



A polyphasic taxonomy of *Daldinia* (Xylariaceae)¹

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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 epitype of *D. eschscholtzii* was selected as representative of the morphochemotype 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. cudonia* is regarded as its synonym. In addition, the following binomials are epi-, iso-, neo- and/or lectotypified: *Daldinia asphalatum*, *D. caldariorum*, *D. clavata*, *D. cuprea*, *D. durissima*, *D. eschscholtzii*, *D. grandis*, *D. loculata*, and *D. vernicosa*. *Annellosporium* and *Versiomyces* are regarded as synonyms of *Daldinia*. Many new synonymies in *Daldinia* are proposed, and some previously published names are rejected. In total, 47 taxa in *Daldinia* are recognised and a key is provided. Their biogeography, chorology, and ecology, as well as the importance of their secondary metabolites, are also discussed. The previous definition of the genus is emended. The species concept is based mainly on morphological and other phenotype-derived characters because, despite diligent search, no molecular data or cultures of several of the accepted species could be obtained. *Daldinia* is segregated into five major groups, 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 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 morphological and chemotaxonomic evidence. In the rDNA based phylogenetic tree, *Daldinia* appears clearly distinct from members of the genera *Annulohypoxylon* and *Hypoxylon*; nevertheless, representatives of small genera of predominantly tropical origin (*Entonaema*, *Phylacia*, *Ruwenzoria*, *Rhopalostroma*, *Thamnomycetes*) 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.

Key words: Ascomycota, biodiversity, chemotaxonomy, systematics, *Xylariales*.

Taxonomic novelties: *Daldinia andina* sp. nov., *D. australis* sp. nov., *D. hausknechtii* sp. nov., *D. rehmi* sp. nov., *D. starbaeckii* sp. nov., *D. theissenii* sp. nov., *D. cahuchosa* comb. nov., *D. nemorosa* comb. nov.

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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* (basonym *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 (1686), who described a "*Fungus fraxineus, niger, durus, orbiculatus*" (Fries 1823). The Tyrolian physician and naturalist, Giovanni Antonio Scopoli, who maintained close contact to Linnaeus, 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

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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**.

