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# A polyphasic taxonomy of *Daldinia* (*Xylariaceae*)

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CBS-KNAW Fungal Biodiversity Centre,
Utrecht, The Netherlands
An institute of the Royal Netherlands Academy of Arts and Sciences

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Cover: Top from left to right: Anamorphic structure of *Daldinia starbaeckii*; stromata of *D. childiae*; ascospores of *Daldinia* sp. PDD 87953. Bottom from left to right: Stromata of *D. placentiformis*; vertical section of a stroma of *D. steglichii*; stroma of *Daldinia* cf. *nemorosa* formed in culture.

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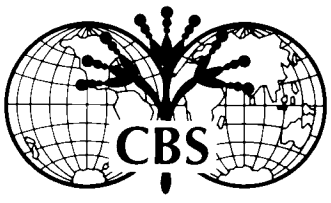


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## CONTENTS

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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*, *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.

**Key words:** Ascomycota, biodiversity, chemotaxonomy, systematics, *Xylariales*.
**Taxonomic novelties:** *Daldinia andina* sp. nov., *D. australis* sp. nov., *D. hausknechtii* sp. nov., *D. rehmii* 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* (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 (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

[1]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**.

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

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. *Peripherica*e. Fries (1823), on the other hand, listed this species in tribe *Pulvinatae,* 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 *Pulvinatae*. Meanwhile, Léveillé (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 (1898, 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 hypoxyloid taxa that lack the conspicuously zonate stromatal interior goes back to Theissen (1909). Arguing that *Hypoxylon placentiforme* had reduced concentric zones, while being otherwise highly similar 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), Thind & 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.

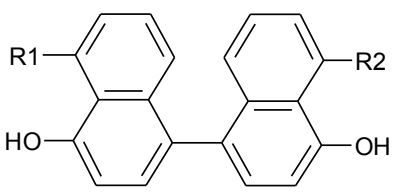
Descriptions of conidial states of *Daldinia* spp. were provided early on by Tulasne &Tulasne (1863) and Molliard (1904), but their significance in the taxonomy of the *Xylariaceae* was only recognised after the 1960s. Anamorphic data from certain *Daldinia* species made it easier to interpret the affinities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

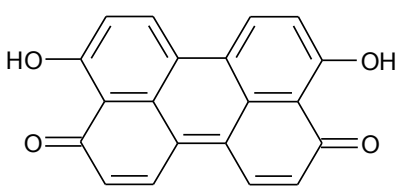
Only two years later, Rogers *et al*. (1999) revised the concept of the type species, based on an original Bolton specimen that disagreed with the concepts of *D. concentrica sensu* Child (1932) and Ju *et al*. (1997), who had regarded this taxon to be almost cosmopolitan and frequent in the USA.. Rogers *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.

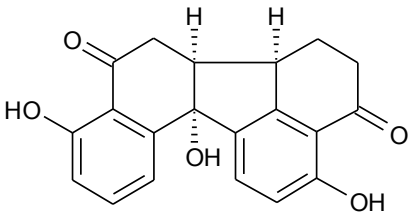
In the past years, the taxonomic work has been supported by intensive collaboration with analytical chemists, and so far over 100 secondary metabolites, the majority of which proved new to science, were identified during our studies from *Daldinia* spp. and related



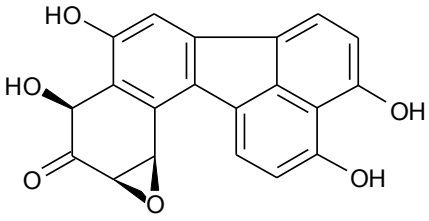

BNT (**1**) R1 = R2 = OH
daldinol (**1a**) R1 = R2 = $OCH_3$



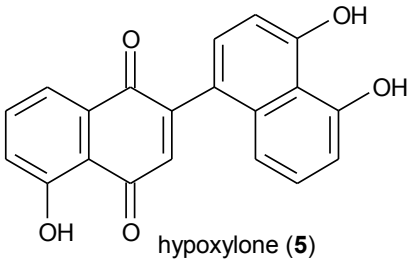

4,9-dihydroxyperylene-3,10-quinone (**2**)



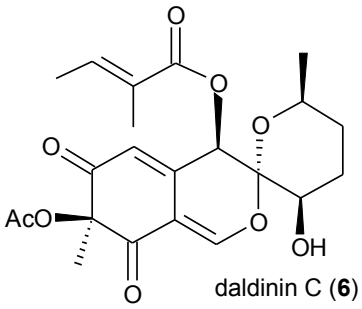

daldinone A (**3**)



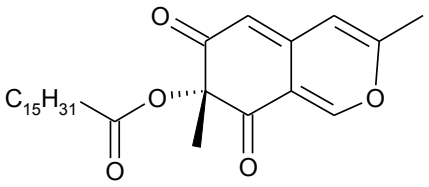

daldinone B (**4**)



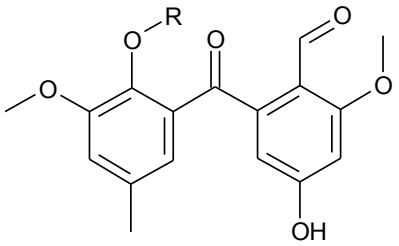

hypoxylone (**5**)



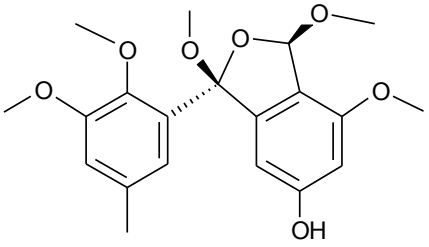

daldinin C (**6**)



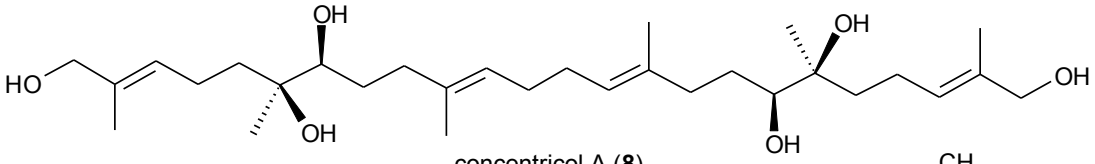

daldinin A1 (**6a**)



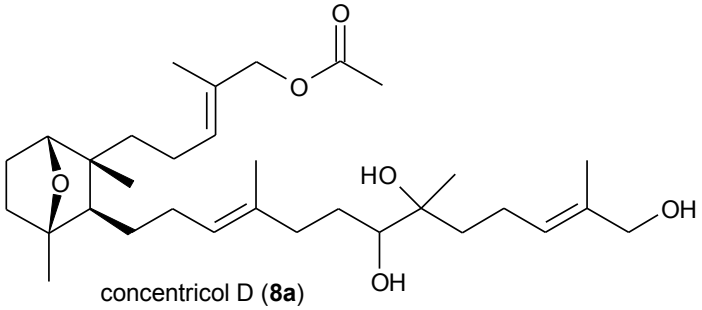

daldinal A (**7**) R = H
daldinal B (**7a**) R = $OCH_3$



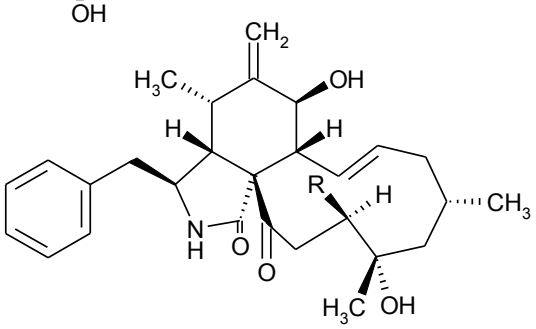

daldinal C (**7b**)




concentricol A (**8**)




concentricol D (**8a**)




10-phenyl-[11]-cytochalasan B (**9**) R = H
10-phenyl-[11]-cytochalasan D (**9a**) R = $OCH_3$

**Fig. 1.** Secondary metabolites from stromata of *Daldinia*. Distribution: **1**: ubiquitous, **2**: *D. petriniae* complex, **1a**, **6–7**: *D. childiae* group; **8**: *D. concentrica* group; **9**: *D. eschscholtzii* group (only 2 representatives out of 16 known compounds of this type are depicted as examples). The remaining depicted molecules are only present as major components in particular species. As discussed earlier on (Stadler 2011), compounds **1–5** are polyketides derived from 1,8-dihydroxynaphthalene biosynthesis and therefore also probably biogenetically related to one another, with **2–5** constituting oxidised forms that are presumably derived from BNT (**1**) or an isomer thereof. Compounds **6** and **7** are polyketides derived from entirely different pathways, whereas concentricols (**8**) are terpenoids derived from the acatate-mevalonate pathway, and cytochalasins (**9**) are of mixed PKS/NRPS origin.

*Xylariaceae*. 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 nrDNA for a number of well-characterised specimens. Similar work was published by Stadler *et*

*al*. (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. childiae*, revealed that *D. concentrica sensu* Rogers *et al.* (1999) and *D. eschscholtzii* contain similar secondary metabolites in their stromata, 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. dennisii* 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 hypoxyloid 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 the stromata. 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, Guidot *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.

Petrini & Petrini (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, Petrini & 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. childiae* 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. childiae* (*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. decipi*ens and an anamorphic xylariaceous fungus they referred to as *Entonaema cinnabarinum* to be associated with woodwasp nests (genus *Xyphidria*). 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 state has fo far been encountered, is not included here. The report of *E. cinnabarinum* 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. childiae*, 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 Ingold (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* (Ingold & 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 (Læssøe 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 generic 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. placentiforme* 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

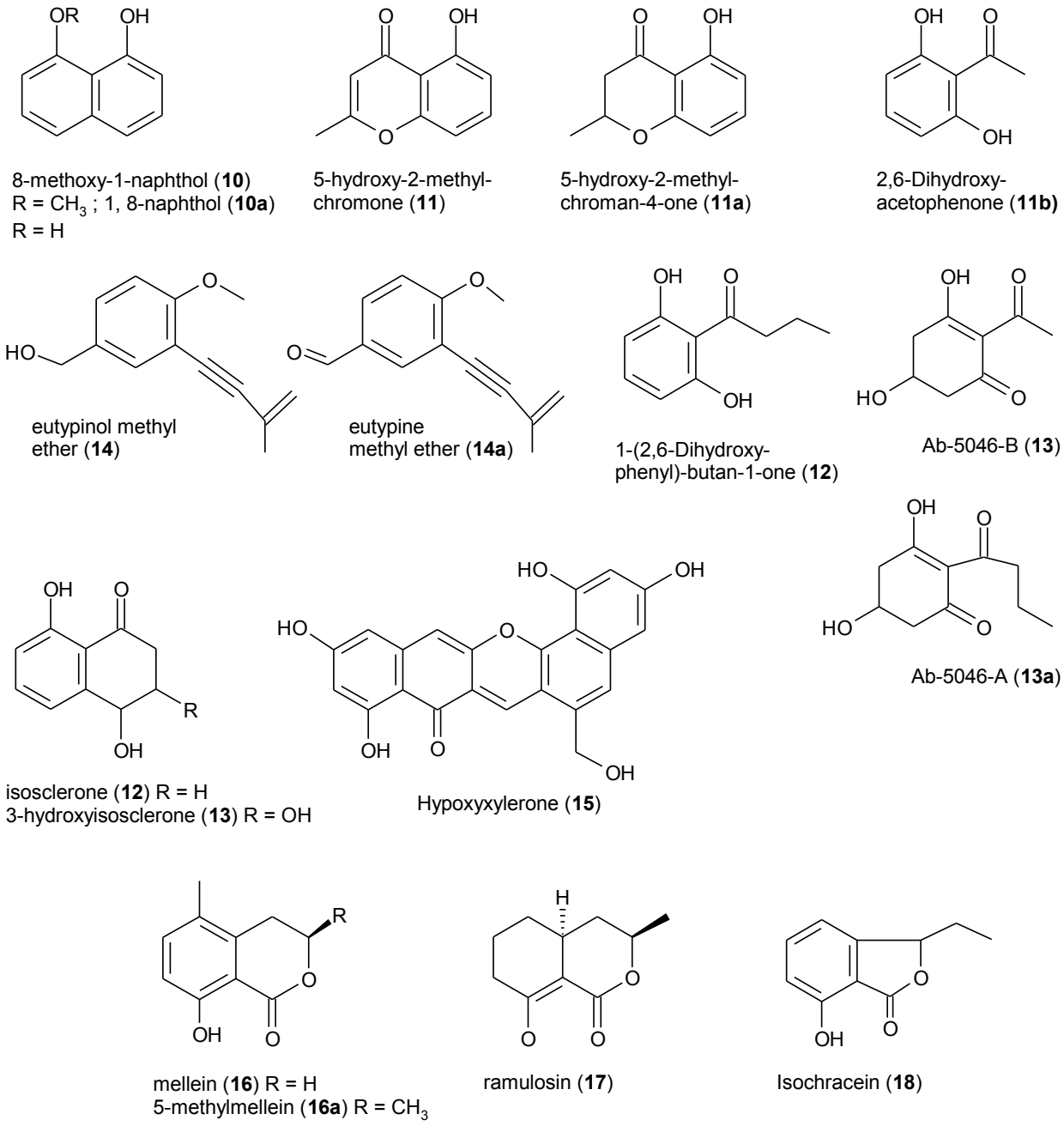



**Fig. 2.** Secondary metabolites from cultures of *Daldinia* and related *Xylariaceae*. Distribution: **10–13**: Ubiquitous in *Daldinia* and immediate allies (*Entonaema*, *Phylacia*, *Rhopalostroma*, *Ruwenzoria* and *Thamnomyces)*. **15**: Green pigment of *Hypoxylon fragiforme*, also present in 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.

methodology (Stadler *et al.* 2004b). 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 "*Xylariacae* 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

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 mellein 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*, *Camillea*, *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 Læssøe (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 (Osemwegie *et al.* 2010), Mexico (Guzman 2008, who even cited *Daldinia* "*fissa*" as an edible mushrooom), 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. childiae* 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 stromata, 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 stromata, 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 dihydroxynaphthalene 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 underexplored 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

