mm thick (Ratio darker/lighter zones 1:5–8), i.e., in the range observed for *D. lloydii*. Also otherwise, the stromatal habit recalls *D. lloydii* very much. It also resembles specimens of *D. petriniae* derived from *Alnus incana* in Europe, with which it even shares the same ascospor dimensions. However, the conidiophores (70–140 × 2.5–3 μm), conidiogenous cells (10–25 × 3–5 μm) and conidia (7–10 × 5.5–7 μm) of the sporothrix-like anamorph of the ex-type culture are slightly smaller than in those of *D. petriniae*. This taxon could eventually be considered a variety or synonym of the latter species, once additional material has been examined. In preparation of this monograph, however, we were not even able to obtain the type material from VLA even 18 months after our request. Therefore, no details and new illustrations of any of the species described by Vassiljeva & Stadler (2008) can be provided here.


**Etyymology:** For the host plant.

**Types:** Russia, Primorsky territory, near Vladivostok, *Carpinus cordata*, N. Vasilyeva, 26 Sep. 1997 (VLA - holotype, WSP - isotype, ex-type culture CBS 122880). Material not re-examined in this study - previously treated as “*Daldinia* sp. from Russian Far East” (Ju et al. 1999).

**Selected illustrations:** Ju et al. (1997), figs 11 (ascosporas) and 44–46 (stromata); Ju et al. (1999) as *Daldinia* sp. from Russian Far East, figs 5–7 (stromata) and 11 (anamorphic structure); Vasilyeva & Stadler (2008), fig. 3 (as *D. carpincola*, stromata in natural habitat).

**Known distribution/host preference of stromata:** Only known from Far Eastern Russia; on *Carpinus cordata*.

**Teleomorph** Similar to *D. decipiens*, except for having smaller asci (p. sp. 80–90 × 8–10 μm, with stipes up to 100 μm long, featuring a discoid amyloid apical ring (0.5 × 3.5 μm) and smaller ascosporas (13–)14–16.5 × (6.5–)7–8(–10) μm, with straight dorsal germ slit spore length, perispore dehiscent in 10 % KOH.
Stromatal secondary metabolites: BNT (1) and other biphenylalene derivatives prevailing.

Cultures and anamorph: Similar to those of D. gelatinosa, except that no formation of stromata has been observed in the ex-type culture.

Notes: Daldinia carpinicola (of which only two collections have so far been reported; cf. Vasilyeva & Stadler 2008), was said to be “endemic” to Eastern Russia. It was not re-examined in the course of this study as we were unable to get the type material from VLA and WSP. The anamorph, which resembles that of D. gelatinosa (see further below in “Notes” to that species), was characterised by Ju et al. (1999, as “Daldinia sp. from Russian Far East”), who had also already stated that this taxon differs from D. decipiens (“Daldinia sp. from Denmark” in Ju et al. 1999) mainly in its ascospore size range and the morphromonology of conidiogenous structures. The morphology of its ascospores is generally in agreement with that of D. gelatinosa, too, aside from the latter species having slightly more narrow spores with more acute ends. A case could even be made to lump this taxon with D. petriniae, too, aside from the latter species having slightly more morphological variation in its ascospore size. We prefer to keep it separate for the time being, until additional material has been encountered and examined.


Etymology: Deceiving; referring to the apparent correspondence of this species to several other members of the genus.

Holotypus: Germany, North Rhine Westphalia, Warstein, Hamorsbruch, on trunk of Betula carlilata, 5 Oct. 2000, H. Wollweber Ww 3811 (M). Treated as “Daldinia sp. from Denmark” by Ju et al. 2001d (figs 1 (stromata of D. concentrica), 2 (anamorph of paratype), and 4a (SEM of ascospores, holotype)).

Selected illustrations: Stadler et al. (2001d) figs 1 (stromata of holotype), 2 (anamorph of paratype), and 4a (SEM of ascospores, holotype).

Known distribution/host preference of stromata: Temperate Northern Hemisphere; most frequently reported from Europe on Betula and other Xylariaceae; only one proven record from Fagus. Anamorph is associated with Xiphydria woodwasps, which may act as dispersal vectors (Srůtka et al. 2007).

Teleomorph: Stromata semiglombose or subsessile, frequently with a short stipe of 3–8 mm height, mostly with fairly conspicuous perithecial outlines at maturity, 0.5–3 × 0.3–3 × 0.6–2 cm; immature stromata often cylindrical; surface of young stromata reddish brown, blackened and dull in age; dull orange brown granules immediately beneath surface, with KOH-extractable pigments Purple (100), Dark Livid (80) or Vinaceous Purple (101); tissue between perithecia brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown or blackish brown, pithy to woody, 0.1–0.5 mm thick, lighter zones fuscous, pithy to woody, persistent, 0.1–1 mm thick (Ratio of darker/lighter zones 1.075–2.), zonation sometimes extending into stipe. Perithecia lanceolate or, less frequently, obovoid, 0.4–0.8 × 0.2–0.4 mm. Ostioles inconspicuous to slightly papillate. Asci 180–210 × 9–10 mm, p. sp. 90–120 mm, stipe 90–100 mm, with discoid, amyloid apical apparatus 0.5–0.8 × 4.5–5.5 µm. Ascospores light brown to dark brown, ellipsoid-inequalitubular to, less frequently, almost equilateral, mostly with narrowly rounded ends, (13–)14–18(–20) × 6.5–10(–11) µm, with straight germ slit over entire spore length on the more convex side; periapex dehiscent in 10 % KOH, appearing smooth under the light microscope, but showing transversal striations by SEM (5.000×); epispore smooth.

Stromatal secondary metabolites: BNT (1) and other biphenylalene derivatives prevailing.

Cultures and anamorph: Colonies on QA reaching the edge of 9 cm diameter in 1–1.5 wk, whitish, felty, azonate, with diffuse margins, becoming Buff (45) to Honey (64) with sporulation; reverse becoming Citrine (13), ultimately becoming blackish with age. Sporulating regions scattered over entire surface of colony. Conidiogenous structure with sporothrix-like or nodulisporium-like branching pattern. Conidiophores frequently arising from characteristic inflated hyphae, unbranched or dichotomously branched, hyaline, coarsely roughened, 50–120 × 2.5–3.5 µm, with 1–2 conidiogenous cells arising from each terminus. Conidiogenous cells terminal or, rarely, intercalary, cylindrical, hyaline, 13–22 × 2.5–5.4 µm. Conidia produced from percurrently proliferating conidiogenous cells or, infrequently, from sympodially proliferating conidiogenous cells. Conidia hyaline, smooth, subglobose to obvoid, frequently with an attenuated base, 7–8 × 4.5–5.5 µm.

Additional specimens examined: Denmark, Sjælland, Petersvaerft, Stensby Skov, Corylus, 21 Oct. 1997, H. Knudsen, treated by Johannesson et al. (2000) as D. decipiens, as “Daldinia sp. from Denmark” by Ju et al. 1999, “Daldinia sp. from Russian Far East”), who had also already stated that this taxon differs from D. decipiens (“Daldinia sp. from Denmark” in Ju et al. 1999) mainly in its ascospore size range and the morphromonology of conidiogenous structures. The morphology of its ascospores is generally in agreement with that of D. gelatinosa, too, aside from the latter species having slightly more narrow spores with more acute ends. A case could even be made to lump this taxon with D. petriniae, too, aside from the latter species having slightly more morphological variation in its ascospore size. We prefer to keep it separate for the time being, until additional material has been encountered and examined.
Notes: This species, previously reported from Germany and Sweden (Stadler et al. 2001e) and France (Stadler et al. 2004d) has now been encountered in Denmark, Spain and England, as well as from the USA and China. It was also present among the specimens labelled Sphaeria concentrica in the Persoon herbarium. Specimen Persoon 271, comprising several rather small substipitate stromata.
on bark of Betula, had been reported as D. concentrica by Ju et al. (1997) and by Rogers et al. (1999) as D. childiae. Indeed, it showed a faint yellow pigment in KOH. However, neither concentricol (a reliable, highly persistent stromatal marker metabolite for the D. concentrica group) nor daldinal and other typical metabolites contained in D. childiae were identified in the crude stromatal extract, and only BNT was detected. This could be due to a similar phenomenon as in the type of D. bakeri, which contained artefacts that are probably fumigants or insecticides (Stadler et al. 2004a).

In addition, some ascospores of up to 19 µm length were observed, matching the characteristics of D. decipiens. The specimens from China deviated slightly from European D. decipiens in having smaller asci (180–200 × 7–8 µm, p. sp. 85–95 × 100–125 µm, with amyloid apical apparatus 0.75–1 × 3.5–4 µm) and ascospores measured only 12–14(–15) × 6–7.5 µm, but their stromatal morphology and HPLC profile, as well as the morphology of their cultures and anamorphic structures did not deviate significantly from the typical form.

The anamorph of this species was identified as a constant associate of certain woodwasps (of the genus Xiphydria), with which it apparently lives in symbiosis (Srůtka et al. 2007, Pažoutová et al. 2010). The woodwasps are highly host-specific, which may account for the apparent host-specificity of the stromata. This phenomenon is being further discussed in the general part (see “Ecology”).


**Etymology:** For the gelatinous interior.

**Holotypus:** USA, New Hampshire, Waterville, wood of Betula alleghaniensis, 9 Aug. 1967, J.D. Rogers (WSP 69649).

**Selected illustrations:** Ju et al. (1997, all from holotype), figs 11 (ascospores) and 44–46 (stromata).

**Known distribution/host preference of stromata:** Temperate Northern Hemisphere, apparently rare; so far found on Betula and Malus.

**Teleomorph:** Stromata turbinate, sessile or short stipitate, surface smooth, wrinkled when rapidly dried, smooth or with inconspicuous perithecial outlines, 0.7–4 × 7–3.5 × 1–3 cm; surface Dark Brick (60), blackened and varnished in age; with dull reddish brown granules immediately beneath surface and with KOH-extractable pigments Dark Livid (80), or without apparent KOH-extractable pigments; tissue between perithecia greyish brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones brown dark brown, pithy to woody, 0.3–0.8 mm thick, lighter zones white to light brown, gelatinous, disintegrating and becoming loculate when dry, 0.2–1.5 mm thick (Ratio darker/lighter zones 1:1–4). Perithecia lanceolate, 0.8–1.2 × 0.2–0.4 mm. Ostioles papillate. Asci 160–240 × 8–10 µm, p. sp. 80–90 µm, stipe 70–150 µm long, with discoid, amyloid apical apparatus 0.5–1 × 3.5–4 µm. Ascospores brown to dark brown, unicellular, ellipsoid-inequilaterial, with narrowly rounded ends, 12.5–16(–17) × 6–8(–10) µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, appearing smooth by LM, but showing conspicuous transverse striation at 2.500–5.000× by SEM; epispore smooth.

**Stromatal secondary metabolites:** BNT (1) and other binaphthalene derivatives prevailing.

**Cultures and anamorph:** Cultures on OA similar to those of D. decipiens (cf. detailed description above), with predominantly sporothrix-like conidiophores up to 120 µm long and annellidic conidiogenesis. The conidiogenous cells (15–35 × 4–6 µm) and conidia (6–7.5 × 4.5–5.5 µm) however, have different dimensions to those of D. decipiens. The culture CBS 116731 produced stromatal primordia of up to 0.9 cm diameter after 2–3 wk, which became covered with the anamorph but never became mature.

Additional specimen examined: Russia, Primorskiy krai, Vladivostok, Botanical Garden near Sanatornaya, Carpinus, 4 Aug. 2003, H. Knudsen (C-F-82770, culture CBS 116731).

Notes: Ju et al. (1997) reported that this species is “reminiscent of D. fissa” (= D. vernicosa), mainly differing from it in its ascospore morphology. Some specimens they actually listed as paratypes (WSP 54679 and WSP 54729 from Idaho, USA) are treated elsewhere herein, because we think they show closer affinities to D. loculata or D. bakeri, and may represent another, yet undescribed taxon. We here report this fungus from Asia (Far Eastern Russia) and were also able to study cultures of this species for the first time. Cultures obtained from the Russian material showed similar microscopic features as the ex-type culture of D. carpincola, which was studied concurrently. Studies of specimens collected from Malus in Canada and the corresponding culture revealed strong similarities to the Russian material, and despite being derived from a non-betulaceous host, we conclude that this material also belongs to D. gelatinosa (see specimens examined section on this taxon). This species contains BNT as major metabolite, and its HPLC profiles resemble that of D. decipiens. Both species have ascospores with rather acute ends, showing transverse striations by SEM (Fig. 62l). Daldinia gelatinosa differs from D. decipiens and D. carpincola mainly in having smaller ascospores with a more regular shape and acute ends, and also differs from D. petriniae in its stromatal anatomy and the dimensions of its anamorphic structures. Daldinia lloydii is also related to them, but differs in its stromatal surface, pigment colours, and in having even more reduced conidiogenous structures. Daldinia barkalovii and D. gorovorae differ in their ascospore sizes and their stromatal morphology.

**Daldinia sp.** with possible affinities with D. gelatinosa. Fig. 63.

**Tanzania,** Eastern Province, Arusha National Park, Mt. Meru crater, 28 May 1968, D.N. Pegler T 1061 as D. eschscholtzii (K(M) 131669).

**Teleomorph:** Stromata depressed-spherical, sessile to subuplicate, deeply shrivelled, without visible perithecial outlines, 0.7–1.4 × 0.5–0.8 cm; surface shiny black with remnants of a Dark Brick (61), umbilicate. Dark reddish brown granules immediately beneath surface, with KOH-extractable pigments Pale Mouse Grey (117); tissue between perithecia blackish, pithy; tissue below perithecial layer strongly gelatinous-hollow, composed of ill-distinct alternating zones, darker zones blackish, 0.2–0.7 mm thick, gelatinous, interspersed with white strands, lighter zones golden brown, 0.15–0.2 mm thick, solid. Perithecia lanceolate, 1 × 0.2–0.25 mm. Ostioles umbilicate. Asci fragmentary, long-stipitate, p. sp.
64–68 × 7–8 µm, with amyloid, discoid apical apparatus, 0.8 × 2.5 µm. Ascospores dark brown, ellipsoid-inequilateral with narrowly rounded ends, 9.5–11.5 × 4.5–6 µm (many collapsed ascospores average narrower), with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, smooth by LM; epispore smooth by LM.