Taxon	MycoBank No.
<i>Daldinia albofibrosa</i> M. Stadler, M. Baumgartner & Wollw. 2001 (p. 57)	MB474115
<i>Daldinia albozonata</i> Lloyd 1919 (p. 59)	MB141379
<i>Daldinia andina</i> Læssøe, J. Fourn. & M. Stadler 2014 (p. 33)	MB800022
<i>Daldinia asphalatum</i> (Link ex Fr.) Sacc. 1882 (p. 106)	MB247095
<i>Daldinia australis</i> J. Fourn. & M. Stadler 2014 (p. 78)	MB563696
<i>Daldinia bakeri</i> Lloyd 1919 (p. 88)	MB246639
<i>Daldinia bambusicola</i> Y.M. Ju, J.D. Rogers & F. San Martín 1997 (p. 60)	MB436494
<i>Daldinia barkalovii</i> Lar.N. Vassiljeva & M. Stadler 2008 (p. 110)	MB511595
<i>Daldinia brachysperma</i> F. San Martín, Y.M. Ju & J.D. Rogers 1997 (p. 60)	MB436495
<i>Daldinia cahuchucosa</i> (Whalley & Watling) M. Stadler & Læssøe 2014 (p. 90)	MB807746
<i>Daldinia caldariorum</i> Henn. 1898 (p. 61)	MB247207
<i>Daldinia carpinicola</i> Lar.N. Vassiljeva & M. Stadler 2008 (p. 111)	MB511594
<i>Daldinia childiae</i> J.D. Rogers & Y.M. Ju 1999 (p. 74)	MB460536
<i>Daldinia clavata</i> Henn. 1902 (p. 65)	MB247027
<i>Daldinia concentrica</i> (Bolton) Ces. & De Not. 1863 (p. 28)	MB146158
<i>Daldinia cuprea</i> Starbäck 1901 (p. 67)	MB146524
<i>Daldinia decipiens</i> Wollw. & M. Stadler 2001 (p. 111)	MB474112
<i>Daldinia dennisii</i> var. <i>dennisii</i> 2004 (p. 35)	MB482298
<i>Daldinia dennisii</i> var. <i>microspora</i> Wollw. & M. Stadler 2004 (p. 35)	MB488679
<i>Daldinia eschscholtzii</i> (Ehrenb.) Rehm 1904 (p. 49)	MB146911
<i>Daldinia gelatinoides</i> Lar.N. Vassiljeva 1998 (p. 92)	MB450312
<i>Daldinia gelatinosa</i> Y.M. Ju, J.D. Rogers & F. San Martín 1997 (p. 113)	MB436496
<i>Daldinia govorovae</i> Lar.N. Vassiljeva & M. Stadler 2008 (p. 115)	MB511596
<i>Daldinia graminis</i> Dargan & K.S. Thind 1985 (p. 121)	MB128584
<i>Daldinia grandis</i> Child 1932 (p. 93)	MB239743
<i>Daldinia hausknechtii</i> J. Fourn. & M. Stadler 2014 (p. 95)	MB488678
<i>Daldinia lloydii</i> Y.M. Ju, J.D. Rogers & F. San Martín 1997 (p. 116)	MB436497
<i>Daldinia loculata</i> (Lév.) Sacc. 1882 (p. 97)	MB239483
<i>Daldinia loculatoides</i> Wollw. & M. Stadler 2004 (p. 99)	MB488678
<i>Daldinia macaronesica</i> M. Stadler, Wollw. & J.M. Castro 2004 (p. 38)	MB488619
<i>Daldinia macrospora</i> F. San Martín, Y.M. Ju & J.D. Rogers 1997 (p. 118)	MB436498
<i>Daldinia martinii</i> M. Stadler, Venturella & Wollw. 2004 (p. 38)	MB489539
<i>Daldinia mexicana</i> F. San Martín, Y.M. Ju & J.D. Rogers 1997 (p. 119)	MB436499
<i>Daldinia nemorosa</i> (M. L. Davey) M. Stadler, J. Fourn. & Læssøe 2014 (p. 100)	MB800145
<i>Daldinia novae-zelandiae</i> Wollw. & M. Stadler 2004 (p. 101)	MB522267
<i>Daldinia palmensis</i> M. Stadler, Wollw. & Tichy 2004 (p. 40)	MB488618
<i>Daldinia petriniae</i> Y.M. Ju, J.D. Rogers & F. San Martín 1997 (p. 103)	MB436500
<i>Daldinia placentifformis</i> (Berk. & M.A. Curtis) Theiss. 1909 (p. 125)	MB438125
<i>Daldinia pyrenaica</i> M. Stadler & Wollw. 2001 (p. 80)	MB474113
<i>Daldinia raimundi</i> M. Stadler, Venturella & Wollw. 2004 (p. 40)	MB489537
<i>Daldinia rehmi</i> Læssøe, M. Stadler & J. Fourn. 2014 (p. 69)	MB512370
<i>Daldinia sacchari</i> Dargan & K.S. Thind 1985 (p. 123)	MB128585
<i>Daldinia singularis</i> Y.M. Ju, Lar.N. Vassiljeva & J.D. Rogers 1999 (p. 120)	MB460421
<i>Daldinia starbaeckii</i> M. Stadler & Læssøe 2014 (p. 69)	MB512385
<i>Daldinia steglichii</i> M. Stadler, M. Baumgartner & Wollw. 2001 (p. 82)	MB474114
<i>Daldinia theissenii</i> Læssøe, J. Fourn. & M. Stadler 2014 (p. 73)	MB564867
<i>Daldinia vanderguchtiae</i> M. Stadler, Wollw. & Brieger 2004 (p. 42)	MB491383
<i>Daldinia vernicosa</i> Ces. & De Not. 1863 (p. 84)	MB249419

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