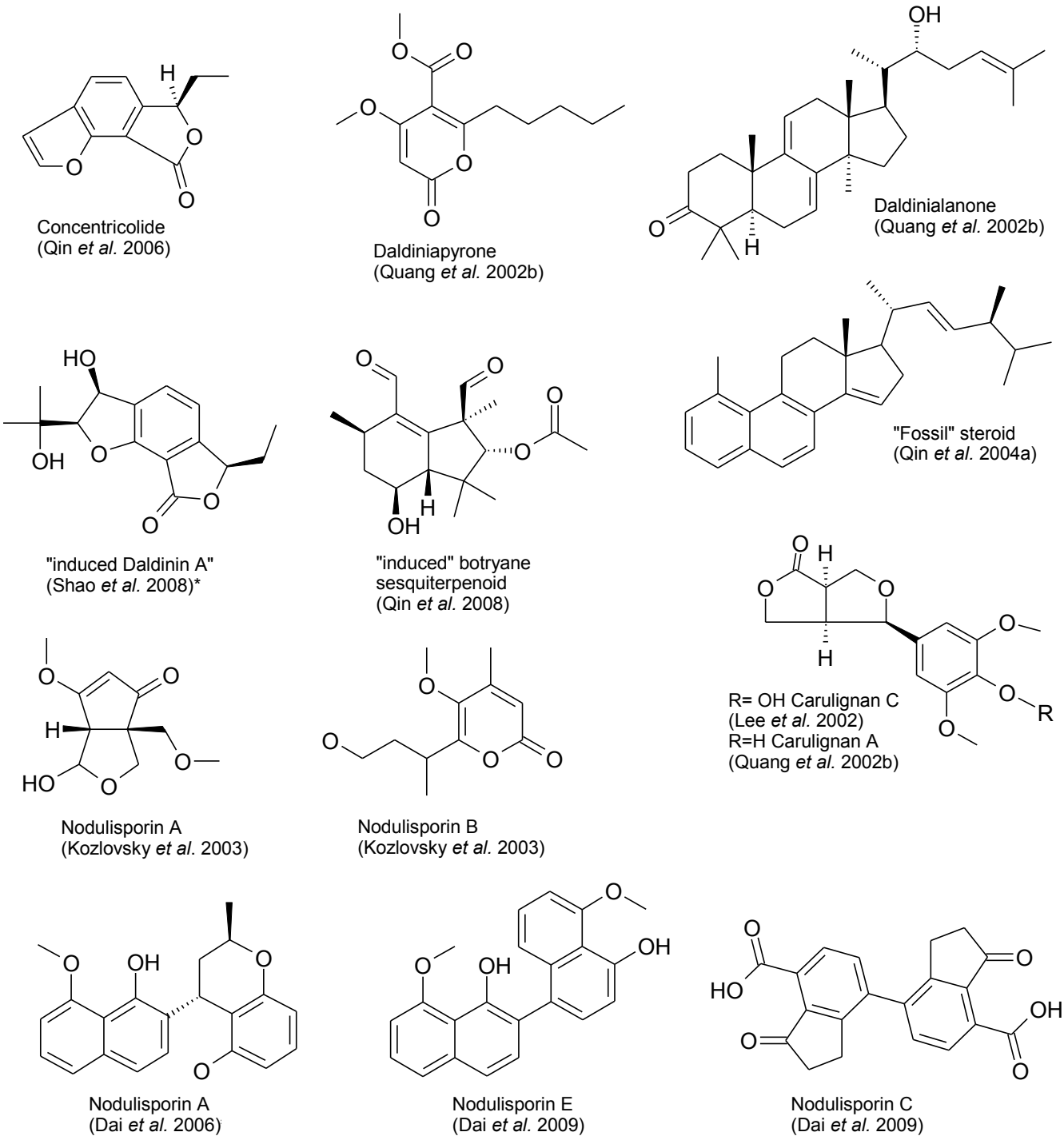



**Fig. 3.** Additional metabolites reported from *Daldinia* that remain to be studied for their chemotaxonomic significance, and Nodulisporins and Nosporins isolated from endophytic *Nodulisporium* strains that resemble *Daldinia* spp. with regard to their metabolite profiles. *not to be confused with the compound that has the same trivial name, published earlier on by Hashimoto *et al.* (1994). **similar to botrydial (compound class not yet detected by us in genuine *Daldinia* strains even by using the culture media published by the authors).

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 naphtoquinones (**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 hypoxylone (**5**) is derived from a different precursor, which has so far not been isolated from any xylariaceous fungus. Species containing hypoxylone, 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. eschscholtzii* and other tropical species, are of mixed PKS/NRPS origin.
- Concentricols (**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. eschscholtzii* 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 *Entonaema* (cf. Stadler *et al.* 2008a), *Rhopalostroma*, *Ruwenzoria*, *Phylacia*, and *Thamnomyces* 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, *i.e.*, *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 felty, 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. caldariorum* 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


**Fig. 4.** Macromorphology of cultures of *Daldinia* spp. (*D. concentrica* group) on 9 cm OA plates (except G on YMG agar) after 2 (A, C, D, G–I) or 4 (B, E, F, J, K) wk of incubation. A, B. *D. concentrica*. A. CBS 113277 (Germany). B. MUCL 51689 (France), with surface covered by secondary mycelium after germination of primary conidia. C. *D. raimundi* MUCL 51680 (France). D. *D. dennisii* var. *dennisii* CBS 114741 ex-type (Australia). E. *D.* cf. *concentrica* MUCL 51268 (D.R. Congo), showing little differentiation even at prolonged incubation time F. *D.* cf. *concentrica* MUCL 45434 (Ethiopia). G, H. *D. dennisii* var. *microspora* (New Zealand). G. ICMP 18264 ex PDD 92220 (YMG). H. ICMP 18261 ex PDD 92967 (OA). I. *D. macaronesica* CBS 113040 (Madeira, YMG). J–L. *D. andina* CBS 116024 (Ecuador). J, K. Culture on YMG, with stromata at margins, K enlarged from J, showing small stromata at the periphery. L. Culture on OA, not differentiating even after prolonged incubation time.

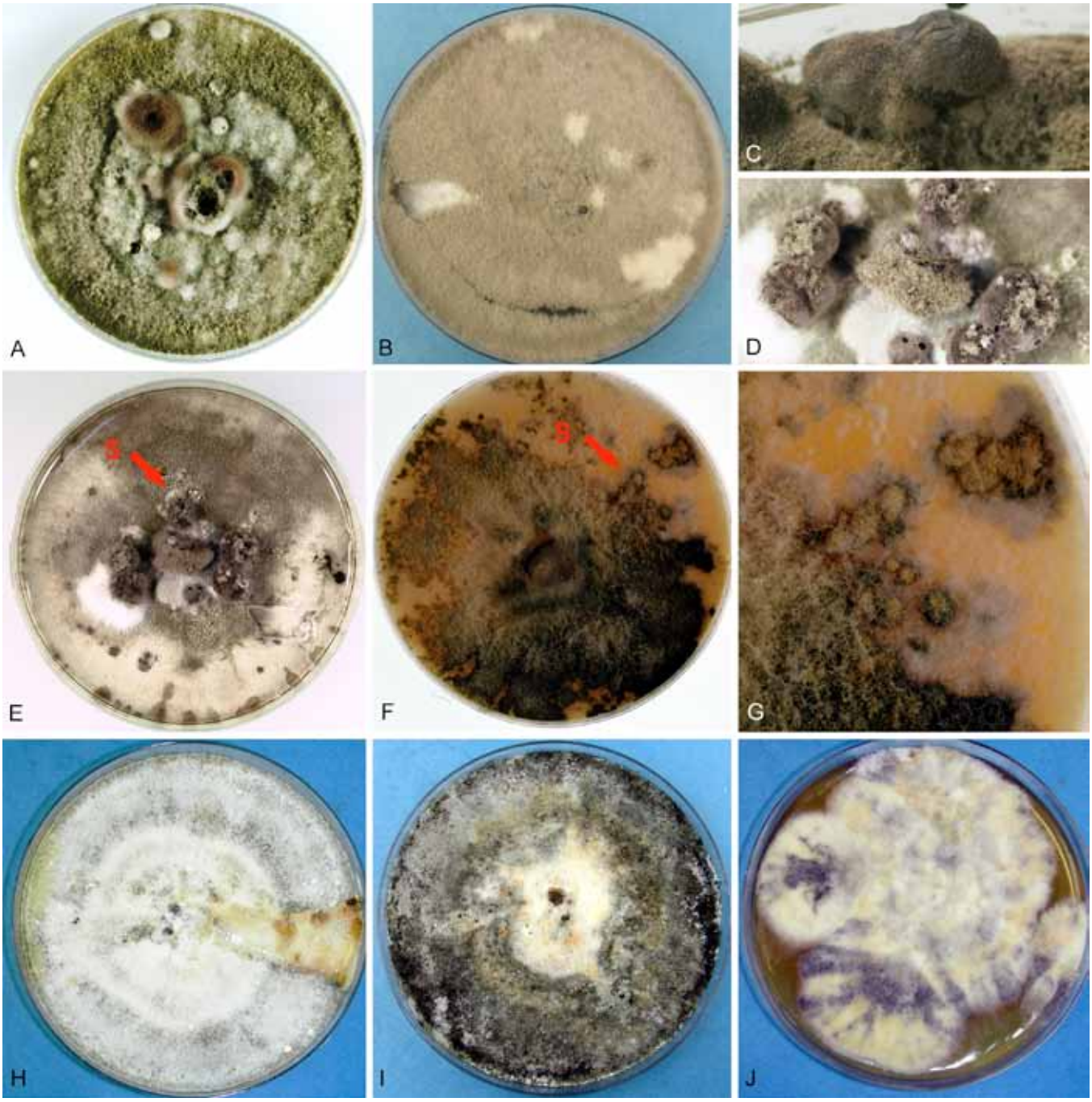



**Fig. 5.** Macromorphology of cultures of *Daldinia* spp. (*D. eschscholtzii* group) on 9 cm OA plates (except G on YMG agar) after 2 (A, C, D, G–J) or 4 (B, E, F) wk of incubation. A, D. *D. eschscholtzii* MUCL47186 (P.R. China). B. *D. starbaeckii* MUCL 45436 ex-type (French Guiana). C, E. *D.* cf. *caldariorum* CBS 113045 (Ecuador). F, G. *D. caldariorum.* ATCC 36660 (UK). H. *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.

*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*, *Ruwenzoria* 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 then 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. childiae* group, produce their conidiophores only after prolonged incubation periods, and in general they become more abundant in the

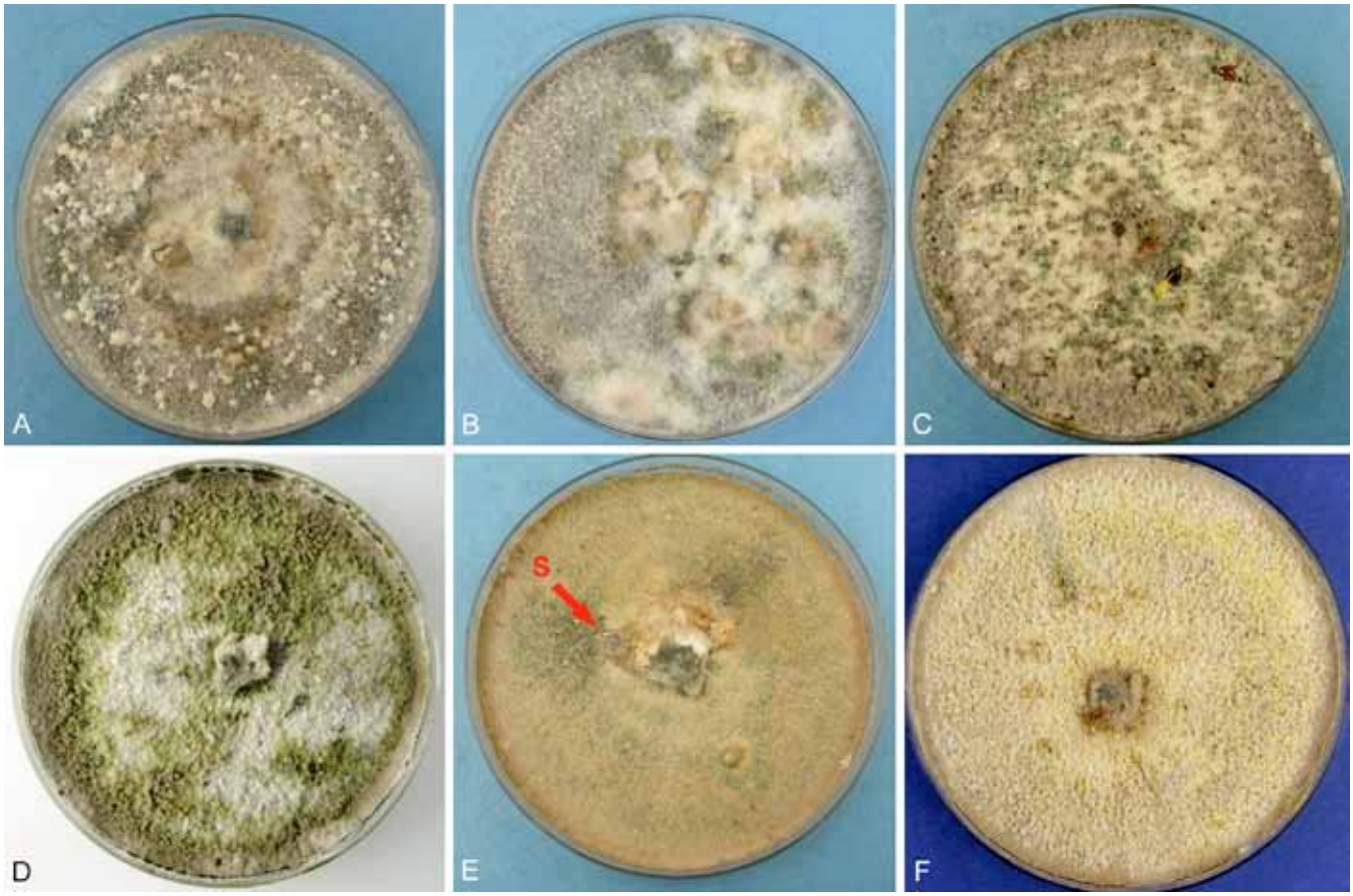



**Fig. 6.** Macromorphology of cultures of *Daldinia* spp. (*D. childiae* group) on 9 cm OA plates after 2 (D, F) or 4 (A–C, E) wk of incubation. A, B. *D. childiae*. A. MUCL 51679 (USA). B. CBS 116993 (Germany). C. *D. australis*. ex-type CBS 116732 (New Zealand). D. *D. pyrenaica* ex-type MUCL 43507 (Spain). E. *D.* cf. *pyrenaica* MUCL 51701ex 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).