Stromatal secondary metabolites: HPLC profiling revealed traces of BNT.

Notes: This collection consists of two intact stromata and a fragment of a third one, they are all fertile but somewhat altered by a drastic drying. The deeply shrunk stromata and the hollow interior most likely correspond to a strongly gelatinous interior as it can be observed in members of the vernicosaloculata group. However, the inequilateral ascospores with a perispore dehiscent in KOH do not fit this group and the combination of characters exhibited by this Daldinia recalls D. gelatinosa, which is considered a member of the petriniae group in this study.

It differs from D. petrinae in having significantly smaller ascospores 9.5–11.5 × 4.5–6 µm vs. 12.5–16(–17) × 6–8(–10) µm and black gelatinous internal zones vs. white to light brown in D. gelatinosa. We refrain from describing it as new due to the scantiness of the material and the absence of cultural data.


Etymology: For the collector of the holotype specimen.

Holotypus: Russia, Primorsky Kray, Reserve Kedrovaya Pad, rotten wood of a deciduous tree, 19 Sep. 1997, O. Govorova (VLA, ex-type culture CBS 122883).

Selected illustrations: Vasilyeva & Stadler (2008, all from holotype), figs 4 (stromata) and 6c, d (anamorph).

Known distribution/host preference of stromata: Far Eastern Russia, only known from type; from unknown substrate.

Teleomorph: Stromata depressed-spherical, sessile, up to 4.5 cm wide; surface roughened with inconspicuous perithecial outlines, dark brown; with KOH-extractable pigments Umber (9), Chestnut.
A polyphasic taxonomy of Dal dinia (Xylariaceae)

(40) or Sepia (63), turning purplish after 5 minutes of incubation; tissue between perithecia greyish brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2–0.8 mm thick, lighter zones white, gelatinous when rehydrated, in places disintegrating and becoming loculate when dry, 0.8–1.5 mm thick (Ratio darker/lighter zones 1:1–3).

Perithecia lanceolate, 0.8–1.2 × 0.3–0.5 mm. Ostioles slightly papillate.

Asci agglutinated and fragmentary, p. sp. 95–125 × 11–13 µm, no stipes and no apical apparatus observed.

Ascospores ellipsoid-inequilateral, with narrowly rounded ends, light brown, (15–)16–18(–20) × 8–10 μm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, epispore smooth by LM, but showing faint transverse striations by SEM (5.000×).

Stromatal secondary metabolites: BNT (1) and a series of hitherto unknown metabolites that were so far not observed in any other specimen of Dal dinia. These unknown compounds are considered responsible for the brownish pigments.

Cultures and anamorph: Colonies on OA reaching the edge of a 9 cm petri dish in 9–11 d, whitish to cream, felty, azonate, with diffuse margins, becoming Isabelline (65) to Honey (45); reverse Citrine (13), melanising with age; sporulating regions scattered over entire surface of colony, Fawn (87). Conidiogenous structure similar to that of D. petriniae, attaining a sporothrix-like to nodulisporium-like branching pattern as defined in Ju & Rogers (1996). Conidiophores up to 210 × 2.5–3.5 µm, with 1–3 conidiogenous cells arising from each terminus. Conidiogenous cells clavate, hyaline, roughened, 10–45 × 3.5–5.5 µm. Conidia exclusively produced from percurrently proliferating conidiogenous cells, hyaline, smooth, subglobose to obovoid, usually with an attenuated, flattened base, (7–)8–11 × 6–7.5 µm.

Notes: The description is modified from Vasilyeva & Stadler (2008) to be in compliance with the current monograph, and further details including molecular data are here presented for the ex-type culture. The gross stromatal morphology and anatomy are similar to D. macrospora and D. gelatinosa, which both deviate in their ascospore sizes and in their stromatal pigments, which, unlike in the D. childiae group, are not due to the presence of dal dinal and dal dinins. The annellidic conidiogenesis of the ex-type culture clearly reveals its affinities to the D. petriniae group. However, its conidiophores are particularly robust, and its conidia are also larger than those of the presumably related taxa.


Etymology: For the eccentric American mycologist, C.G. Lloyd, who described the type specimen sub Hypoxylon fissum.

≡ Hypoxylon fissum Lloyd, Mycol. Writings 7: 1121. 1922; non Daldinia fissa Lloyd, 1924.

Holotypus: USA, New York, C.E. Fairman in ex Lloyd herb. no 11522 (BPI 715091).

Selected illustrations: Lloyd (1922) fig. 2141 (type, stromata); Ju et al. (1997), figs 13 (ascospores), 47, 48 (stromata); Wollweber & Stadler (2001), Abb. 11 (stromata).

Known distribution/host preference of stromata: Temperate regions of Europe and America; so far exclusively found on Betula.

Teleomorph: Stromata hemispherical to pulvinate, sessile or rarely subsessile, with inconspicuous perithecial outlines, 1–3 × 1–3 × 1–1.5 cm; surface dark brown to blackish, especially in young state densely covered with a Fulvous (43) coating, characteristically cracking into polygonal scales; with dull reddish brown granules immediately beneath surface and with KOH-extractable pigments Olivaceous (48) to Fawn (87); tissue between perithecia brown,
Fig. 64. Teleomorphic and anamorphic characteristics of Daldinia lloydii. A–C, P. Ww 3829 (Germany, immature). D, E, C.F. Specimen C-71601 (Denmark, immature). F. Ww 3893 (Germany, immature). G–I, MB 4018 (USA). J–O. PRM 875256 (Slovakia) A, D, G, J. Stromatal habit. (A stromatal pigments in 10 % KOH inserted). B, E, F, H, K, L. Stromata in longitudinal section showing internal concentric zones and perithecial layer (F: stromatal pigments in 10 % KOH inserted). C. Conidiogenous structure present on immature stroma, observed in SDS. I, M. Close-up on stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). N. Ascospores in SDS. O. Ascospores in KOH, showing dehiscing perispore. P. Ascospores by SEM (10,000×). Scale bars A, B D–H, J–L = 5 mm; I, M = 1 mm; C, N, O = 10 µm; P = 5 µm.
pithy to woody; tissue below peritrichal layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2–0.3 mm thick, lighter zones while to pale brown, mixed with pithy to woody and gelatinous materials, persistent, 0.1–0.5 mm thick (Ratio darker/lighter zones 1.2–3.1); frequently the horizontal zonation of the entostroma does not reach into the lower portions of struma, which are composed of fibrous, woody tissue and vertically, rather than horizontally zonate. *Peniophora* obviod to lanceolate, 1 × 0.3–0.4 mm. Ostioles umbilicate to inconspicuous. Asci 190–210 × 9.5–10.5 µm, p. sp. 90–100 µm, stipes 100–110 µm, with amyloid, discoid apical apparatus 0.5–0.75 × 4–5 µm. Ascospores dark brown, highly variable, ellipsoid-inquadrilateral, with narrowly to, less frequently, broadly rounded ends, occasionally pinched (11–)12–18 × 6–8–(9) µm, with straight to slightly undulate germ slit sori length on convex side; perispor dehiscent in 10 % KOH, smooth by LM, but showing conspicuous transverse striations by SEM (2.500–5.000×); epispore smooth.

**Stromatal secondary metabolites:** BNT (1) only present in traces; major stromatal constituents are presumably perylene quinones (e.g., 2), which account for the greenish stromatal pigments in KOH.

**Cultures and anamorph:** Only one specimen was so far cultured, but it did not differentiate much on OA and YM agar. The anamorph observed on young stromata showed a similar morphology to that of cultures of *D. petriniae*, albeit mainly unbranched sporothrix-like conidiophores up to 80 µm high with a single terminal conidiogenous cell (18–35 × 3.5–5.5 µm) were observed (Fig. 64C). *Conidia* are produced exclusively in an annelidic manner. They are slightly smaller than in *D. petriniae* (6–8 × 3–4 µm), which is actually in accordance with observations by Lloyd (1922) on the type specimen.


Notes: This species is commonly associated with Betula and has been infrequently collected in Northern and Central Europe and (predominantly north-eastern) USA. We report it here from England, Hungary, Slovenia, Slovakia, and Sweden for the first time. It can most easily be recognised by its characteristic, cracked stromatal surface, a feature that is also occasionally observed in *D. concentrica*. However, the stromata of the type species only crack into a fine network at maturity and never show conspicuous scales that can already be seen with the naked eye (aside from not usually being associated with Bulatulaeae). Along with its dense olivaceous pigments, which were only faint in the type specimen of *D. lloydii*, the surface characteristics are sometimes almost sufficient to identify even immature material, since the disruption of the surface occurs quite early in its development. Another feature that is characteristic of this species is the lack of concentric zones near the base of the stromata, which may have led Lloyd to originally assign it to Hypoxylon. The pigments of *D. lloydii* (and *D. petriniae* p.p., see below) are in fact perylene quinones, as previously demonstrated for Thamnomyces (Stadler et al. 2010a).

**Daldinia macrospera** F. San Martin, Y.M. Ju & J.D. Rogers, Mycotaxon 61: 274. 1997. Fig. 65.

**Etymology:** For the large ascospores.


Known distribution/host preference of stromata: Mexico and Ecuador.

**Teleomorph:** Stromata turbinate, short stipitate, wrinkled, with inconspicuous perithecial outlines, 3 × 3 × 2.7 cm; surface Grayish Sepia (106); with dull brown granules immediately beneath surface and without apparent KOH-extractable pigments; tissue between perithecia greyish brown, pithy to woody, tissue below peritrichal layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2–0.8 mm thick, lighter zones white, gelatinous when fresh, disintegrating and becoming loculate when dry; 1–3 mm thick (Ratio darker/lighter zones 1.1–5). *Periophora* lanceolate, 1.6–2 × 0.4–0.5 mm. Ostioles papillate. Asci fragmentary in material studied, p. sp. 100–120 × 12–14 µm, with amyloid, discoid apical
Spatula apparatus, 1 × 4 µm. Ascospores brown, ellipsoid-in-equi lateral with narrowly rounded ends, 22.5–30 × 8.5–10.5 µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, smooth both by LM and SEM (10.000×); epispore smooth.

**Stromatal secondary metabolites**: BNT (1) and other binaphthalene derivatives prevailing.

**Cultures and anamorph**: Unknown, except for some small fragmentary sporothrix-like conidiophores on the stromatal surface of the specimen from Ecuador, which were reminiscent of the conidiophores of *D. petriniae*.

Additional specimen examined: Ecuador, vicinity of Huigra, mostly on the Hacienda de Licay, Aug. 1918, N. & G. Rose 23729 as *D. concentrica* (FH 220988).

Notes: This species was described by Ju et al. (1997) from Mexico and here reported from Ecuador, based on an old specimen in FH. It is the only species in the genus that has ascospores up to 30 µm long. The stromata contains BNT and further naphthalenes as prevailing secondary metabolites, which agrees with the purple pigments in KOH reported by Ju et al. (1997) that we failed to observe. Furthermore, its ascospores were found smooth by SEM (Fig. 65I). Its stromatal anatomy is reminiscent of *D. govorovae*, from which it mainly differs by the much larger ascospores. This species is tentatively assigned to the *D. petriniae* group because the aforementioned similarity of the stromata of a species that was shown to produce conidia from percurrently proliferating conidiogenous cells, and from remnants of what are probably sporothrix-like conidiophores on the stromatal surface in the specimen in FH. It is the only species in this group that has smooth ascospores by SEM and might eventually be proven to have different affinities, once fresh material can be studied.

Etymology: For Mexico.


Selected illustrations: Ju et al. (1997, all from isotype), figs 16 (ascospores) and 53–55 (stromata).

Known distribution/host preference of stromata: Only known from *Quercus* in Mexico.

Teleomorph: Stromata turbinate or irregularly depressed-spherical, sessile or short stipitate, wrinkled, lacking perithecial outlines, 0.7–3.5 × 0.7–3 × 1–3 cm; surface Dark Brick (60), blackened and varnished in age; dull reddish brown granules immediately beneath surface, with KOH-extractable pigments weak Isabelline (65) or Honey (64); tissue between perithecia grayish brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.3–0.7 mm thick, lighter zones white, gelatinous, disintegrating and becoming loculate when dry, 0.7–1.5 mm thick (Ratio darker/lighter zones 1:2), whole interior eventually turning hollow. Perithecia lanceolate, 0.8–1.2 × 0.3–0.4 mm. Ostioles papillate Asci 195–250 × 8–10 µm broad, p. sp. 80–90 µm, stipes 110–160 µm, with amyloid, discoid apical ring, 1 × 3.5–4 µm. Ascospores brown to dark brown, ellipsoid-inquillateral with narrowly rounded ends, 12.5–15.5 × 6.5–7.5 µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH, appearing smooth by LM but showing inconspicuous transverse striations by SEM (5.000–10.000×); episipore smooth.

Cultures and anamorph: See Notes.
Notes: We agree with Ju et al. (1997) that *D. mexicana* is generally in agreement with *D. gelatinosa* with regard to its teleomorphic morphology, and its ascosporous also show inconspicuous transverse striations by SEM (see Fig. 66H). Nevertheless, this species turned out to be problematic with respect to its chemical traits. HPLC of the type material revealed that it lacks daldinal and daldinin type secondary metabolites as usually found in *Daldinia* spp. with yellowish stromatal pigments. The pigments in KOH were less intense than typically observed in the *D. chilidae* group. HPLC profiling revealed traces of perylene quinones, which may account for the pigment colours in KOH. A culture was also obtained from the perithecial contents when the isotype material was studied in 2000, i.e. three years after publication of the protologue. This culture was reminiscent of the *D. petriniae* group (Fig. 15K) and showed essentially the same features as the cultures of *D. gelatinosa* described above, with percurrently proliferating conidiophores up to 110 µm high, and conidiogenous cells 14–34 × 4–5 µm, conidia measuring 6–7 × 4–5.5 µm. These features would be in strong accordance with our suspicion that *D. mexicana* has affinities to *D. gelatinosa* and thus, the *D. petriniae* group. The molecular data (see Results on molecular phylogeny), as well as the morphological similarities to *D. gelatinosa*, would agree with the culture being genuine. However, although we have been able to obtain viable genuine cultures from some other *Daldinia* specimens even several years after collection, we think that fresh material of this fungus from Mexico should be made available for confirmation. Notably, even not even a collection date was given for the type collection, and the culture we obtained could as well be an artifact.