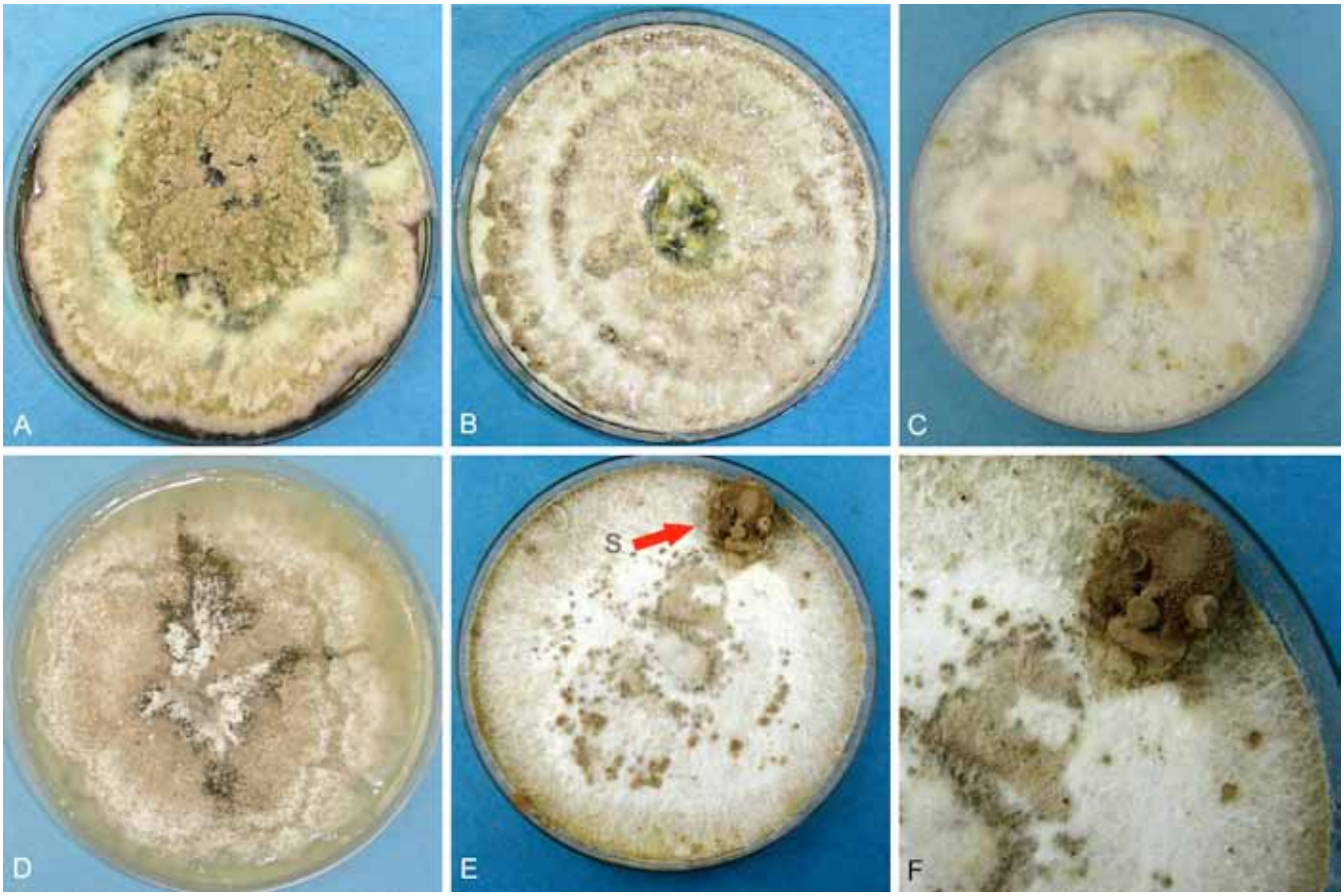



**Fig. 8.** Macromorphology of cultures of *Daldinia* spp. (*D. petriniae* group and *D.* cf. *nemorosa)* on 9 cm YMG (A, C, D) or OA (B, E, F) plates after 2 (C, D) or 4 (A, B, E, F) wk of incubation. A, B. *D. petriniae* MUCL 51850 (Switzerland). C. *D. lloydii* CBS 113483 (Germany), showing the characteristic 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.

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 conidiophores. 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 *Xylariaceae*, 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*",

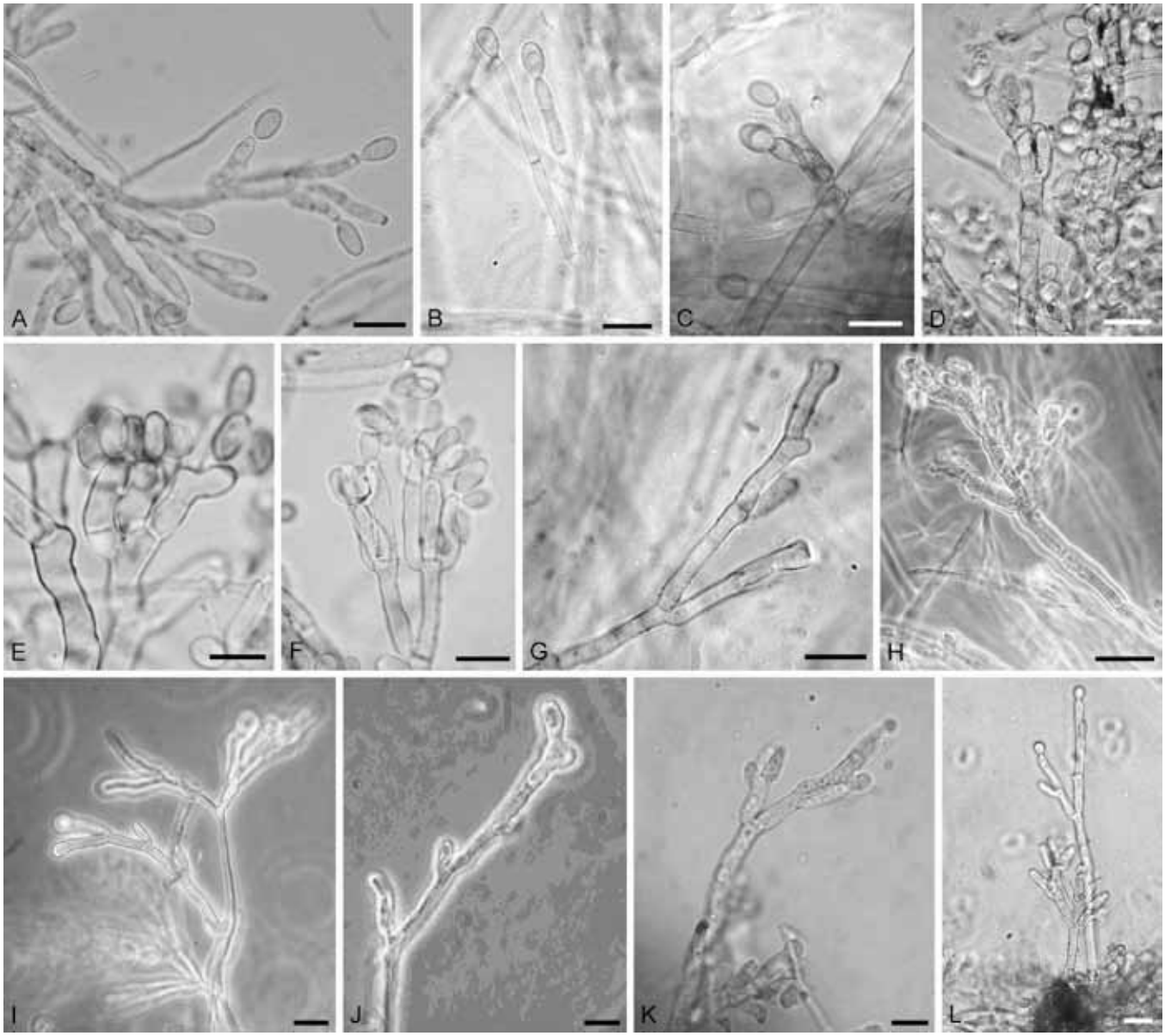



**Fig. 9.** Photomicrographs of anamorphic structures of the *Daldinia concentrica* complex from OA culture,1000×, showing nodulisporium-like conidiophores if not indicated otherwise. A, C. *D. concentrica*. A. Regular conidiophore of MUCL 51689 ex *Ww 2357* (France). B, C. Aberrant sporothrix-like conidiophores 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.

but describes the different stages of complexity that can occur in conidiophores of the *Xylariaceae* as "nodulisporium-like[2]" 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

[2]Ju & 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.

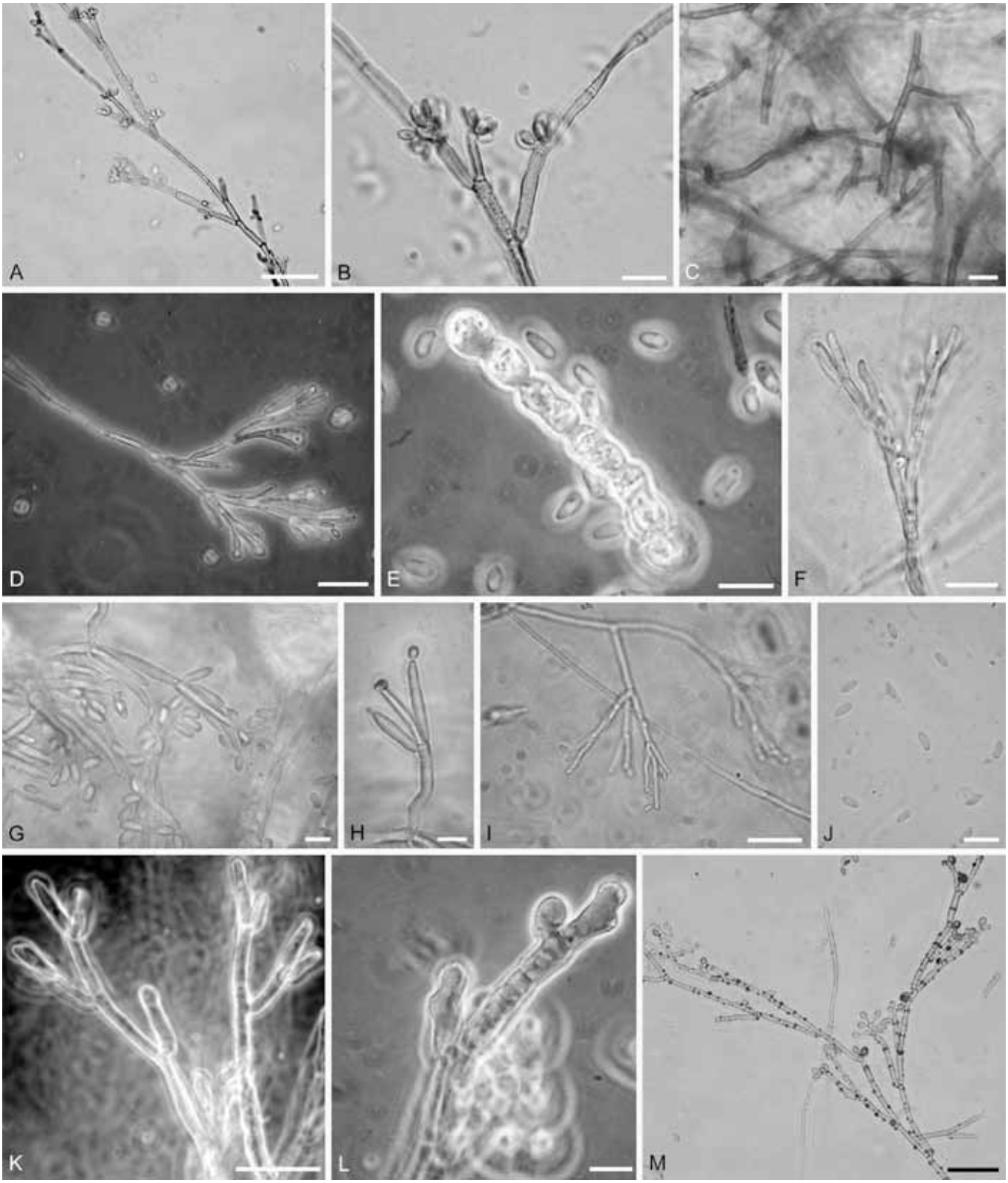



**Fig. 10.** Photomicrographs of (nodulisporium-like) anamorphic structures of the *Daldinia eschscholtzii* group. Part 1. A–F: Typical form of *D. eschscholtzii.* A, B: MUCL 43508 (Papua New Guinea), showing conidiophores with intercalary conidiogenous cells. C–E: CBS 113042 (Peru). C. Inflated melanised hyphae. D. Conidiophore. E. Chlamydospores in old cultures. F. MUCL 44145 (Cuba, *Pinus*), terminal conidiogenous cells. G–J. Aberrant forms of *D. eschscholtzii* with typical teleomorph from Malaysia. G, H: CBS 116041 ex AJSW 914–93, showing larger conidiogenous cells (H) and conidia (G, H). I, J: CBS 116036 ex AJSW 637, showing smaller conidiophores (I) and more slender conidia (J) than the typical form. K–M: *D. theissenii*. L, M, CBS 113043 (Peru, ex-type), showing conidiophore (K) and conidiogenous cells in the stage of conidiation (L); M: CBS 113044 (Argentina), showing conidiogenous hyphae covered with blackish exsudates in aged cultures and conidiogenous cells. Scale bars A, F, I, K, M = 25 µm; B, C–E, G, H, J, L = 10 µm.