In contrast, a specimen from Eastern Russia described and cultured as *‘D. cf. mexicana’* by Ju et al. (1999) contained the compounds that are typically found in *D. chilidae* and the remainder of this species group. This specimen (Russia, Primorsky Territory, reserve ‘Kedrovaya Pad’, 19 Sep. 1997, O. Govorova, specimen in VLA, n.v., and WSP; culture Ww 3844, in pers. coll. STMA, deposited with MUCL) was later sent to us by J.D. Rogers, cultured by us in an independent experiment and studied. While we failed to observe an anamorph, the molecular data (see Results on molecular phylogeny) point toward it being closely related to the strain we obtained from the isotype specimen of *D. mexicana*. Interestingly, both cultures appeared related to the *D. petriniae* group.

Because of various similarities to *D. gelatinosa*, we assume that *D. cf. mexicana sensu* Ju et al. (1999) also constitutes a member of the *D. petriniae* group. However, the anamorph of the Russian specimen of *D. cf. mexicana* was revealed by Ju et al. (1999) to have a holoblastic, rather than annelidic conidiogenesis. We doubt that this Russian fungus is really identical with *D. mexicana*, but fresh, culturable material from Mexico must be made available before a final conclusion on this matter can be reached.

*Daldinia singularis* Y.M. Ju, Lar. N. Vassiljeva & J. D. Rogers, Mycotaxon 71: 405. 1999. Fig. 67.

Etymology: Unique (¿; not stated explicitly in the protologue).

Types: Russia: Primorsky Territory, near Vladivostok, twigs of *Carpinus cordata*, 26 Sep. 1997, L. Vasilieva (VLA – holotype n.v., WSP – isotype, culture not apparently deposited in a public collection, but GenBank Acc. Nos of DNA sequences were released as AY951700 and AY951812 by Hsieh et al. (2005)).

Selected illustrations: Ju et al. (1999), figs 1, 2 and 4 (stromata), 3 (culture) and 8, 9 (anamorph).

Known distribution/host preference of stromata: Far Eastern Russia, on *Carpinus*.

For a detailed description of the teleomorphic and anamorphic features of this fungus see Ju et al. (1999).

Notes: This fungus has so far only been found on *Carpinus* in Far Eastern Russia. It is characterised by its small stromata, highly reducedascal apicalapparati, and ellipsoid-equilateral to reniform ascospores. Moreover, it produces intercalary coil-like twists in culture and has an annelidic conidiogenesis (Ju et al. 1999). HPLC of the isotype revealed BNT and further binaphthyls major metabolites, in agreement with its purple pigments in KOH (Stadler et al. 2001a, b). SEM showed the ascospore perispore to be smooth at 12,000× (data not shown). Our observations on the holotype match very well the original description (thus it does not seem necessary to redo the full description) except regarding the reaction of perispores in 10 % KOH (Fig. 67F, G). While they were reported to be indehiscent by Ju et al. (1999), we observed the dehiscence of the perispore in a significant number of cases. As illustrated above, the perispores are very thin and fragile, they break off readily and therefore can be easily overlooked because of their migration towards the edges of the slide when the cover slip is laid down on the drop of KOH containing the ascospores.

Group F: Sugarcane-associated *Daldinia* spp. from Asia and further taxa with unclear affinities (Figs 68–72)

The species treated in this chapter are difficult to accommodate in either of the foregoing ones, because cultures, anamorphs, and molecular data are not yet available, and partly because their known characteristics point towards their having intermediate status between two or more of the groups defined earlier on. Aside from two apparently endemic species from South Asia and one new species collected in Ecuador, we have also accommodated two yet unnamed species that are so far only known from one or few herbarium collections and provide preliminary descriptions that illustrate the diversity within the genus and may facilitate re-collection of these interesting taxa. A complete compilation of chorological and biogeographic data of all accepted taxa of *Daldinia* is given in Table 12.

*Daldinia graminis* Dargan & K.S. Thind, Kavaka 12(2): 115. 1985 [1984]. Fig. 68.

Etymology: For the “graminaceous”, i.e. poaceous, host.


Selected illustrations: Dargan & Thind (1984, from holotype), Plate II, figs 8–15; Ju et al. (1997, from isotype), figs 85–86 (stromata and ascospores).

Known distribution/host preference of stromata: Only known from the type; from sugarcane in India.
**Telemorph:** Stromata turbinate, sessile or with narrow connective, with inconspicuous perithecial outlines, 0.5–0.7 × 5–7 × 0.25–0.35 cm; surface Violaceous Grey (116) to Sepia (63), dull reddish brown granules immediately beneath surface, without apparent KOH-extractable pigments; tissue between perithecia whitish or grey, pithy; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy, 0.1–0.2 mm thick, lighter zones cream, pithy to loculate, persistent, 0.2–0.5 mm thick (Ratio darker/lighter zones 1:2–5). *Perithecia* obovoid to lanceolate, 0.7–0.85 × 0.3–0.35 mm. Ostioles inconspicuous. *Asci* with spores arranged partially biseriately, 190–215 µm × 16–19 µm, p. sp. 95–110 µm, stipes 90–110 µm, with amyloid, discoid apical apparatus 1 × 4–4.5 µm. Ascospores brown, ellipsoid-inequilateral, with narrowly rounded, sometimes almost acute ends, 20–26(–30) × 7.5–9 µm, with straight germ slit much less than spore length on convex side; perispore indehiscent in 10 % KOH; appearing smooth by LM, not yet studied by SEM.

**Stromatal metabolites:** Large amounts of cytochalasins and traces of BNT.

**Notes:** See Ju et al. (1997) for telemorphic characters (the above description is largely in accordance with them) and Stadler et al. (2004d) for HPLC profiles. *Daldinia graminis* mainly differs from *D. sacchari* in ascospore morphology. The biology and anamorphic characters remain to be evaluated when further material becomes available.

*Daldinia sacchari* Dargan & K. S. Thind, Kavaka 12(2): 114. 1985 [1984]. Fig. 69.

**Etymology:** For the host *Saccharum* (sugarcane).

**Types:** India. Punjab (Union Territory), Haryana, Chandigarh, burnt stems of *Saccharum munja*. 20 Aug. 1966, H.S. Chahal 70 (PAN – holotype n.v., K(M) 36398 – isotype).

**Selected illustrations:** Dargan & Thind (1984, from holotype), Plate II, figs 1–7 (stromata and ascospores); Ju et al. (1997, from isotype), figs 62–64 (stromata) and 69 (ascospores).
**Table 12.** Biogeography, apparent host specificity, stromatal pigments in KOH and (where known) mode of conidiogenesis of all *Daldinia* spp. treated herein.

<table>
<thead>
<tr>
<th>Species/Variety (Daldinia)</th>
<th>Pigmens</th>
<th>Biogeography (preferred host plants)</th>
<th>Conidiogenesis*</th>
</tr>
</thead>
<tbody>
<tr>
<td>albofibrosa</td>
<td>Yellow-brown</td>
<td>Papua New Guinea</td>
<td>H</td>
</tr>
<tr>
<td>albozonata</td>
<td>Weak purple or none</td>
<td>Africa</td>
<td>U</td>
</tr>
<tr>
<td>andina</td>
<td>Dense purple</td>
<td>Ecuador</td>
<td>U</td>
</tr>
<tr>
<td>asphaltum</td>
<td>Purple</td>
<td>Tropical and subtropical America, P.R. China</td>
<td>A</td>
</tr>
<tr>
<td>australis</td>
<td>Yellow-brown</td>
<td>Southern Hemisphere (Australia, New Zealand); Hawaii (Metrosideros)</td>
<td>H</td>
</tr>
<tr>
<td>bakeri</td>
<td>Purple (faint yellow in type specimen due to artefacts)</td>
<td>Australia, New Zealand</td>
<td>U</td>
</tr>
<tr>
<td>bambusicola</td>
<td>Purple</td>
<td>Asia (original); USA (imported), (bamboo)</td>
<td>H</td>
</tr>
<tr>
<td>barkalovi</td>
<td>Weak purple</td>
<td>Russian Far East (Alnus)</td>
<td>A</td>
</tr>
<tr>
<td>brachysperma</td>
<td>Purple or none</td>
<td>America (Mexico)</td>
<td>U</td>
</tr>
<tr>
<td>calfariorum</td>
<td>Dense purple</td>
<td>Cosmopolitan, moderate and warmer climates (burnt Ulex)</td>
<td>H</td>
</tr>
<tr>
<td>childiae</td>
<td>Yellow-brown</td>
<td>Cosmopolitan (moderate and warmer climates)</td>
<td>H</td>
</tr>
<tr>
<td>clavata</td>
<td>Purple</td>
<td>Tropical Africa and America</td>
<td>U</td>
</tr>
<tr>
<td>concentrina</td>
<td>Weak purple</td>
<td>Europe (warmer temperate climates), (Fraxinus)</td>
<td>H</td>
</tr>
<tr>
<td>cuprea</td>
<td>grey or brown vinaceous</td>
<td>Tropical South America (and Africa?)</td>
<td>U</td>
</tr>
<tr>
<td>decipiens</td>
<td>Purple</td>
<td>Northern temperate Europe, (Betula and other Betulaceae)</td>
<td>A (p)</td>
</tr>
<tr>
<td>dennisii var. dennisii</td>
<td>Purple</td>
<td>Australia, New Zealand</td>
<td>H</td>
</tr>
<tr>
<td>dennisii var. microspora</td>
<td>Purple</td>
<td>Southern Hemisphere (not yet reported from South America)</td>
<td>H</td>
</tr>
<tr>
<td>eschscholtzii</td>
<td>Weak purple or none</td>
<td>Panropical, warmer climates outside Europe</td>
<td>H</td>
</tr>
<tr>
<td>gelatinoides</td>
<td>Dense purple</td>
<td>Asia (Russian Far East, Japan)</td>
<td>H</td>
</tr>
<tr>
<td>gelatinosa</td>
<td>Purple</td>
<td>Northern temperate zones (circumpolar), (Betulaceae)</td>
<td>A (p)</td>
</tr>
<tr>
<td>gorovorvae</td>
<td>Olivaceous</td>
<td>Russian Far East</td>
<td>E</td>
</tr>
<tr>
<td>graminis</td>
<td>Weak purple or none</td>
<td>Asia (India), (Saccharum)</td>
<td>U</td>
</tr>
<tr>
<td>grandis</td>
<td>Dense purple</td>
<td>America (warmer climates)</td>
<td>U</td>
</tr>
<tr>
<td>lloydii</td>
<td>Dense olivaceous</td>
<td>Northern temperate zones (circumpolar), (Betula)</td>
<td>A (p)</td>
</tr>
<tr>
<td>loculata</td>
<td>Dense purple</td>
<td>Northern temperate zones (circumpolar), (Betula and other Betulaceae)</td>
<td>H</td>
</tr>
<tr>
<td>loculatoides</td>
<td>Dense purple</td>
<td>Northern temperate zones (America, Europe)</td>
<td>H</td>
</tr>
<tr>
<td>macaronesica</td>
<td>Weak purple</td>
<td>Macaronesian Islands, (Lauraceae)</td>
<td>H</td>
</tr>
<tr>
<td>macrospora</td>
<td>Dense purple</td>
<td>America (Mexico)</td>
<td>U</td>
</tr>
<tr>
<td>mexicana</td>
<td>Yellow</td>
<td>America (Mexico), (Quercus)</td>
<td>U</td>
</tr>
<tr>
<td>novae-zelandiae</td>
<td>Purple</td>
<td>Australia, New Zealand (Nothofagus)</td>
<td>H</td>
</tr>
<tr>
<td>palmensis</td>
<td>Weak purple</td>
<td>Canary Islands, (Laurus)</td>
<td>H (p)</td>
</tr>
<tr>
<td>petriniae</td>
<td>Purple or olivaceous</td>
<td>Northern temperate zones (circumpolar), (Alnus and other Betulaceae)</td>
<td>A</td>
</tr>
<tr>
<td>pyrenaca</td>
<td>Yellow-brown</td>
<td>Europe (temperate zones), (Quercus)</td>
<td>H</td>
</tr>
<tr>
<td>raimundi</td>
<td>Weak purple</td>
<td>Europe (warmer temperate zones), (Quercus)</td>
<td>H</td>
</tr>
<tr>
<td>sacchari</td>
<td>Weak purple</td>
<td>Asia (India, Pakistan), (Saccharum)</td>
<td>U</td>
</tr>
<tr>
<td>singularis</td>
<td>Dense purple</td>
<td>Asia (Russian Far East)</td>
<td>H</td>
</tr>
<tr>
<td>steglichii</td>
<td>Yellow-brown</td>
<td>Tropical Asia, New Guinea</td>
<td>H</td>
</tr>
<tr>
<td>theisseni</td>
<td>Purple</td>
<td>Tropical America</td>
<td>H</td>
</tr>
<tr>
<td>vanderguchtiae</td>
<td>Weak purple</td>
<td>Europe (UK, Channel Islands)</td>
<td>H</td>
</tr>
<tr>
<td>vernicosa</td>
<td>Dense purple</td>
<td>Northern temperate zones (circumpolar)</td>
<td>H</td>
</tr>
</tbody>
</table>

*Conidiogenesis: H: holoblastic; A: Annellidic; U: Unknown; p: Predominantly. Host genera in brackets need to be confirmed by further collection work. In some cases only the predominant host is indicated.*

**Known distribution/host preference of stromata:** Only known from the Punjab (a territory located at the border between India and Pakistan); on sugarcane.

**Teleomorph:** Stromata turbinate, sessile or subsessile, with inconspicuous to conspicuous perithelial outlines, 0.8–1× 0.8–1 × 0.6–1 cm; surface areolate, Vinaceous Buff (86) to Grayish Sepia (106); dull reddish brown granules immediately beneath surface forming a very thin crust 20–25 µm thick, without apparent KOH-extractable pigments; tissue between perithecia white, pithy; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy, 0.1–0.3 mm thick, lighter zones
white to cream, pithy to fibrous, strongly loculate persistent, 1–2 mm thick (Ratio darker/lighter zones 1:4–10). Perithecia elongated-obovoid, 0.7–0.8 × 0.3–0.35 µm. Ostioles inconspicuous. Ascii 140–175 × 9.5–11 µm, p. sp. 90–110 µm, stipes 50–65 µm, with amyloid, discoid apical apparatus, 0.8–1 × 2.5–3.5 µm. Ascospores brown, ellipsoid-inequilateral, mostly with narrowly rounded ends, 14.5–18 × 6.5–8 µm, with straight germ slit spore length or nearly so on convex side; perispore indehiscent in 10 % KOH; appearing smooth by LM, appearing almost smooth with faint ridges by SEM (5,000×).