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

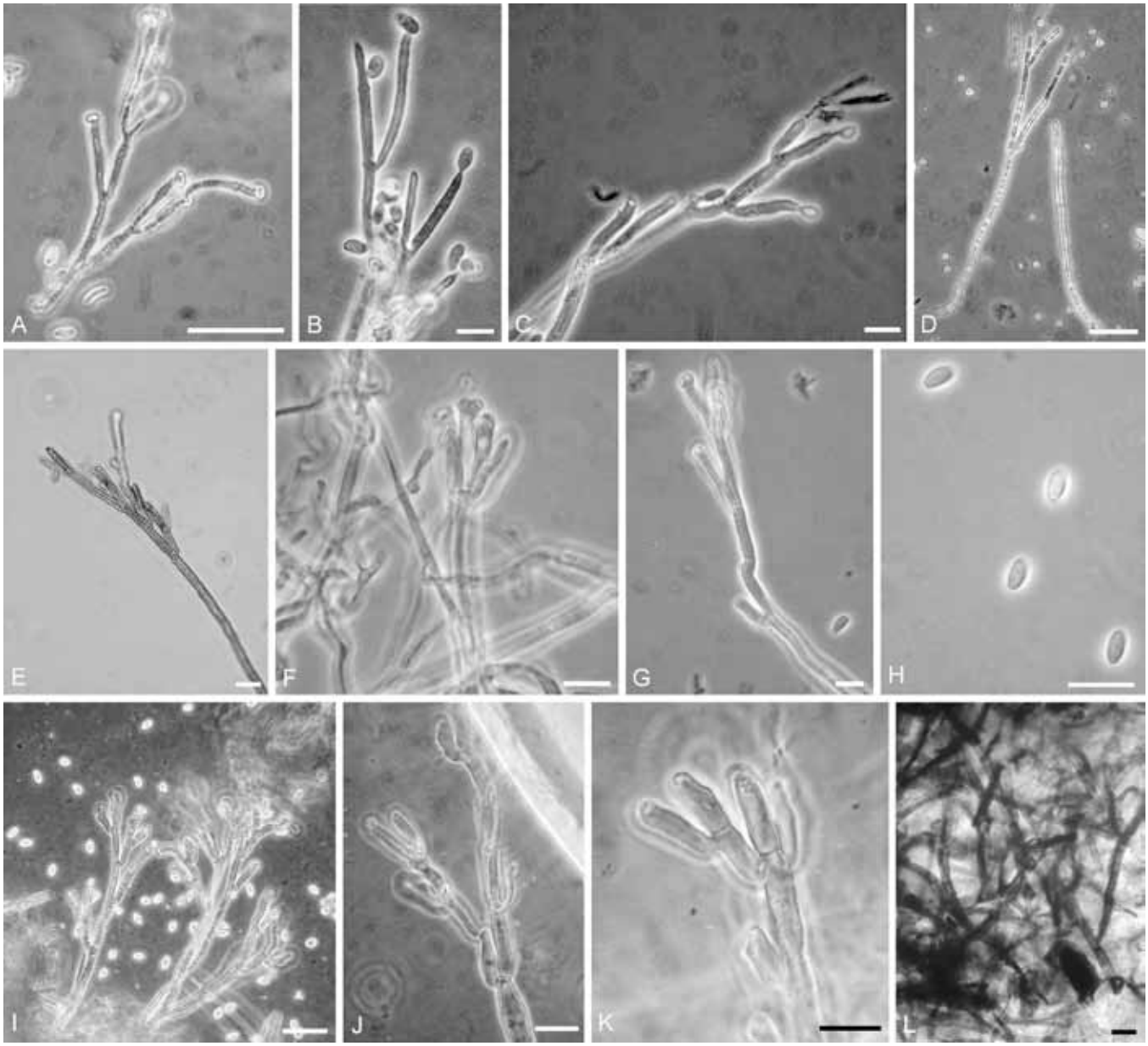



**Fig. 11.** Photomicrographs of (nodulisporium-like) anamorphic structures of the *Daldinia eschscholtzii* group. Part 2. A–D: *D. starbaeckii*, several strains, showing conidiophores with virgariella-like branching patterns. A. MUCL 52886 (Martinique), B, C. MUCL 45436, ex-type (French Guiana). D. CBS 116026 (Ecuador), E–H. *D. albofibrosa*, MUCL 38738, ex-type (Papua New Guinea). I–L. *D. caldariorum*. I. CBS 113045 (Ecuador), conidiophores and conidia. J. KC1523 (UK, from *Ulex*), conidiophore. K. MUCL 47715 (South Africa), conidiogenous cells. L. Inflated melanised hyphae. Scale bars A, D, I = 25 µm; B, C, E–H, J–L = 10 µm.

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 *Annulohypoxylon*, 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 teleomorph 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 teleomorph 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.

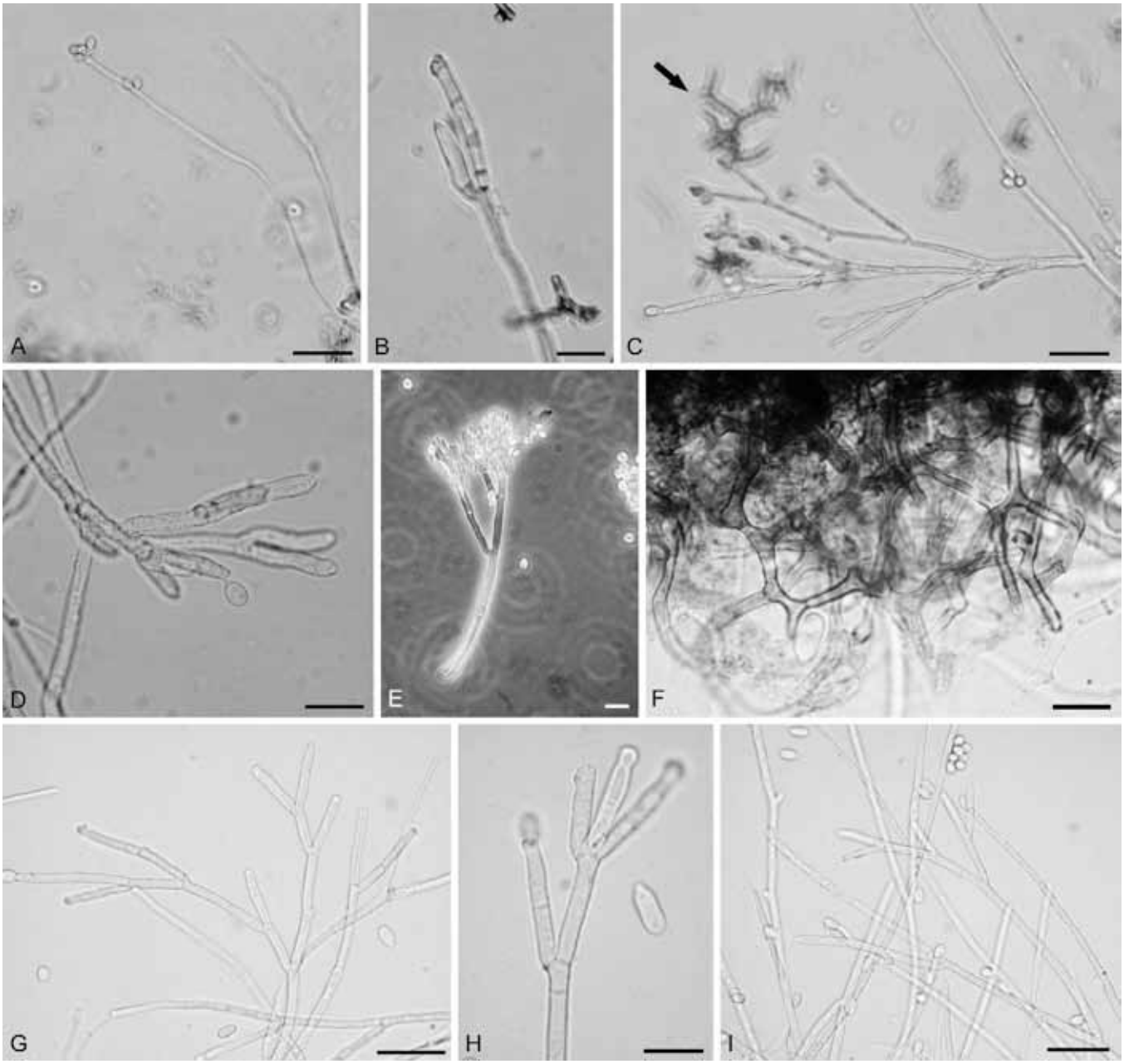



**Fig. 12.** Photomicrographs of anamorphic structures of the *Daldinia childiae* complex from OA culture. Part 1. A–C: *D. pyrenaica*, ex-type culture (Spain, MUCL 43507). A. Unbranched sporothrix-like conidiophores. B.Tip of branched sporothrix-like conidiophore. C. Nodulisporium-like conidiophores, and stromatic structure in the background, indicated by an arrow. D, E. *D. childiae*. D. *Ww 3714* (Switzerland), tip of conidiophore showing nodulisporium-like branching pattern. E. TL-9493 (Ecuador), conidiophore. F–I. *D. steglichii* (La Réunion, MUCL 53886). F. Stromatic structures arising from inflated hyphae. G. Young conidiophore, showing a virgariella-like branching pattern. H. Fully developed conidiophore showing a nodulisporium-like branching pattern with three conidiogenous cells. I. Conidiophores and conidia. Scale bars A, C, G, I = 25 µm; B, D–F, H = 10 µm. A–D were recorded by M. Briegert née Baumgartner in the course of her Diploma thesis (Baumgartner 2001).

## MATERIALS AND METHODS

*Abbreviations/Acronyms*: **AJSW**: personal herbarium of A.J.S. Whalley, Liverpool, UK. **BNT**: 1,1´–Binaphthalene–4,4'–5,5'–tetrol. **DAD**: Diode Array Detection. **JF**: personal herbarium of J. Fournier. **HPLC**: High Performance Liquid Chromatography. **JDR**: personal herbarium of J.D. Rogers, Pullman, Wa., USA. **KC**: accession numbers for cultures deposited at Kew, UK. **Kr**: personal herbarium of H. Kreisel, Potthagen, Germany. **LM**: Light Microscopy, **MS**: Mass Spectrometry. **SEM**: Scanning Electron Microscopy. **SDS:** Sodium Dodecyl Sulphate**. STMA**: personal herbarium and culture collection of M. Stadler. **TL**: fungarium of T. Læssøe (housed in C or K with duplicates of some in QCA, QCNE). **Ww**: herbarium and notebook of H. Wollweber, used as identifier for specimens located in the mycological herbarium previously housed at the Fuhlrott–Museum, Wuppertal, Germany (**WUP**). **UV/Vis**: ultraviolet/visible. **YMJ**: personal herbarium and culture collection of Yu-Ming Ju, Taipei, Taiwan.

### 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]"

[3]Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih

[4]CABI Bioscience, CBS and Landcare Research: www.indexfungorum.org (last access 14 April 2012).

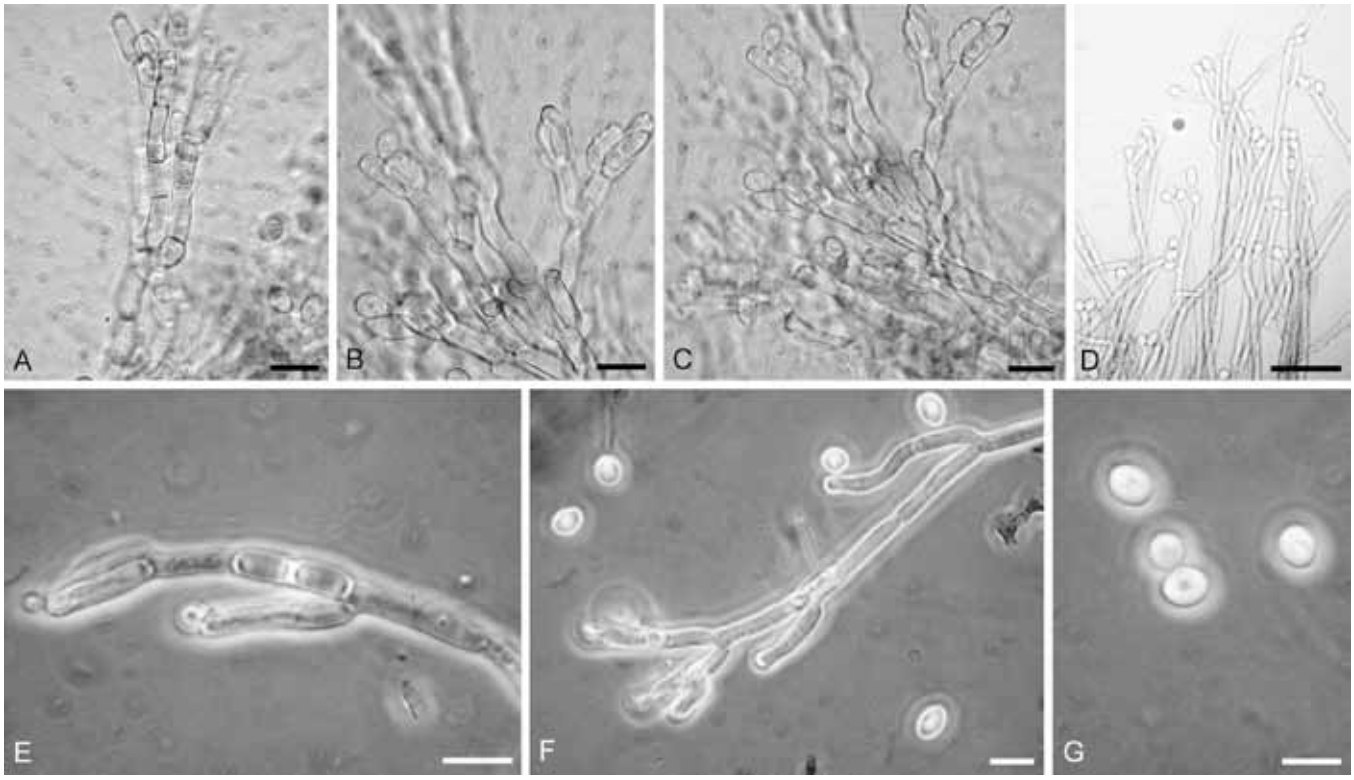



**Fig. 13.** Photomicrographs of anamorphic structures of the *Daldinia childiae* complex. Part 2. A–D. *D. australis* PDD 81102 (New Zealand), A–C. Nodulisporium-like branching pattern in OA culture after 3 wk. D. Virgariella-like anamorph on stromata. E–G. *D.* cf. *pyrenaica*, CBS 117736 (Ukraine). Virgariella-like conidiophores and subglobose conidia. Scale bars A–C, E–G = 10 µm; D = 25 µm.

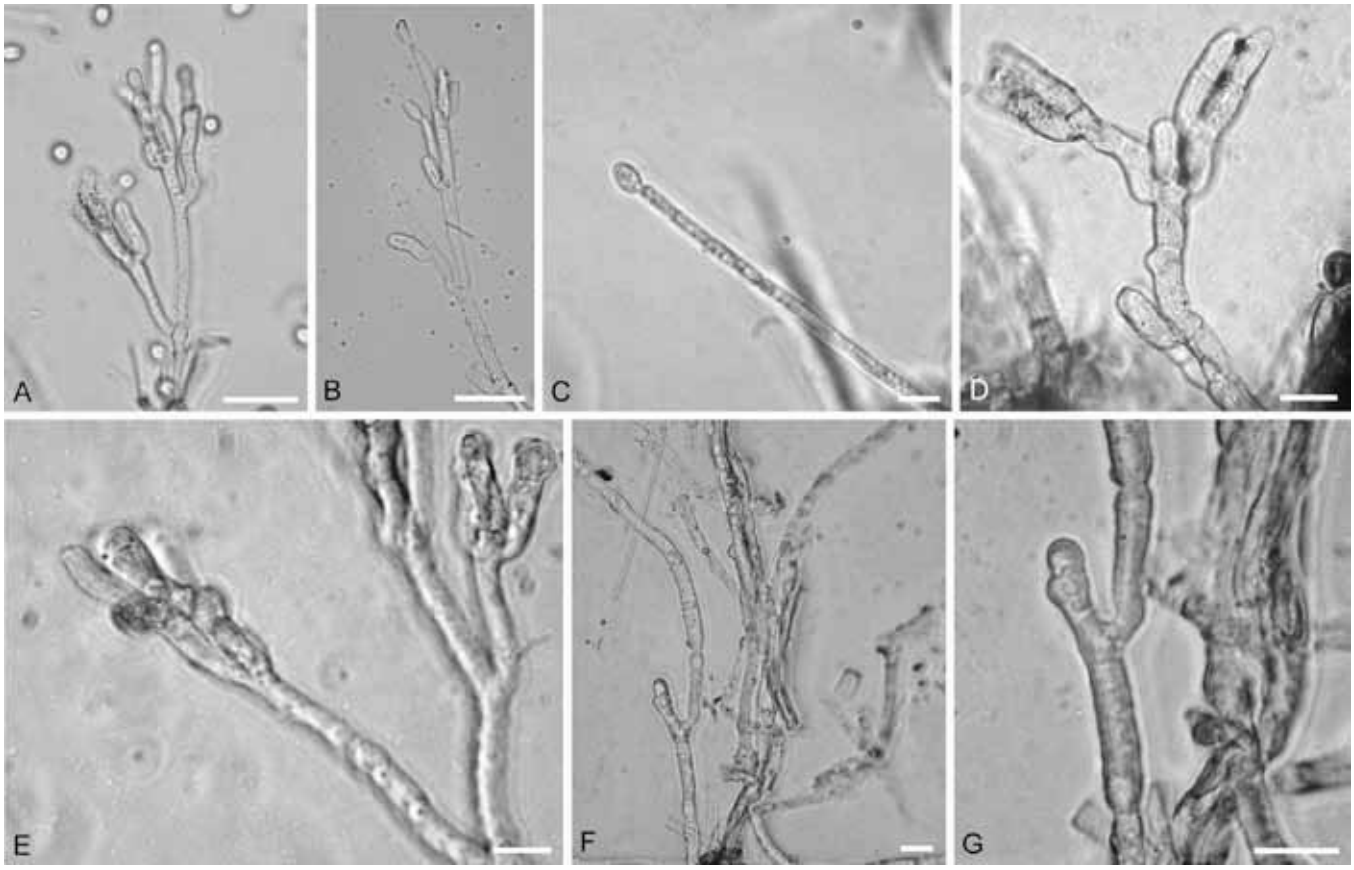



**Fig. 14.** Photomicrographs of anamorphic structures of the *Daldinia vernicosa/loculata* complex (from OA culture, phase contrast, 1000×). A. *D. loculata*. Nodulisporium-like conidiophore of MUCL 51688 (Sweden). B, C. *D. vernicosa.* nodulisporium-like (B) and sporothrix-like (C) conidiophores of 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.

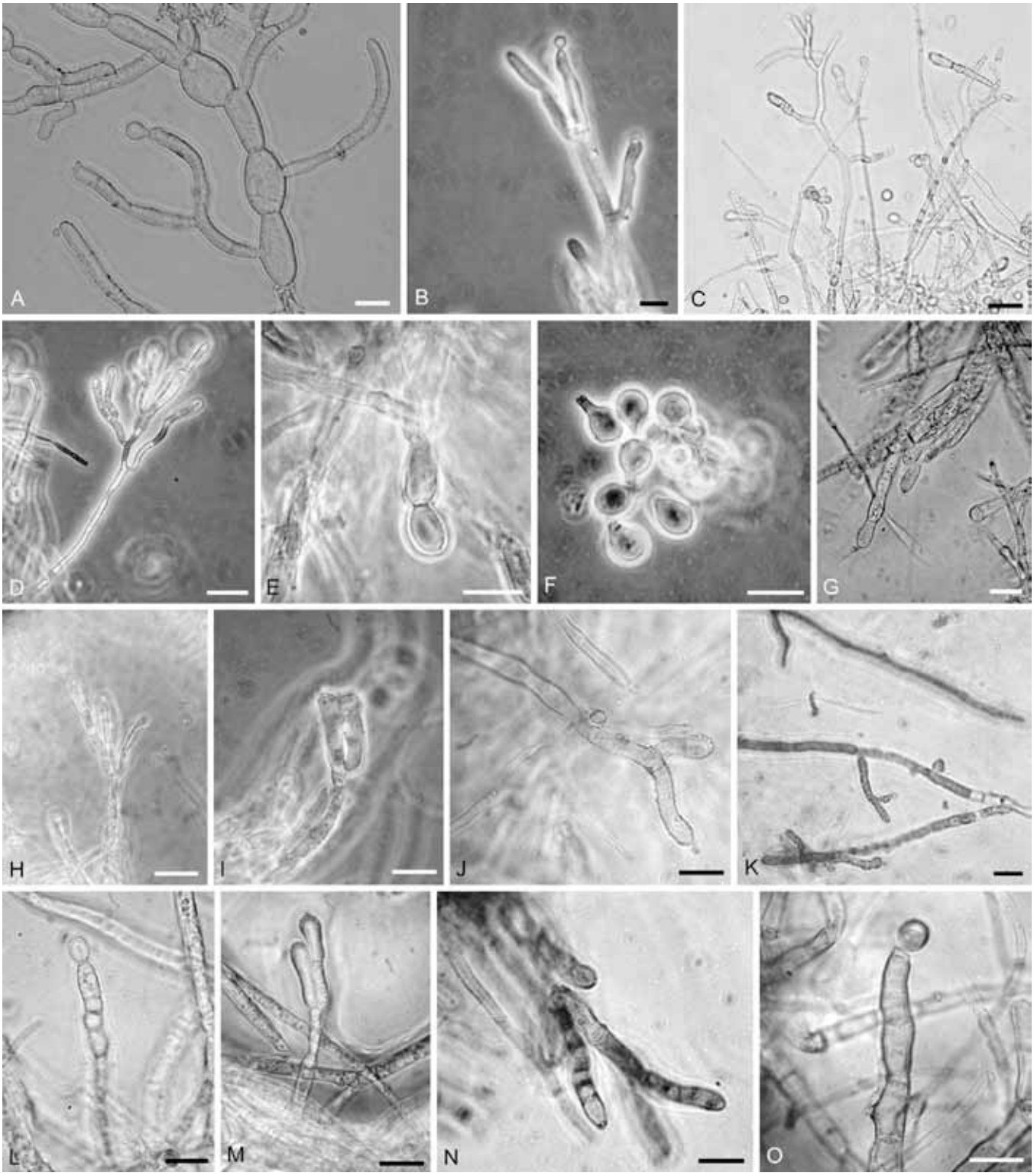



**Fig. 15.** Photomicrographs of anamorphic structures of the *Daldinia petriniae* complex. A, B: *D. petriniae*. A, MUCL 49213 (Sweden), inflated hyphae bearing conidiophores. B. CBS 119988 (Austria), conidiophores. C. *D. decipiens*, CBS 122879 (Sweden), conidiophores. D–F. *D. gelatinosa* CBS 116731 (Russia), D. Nodulisporium-like conidiophores. E. Sporothrix-like conidiophores. F. Conidia with characteristic attenuations that are often observed in this species complex. G-I *D. lloydii* CBS 113483 (Germany), conidiophores. J. *D. carpinicola*, ex-type culture CBS 122880, condidiophore. K. *D. mexicana*, culture isolated from isotype, specimen several years after collection, showing pigmented hyphae from which sporothrix-like conidiophores arise. L, M. *D. barkalovii*, ex-type culture CBS 116999, conidiophores. N, O. *D. govorovae*, ex-type culture CBS 122883. N. Conidiophore. O. Conidiophore with conidium attached. Scale bars C, D, H = 25 µm; A, B, E–G, I–O = 10 µm.

(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

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 apparati, conidiophores, and conidiogenous 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 $N_2$. 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 obovoid. 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, felty, 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 Læssøe *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

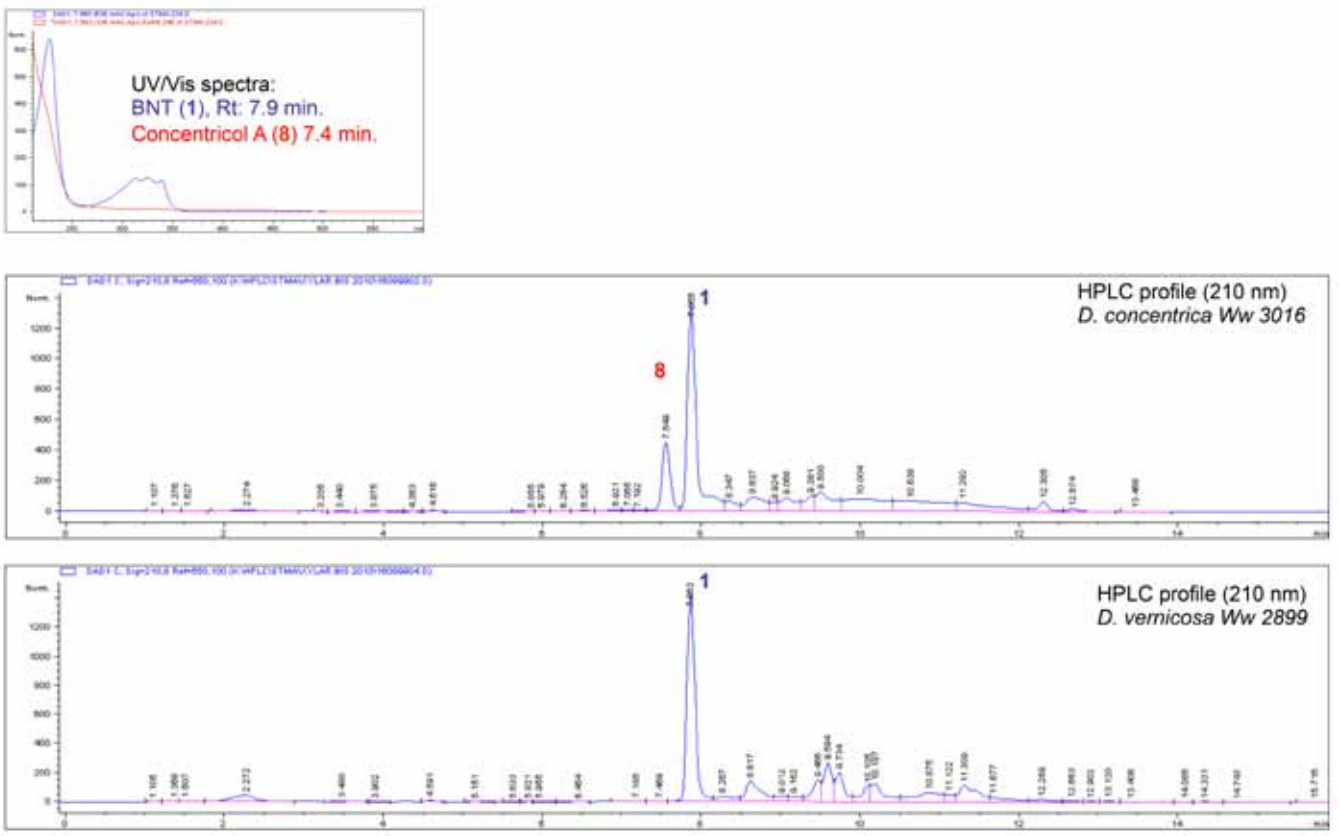



**Fig. 16.** Representative HPLC profiles (210 nm) of stromatal methanol extracts of *Daldinia concentrica* and *D. vernicosa* and DAD spectra of characteristic metabolites. The profiles are rather characteristic of the respective groups as defined in the taxonomic parts. Whereas the profile of *D. concentrica* and other members of this species complex is dominated by BNT (**1**) and concentricol A (**8**), the profile of *D. vernicosa* mainly reveals BNT (**1**) and other compounds which are presumably binaphthyl derivatives.