Stromatal metabolites: Large amounts of cytochalasins and traces of BNT.

Notes: See Ju et al. (1997) for teleomorphic characters (the description above largely agrees with them) and Stadler et al. (2004d) for HPLC profiles. This species is undoubtedly closely related to *D. graminis*. Both are apparently restricted to burnt sugarcane in South Asia, but are as now only known from a few collections, hence their ecology should be verified by further field work. It has not yet been studied for anamorphic characters, but its secondary metabolites appear to be similar to those of *D. eschscholtzii*. Some peculiar features of these species that deviate from most other members of the genus are the thin stromatal crust, resulting in a particular uneven stromatal surface as the perithecia become mature, and the relatively thick ascus apical apparatus.

Stadler et al. (2004d) reported a specimen from Pakistan, Punjab, Ladhar, Sheikhpura, on burnt culms of *Saccharum* sp., 14 Sep. 1980, S. Ahmad 27903 (K(M) 120963), with yet smaller ascospores 12–15 × 6–7.5 µm. This specimen resembled *D. eschscholtzii* even more closely than the type specimen of *D. sacchari*. 

Fig. 68. Teleomorphic characteristics of *Daldinia graminis*. Isotype, K(M) 36396 (India). A–C. Stromatal habit. D, E. Stroma in longitudinal section showing internal concentric zones and perithecial layer. F. Ascospores in SDS, showing germ slits. G. Ascospores in KOH, showing non-dehiscing perispore. H. Ascus top in Melzer’s reagent revealing amyloid apical apparatus. Scale bars A–E = 2 mm; F–H = 10 µm.
Daldinia sp. WSP54679. Fig. 70.

Known distribution: So far only known from two collections in USA.

Teleomorph: Stromata subglobose or irregularly turbinate to cylindro-clavate, subsessile to distinctly stipitate, stipes obconical and not clearly distinct from fertile part, with perithecial outlines exposed, 1.5–3.8 × 2.6–3.9 cm; surface black to shiny black, hard-textured, with dark reddish brown to blackish granules immediately beneath surface, with KOH-extractable pigments dilute Vivid Violet (79); tissue between perithecia brown, pithy; tissue below perithecial layer composed of alternating zones, extending into stipe, darker zones brown, pithy, 0.5–1 mm thick, lighter zones cream-coloured, fibrous and often loculate, 0.5–1.5 mm thick (Ratio darker/lighter zones 1:1–3). Perithecia lanceolate, 0.8–0.9 × 0.3–0.35 mm. Ostioles umbilicate, inconspicuous. Asci 230–270 × 9.5–11.5 µm, p. sp. 80–100 µm, stipes 140–180 µm long, with amyloid, discoid apical apparatus 0.8–1 × 3.5–4 µm. Ascospores dark brown, ellipsoid often almost equilateral with narrowly to broadly rounded ends, 13–16 × 6.8–7.5 µm, with straight germ slit spore length; perispore at times dehiscent in 10 % KOH, very thin and fragile, smooth by LM; epispore smooth by LM.

Cultures and anamorph: Unknown.

Stromatal secondary metabolites: BNT (1) and other binaphthalene derivatives prevailing.

Specimens examined: USA. Idaho, Valley Co., Head of Split Cr., on the ground, 18 Aug. 1964, Larry Kistler, det. Paul Miller as D. concentrica (WSP54679); Idaho, Valley Co., Snowslide Lake, on the ground, 18 Aug. 1964, Kenneth Harrison (WSP54729), see Ju et al. (1997) sub D. gelatinosa.
Notes: This *Daldinia* is represented by two collections from the same area, both in very good condition but too ancient to be cultured. One of them was actually cited as paratype of *D. gelatinosa* by Ju et al. (1997), but we found upon re-examination of the material from WSP that it strikingly differs from the holotype of that taxon in both its macroscopic characteristics of the stromata and its ascospore morphology. It rather resembles *D. bakeri* by having large black stromata with a warty surface, purple KOH-extractable pigments, pale loculate internal zones and almost equilateral ascospores with similar size range. However, it differs markedly from *D. bakeri* in having some ascospores with dehiscing perispore, a character not found in the taxa around *D. vernicosa*. Moreover, both collections were made in two different localities “on the ground”, which is a very unusual substrate for a *Daldinia*, although some remnants of woody material attached to the base of the stipes of some stromata suggest an occurrence on buried wood. The packet of WSP 54679 contains an annotation by Yu-Ming Ju (22 May 1995) reading “a new species of *Daldinia*, which supports our opinion on these collections, but also reflects the difficulties to erect a new taxon based on teleomorph morphology alone. This is why we consider this species as a dubious member of the *vernicosa-loculata* group, the status of which should be evaluated based on further cultural and molecular data.

*Daldinia ‘bakeri’* sensu Dennis (1963) p.p. Fig. 71.

Known distribution: So far only known from one collection in Central Africa.

Teleomorph: Stromata turbinate, subsessile, with perithecial outlines not exposed but deeply wrinkled due to drastic drying, with a deep median furrow, 4.2 × 3 cm; surface shiny black, with dull reddish brown granules immediately beneath surface with KOH-extractable pigments absent; tissue between perithecia dark brown, pithy; tissue below perithecial layer composed of alternating zones, extending into base, darker zones dark brown, pithy to woody, 0.2–0.5 mm thick, lighter zones golden brown, pithy, solid, 1–1.5 mm thick. Perithecia lanceolate, 1.2–1.4 × 0.25–0.35 mm. Ostioli umbilicate to slightly papillate, often at the centre of a low raised tunicle 0.12–0.2 mm diam. Ascii fragmentary, not measured, with amyloid, discoid apical apparatus 0.8 × 2 μm. Ascospores brown to dark brown, ellipsoid-inequilateral with most often narrowly rounded ends, 14.5–17 × 7–8.5 μm, with straight germ slit spore length; perispore dehiscent in 10 % KOH, smooth by LM; epispore smooth by LM.

Cultures and anamorph: Unknown.

Stromatal secondary metabolites: traces of BNT (1).

Specimen examined: D.R. Congo, Kalonge, ombrophile forest, on dead wood, 14 Feb. 1953, H. Frederiq in herb. G.F. de Witte 10357 (BR–Myc 103067,62; mixed with *Ruwenzeria pseudoannulata*).

Notes: As stated earlier (Stdler et al. 2010a), in the packet BR–Myc 103067,62 labelled *Daldinia bakeri*, a *Daldinia* sp. was encountered, mixed with three smaller stromata of another dalidnoid ascomycete that represents the new genus and species *Ruwenzeria pseudoannulata*. Thus, it is difficult to reassess which part of the specimen Dennis (1963) had in mind, when he determined it as *D. bakeri*. The *Daldinia* element, indeed, externally resembles *D. bakeri* by its blackish nodulose stromata, but when the stroma is cut open the interior appears very different from that of *D. bakeri* in being compact, in shades of pale brown and the zonation much less contrasted.

Microscopically, the inequilateral ascospores with dehiscent perispore are very different from those of *D. bakeri* and other members of the *vernicosa-loculata* group as defined herein. As the HPLC profile is rather inconclusive and as we lack cultural and molecular data the status of this taxon remains unsettled until fresh material becomes available.

*Daldinia placentiformis* (Berk. & M.A. Curtis) Theissen, Ann. Mycol. 7: 4. 1909. Fig. 72.


For synonyms, which, however, need to be revised according to the current concept, see Ju & Rogers (1996), sub *H. placentiforme* and Hladkí & Romero (2006).

Selected illustrations: Dennis (1963), as *Hypoxylon congoense*, fig. 17C (stromata); Ju & Rogers (1996), as *Hypoxylon placentiforme*, fig. 18B (anamorph).

Geographic distribution/host specificity: Circumtropical fide Ju & Rogers (1996), host plants not recorded.

Description based on the material illustrated below (which agrees with the holotype specimen):

Teleomorph: Stromata hemispherical, pulvinate or peletate, base broadly attached to substrate or constricted, often coalescent, with inconspicuous perithecial outlines, 0.6–2 × 0.4–0.5 cm; surface Vinaceous Grey (116) (immature) to Brown Vinaceous (84), pruinose, wrinkled to slightly nodulose, margin thin and undulate; dark orange brown granules forming a thin crust above perithecia, with Dull Green (70) KOH-extractable pigments; tissue between perithecia dark brown; tissue below perithecial layer 2.5–3.5 mm thick, brown with radially oriented black strands in upper part, somewhat lamellate in places, blackish brown and solid in lower part. Perithecia lanceolate 1.3–1.5 × 0.3–0.4 mm. Ostioli umbilicate to slightly raised discoid. Ascii fragmentary, not measured, with amyloid, discoid apical apparatus 0.5 × 3–3.5 μm. Ascospores dark brown ellipsoid-inequilateral with narrowly rounded ends, 14.5–16 × 6.5–7 μm, with straight germ slit spore length on most convex side; perispore dehiscent in 10 % KOH, smooth by LM and SEM; epispore smooth.

Cultures and anamorph: See Ju & Rogers (1996) as *H. placentiforme*. The cultures described there are derived from material collected in Mexico, which we have been unable to study and showed a nodulisporium-like anamorph. The dimensions of the conidiogenous structures closely resemble those of *D. eschscholtzii*. 

---

www.studiesinmycology.org

A POLYPHASIC TAXONOMY OF *Daldinia* (Xylariaceae)
Specimens examined: **Australia**, Tasmania, L. Rodway in Lloyd herb. 10720, det. J. H. Miller as *H. sclerophaeum*, mixed with *H. cf. crocopeplum* (BPI 716664); sine loc., ex herb. Berkeley S 54, as *H. sclerophaeum*, (K(M) 140189). **Brazil**, Rio Grande do Sul, Sao Leopoldo, 1907, J. Rick 335, (BPI 591442, PC 89194); same locality, Theissen 4396, det. C. G. Lloyd as *Hypodiscus rickii*, see Ju & Rogers (1996) as *H. placentiforme* (BPI 594123); Parecy, 1924, J. Rick 454 as *Hypodiscus rickii* (BPI 594123); exact locality unknown; J. Rick in Lloyd herb. 11494 as *H. corium* ined., rev. Ju & Rogers (1996) as *H. placentiforme* “BPI 11494” (BPI 716350). **Chile**, Temuco, Novena Región de la Araucanía, Sector Collimallín, on burnt stems and branches of *Ulex europeaus* (dead wood), 7 Sep.1996,

**Fig. 70.** Teleomorphic characteristics of *Daldinia* sp. WSP54679 (USA). A, B. Stromatal habit. C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). F. Ascospores in SDS, showing germ slit. G, I. J. Ascospores in KOH, showing non-dehiscing perispores (G) or rarely dehiscing perispores (I, J). H. Ascus top in Melzer’s reagent revealing amyloid apical apparatus. Scale bars A–C = 1 cm; D, E = 1 mm; F–J = 10 µm.

**Notes:** Daldinia placentiformis is derived from the neotropics, well-characterised by its pulvinate to peltate stromata with vinaceous surface, greenish pigments in KOH and ascospores with smooth dehiscent perispore and long germ slit. Collections from New Zealand feature more massive stromata with more purplish surface and are associated with Nothofagus, they might represent a distinct taxon (Ju & Rogers 1996). Hellwig et al. (2005) have reported that the green pigments of the holotype specimen are due to the presence of large amounts of daldinone A (2), which was also confirmed by studies of fresh specimens. However, as already demonstrated by Bitzer et al. (2008), the concept of this species presented by Ju & Rogers (1996) needs to be revised. In the study by Bitzer et al. (2008), material from Africa was cultured and sequenced and found to deviate in its morphological and chemical characters from the typical form that occurs in the neotropics. The sequence of this specimen is included here in the phylogenetic tree (see Results on molecular phylogeny). Both specimens showed the same HPLC profiles as the concurrently examined Daldinia spp. in culture. According to our preliminary results, this species will in all likelihood need to be segregated into various new taxa, but this affords the availability of additional, fresh material. As pointed out in the general taxonomic part and confirmed here by a phylogenetic study using a large number of specimens, there is no doubt that this species has close affinities to Daldinia; however, it remains to be seen whether this holds true for other taxa featuring massive stromata with long tubular perispories.

We have therefore only described the teleomorph of what we regard the typical form and listed some specimens that appeared in agreement with the type material even with respect to their HPLC profiles.

**Dichotomous key to Daldinia**

This key is based on that by Rogers et al. (1999) and subsequent additions. As far as possible, we have keyed out teleomorphic characters that can be easily recognised in freshly collected specimens. On the other hand, many of the currently accepted Daldinia spp. can hardly be identified without the aid of SEM and in the absence of cultures. This cannot be helped, since anamorphic characters have become important in the current taxonomic concepts of the Xylariales, while SEM is frequently a valuable diagnostic tool that allows for identification of material that cannot be cultured. We have tried to use the aforementioned features as late as possible in the key, or only added them as additional information. Hence, SEM...
Fig. 72. Stromatal and teleomorphic characteristics of Daldinia placentiformis. A. MP 4573 (Panama; not fully mature). B–E, G–I. AC 25 (Panama). F. Rick 335 (Brazil). A–C. Stromatal habit (A: in situ, B: top view, C: lateral view). D, F. Stromata in longitudinal section showing azonate interior and perithecial layer. E. Stromatal surface showing slightly raised-discoid ostioles, with stromatal pigments in 10 % KOH inserted. G. Ascospores in SDS, showing a germ slit. H. Ascospore in KOH, showing dehiscing perispore. I. Ascus top with amyloid apical apparatus (mounted in Melzer’s reagent). Scale bars A = 1 cm; B–D, F = 5 mm; E = 0.5 mm; G–H = 10 µm; I = 5 µm.
A polyphasic taxonomy of Dalldinia (Xylariaceae)

is used mainly to discriminate some species pairs, but if cultures are available, it mostly becomes expedient, and vice versa. Although HPLC data have occasionally proved to be more conclusive, the key works well with KOH-extractable stromatal pigments. Our results are based on a large number of fresh collections and therefore differ in several instances from those presented by Ju et al. (1997). In some cases, HPLC profiling has provided evidence that the apparent pigments of the old herbarium specimens are artificial (see D. bakeri, Stadler et al. 2004a), hence the diagnostic importance of these pigment colours is generally much higher for determination of fresh material, and even then it should not be old and overmature (Wollweber & Stadler 2001). For discrimination of closely related species, the Tables in the taxonomic part may be useful, since they can be used as synoptic keys.

1 Perispore not dehiscent in 10 % KOH ................................................................. I
2 Perispore dehiscent in 10 % KOH ............................................................... I
2 KOH-extractable pigments violaceous, purple or absent .................................................... II
2 KOH-extractable pigments differently coloured ........................................................ III
3 KOH-extractable pigments olivaceous, sepia or umber .................................................... III
3 KOH-extractable pigments cinnamon or orange brown .................................................. IV

I – Perispore not dehiscent in 10 % KOH

1 On sugarcane. Known from India ................................................................. 2
2 On woody, dicot. substrates ................................................................. 3
2 Ascospores 20–26 × 7.5–9 µm, with short germ slit .................................................. D. graminis (p. 120)
2 Ascospores 14.5–18 × 6.5–8 µm, with germ slit spore length ................................ D. sacchari (p. 122)
3 Interior distinctly loculate (gelatinous in fresh condition) ........................................... 4
3 Interior not or hardly loculate (not distinctly gelatinous when fresh) .................... 9
4 Ascospores 16–23 × 8–13 µm ........................................................................ D. novae-zelandiae (p. 100)
4 Ascospores not over 17 µm long ........................................................................ 5
5 Internal loculate zones black; ascospores 13.5–17 × 7–8.5 µm ................................. D. cf. bakeri Tanzania (p. 90)
5 Internal loculate zones whitish to cream-coloured or grey brown ......................... 6
6 Stromata occurring on wood of fire-damaged trees; ascospores 11.5–15 × 6.5–8(–9) µm D. vernicosa (p. 83)
6 Stromata not associated with fire-damaged trees .................................................... 7
7 Stromatal surface even, without visible perithecial outlines; ascospores 12–13 × 6–8 µm, interior becoming hollow D. gelatinoides (p. 92)
7 Stromatal surface nodulose with perithecial outlines slightly exposed; ascospores larger, interior not becoming hollow ....................... 8
8 Ascospores 13–16 × 7.5–9 µm, with perispore consistently indehiscent; on wood .................................................. D. bakeri (p. 88)
8 Ascospores 13–16 × 6.8–7 µm, with perispore infrequently dehiscent; reported as “on the ground”. Dalldinia sp. “Idaho” (USA) (p. 124)
9 Stromata occurring on wood of fire-damaged trees; known from Northern Hemisphere, temperate to boreal distribution ........................................ 10
9 Stromata not associated with fire-damaged trees; temperate to tropical distribution ........................................ 11
10 Ascospores 11–14(–15) × 6–8 µm .................................................................. D. loculata (p. 96)
10 Ascospores 15–19 × 7–9 µm ........................................................................ D. loculatoide (p. 99)
11 Perithecia obovoid, asci lacking apical apparatus. Ascospores 14.5–16 × 8–8.5 µm D. cf. bakeri Senegal (p. 89)
11 Perithecia elongate ellipsoid to lanceolate, asci with apical apparatus .................... 12
12 Ascospores 17–22 × 7–10 µm ........................................................................ D. grandis (p. 92)
12 Ascospores 13–17 µm long ............................................................................ 13
13 Stromatal interior black and very hard textured; ascospores 13–17 × 7.5–9 µm. Known from Australia D. cauchucosa (p. 90)
13 Stromatal interior grey brown, woody to fibrous; ascospores 13–16 × 7–8 µm. Known from La Réunion D. hausknecithii (p. 95)

In case the identity of the UAMH specimens with D. nemorosa were proven, this species would also key out here, but differs from D. loculatoide in its annelidic conidiogenesis.
II - KOH-extractable pigments violaceous, purple or absent

1. Stromata very small, rarely over 1 cm in greatest dimension ........................................... 2
2. Stromata larger ...................................................................................................................... 5
3. Perithecia lanceolate; ascospores 9.5–11.5 × 4.5–6 µm. Known from Tanzania .................. Daldinia sp. K(M) 131689 (p. 113)
4. Perithecia obvoid ................................................................................................................ 3

5. Ascospores 6.5–7.5 × 3–4 µm; interior predominantly white. Known from Mexico .................. D. brachysperma (p. 60)
6. Ascospores larger, interior brownish ..................................................................................... 4

7. Ascospores 8–11 × 4–5.5 µm, with germ slit on the less convex side. Widespread in the tropics extending to warm temperate climates, often on Ulex ........................................................................................................ D. caldariorum (p. 60)
8. Ascospores 9–11 × 4–5.5 µm, with germ slit on the more convex side. Known from Far Eastern Russia on Carpinus ................. D. singularis (p. 120)

9. Stromata upright, distinctly stipitate ..................................................................................... 6
10. Stromata turbinate to hemispherical ..................................................................................... 9

11. Stromatal interior brownish; ascospores 12.5–16.5 × 6–8 µm. Known from Brazil ................ D. asphalatum (p. 106)
12. Stromatal interior predominantly white; ascospores less than 12 µm long ......................... 7

13. Ascospores 7–9 × 3–4 µm. Known from tropical Africa ....................................................... D. albozonata (p. 58)
14. Ascospores larger ................................................................................................................ 8

15. Ascospores 8–11.5 × 4–5.5 µm; ostioles inconspicuous ......................................................... D. clavata (p. 65)
16. Ascospores 10–11.5 × 4.5–5.5 µm; ostioles discoid-papillate ................................................ D. cuprea (p. 67)
17. KOH-extractable pigments absent or appearing with delay (several minutes) ...................... 10
18. KOH-extractable pigments present, at least in mature stromata ........................................ 12

19. KOH-extractable pigments appearing with delay (several minutes). Ascospores 11–13(−14.5) × 5–6.5 µm. Widespread and common in the tropics ................................................................. D. eschscholtzii (p. 47)
20. KOH-extractable pigments absent ....................................................................................... 11

21. Species known from Northern Hemisphere, with temperate to warm temperate distribution ................................................................................................................................. 13
22. Species with tropical distribution ........................................................................................ 23

23. Species occurring on Betulaceae ......................................................................................... 14
24. Species occurring on other hosts ........................................................................................ 18

25. KOH-extractable pigments vinaceous grey to pale violet .................................................... 15
26. KOH-extractable pigments dense violet ............................................................................. 16

27. Stromatal surface wrinkled with ochre wavy stripes; ascospores 12–14 × 6–7 µm. Known from Far Eastern Russia ......................... D. barkalovii (p. 110)
28. Stromatal surface slightly nodulose, lacking stripes; ascospores 12.5–16.5 × 6.5–7.5 µm. Known from northern temperate-boreal zones ................................................................. D. petriniae (p. 102)
29. Stromata almost sessile. Ascospores 12.5–16 × 6–8 µm ......................................................... D. gelatinosa (p. 113)
30. Stromata usually distinctly stipitate. Ascospores averaging longer ..................................... 17

31. Ascospores 14–16.5 × 7–8 µm. Known from Far Eastern Russia ........................................ D. carpinicola (p. 111)
32. Ascospores 14–18(−19) × 6.5–10 µm. Known from temperate Northern Hemisphere .......... D. decipiens (p. 111)

33. Ascospores 13–17.5 µm long ................................................................................................. 19
34. Ascospores 10–14 µm long .................................................................................................. 21

35. Widespread in Europe; ascospores 13–17.5 × 6–7.5 µm ....................................................... D. concentrica (p. 28)
36. Known from southern Europe, North Africa and the Macaronesian Islands ......................... 20
A POLYPHASIC TAXONOMY OF Daldinia (Xylariaceae)

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>20</td>
<td>Known from the Macaronesian Islands; ascospores 14–17 × 6–8 µm</td>
<td>D. macaronesica (p. 38)</td>
</tr>
<tr>
<td>20</td>
<td>Known from southern Europe and North Africa; ascospores 13–17 × 5–7 µm</td>
<td>D. martini (p. 38)</td>
</tr>
<tr>
<td>21</td>
<td>Known from Canary Islands, on Laurus. Ascospores 11–13 × 5.5–6.5 µm</td>
<td>D. palmensis (p. 40)</td>
</tr>
<tr>
<td>21</td>
<td>Not known from Laurus nor the Canary Islands</td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>Known from UK, on Acer. Ascospores 10–14 × 5–7 µm</td>
<td>D. vanderghuchtiae (p. 42)</td>
</tr>
<tr>
<td>22</td>
<td>Known from Mediterranean and Western Europe, on Quercus ilex. Ascospores 12–14 × 6–7 µm</td>
<td>D. raimundi (p. 40)</td>
</tr>
<tr>
<td>23</td>
<td>On bamboo; ascospores 8.5–11 × 4–5 µm. Known from Thailand</td>
<td>D. bambusicola (p. 60)</td>
</tr>
<tr>
<td>23</td>
<td>On dicot. wood; ascospores larger</td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>Stromata hemispherical to depressed-spherical, sessile</td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>Stromata turbinate, more or less stipitate</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>Ascospores 12.5–15.5 × 6–6.8 µm with short germ slit. Known from D.R. Congo</td>
<td>Daldinia sp. (MUCL51268) (p. 43)</td>
</tr>
<tr>
<td>25</td>
<td>Ascospores with germ slit spore length</td>
<td></td>
</tr>
<tr>
<td>26</td>
<td>Ostioles papillate. Ascospores 12–14.5 × 6–6.5 µm. Known from Mexico</td>
<td>Daldinia sp. Martin 910 (NY) (p. 55)</td>
</tr>
<tr>
<td>26</td>
<td>Ostioles inconspicuous to slightly papillate. Known from Australia and New Zealand</td>
<td></td>
</tr>
<tr>
<td>27</td>
<td>Ascospores 16–18 × 6–8 µm</td>
<td>D. dennisii (P. 35)</td>
</tr>
<tr>
<td>27</td>
<td>Ascospores 12–15 × 6–8 µm</td>
<td>D. dennisii var. microspora (p. 35)</td>
</tr>
<tr>
<td>28</td>
<td>Ascospores 9–12 µm long</td>
<td></td>
</tr>
<tr>
<td>28</td>
<td>Ascospores 16–21.5 µm long</td>
<td></td>
</tr>
<tr>
<td>29</td>
<td>Ascospores 9.5–10.5 × 4.5–5.5 µm</td>
<td>D. rehmi (p. 68)</td>
</tr>
<tr>
<td>29</td>
<td>Ascospores 9–12 × 5–6 µm, relatively more slender</td>
<td>D. theissenii (p. 72)</td>
</tr>
<tr>
<td>30</td>
<td>Ascospores 16–18 × 7–8 µm. Known from Malawi</td>
<td>Daldinia sp. Rammeloo (p. 45)</td>
</tr>
<tr>
<td>30</td>
<td>Ascospores 17.5–21.5 × 7–10 µm. Known from Ecuador</td>
<td>D. andina (p. 33)</td>
</tr>
</tbody>
</table>

* The identification of the following six species (couplets 19–22) can hardly be based on teleomorphic morphological characters; additional discriminant characters are available in Tables 3 and 4.

**III - KOH-extractable pigments olivaceous, sepia or umber**

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>KOH-extractable pigments umber or sepia (in shades of brown)</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>KOH-extractable pigments olivaceous to greenish</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Interior gelatinous-loculate; ascospores 16–18 × 8–10 µm. Known from Far Eastern Russia</td>
<td>D. govorovae (p. 114)</td>
</tr>
<tr>
<td>2</td>
<td>Interior fibrous-loculate; ascospores 14–15.5 × 7–8 µm. Known from tropical and subtropical regions of South and East Asia</td>
<td>D. steglichii (p. 82)</td>
</tr>
<tr>
<td>3</td>
<td>Stromata erect, distinctly stipitate; ascospores 12.5–16.5 × 6–8 µm. Known from tropical and subtropical North and South America, P.R. China</td>
<td>D. asphalatum (p. 106)</td>
</tr>
<tr>
<td>3</td>
<td>Stromata turbinate to hemispherical</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Ascospores 9–12 µm long</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Ascospores 12–23 µm long</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Stromatal interior predominantly white. Ascospores 9–10.5 × 4–4.5 µm. Known from New Guinea and South East Asia</td>
<td>D. albofibrosa (p. 57)</td>
</tr>
<tr>
<td>5</td>
<td>Stromatal interior predominantly brown. Known from neotropics</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Ostioles inconspicuous. Ascospores 10–12 × 5–6 µm</td>
<td>D. starbaeckii (p. 69)</td>
</tr>
<tr>
<td>6</td>
<td>Ostioles discoid-papillate. Ascospores 9.5–11 × 5–6 µm</td>
<td>D. cf. starbaeckii (p. 71)</td>
</tr>
<tr>
<td>7</td>
<td>Stromatal interior gelatinous, hollow. Ascospores 12.5–15.5 × 6.5–7.5 µm. Known from Mexico</td>
<td>D. mexicana (p. 118)</td>
</tr>
<tr>
<td>7</td>
<td>Stromatal interior woody-fibrous, solid. Known from North temperate Hemisphere</td>
<td></td>
</tr>
</tbody>
</table>
Molecular phylogeny (Figs 73, 74, for corresponding specimen data see Table 13)

The species groups outlined in this monograph were mostly recognised as reasonably well supported groupings by the ITS rRNA gene phylogeny (i.e. likelihood bootstrap support >70%). However, the backbone of the tree, i.e. the relationships among the species complexes were consistently weakly supported (94–4%). These relationships are recognisable from the topology of the most likely tree, but not discussed further here.