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 be 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

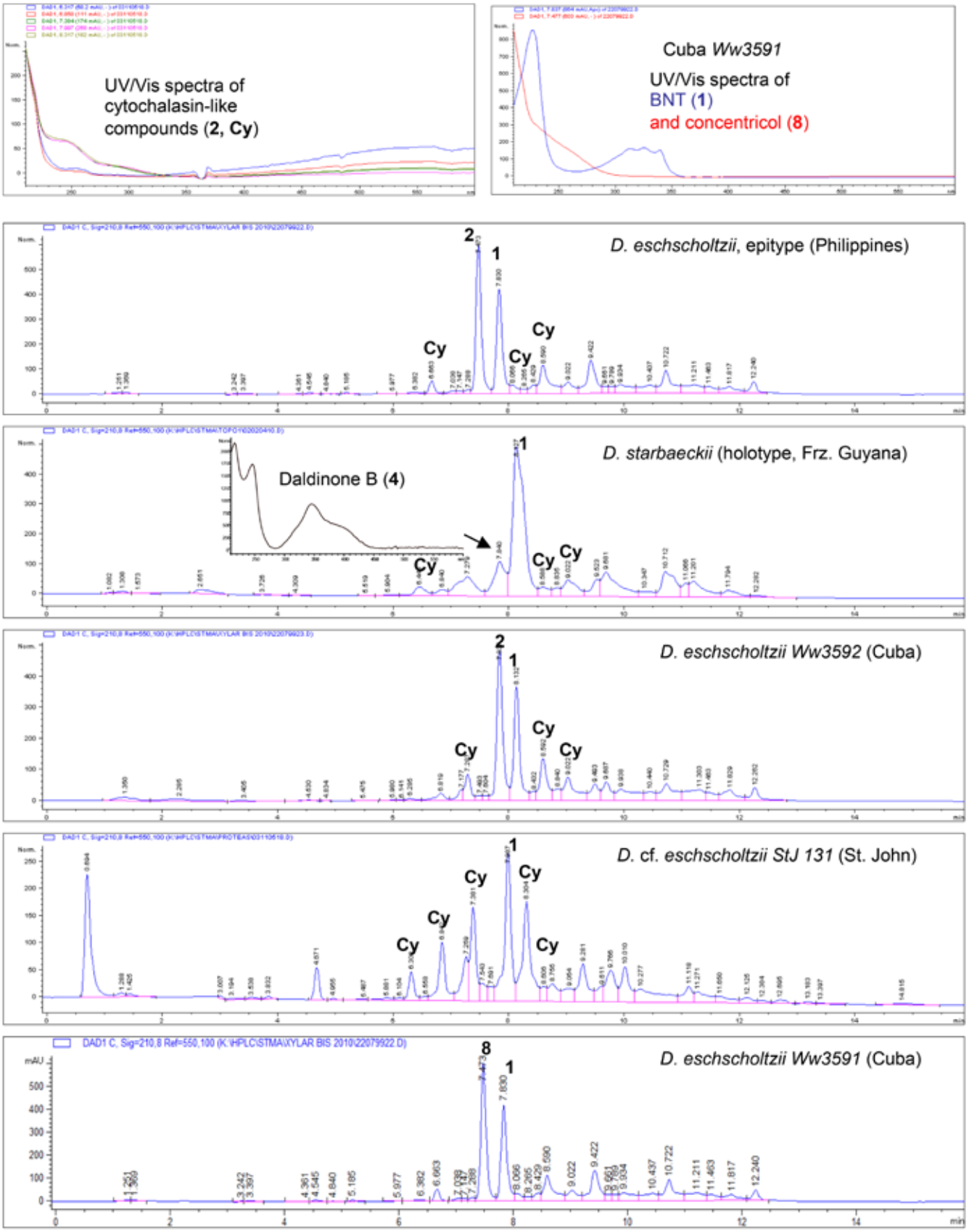



**Fig. 17.** Representative HPLC profiles (210 nm) of some specimens of the *Daldinia eschscholtzii* group and DAD spectra of characteristic metabolites. Most of these specimens contain cytochalasins (*e.g.*, **9**) in large amounts (see DAD spectra above left) and only traces of BNT (**1**), but some 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.

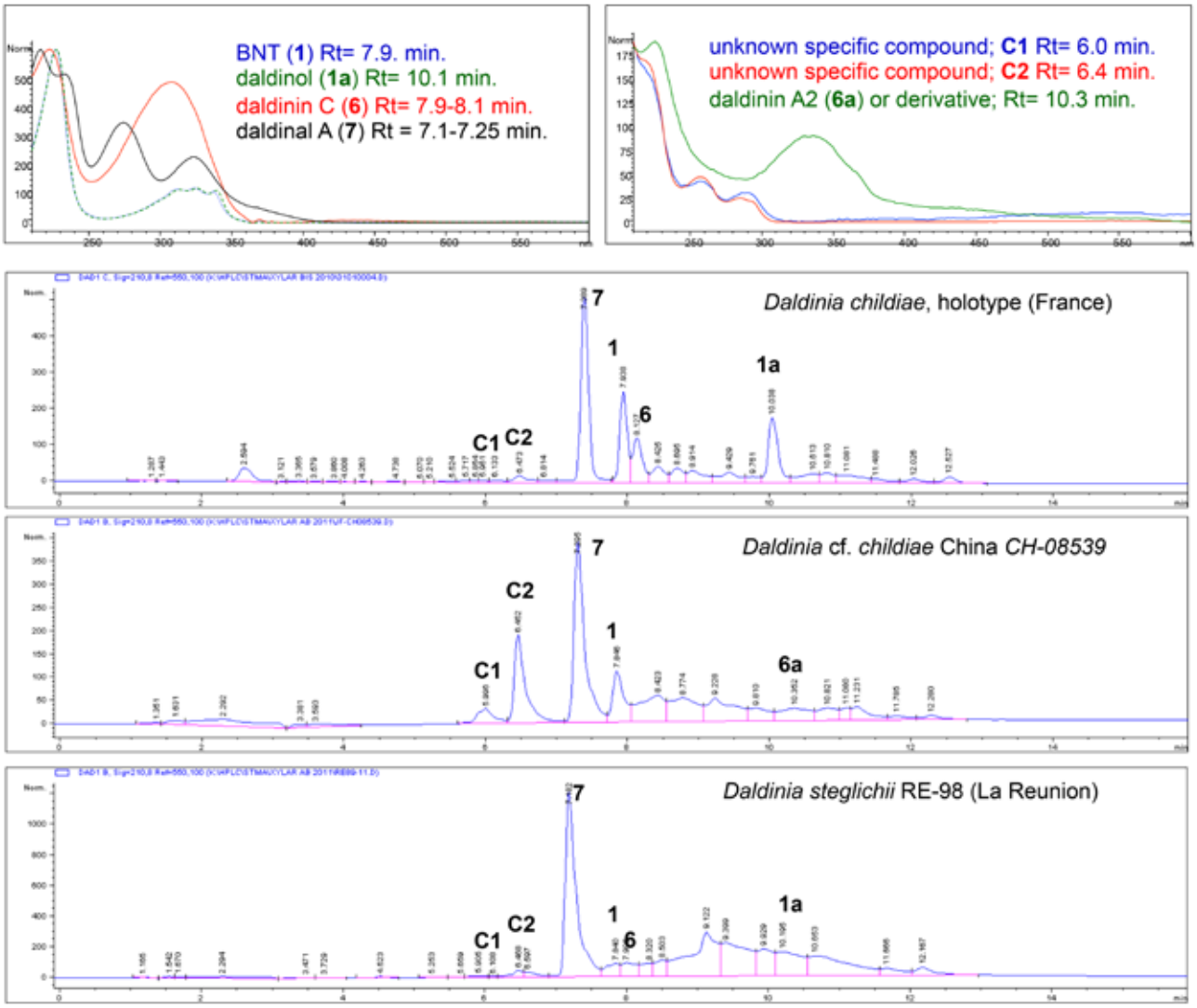



**Fig. 18.** Representative HPLC profiles (210 nm) of stromatal methanol extracts of some specimens of the *Daldinia childiae* group and DAD spectra of characteristic metabolites. The profile of *D. childiae* is also characteristic of *D. australis* and *D. pyrenaica*. *Daldinia* cf. *childiae* from P.R. China and *D. steglichii* differ in containing no detectable amounts or only minor quantities of daldinol (**1a**) and daldinin C (**6**), respectively. All species of this complex are characterised by daldinal A (**7**) being by far the most prominent stromatal metabolite. Compounds with spectral characteristis reminiscent of daldinin 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.

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

***Daldinia* Ces. & De Not.**, Comment. Soc. crittog. Ital. 1 (no. 4): 197. 1863; [*nom. cons.*], emend. M. Stadler, J. Fourn. & Læssøe.

**Kingdom** Fungi, **Division** Ascomycota, **Subdivision** Pezizomycotina, **Class** Sordariomycetes, **Subclass** Xylariomycetidae, **Order** *Xylariales*, **Family** *Xylariaceae*.

*Anamorph***:** Where known *nodulisporium*-like (cf. Ju & Rogers 1996, Ju *et al.* 1997)

**Typus**: *D. concentrica* (Bolton: Fr.) Ces. & De Not. Comm. Soc. crittog. Ital. 1 (no. 4): 197. 1863. [≡ *Sphaeria concentrica* Bolton: Fr.]

≡ *Peripherostoma* S.F. Gray, Nat. Arr. Brit. Pl. I: 513. 1821; [nom. rejic., ICBN Art. 14.4].

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

≡ *Stromatosphaeria* Grev., Fl. Edinensis: 355. 1824; [nom. rejic., ICBN Art. 14.4].

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

≡ *Hemisphaeria* Klotzsch, Acad. Caes. Leop. Nova Acta 19: 241. 1843; [nom. rejic., ICBN Art. 14.4].

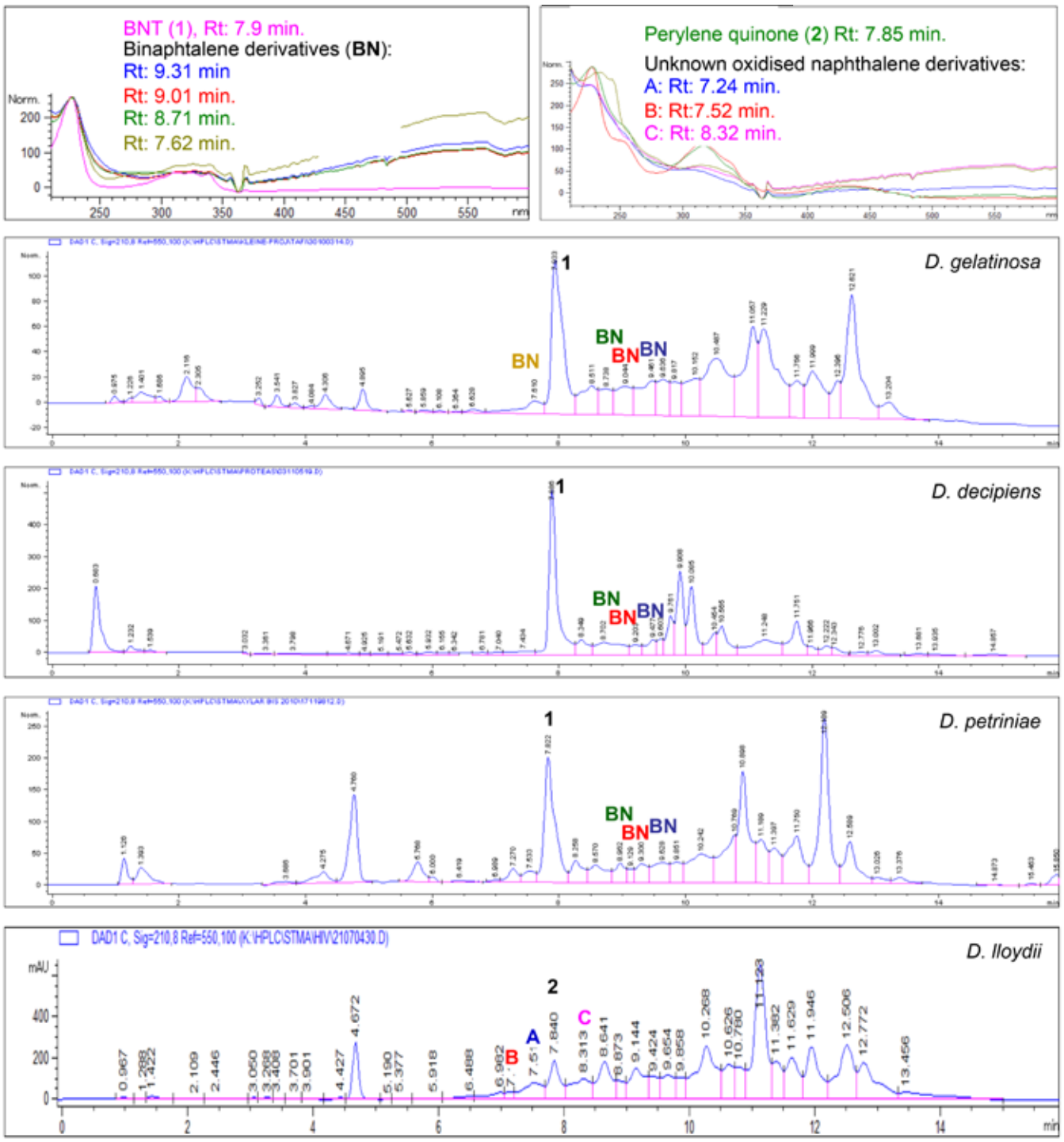



**Fig. 19.** Representative HPLC profiles (210 nm) of stromatal methanol extracts of the holotype specimens of four species of the *Daldinia petriniae* group and DAD spectra of characteristic metabolites. All profiles, except for that of *D. lloydii* reveal mainly BNT (**1**) and compounds with similar 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.

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

= *Versiomyces* Whalley & Watling, Notes R. bot. Gdn Edinb. 45: 401.1989.

**Typus**: *V. cahuchucosus* Whalley & Watling

= *Annellosporium* M.L. Davey, Karstenia 50: 3. 2010.