The general topology of the phylogenetic tree, however, was found in agreement with the hypothesis on evolution of hypoxylloid Xylariaceae by Ju & Rogers (1996). For instance, H. monticulorum and H. submonticulorum appeared basal in this clade. However, as in previous phylogenies based on ITS rDNA sequences (Suwanassai et al. 2005, Bitzer et al. 2008, Tang et al. 2009), the genera Annulohypoxylon and Hypoxylon were not fully resolved. In accordance with morphological and chemical data, H. laschii and H. gibraicenae (cf. Stadler et al. 2004, Fournier et al. 2010b) were shown to have affinities to the H. rubiginosum complex. Also in agreement with the afore mentioned previous phylogenetic studies, all sequences of Daldinia clustered as sister group to a clade comprising Annulohypoxylon and Hypoxylon spp. While Pyrenomyxa morganii and Thuenemella cubispora, two taxa that differ from Hypoxylon by their aberrant ascal and ascospore morphology, were found nested in Hypoxylon, the Daldinia clade included sequences from taxa of Entonaea, Phylacia, Rhopalostroma, Ruwenzonia, and Thamnomyces. Accordingly, neither Hypoxylon nor Daldinia appear monophyletic in their current circumscriptions. However, based on the currently available still patchy data background, we consider it premature to draw taxonomic consequences.

Sequences of the D. eschscholtzii group appear in clade B, which is a sister group to a clade (B1) comprising members of other daldinoid genera (i.e. Phylacia, Rhopalostroma and Thamnomyces). Ruwenzonia pseudanoannulata, Entonaea liquescens and Daldinia placentiformis cluster outside the major groups of Daldinia, but become nested within the D. eschscholtzii clade, if the taxon selection is restricted to the daldinoid taxa, allowing for more informative reliably alignable characters to be included in the phylogenetic analyses (data not shown). According to this analysis, D. albiflora and D. clavata also cluster within the D. eschscholtzii clade. Interestingly, strain CBS 222.61, presumably originating from the work by Martin (1969) as D. eschscholtzii, is nested in a clade comprising Hypoxylon spp. and closely related to H. fragiforme. It certainly does not represent D. eschscholtzii or another Daldinia sp., since its HPLC profiles in culture (mellein derivatives being the major metabolites and naphthols and chromones being absent) were also atypical of Daldinia. The taxonomy of this strain should therefore be changed to Hypoxylon.

Clade A predominantly comprised sequences of D. concentrica and allies. The sequences of both specimens of D. steiglichii studied cluster within clade A despite the highly similar morphology and secondary metabolite profiles of D. steiglichii to the D. childiae group. The tropical D. andina and the yet unnamed species from D. R. Congo (D. cf. concentrica MUCL 51268) appear closely related to the remainder of the species of the D. concentrica group. Those, however, could not be resolved based on ITS sequence data. Interestingly, D. cf. grandis from New Zealand (IMCP 18266) also clustered here, suggesting that it has affinities to the D. concentrica group as well, although its morphology actually recalls that of D. loculata, D. loculatoideae and the type material of D. grandis.

Group D, comprising sequences of members of the D. vernicosus/D. loculata group, appears as a sister group to D. concentrica and allies. This clade is separated into three major lineages, comprising (D1) D. vernicosus/D. gelatinoides, (D2) D. novae-zelandiae and (D3) D. hausknechti/D. loculata/D. loculatoideae, respectively. Anellerosporium nemorosum is included in the clade C3, confirming results by Davey (2010) on its phylogenetic affinities to D. loculata. The only remarkable morphological difference of A. nemorosum to the remainder of the D. vernicosus/loculata group is the presence of annellidic conidiogenesis. The anamorphic morphology of A. nemorosum (D. nemorosum comb. nov.) is similar to that of members of the D. petriniae group, but such an annellidic conidiogenesis also occurs in D. palvensis (which is clearly a member of the D. concentrica group). This feature could therefore easily have arisen convergently several times during evolution of these predominantly endophytic ascomycetes by reduction of the conidiophores.

The sequence data of D. mexicana and D. cf. mexicana appear basal to two groups C (comprising the remainder of the D. childiae group) and E (comprising exclusively members of the D. petriniae group). Both of these clades do not appear to be fully resolved with respect to the morphological species concepts but are clearly recognisable as coherent groups in the genus.

In summary, the ITS rRNA region appears to be informative for Daldinia mostly at the level of species complexes, even though
The major clades found in the phylogenetic study are largely in agreement with the concept based on a combination of various phenotype-based characters. Only in a few cases, the generated sequences were apparently specific to a given species, and the more representatives were available for a given taxon, the higher the infraspecific variability observed. As mentioned in some instances in the taxonomic part, care should be taken by interpretation of such DNA sequences for endophytes and environmental samples with respect to species assignments. Even though the phylogenetic study did not consider certain aberrant parts of the ITS rRNA gene region, which may prove more informative for species recognition, a general “molecular identification” of Dalldinia species seems to be rather difficult. However, as the most commonly sequenced region, ITS sequence data represent a valuable link between taxonomic and environmental studies. This may eventually lead to insights into the life cycles of fungi with inconspicuous growth on substrates or hosts different to those of stromata formation (cf. Bills et al. 2012).

OUTLOOK AND DISCUSSION

This monograph summarises the results of over a decade of intensive work on the genus Dalldinia. Due to the fact that it was paralleled by studies on related genera like Hypoxylon, Phylacia, Rhopalostroma, and Thamnomyces, the results are now more conclusive because they can be viewed in a broader context.

As shown in Table 14, several of the species defined by Ju et al. (1997) were recognised as complexes and resolved.

Our recent studies (Stadler et al. 2004a, 2005, Bitzer et al. 2008) in agreement with molecular data (Triebel et al. 2005, Hsieh et al. 2005) revealed that the concept of Dalldinia, hitherto based on features relating to stromatal anatomy is no longer tenable. Therefore, the generic description was modified from that of Ju et al. (1997), to accommodate azonate Dalldinia spp. (e.g., D. placentiformis, D. gelatinoides and Versiomyces cahucuchosus) and allow to accommodate further members of the genus that might in future be revealed to belong to this phylogenetic lineage. The new generic concept including D. placentiformis, previously recognised in Hypoxylon is strongly supported by micromorphological, chemotaxonomic and molecular data (cf. Hsieh et al. 2005, Bitzer et al. 2008). The non-azonate Dalldinia species included in this monograph have essentially the same specific metabolites in their stromata and cultures, their spores are indistinguishable from those of true Dalldinia spp., and their DNA sequences, where available, appear nested inside monophyletic clades comprising Dalldinia (cf. phylogenetic tree in Fig. 73).

A problem for some taxonomists may arise from the fact that in molecular phylogenies Hypoxylon appears paraphyletic when Dalldinia is included. Preliminary results on Entontaema (Triebel et al. 2005), Phylacia (Bitzer et al. 2008), Rhopalostroma (Stadler et al. 2010a) and Thamnomyces (Stadler et al. 2010b) revealed that even Dalldinia appears paraphyletic with respect to these smaller genera. However, we agree with Uwe Braun (2012), who gave a clear outline of certain challenges and problems of modern fungal taxonomy under the rules of the new nomenclature. Among other issues, this author emphasised that the experts who are in charge of monographic work should best determine for themselves how to deal with difficult and widely unknown taxa.

A puristic approach favouring the principle of monophyly might actually result in drastic nomenclatural changes in the Xylariaceae, leaving only a few genera, aside from the largest ones (Xylaria and Hypoxylon), which are themselves in desperate need of revision, using polythetic concepts. An alternative could be excessive splitting of Hypoxylon into smaller taxonomic entities, since neither the study by Hsieh et al. (2005) on α-actin and β-tubulin sequences nor the available data on rDNA (Kuhnert et al. 2014) suggest that this genus exclusive of Dalldinia and related tropical taxa is homogeneous. It cannot even be excluded that Hypoxylon may eventually be restricted to a group of species comprising H. fragiforme and its immediate allies, in which case probably several new genera would need to be erected. However, in this genus, a large percentage of the currently accepted species remain to be found in fresh state and analysed by modern methodology. Moreover, Hypoxylon placentiforme sensu Ju & Rogers (1996) is certainly not the only species described in this monograph that will in future be revealed to constitute a heterogeneous species complex. The affinities of Annullohypoxylon to Hypoxylon and the reason for the discrepancies between molecular phylogenies based on rDNA vs. housekeeping genes should also be further clarified.

We feel that all measures that may result in drastic nomenclatural changes (i.e., changes at the generic rank or below) should only be undertaken as significant amounts of additional data on the core groups of this hyper-diverse fungal family have become available and at least the type species of all genera and the most important species have been properly typified and their cultures and conidial stages studied for comparison. This may not be an easy task, since it took us almost a decade to locate and study suitable material in Dalldinia. Still, one third of the taxa accepted here are only known from their teleomorphic characters, whereas anamorphic and molecular data are still amiss. It might be feasible to solve the problem by applying taxonomic changes at the suprageneric rank.

The chorological and molecular data also allow us to attain a better picture on the diversity and biogeography of Dalldinia. It is, for instance, rather interesting that members of the D. concentrica group have a rather bipolar distribution in the temperate climate zones of both Hemispheres, but are apparently absent in Northern Asia and America, and that so far no member of the D. petriniae group was found outside the temperate Northern Hemisphere. The data available also point toward a rather high diversity of Dalldinia (and in particular, the D. petriniae group) in Far Eastern Russia, but notably the endemic species described by Vasilyeva (1998), Ju et al. (1999) and Vasilyeva & Stadler (2008) are only known from one or a few collections and appear to some extent related to other, more widely distributed species. In any case, the statement by Ju et al. (1997) that Dalldinia has its greatest diversity in Mexico might have been due to biased sampling, and additional species can probably still be found from many other regions of the world. However, at this time we feel we have run out of options to contribute data based on herbarium specimens; fresh material will be desperately needed to resolve the open questions. In fact, the conspicuous stromata of Dalldinia are certainly not as hard to find as those of many other pyrenomycetes. Hence, we hope that this monograph can raise interest among the field mycologists, so they can retrieve fresh material of all the insufficiently known taxa included in the present study, so the picture of global biodiversity in Dalldinia will soon get more complete.

Another avenue for future research on xylariaceous endophytes was recently outlined in the study by Bills et al. (2012), where the teleomorph of the producer organism of the nodulisporic acids, which are potent natural insecticides that made it into pharmaceutical development, was identified based on a combination of field work, classical morphology, HPLC profiling studies and multi-gene genealogies. This study describes how a
The clade including 81 sequences from the genus Daldinia was supported by a bootstrap value of 90% (Fig. 74). D. eschscholtzii, the type species, and D. starbaeckii, whose type material was provided by D. starbaeckii, were used as outgroups. Bootstrap values for the clades supported by more than 70% are indicated in Fig. 74. The clade containing D. eschscholtzii and D. starbaeckii is shown separately (Fig. 74).
Fig. 74. Phylogenetic relationships among *D. concentrica*, *D. childiae*, *D. vernicosa/loculata*, *D. petriniae* and their respective allies. Section from Fig. 73.
<table>
<thead>
<tr>
<th>Species</th>
<th>Acc. No. (GenBank)</th>
<th>Specimen/ Strain No.</th>
<th>References</th>
<th>Host/Country</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annulohypoxylon cohaerens</td>
<td>AY616687</td>
<td>M-0066231 (CBS 114744)</td>
<td>Triebel et al. (2005)</td>
<td>Fagus, Germany</td>
</tr>
<tr>
<td>Annulohypoxylon minutellum</td>
<td>JX658447</td>
<td>CBS 119015</td>
<td>Bitzer et al. (2008), Stadler et al. (2013)</td>
<td>Castanea, Portugal</td>
</tr>
<tr>
<td>Annulohypoxylon multifforme</td>
<td>AY616706</td>
<td>M-0067221</td>
<td>Triebel et al. (2005)</td>
<td>Betula, Germany</td>
</tr>
<tr>
<td>Annulohypoxylon stigyum</td>
<td>JX658526</td>
<td>CBS 119027</td>
<td>Bitzer et al. (2008)</td>
<td>Malaysia</td>
</tr>
<tr>
<td>Biscogniauxia nummularia</td>
<td>JX658444</td>
<td>MUCL 51395</td>
<td>Bitzer et al. (2008)</td>
<td>Fagus, France</td>
</tr>
<tr>
<td>Calceomyces lactuosus</td>
<td>JX658530</td>
<td>CBS 633.88</td>
<td>Present study</td>
<td>Japan (T)</td>
</tr>
<tr>
<td>Daldinia albofibrosa</td>
<td>JX658518</td>
<td>CBS 117737</td>
<td>Present study</td>
<td>Malaysia</td>
</tr>
<tr>
<td>Daldinia barkalovii</td>
<td>JX658537</td>
<td>CBS 116999</td>
<td>Vasilyeva &amp; Stadler (2008)</td>
<td>Russia (T)</td>
</tr>
<tr>
<td>Daldinia andina</td>
<td>AM749918</td>
<td>CBS 114736</td>
<td>Bitzer et al. (2008) as D. grandis</td>
<td>Ecuador</td>
</tr>
<tr>
<td>Daldinia australis</td>
<td>JX658544</td>
<td>MUCL 47964</td>
<td>Present study</td>
<td>P.R. China</td>
</tr>
<tr>
<td>Daldinia eschscholtzii</td>
<td>JX658548</td>
<td>MUCL 47966</td>
<td>Present study</td>
<td>P.R. China</td>
</tr>
<tr>
<td>Daldinia bambusicola</td>
<td>JX658436</td>
<td>CBS 122872</td>
<td>Ju et al. (1997)</td>
<td>Thailand (T)</td>
</tr>
<tr>
<td>Daldinia barkalovii</td>
<td>JX658537</td>
<td>CBS 116999</td>
<td>Vasilyeva &amp; Stadler (2008)</td>
<td>Russia (T)</td>
</tr>
<tr>
<td>Daldinia carpincola</td>
<td>JX658442</td>
<td>CBS 122880</td>
<td>Vasilyeva &amp; Stadler (2008), Ju et al. (1999)</td>
<td>Carpinus, Russia (T)</td>
</tr>
<tr>
<td>Daldinia cf. australis</td>
<td>JX658547</td>
<td>MUCL 53761</td>
<td>Present study</td>
<td>Australia</td>
</tr>
<tr>
<td>Daldinia cf. concentrica</td>
<td>JX658473</td>
<td>MUCL 45434</td>
<td>Present study</td>
<td>Ethiopia</td>
</tr>
<tr>
<td>Daldinia cf. dennisi var. microspora</td>
<td>JX658539</td>
<td>ICMP 18265</td>
<td>Present study</td>
<td>New Zealand</td>
</tr>
<tr>
<td>Daldinia cf. eschscholtzii</td>
<td>JX658456</td>
<td>KC 1690</td>
<td>Bitzer et al. (2008)</td>
<td>Venezuela</td>
</tr>
<tr>
<td>Daldinia cf. grandis</td>
<td>JX658543</td>
<td>ICMP 18266</td>
<td>Present study</td>
<td>Weinmannia, New Zealand</td>
</tr>
<tr>
<td>Daldinia cf. mexicana</td>
<td>JX658460</td>
<td>Ww 3844/MUCL</td>
<td>Ju et al. (1999)</td>
<td>Far Eastern Russia</td>
</tr>
<tr>
<td>Daldinia cf. pyrenaica</td>
<td>JX658515</td>
<td>MUCL 47221</td>
<td>Present study</td>
<td>Populus, Ukraine</td>
</tr>
<tr>
<td>Daldinia cf. caldariorum</td>
<td>JX658453</td>
<td>CBS 113045</td>
<td>Present study</td>
<td>Ecuador</td>
</tr>
<tr>
<td>Daldinia clavata</td>
<td>JX658546</td>
<td>MUCL 47436</td>
<td>Present study</td>
<td>Gabon</td>
</tr>
<tr>
<td>Daldinia cinnamomea</td>
<td>AY616683</td>
<td>CBS 113277</td>
<td>Triebel et al. (2005)</td>
<td>Fraxinus, Germany</td>
</tr>
<tr>
<td>Daldinia cinnamomea</td>
<td>AY616682</td>
<td>CBS 113278</td>
<td>Triebel et al. (2005)</td>
<td>Fraxinus, UK</td>
</tr>
<tr>
<td>Daldinia carpinicola</td>
<td>JX658457</td>
<td>CBS 117124</td>
<td>Present study</td>
<td>Platanus, Greece, Crete</td>
</tr>
<tr>
<td>Daldinia childiae</td>
<td>JX658533</td>
<td>KC 1693</td>
<td>Present study</td>
<td>Quercus, UK</td>
</tr>
<tr>
<td>Daldinia eschscholtzii</td>
<td>JX658469</td>
<td>KC1697</td>
<td>Present study</td>
<td>Fraxinus, US</td>
</tr>
<tr>
<td>Daldinia eschscholtzii</td>
<td>JX658472</td>
<td>KC1697</td>
<td>Present study</td>
<td>Fagus, UK</td>
</tr>
<tr>
<td>Daldinia eschscholtzii</td>
<td>JX658454</td>
<td>MUCL 46679</td>
<td>Present study</td>
<td>Acacia, Italy</td>
</tr>
<tr>
<td>Daldinia eschscholtzii</td>
<td>JX658445</td>
<td>MUCL 51681</td>
<td>Present study</td>
<td>Fraxinus, France</td>
</tr>
<tr>
<td>Daldinia eschscholtzii</td>
<td>JX658471</td>
<td>MUCL 54179</td>
<td>Bitzer et al. (2008)</td>
<td>Fagus, Germany</td>
</tr>
<tr>
<td>Daldinia eschscholtzii</td>
<td>JX658474</td>
<td>MUCL 52885</td>
<td>Present study</td>
<td>Greece, Rhodes</td>
</tr>
<tr>
<td>Species</td>
<td>Acc. No. (GenBank)</td>
<td>Specimen/ Strain No.</td>
<td>References</td>
<td>Host/Country</td>
</tr>
<tr>
<td>---------</td>
<td>-------------------</td>
<td>----------------------</td>
<td>------------</td>
<td>--------------</td>
</tr>
<tr>
<td>Daldinia decipiens</td>
<td>JX658455</td>
<td>CBS 116997</td>
<td>Present study</td>
<td>Alnus, Russia</td>
</tr>
<tr>
<td></td>
<td>JX658441</td>
<td>CBS 122879</td>
<td>Ju et al. (1999), stadler et al. (2001d)</td>
<td>Betula, Sweden (PT)</td>
</tr>
<tr>
<td></td>
<td>JX658476</td>
<td>MUCL 44610, CBS 113046</td>
<td>stadler et al. (2004d), bitzer et al. (2008)</td>
<td>Carpinus, Denmark</td>
</tr>
<tr>
<td></td>
<td>JX658524</td>
<td>MUCL 52699</td>
<td>Present study</td>
<td>Betula, Germany</td>
</tr>
<tr>
<td>Daldinia dennisii</td>
<td>JX658477</td>
<td>CBS 114741</td>
<td>stadler et al. (2004c), bitzer et al. (2008)</td>
<td>Phitosporum, Australia (T)</td>
</tr>
<tr>
<td></td>
<td>JX658479</td>
<td>CBS 114742</td>
<td>stadler et al. (2004c), bitzer et al. (2008)</td>
<td>Elaeocarpus, Australia (PT)</td>
</tr>
<tr>
<td>Daldinia dennisii var. microspora</td>
<td>JX658478</td>
<td>MUCL 45010</td>
<td>bitzer et al. (2008)</td>
<td>Podocarpus, South Africa</td>
</tr>
<tr>
<td></td>
<td>JX658538</td>
<td>ICMP16264</td>
<td>Present study</td>
<td>Beilschmiedia, New Zealand</td>
</tr>
<tr>
<td>Daldinia eschscholtzii</td>
<td>HE590883</td>
<td>CALP 11206</td>
<td>Present study</td>
<td>Philippines (ET)</td>
</tr>
<tr>
<td></td>
<td>JX658497</td>
<td>CBS 113042</td>
<td>bitzer et al. (2008)</td>
<td>Peru</td>
</tr>
<tr>
<td></td>
<td>AY616684</td>
<td>CBS 113047</td>
<td>triebel et al. (2005)</td>
<td>Thailand</td>
</tr>
<tr>
<td></td>
<td>JX658500</td>
<td>CBS 116032</td>
<td>bitzer et al. (2008)</td>
<td>Australia</td>
</tr>
<tr>
<td></td>
<td>JX658498</td>
<td>CBS 116035</td>
<td>bitzer et al. (2008)</td>
<td>Malaysia</td>
</tr>
<tr>
<td></td>
<td>JX658492</td>
<td>CBS 116037</td>
<td>bitzer et al. (2008)</td>
<td>Malaysia</td>
</tr>
<tr>
<td></td>
<td>JX658499</td>
<td>CBS 116037</td>
<td>bitzer et al. (2008)</td>
<td>Malaysia</td>
</tr>
<tr>
<td></td>
<td>JX658489</td>
<td>CBS 117735</td>
<td>bitzer et al. (2008)</td>
<td>Cameroon</td>
</tr>
<tr>
<td></td>
<td>JX658481</td>
<td>CBS 117740</td>
<td>bitzer et al. (2008)</td>
<td>Burkina Faso</td>
</tr>
<tr>
<td></td>
<td>JX658491</td>
<td>CBS 117741</td>
<td>bitzer et al. (2008)</td>
<td>Malaysia</td>
</tr>
<tr>
<td></td>
<td>JX658438</td>
<td>CBS 122876</td>
<td>Ju et al. (1997)</td>
<td>USA, Texas</td>
</tr>
<tr>
<td></td>
<td>JX658439</td>
<td>CBS 122877</td>
<td>Ju et al. (1997)</td>
<td>Ficus, Thailand</td>
</tr>
<tr>
<td></td>
<td>JX658440</td>
<td>CBS 122878</td>
<td>Ju et al. (1997)</td>
<td>Guadeloupe</td>
</tr>
<tr>
<td></td>
<td>JX658496</td>
<td>KC 1616</td>
<td>bitzer et al. (2008)</td>
<td>Saint Lucia</td>
</tr>
<tr>
<td></td>
<td>JX658490</td>
<td>KC 1699</td>
<td>bitzer et al. (2008)</td>
<td>Mexico</td>
</tr>
<tr>
<td></td>
<td>JX658493</td>
<td>MUCL 38740</td>
<td>bitzer et al. (2008)</td>
<td>Papua New Guinea</td>
</tr>
<tr>
<td></td>
<td>JX658486</td>
<td>MUCL 41777</td>
<td>bitzer et al. (2008)</td>
<td>Sixygiom jambos, Cuba</td>
</tr>
<tr>
<td></td>
<td>JX658494</td>
<td>MUCL 41778</td>
<td>bitzer et al. (2008)</td>
<td>Bucida palustris, Cuba</td>
</tr>
<tr>
<td></td>
<td>JX658495</td>
<td>MUCL 43508</td>
<td>bitzer et al. (2008)</td>
<td>Papua New Guinea</td>
</tr>
<tr>
<td></td>
<td>JX658484</td>
<td>MUCL 45434</td>
<td>bitzer et al. (2008)</td>
<td>Benin</td>
</tr>
<tr>
<td></td>
<td>JX658482</td>
<td>MUCL 47965</td>
<td>bitzer et al. (2008)</td>
<td>P.R. China</td>
</tr>
<tr>
<td>Daldinia gelatinoides</td>
<td>GQ355621</td>
<td>MUCL 46173</td>
<td>bitzer et al. (2008), stadler et al. (2008a)</td>
<td>Kalopanax, Far Eastern Russia</td>
</tr>
<tr>
<td>Daldinia gelatinosa</td>
<td>JX658458</td>
<td>UAMH 7406</td>
<td>Present study</td>
<td>Malus, Canada</td>
</tr>
<tr>
<td></td>
<td>JX658503</td>
<td>CBS 116730</td>
<td>Present study</td>
<td>Far Eastern Russia</td>
</tr>
<tr>
<td>Daldinia govorovae</td>
<td>JX658443</td>
<td>CBS 122883</td>
<td>Vasilyeva &amp; Stadler (2008)</td>
<td>Far Eastern Russia (T)</td>
</tr>
<tr>
<td>Daldinia hausknechtii</td>
<td>JX658521</td>
<td>CBS 119995</td>
<td>La Réunion (T)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>JX658457</td>
<td>CBS 113483</td>
<td>bitzer et al. (2008)</td>
<td>Betula, Germany</td>
</tr>
<tr>
<td>Daldinia loculata</td>
<td>AF176965</td>
<td>CBS 114738</td>
<td>Johansson et al. (2000)</td>
<td>Betula, UK (ET)</td>
</tr>
<tr>
<td></td>
<td>AF176964</td>
<td>TL 4613 (C)</td>
<td>Johansson et al. (2000)</td>
<td>Betula, Far Eastern Russia</td>
</tr>
<tr>
<td>Daldinia loculatoidea</td>
<td>AF176982</td>
<td>CBS 113279</td>
<td>Johansson et al. (2000) as D. grandis</td>
<td>Fagus, UK (T)</td>
</tr>
<tr>
<td></td>
<td>AM407726</td>
<td>CBS 116729</td>
<td>bitzer et al. (2008), sequenced by S. Pazoutova</td>
<td>Czech Republic, Betula</td>
</tr>
<tr>
<td>Daldinia macaronesica</td>
<td>JX658459</td>
<td>UAMH 9035</td>
<td>Present study</td>
<td>Populus, Canada</td>
</tr>
<tr>
<td></td>
<td>JX658505</td>
<td>MUCL 52884</td>
<td>stadler et al. (2004c)</td>
<td>La Gomera</td>
</tr>
<tr>
<td></td>
<td>JX658504</td>
<td>CBS 113040</td>
<td>stadler et al. (2004c)</td>
<td>Ocotea, Madeira (PT)</td>
</tr>
<tr>
<td></td>
<td>JX658506</td>
<td>Ww4196 (M)</td>
<td>stadler et al. (2004c)</td>
<td>Ocotea, La Palma (T)</td>
</tr>
<tr>
<td>Daldinia martini</td>
<td>JX658507</td>
<td>CBS 113041</td>
<td>stadler et al. (2004c)</td>
<td>Quercus, Italy (T)</td>
</tr>
<tr>
<td>Daldinia mexicana</td>
<td>JX658508</td>
<td>Ww 3843/MUCL</td>
<td>Ju et al. (1997)</td>
<td>Quercus, Mexico (T)</td>
</tr>
<tr>
<td>Daldinia nemorosa</td>
<td>HM114296</td>
<td>UAMH 11227</td>
<td>Davey (2010) as Annellosporum</td>
<td>Soil, Canada</td>
</tr>
<tr>
<td>Daldinia novae-zelandiae</td>
<td>JX658437</td>
<td>CBS 122873</td>
<td>Present study</td>
<td>New Zealand</td>
</tr>
<tr>
<td></td>
<td>JX658540</td>
<td>ICMP18269</td>
<td>Present study</td>
<td>New Zealand</td>
</tr>
<tr>
<td></td>
<td>JX658509</td>
<td>CBS 114739</td>
<td>stadler et al. (2004d)</td>
<td>New Zealand (PT)</td>
</tr>
</tbody>
</table>
Table 13. (Continued).