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

= ***Daldinia nemorosa* (M. L. Davey), M. Stadler, J. Fourn. & Læssøe, comb. nov. [MycoBank MB800145]**[5]

*Basionym*: *Annellosporium nemorosum* M.L. Davey, Karstenia 50: 3. 2010.

**Emended generic description:**
*Teleomorph*: *Stromata* conspicuous, spherical, depressed-spherical, placentiform, peltate, turbinate, clavate, or cylindrical, sessile, subsessile to stipitate, solitary to aggregated, outline smooth or with inconspicuous to conspicuous perithecial outlines. *Surface* coloured, often brown or purple in young stromata, 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* obovoid to lanceolate. *Ostioles* inconspicuous, umbilicate, discoid/annulate, slightly papillate, discoid papillate or papillate. *Asci* eight-spored, cylindrical, often very long-stipitate, with ascospores arranged uniseriately or, rarely, partly biseriately, with apical apparatus ± discoid, amyloid, rarely inamyloid. *Ascospores* brown to dark brown, unicellular in both mature and immature states, inequilaterally ellipsoid 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**) Ab-5046-B (**14**) always produced on solid and liquid media, such as yeast-malt glucose medium. Eutypinol methyl ether (**11**) and eutypine methyl ether (**12**) also present in some species, but mellein and 5-methylmellein (**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. childiae* group; D: *D. vernicosa/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:

- Ascospore shape and colour
- Dehiscence and ornamentation of ascospore perispore
- Colour of stromatal pigments in KOH (and, accordingly, presence of characteristic pigments and other secondary metabolites)
- 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 ascal apical apparati
- 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 concentricol 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.

[5]The ex-type strain of this species was not studied by us; therefore we have not included a detailed description.

**Table 2.** Salient characters of the major groups of *Daldinia.*

| Group | Perispore dehiscence (KOH) | Predominant stromatal metabolites | Ascospore ornamentation (SEM) | Ascospore shape | Conidiogenesis |
|---|---|---|---|---|---|
| *D. concentrica* group | + | BNT, **concentricols** | Species specific (smooth or striate) | Inequilateral; narrowly rounded ends | Mostly holoblastic |
| *D. eschscholtzii* group | +/- | BNT, **cytochalasins** | Species specific (smooth or striate) | Inequilateral; mostly narrowly rounded ends | Holoblastic |
| *D. graminis*/*D. sacchari* | - | BNT, **cytochalasins** | Conspicuously striate | Inequilateral; narrowly rounded ends | Unknown |
| *D. childiae* group | | BNT, **daldinal**, **daldinins** | Conspicuously striate | Inequilateral; narrowly rounded ends | Holoblastic |
| *D. vernicosa/loculata* group | - | BNT | **Smooth** | **Equilateral to inequilateral; broadly rounded ends** | Holoblastic |
| *D. petriniae* group | + | BNT, **perylene quinones** | Conspicuously striate | Inequilateral; narrowly rounded ends | **Annellidic** |

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 dehiscent 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 mature state, owing to the presence of BNT (**1**). Interestingly, stromata of all northern temperate species of this group, of which a significant number of specimens was studied, become mature in the spring (February-May, depending on the geographic region). In contrast, stromata of all other *Daldinia* spp. of the temperate Northern Hemisphere usually become mature later in the year. A common chemotaxonomic marker molecule which is present as major stromatal metabolite in all African and European specimens so far studied by HPLC profiling is concentricol A (**8**; see HPLC chromatogram in Fig. 16). This compound co-occurs with BNT (**1**), except in the majority of *D. dennisii* specimens and *D. andina*.

A synpopsis 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.

***Daldinia concentrica*** (Bolton: Fr.) Ces. & De Not., Comm. Soc. crittog. Ital. **1**(no. 4): 197. 1863.
Figs 4A, B, 9A–C, 20, 21.

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

≡ *Sphaeria concentrica* Bolton, Hist. Fung. Halifax III: 180. 1789; Bolton : Fr., Syst. Mycol. II: 331. 1823; non Wahlenberg, 1812.
≡ *Peripherostoma concentricum* (Bolton: Fr.) Gray, Nat. Arr. Brit. Pl. I: 513. 1821.
≡ *Stromatosphaeria concentrica* (Bolton: Fr.) Grev., Fl. Edinensis: 355. 1824.
≡ *Hypoxylon concentricum* (Bolton: Fr.) Grev., Scot. Crypt. Fl. VI: pl. 324. 1828.
≡ *Hemisphaeria concentrica* (Bolton: Fr.) Klotzsch, Acad. Caes. Leop. Nova Acta 19: 241. 1843.

*Holotype*: Bolton, J. 1789. A history of fungusses growing about Halifax III. Huddersfield, plate 180. *Supporting material* (*fide* Rogers *et al.* 1999): **UK**, Captn Hope's Pleasure grounds, sent by E. Robson to J. Bolton, on stumps placed for seats, apparently immature (SUN).

*Epitype* (selected by Rogers *et al.* 1999): **UK**, England, Durham, Cassop Vale, May 1975, *Fraxinus*, A.J.S. Whalley *234* (K(M) 171995).

**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).

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

**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.

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

= ? *Valsa tuberosa* Scop., Fl. Carniol. II, ed. 2: 399. 1772.
≡ *Sphaeria tuberosa* (Scop.) Timm, Fl. Megapol. Prodr., p. 279. 1788.
≡ *Daldinia tuberosa* (Scop.) J. Schröt., Jahresber. Schles. Ges. Vaterl. Cult. 59: 464. 1881.
≡ *Hypoxylon tuberosum* (Scop.) Wettst., Verh. K. K. Zool.-Bot. Ges. Wien 35: 591. 1885.
= *Lycoperdon fraxineum* Hudson, Fl. Angl. ed. 2, II: 641. 1778.
= *Sphaeria fraxinea* Sibth., Fl. Oxon.: 401. 1794.
= ? *Sphaeria tunicata* Tode, Fung. Mecklenb. Sel. II, p. 59. 1791.

*Selected illustrations*: Whalley & Watling (1980), figs 1, 2 (teleomorph and SEM of anamorph); Petrini & 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).

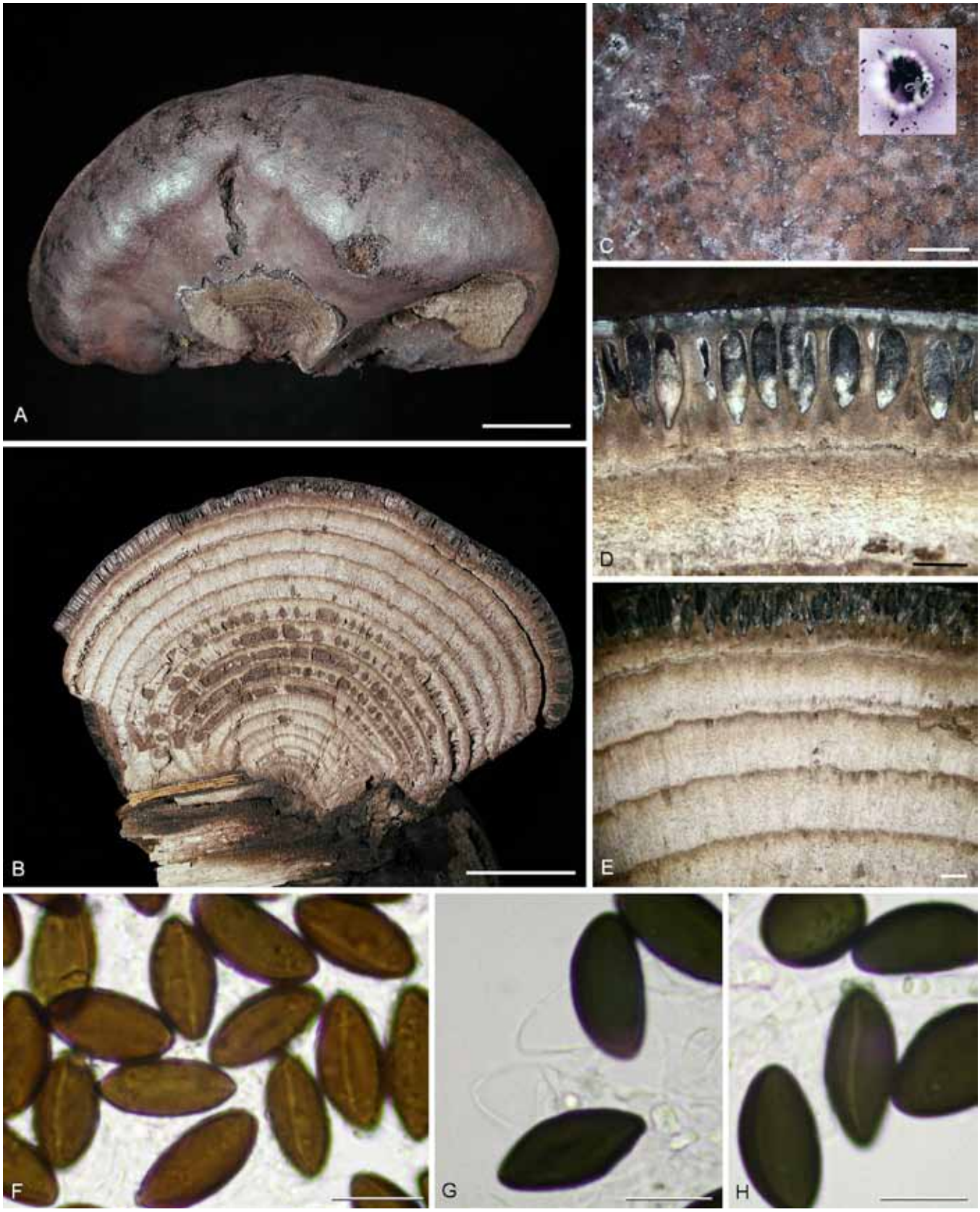



**Fig. 20.** Teleomorphic characteristics of *Daldinia concentrica.* Epitype K(M) 171995 (UK). A. Stromatal habit. B, D, E. Stroma in longitudinal section showing internal concentric zones and perithecial layer. C. Stromatal surface showing the characteristic reticulate surface structure, with stromatal pigments in 10 % KOH inserted. F. Ascospores in SDS. G, H. Ascospores in KOH, showing dehiscing perispore and sigmoid germ slit. Scale bars A, B = 1 cm; C–E = 1mm; F–H = 10 µm.

*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.

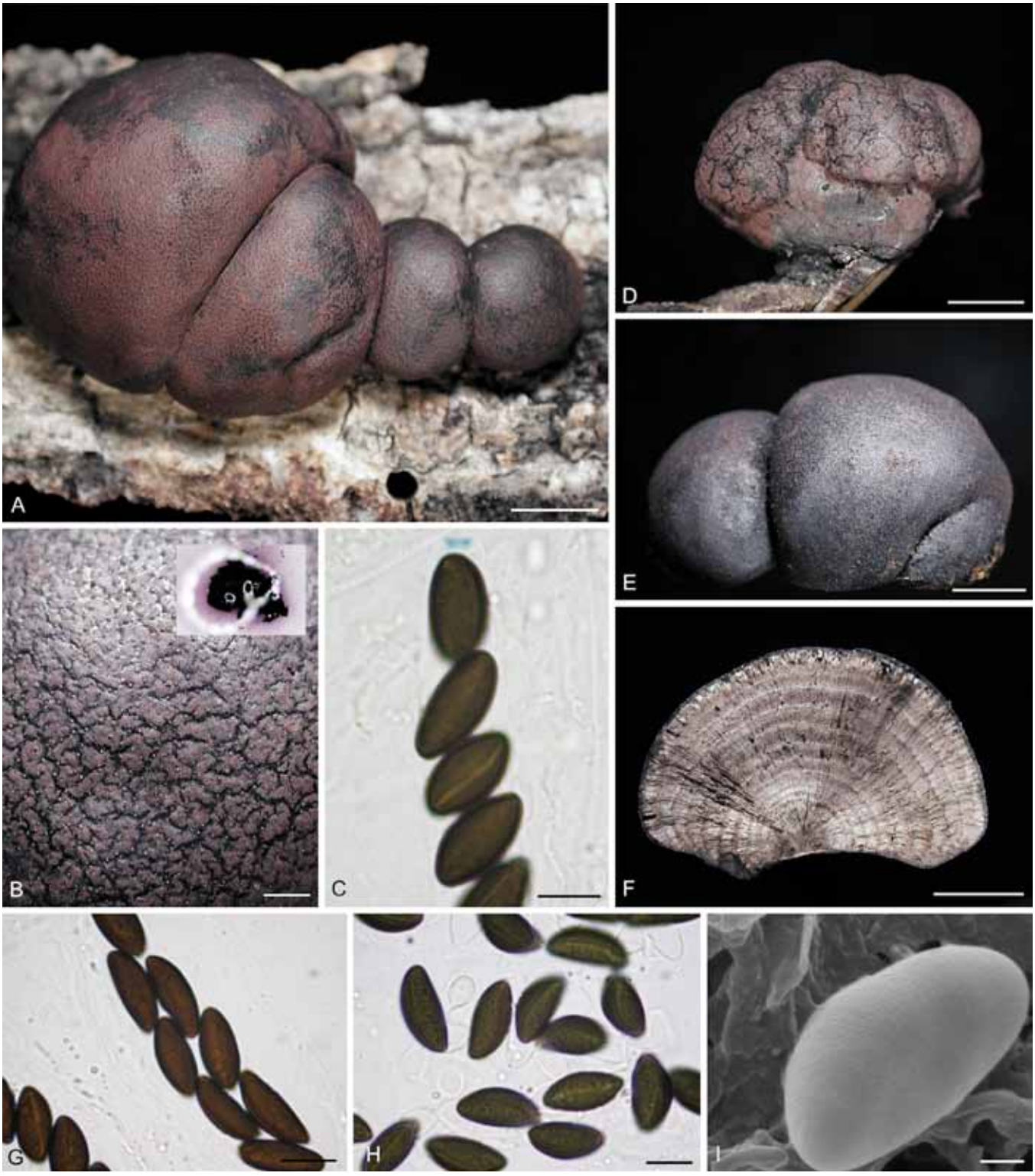



**Fig. 21.** Teleomorphic characteristics of *Daldinia concentrica*. A–C, F–H. *JF-09129* (*Fraxinus*, France). D. *JF-08146* (*Ailanthus*, France). E. *JF-05055* (*Fraxinus*, France). I. *Ww 3739* (*Fraxinus*, Germany). A, D, E. Stromatal habit. B. Stromatal surface showing the characteristic reticulate surface structure, with stromatal pigments in 10 % KOH inserted. C. Ascospores and ascus in Melzer's reagent, revealing amyloid apical rings. F. Stroma in longitudinal section showing internal concentric zones and perithecial layer. G. Ascospores in SDS. H. Ascospores in KOH, showing dehiscing perispore and straight to sigmoid germ slits. I. Ascospores by SEM (10.000×). Scale bars A, D, E, F = 1 cm; B = 1 mm; C, G, H = 10 µm; I = 2 µm.