<table>
<thead>
<tr>
<th>Species</th>
<th>Acc. No. (GenBank)</th>
<th>Specimen/ Strain No.</th>
<th>References</th>
<th>Host/Country</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daldinia palmentensis</td>
<td>JX658510</td>
<td>CBS 113039, MUCL 44616</td>
<td>Stadler et al. (2004c)</td>
<td>Laurus, La Palma (T)</td>
</tr>
<tr>
<td>Daldinia petriniae</td>
<td>JX658512</td>
<td>MUCL 49214, CBS 119988</td>
<td>Bitzer et al. (2008)</td>
<td>Alnus incana, Austria</td>
</tr>
<tr>
<td></td>
<td>JX658514</td>
<td>CBS 116728</td>
<td>Bitzer et al. (2008)</td>
<td>Alnus, Liechtenstein</td>
</tr>
<tr>
<td></td>
<td>JX658461</td>
<td>CBS 116994</td>
<td>Present study</td>
<td>Betula, Far Eastern Russia</td>
</tr>
<tr>
<td>Daldinia placentaformis</td>
<td>AM749921</td>
<td>MUCL 47603</td>
<td>Bitzer et al. (2008)</td>
<td>South Africa</td>
</tr>
<tr>
<td>Daldinia pyrenaica</td>
<td>AM749927</td>
<td>MUCL 43749</td>
<td>Bitzer et al. (2008)</td>
<td>Quercus, Spain (T)</td>
</tr>
<tr>
<td>Daldinia raimundi</td>
<td>JX658517</td>
<td>CBS 113038</td>
<td>Stadler et al. (2004c)</td>
<td>Quercus, Italy (T)</td>
</tr>
<tr>
<td></td>
<td>JX658446</td>
<td>MUCL 51689</td>
<td>Present study</td>
<td>Quercus, France</td>
</tr>
<tr>
<td>Daldinia sp. nov. (ct. concentrica)</td>
<td>JX658522</td>
<td>MUCL 51268</td>
<td>Present study</td>
<td>D.R. Congo</td>
</tr>
<tr>
<td>Daldinia starbaecki</td>
<td>JX658489</td>
<td>CBS 116727</td>
<td>Bitzer et al. (2008)</td>
<td>Ecuador</td>
</tr>
<tr>
<td></td>
<td>JX658487</td>
<td>MUCL 44145</td>
<td>Bitzer et al. (2008)</td>
<td>Cuba</td>
</tr>
<tr>
<td></td>
<td>JX658488</td>
<td>MUCL 45436</td>
<td>Present study</td>
<td>French Guiana (T)</td>
</tr>
<tr>
<td></td>
<td>JX658485</td>
<td>MUCL 52886</td>
<td>Present study</td>
<td>Martinique</td>
</tr>
<tr>
<td>Daldinia steiglichii</td>
<td>JX658534</td>
<td>MUCL 43512</td>
<td>Van der Gucht (1994), Stadler et al. (2001c)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>JX658545</td>
<td>MUCL 53886</td>
<td>Present study</td>
<td>New Guinea (PT)</td>
</tr>
<tr>
<td>Daldinia theissenii</td>
<td>JX658468</td>
<td>BCRC 34045, CBS 122875</td>
<td>Ju et al. (1997) as D. clavata</td>
<td>Mexico</td>
</tr>
<tr>
<td></td>
<td>AM749931</td>
<td>CBS 113044</td>
<td>Bitzer et al. (2008)</td>
<td>Argentina</td>
</tr>
<tr>
<td>Daldinia vanderguchtiae</td>
<td>JX658520</td>
<td>CBS 113036</td>
<td>Stadler et al. (2004c)</td>
<td>Acer, UK, Jersey (T)</td>
</tr>
<tr>
<td>Daldinia vernicosa</td>
<td>EF026146</td>
<td>BCRC 34048</td>
<td>Ju et al. (1999), Bitzer et al. (2008)</td>
<td>Fagus, Germany (ET)</td>
</tr>
<tr>
<td></td>
<td>JX658501</td>
<td>CBS 119314</td>
<td>Bitzer et al. (2008)</td>
<td>Carpinus, Germany</td>
</tr>
<tr>
<td></td>
<td>JX658448</td>
<td>CBS 119315</td>
<td>Bitzer et al. (2008)</td>
<td>Corylus, Germany</td>
</tr>
<tr>
<td></td>
<td>AM749925</td>
<td>CBS 119316</td>
<td>Ju et al. (1999), Bitzer et al. (2008)</td>
<td>Fagus, Germany (same locality as ET)</td>
</tr>
<tr>
<td></td>
<td>JX658470</td>
<td>CBS 139.73</td>
<td>Triebel et al. (2005)</td>
<td>Netherlands, originally dep. as D. concentrica</td>
</tr>
<tr>
<td></td>
<td>JX658502</td>
<td>CBS 157.32</td>
<td>Child (1932)</td>
<td>USA, Missouri</td>
</tr>
<tr>
<td></td>
<td>JX658519</td>
<td>CBS 161.31</td>
<td>Child (1932)</td>
<td>USA (T of D. simulans)</td>
</tr>
<tr>
<td>Entonaea liquescens</td>
<td>AY616686</td>
<td>ATCC 46302</td>
<td>Rogers (1982), Triebel et al. (2005)</td>
<td>USA, Florida</td>
</tr>
<tr>
<td>Graphostroma platyptoma</td>
<td>JX658535</td>
<td>CBS 270.87</td>
<td>Pirozynski (1974)</td>
<td>Crataegus, France (T)</td>
</tr>
<tr>
<td></td>
<td>JX658542</td>
<td>MUCL 53890</td>
<td>Present study</td>
<td>Quercus, France</td>
</tr>
<tr>
<td>Hypoxylon anthochromum</td>
<td>JX658532</td>
<td>FU69799, STMA07040, MUCL 49881</td>
<td>Bitzer et al. (2008)</td>
<td>Panama</td>
</tr>
<tr>
<td>Hypoxylon fragiforme</td>
<td>AY616690</td>
<td>CBS 114745</td>
<td>Triebel et al. (2005)</td>
<td>Fagus, Germany</td>
</tr>
<tr>
<td>Hypoxylon fuscom</td>
<td>AY616693</td>
<td>CBS 113049</td>
<td>Triebel et al. (2005)</td>
<td>Corylus, Germany</td>
</tr>
<tr>
<td>Hypoxylon gibricense</td>
<td>JX658523</td>
<td>MUCL 52698</td>
<td>Fournier et al. (2010b)</td>
<td>Portugal (T)</td>
</tr>
<tr>
<td>Hypoxylon haematostroma</td>
<td>AM749924</td>
<td>MUCL 47600</td>
<td>Bitzer et al. (2008)</td>
<td>Panama</td>
</tr>
<tr>
<td>Hypoxylon howeanum</td>
<td>AM749928</td>
<td>MUCL 47599</td>
<td>Bitzer et al. (2008)</td>
<td>Acer, Germany</td>
</tr>
<tr>
<td>Hypoxylon laschii</td>
<td>JX658525</td>
<td>MUCL 52796</td>
<td>Present study</td>
<td>Fraxinus, France</td>
</tr>
<tr>
<td>Hypoxylon monticulosum</td>
<td>DQ223748</td>
<td>SUT080</td>
<td>Suwanassai et al. (2005)</td>
<td>Thailand</td>
</tr>
<tr>
<td>Hypoxylon nicaraguense</td>
<td>AM749922</td>
<td>CBS 117739</td>
<td>Bitzer et al. (2008)</td>
<td>Burkina Faso</td>
</tr>
<tr>
<td>Hypoxylon petriniae</td>
<td>AM749923</td>
<td>CBS 114746</td>
<td>Bitzer et al. (2008)</td>
<td>Fraxinus, France (T)</td>
</tr>
<tr>
<td>Hypoxylon polyurus</td>
<td>AM749941</td>
<td>MUCL 49339</td>
<td>Bitzer et al. (2008)</td>
<td>Ivory Coast</td>
</tr>
<tr>
<td>Hypoxylon rubiginosum</td>
<td>AM749936</td>
<td>CBS 119309</td>
<td>Bitzer et al. (2008)</td>
<td>Fraxinus, Germany</td>
</tr>
<tr>
<td>Hypoxylon sp.</td>
<td>JX658483</td>
<td>CBS 222.61</td>
<td>Martin (1969) as D. eschscholtzi; taxonomy revised here</td>
<td>Mexico</td>
</tr>
<tr>
<td>Hypoxylon submonticulosum</td>
<td>JX658449</td>
<td>CBS 115280</td>
<td>Present study</td>
<td>Ulmus, France</td>
</tr>
<tr>
<td>Nodulisporium africanum</td>
<td>JX658527</td>
<td>MUCL 3531</td>
<td>Bitzer et al. (2008)</td>
<td>D.R. Congo</td>
</tr>
<tr>
<td>Nodulisporium gregarinum</td>
<td>JX658528</td>
<td>MUCL 3630</td>
<td>Bitzer et al. (2008)</td>
<td>Morus alba, Pakistan</td>
</tr>
<tr>
<td>Nodulisporium indicum</td>
<td>JX658529</td>
<td>CBS 124.83</td>
<td>Bitzer et al. (2008)</td>
<td>India (T)</td>
</tr>
</tbody>
</table>
A POLYPHASIC TAXONOMY OF DALDINIA (XYLARIACEAE)

Table 13. (Continued).

<table>
<thead>
<tr>
<th>Species</th>
<th>Acc. No. (GenBank)</th>
<th>Specimen/ Strain No.</th>
<th>References</th>
<th>Host/Country</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phylacis poculiformis</td>
<td>FN456830</td>
<td>CBS 123581</td>
<td>Stadler et al. (2010a)</td>
<td>Panama</td>
</tr>
<tr>
<td>Phylicia saurana</td>
<td>AM749919</td>
<td>CBS 119992</td>
<td>Bitzer et al. (2008)</td>
<td>Panama</td>
</tr>
<tr>
<td>Pyrenomyxa morganii</td>
<td>AM749920</td>
<td>CBS 116990</td>
<td>Stadler et al. (2005), Bitzer et al. (2008)</td>
<td>Far Eastern Russia (T)</td>
</tr>
<tr>
<td>Rhopalosporia angolensis</td>
<td>FN821965</td>
<td>CBS 123614</td>
<td>Stadler et al. (2010c)</td>
<td>Burkinaaso</td>
</tr>
<tr>
<td>Ruwenzoriza pseudoannulata</td>
<td>GU053586</td>
<td>MUCL 51394</td>
<td>Stadler et al. (2010b)</td>
<td>D.R. Congo (T)</td>
</tr>
<tr>
<td>Thamnomyces camerunensis</td>
<td>FN498282</td>
<td>MUCL 51396</td>
<td>Stadler et al. (2010a)</td>
<td>Cameroon</td>
</tr>
<tr>
<td>Thuemenella cubispora</td>
<td>JX058531</td>
<td>CBS 119807</td>
<td>Present study</td>
<td>USA</td>
</tr>
</tbody>
</table>

Table 14. Comparison of the species concepts of Ju et al. (1997) and Rogers et al. (1999) with the currently proposed taxonomy of Daldinia. *These taxa, here circumscribed as the “D. concentrica group”, roughly correspond to the concept of Rogers et al. (1999) for Daldinia concentrica.

<table>
<thead>
<tr>
<th>Taxon Ju et al. (1997, 1999)</th>
<th>Taxon (present study)</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. clavata</td>
<td>D. albozonata + D. clavata + D. theissenni</td>
</tr>
<tr>
<td>D. grandis</td>
<td>D. andina + D. grandis + D. novae-zelandiae + D. loculatooides (+ D. hausknedti?)</td>
</tr>
<tr>
<td>D. cucudina</td>
<td>D. aspahletum</td>
</tr>
<tr>
<td>D. concentrica</td>
<td>D. chitidae (+ D. australis + D. pyrenaica?)</td>
</tr>
<tr>
<td>D. sp. from Russian Far East</td>
<td>D. carpincola</td>
</tr>
<tr>
<td>D. sp. from Denmark</td>
<td>D. decipiens</td>
</tr>
<tr>
<td>D. eschscholtzi</td>
<td>D. eschscholtzi + D. rehmii + D. starbaeccki, (+ D. vanderguchtiae?)</td>
</tr>
<tr>
<td>D. fissa</td>
<td>D. vernicosa (+ D. gelatinoides)</td>
</tr>
<tr>
<td>D. gelatinosa</td>
<td>D. gelatinosa (+ D. sp. nov. ined., cf. D. bakeri, represented by WSP 54679/WSP 54729 from Idaho)</td>
</tr>
<tr>
<td>Hypoxylon placentiforme</td>
<td>D. placentiformis</td>
</tr>
<tr>
<td>Versiomyces cahucuchosus</td>
<td>D. cahucuchosa</td>
</tr>
</tbody>
</table>

The sequenced strain was supposedly obtained from a "blood culture", according to the title of the paper, while the abstract also mentions a "draft genome sequence of a member of the Xylariaceae". Unfortunately, the sequenced strain was not commented on further here. However, evaluation of the sequence data by "genome mining" using modern bioinformatics tools, as well as additional genome sequencing of other, well-characterised and unambiguously identified vouchers strains from the family may facilitate not only functional genomics studies of their secondary metabolites, but ultimately yield reliable molecular marker genes for a molecular phylogeny based on biologically relevant, unique features that encode for the salient characters of the phenotypes.

ACKNOWLEDGEMENTS

We gratefully acknowledge the support by the curators and staff of the herbaria mentioned in the taxonomic part, especially to Begoña Aguirre-Hudson and Brian Spooner (K), Anna-Lena Anderberg (S), Margarita Dueñas (MA), Ellen Bloch (NY), Erin McCray & Amy Rossman (BPI), Teresa H. Quimio (CALP), Mieke Verbeken (M), Genevieve Lewis-Gentry (FH), André Frature (BR), Brian J. Coppins (E), Eric McKenzie (PDD), Robert Lücking (F), Markus Scholler (KR), Herbert Boyle (GLM), Andreas Gminder & Martin Neibel (ST), David Minter (CABI), Svengunnar Ryman (UPS) and Harrie Sipman (B), who searched extensively for important specimens on our request or provided us with their entire and extensive collections of material. Lynne Sigler (UAMH) is thanked for providing specimens and cultures, and the staff of CBS and MUCL for safekeeping our numerous cultures that we have deposited over the past years and for their efforts to keep them available to others for study.

Special thanks go to our colleagues Beatrice Sem-Irlet, D. Jean Lodge, Esperanza Beltrán, Larissa Vasilyeva, Laura Guzmán-Davalos, Meike Piepenbring, Alain Gardiennet, Alexander Akulov, Alfred Grammo, Anthony Whalley, Anton Hausknecht, Björn Nordén, Christian Lechat, Christine Lécuru, Daniel Remy, David Rambold, in whose laboratory at the university of Bayreuth most of the sequence data presented here were generated, is also thanked for providing infrastructure and support. Markus Scholler and Dagmar Triebel are also thanked for arranging international loan transactions on our behalf.

We also wish to thank Klaus Ide (Bayer Technology Services, Leverkusen, Germany) for help with SEM, Dirk Müller (IMD, Dortmund) for performing HPLC–
REFERENCES


Braun U (2012). The impacts of the discontinuation of dual nomenclature of


Child M (1932). The genus Xylariaceae and the daldinoid

Cesati V, De Notaris G (1863). Schema di classificazione degle sferiacei italici


A POLYPHASIC TAXONOMY OF DALDINIA (XYLARIACEAE)


Ng IS, Chen PT, Ju YM, Tsai SW (2010). Novel cellulase screening and optimisation production from the wood-decaying Xylariaceae: Daldinia species. Applied Biochemistry and Biotechnology, published online (http://dx.doi.org/10.1007/s12010-010-9102-1)