*Teleomorph*: *Stromata* hemispherical to depressed-spherical, widely attached to the substrate, very rarely substipitate, 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 length on convex side; perispore dehiscent in 10 % KOH, appearing smooth, showing very faint ridges by SEM only at 10.000×.

*Cultures and anamorph*: Colonies on OA reaching the edge of 9 cm Petri dish in 8–11 d, at first whitish, felty, azonate, with diffuse margins, becoming tan to grey with green tones; reverse Citrine (13) or Dull Green (70). Sporulating regions scattered over entire surface of colony, Buff (45) to Honey (64). Conidiogenous structure nodulisporium-like. *Conidiophores* up to 300 × 3–3.5 µm, di- or trichotomously branched, hyaline, roughened, 3.5–4.5 µm diam, with 2–4 conidiogenous cells arising from each terminus. *Conidiogenous cells* cylindrical, hyaline, finely roughened, 10–25 × 3–4 µm. *Conidia* produced holoblastically in sympodial sequence, hyaline, smooth to finely roughened, ellipsoid, often with flattened base, (5.5–)6.5–8(–9) × 3.5–4.5 µm.

*Additional specimens examined*: **Austria**, Carinitha, Spittal, Lieserweg toward Seeboden, near Millstädter See, on wood of *Alnus*, 21 Jul. 1991, H. Staub (KR 12095). **Belgium**, Antwerpen, Ravels, 8 Aug. 1942, N. Tuymans *3930* (BR–Myc 072810,60); Wijnegem, on dead trunk, 14 Apr. 1996*,* J. Volders (BR–Myc 1389686.82); Brabant, Bruxelles, 1906, E. Bommer & M. Rousseau (BR–Myc 072814,64); Groenendahl, Hoeilaart, on tree trunk, 1882, E. Bommer & M. Rousseau ex Gravis (BR–Myc 072820,70); Kerkom, Sep. 1960, P. Martens (BR–Myc 072809,59); Meise, 10 Jan. 1989, H. de Meulder *4887* (BR–Myc 013638,58); Oud–Heverlee, Kouterbos, *Populus*, 24 Mar. 1994, J. Monnens *94.02* (BR–Myc 033502,35); Villers–la–Ville, *Fraxinus*, 5 May 1984, P. Piret (BR–Myc 072832,82); same loc. and host, 9 May 1986, J. Rammeloo *8653* ex herb. Piret (BR–Myc 001769,23); same loc. and host, 8 May 1987, P. Piret (BR–Myc 018963,48); Zemst Laar, Keempoel, Aug. 1969, N. Cnops (BR–Myc 017791.40); Hainaut, Ath, *Betula alba*, Aug. 1915, A.S. Gilson (BR–Myc 072818,68); Bouffioulx, on cf. *Populus*, 24 Apr. 1955, P. Heinemann *2118* (BR–Myc 072819,69); Limburg, Kanne, 15 May 1980, J. Rammeloo *6814* (BR–Myc 072827,77); same locality, *Fraxinus*, 1964, J. Moens (BR–Myc 072830,80); Oost–Vlaanderen, Natuurpark Scheldeland, *Populus*, 5 Sep. 1970, J. Moens *1190* (BR–Myc 072829,79); Overmere, Carnardiére, *Fraxinus*, 1912*,* E. Bommer & M. Rousseau (BR–Myc 072824,74); same locality, *Fraxinus*, 1913*,* E. Bommer & M. Rousseau (BR–Myc 072813,63); same locality, *Fraxinus*, 21 Jun. 1906, P. Nypels (BR–Myc 072817,67); same locality, *Fraxinus*, Apr. 1914*,* E. Bommer & M. Rousseau (BR–Myc 072823,73); same locality, *Fraxinus*, no date*,* E. Bommer & M. Rousseau (BR–Myc 072821,71); Overmere, Oct. 1915, M. Beeli *100* (BR–Myc 072807,57); Overmere, Donk, Jul. 1965, J. Moens, det. K. Laureys (BR–Myc 072831,81); West–Vlaanderen, Adinkerke, on trunk of cf. *Populus*, 3 May 1955, P. Heinemann *2120* (BR–Myc 072826,76); West-Vlanderen, de Haan, on cf. *Populus*, 1912*,* E. Bommer & M. Rousseau (BR–Myc 072825,75); exact locality unknown, 1900, L. Imler ex herb. Frison (BR–Myc 044615,62). **Bulgaria**, natural territory Ropotamo, autocamping "Arkutino", on living trunk of *Fraxinus*, 14 Jun. 1977, J. Kuthan (PRM 824793). **France**, Aude: Saint Papoul, in a private garden, on *Populus* sp., 4 Jun. 2010, *JF-10076* (JF). Côte d'Or: Bomberain, road to Bèze, on *Ailanthus altissima,* 12 Feb. 2008, A. Parizot & A. Gardiennet, kept ripening by JF outside in his garden until late May 2008, *JF-08146*; Deux Sèvres, Virollet, Forét de Chizé, *Fagus sylvatica*, 26 Apr. 2004, Ch. Lécuru, *JF-04045* (KR, culture MUCL 51681); Maillezais, *Fraxinus*, 27 Jun. 1999, M. Stadler, *Ww 3589* (KR 0026329); Haute Garonne, Vigoulet Auzil, on *Fraxinus excelsior*, 30 Apr. 2000, *JF-00053* (JF). Pas–de–Calais, Wissant, *Fraxinus excelsior*, no date, C. & E. Bommer (BR–Myc 0993369,55, culture MUCL 51681); Var, Chateau Vert, banks of Argens brook, on *Fraxinus excelsior*, 29 Apr. 2010, Paul Pirot, *JF-10058* (JF); Vendée: Mervent, Pont du Déluge, on *Fraxinus excelsior*, 12 May 2009, Pierre Lejay, *JF-09128* (JF); exact locality unknown, Bretagne, *Fagus*, 25 Aug. 1992, H. Wollweber *Ww 2357* (KR 0026337, culture MUCL 51689). **Germany**, Mecklenburg-Vorpommern, Burgruine Landskorn, *Fraxinus excelsior*, Apr. 2011, K. Toballa, comm. H. Kreisel, *STMA11178* (KR, culture MUCL 53970); Greifswald, Lubzower Forst, dead wood of cf. *Fraxinus excelsior*, 2 May 2007, N. Amelang, *STMA 07014* (KR, culture CBS 121672, MUCL 49333); North Rhine Westphalia, Bergkamen, on fallen trunk of *Fagus sylvatica*, 13 Feb. 2000, H. Wollweber *Ww 3747* (WUP); Bielefeld, Brönninghausen, on *Fagus*, 16 Jun. 1996, H. Wollweber *Ww 3080* (WUP)*;* Cologne, Zoo, *Fagus*, 7 Apr. 1995, B. &. M. Stadler, *STMA 05061* (STMA, culture MUCL 54179); Haan-Gruiten, Neandertal, Winkelsmühle, 5 Jun. 2001 (M, culture CBS 113277, GenBank Acc. No. AY616683, see Triebel *et al.* 2005); same locality and host, 24 Sep. 2004, M. Stadler (BPI 863987); same locality and host, 26 Aug. 2005, B. & M. Stadler *STMA 06222A* (PDD 77090); same locality and host, 7 Apr. 1998, H. Wollweber, *Ww 3316* (KR 0026339); same locality and host, B. & M. Stadler (KR 0012090); exact locality unknown, *Alnus*, 5 Mar. 1989, I. & W. Sonneborn in herb. Krieglsteiner *KR 319/89, Ww 4104* (STU, WUP); Rheinland-Pfalz, exact locality unknown, *Alnus*, 17 Sep. 1989, G.J. Krieglsteiner *KR 593/89* (STU, WUP). **Greece**, Isle of Crete, Jrini Gorge, on dead *Platanus orientalis*, Aug. 1998, D. Weiß ex herb. D. Benkert (B, culture CBS 117124); Isle of Rhodes, unidentified broadleaved wood, 20 Oct. 2004, F. Dämmrich, comm. M. Eckel, *STMA 05058,* K(M) 130020 (culture KC1696, MUCL 52885). **Italy**, Napoli, 1883, E. Bommer & M. Rousseau ex herb. Gravis (BR–Myc 0993368,54); Pisa, *Populus*, Apr. 1992, F. Bellu, *Ww 3598* (WUP ex Museo Cantonale Ticino, see Stadler *et al.* 2001a); Sicily, Catania, Natural Reserve Simeto, *Acacia cyanophylla*, 7 Apr. 2001, A. Lantieri (BR-Myc 149948.83, culture MUCL 46679); Palermo, Bosco della Ficuzza, *Quercus pubescens*, Mar. 2003, G. Venturella (PAL, culture MUCL 49358); exact locality unknown, 1860, De Notaris (CWU R 570), probably material studied by Cesati & De Notaris (1863). **Netherlands**, Zeeland, S of Beveland, *Ulmus*, 16 Mar. 1952, B.J.J.R. Walbrecht (UPS). **Serbia**, Pirot ("SE Serbia"), on oak wood in cellar, Sep. 1900, collector unknown (B70 0009601). **Spain**, Cordoba, Lucena, on dead wood in public park, 29 Aug. 1998, J. Carlos & J. Pablo Campos (MA 40250); Jaen, Linares, *Salix babylonica*, 23 Nov.1997, F.D. Calonge (MA 39285); Logroño, Brieva de Cameros, trunk of *Carpinus*, M. Barba (MA 33555); Madrid, Aldea del Fresno, *Fraxinus*, A. Moreno, 20 Mar.1982 (MA 13425); same locality, *Fraxinus*, Nov. 1994, F.D. Calonge (MA 33257); El Escorial, *Populus*, 30 Mar. 1987, D. Gutierrez (MA 19453); same locality, Finca La Pizarrera, *Fraxinus*, 15 Jun. 1988 J.M. Castellano (MA 21129); Villa del Prado, dead wood, 4 May 1997, F.D. Calonge (MA 36716); same locality, *Fraxinus*, 16 May 1999, J.C. Campos (MA 41312); Mallorca, Sporlas, on deed branch of *Ulmus minor*, 11 Sep. 1987, A. Martínez de Azagra (MA 22456). **Switzerland**, Bern, Belp, Belpberg, 600 m, on cf. *Juglans* in beech forest, 5 Apr. 1998, B. Senn-Irlet, H. Wollweber *Ww 3717* (BERN, WUP). **UK**, England, Berkshire, Kintbury, Inkpen, 21 Jan. 1978, D.W. Minter (IMI 225370); Buckinghamshire, High Wycombe, Hazlemere, Penn Wood, *Fagus sylvatica,* 10 Feb. 2009, P. Cullington (K(M) 162574[6]; Devon, Slapton woods, "*Fraxinus excelsior* and *Acer* sp.", 2 Apr. 1978, Asperges (BR–Myc 093356,41); Devon, exact locality not stated, *Fraxinus excelsior*, 1994, collector not stated (IMI 362151); Castle Eden Dene NNR, A.J.S. Whalley *240* – K(M) 171997; Witton Le Wear, Whalley *230* – K(M) 171996; Greater London, London, Regents Park, unburnt part of living *Fagus sylvatica*, internal wood damaged by fire at the base, 6 Mar. 2005, K. Mottram, *STMA 05063*, K(M) 130021, culture KC1697. Herefordshire, Ledbury, on attached branch of *Quercus robur*, 16 Jun. 2002, comm. E. Blackwell, K(M) 98806, culture KC 1693. Norfolk, King`s Lynn, on putrid trunk of *Fraxinus excelsior*, 1874, ex herb. C.B. Plowright, de Thümen, Mycotheca universalis *No. 69* (BR–Myc 0993363,49; 5 packets in NY); same locality, no date, M.C. Cooke, Fungi Britannici Exsiccati, 2th Ed. *216*, in herb. Saccardo (PAD). Hertfordshire, near Buntingford, Wyddial, Caprons wood, on old dead, standing tree of *Prunus spinosa*, 6 Mar. 2002, K. Robinson, K(M) 95236, culture KC 1686; near Baldock, Weston Hills, on fallen log of *Fagus sylvatica*, 8 Apr. 2002, K. Robinson, K(M) 98272, culture KC 1689. North Yorkshire, north of Thornton le Dale, *Fraxinus excelsior*, 9 May 2005, W. Jaklitsch *WJ3137* (WU); Somerset, *Fraxinus*, 1957, collector not stated (IMI 70208); Suffolk, Stonham Aspal, 'Lagand', on unburnt trunk, *Betula* sp., 25 Apr. 2009, N. Mahler, K(M) 163123; Surrey, Ranmore Co., *Fagus sylvatica*, 18 Dec. 1955, Booth (IMI 60994); Kew Gardens Conservation Area, *Fagus sylvatica*, 24 Nov. 2001, A. Henrici, K(M) 91667, culture KC 1688. West Sussex, Lime Regis Underclif on trunk of a fallen ash (*Fraxinus*), 10 Apr. 1976, G. Raeymakers *14* (BR–Myc 093356,42); Upper Yorkshire, Victoria, ex herb. G. Massee, "purchased 1909" (NY); Lancashire, Liverpool, Speke Hall, *Fraxinus excelsior*, 10 Sep. 1972, BMS Foray, J.A. Nannfeldt (UPS); West Yorkshire, Halifax, Black Brook, *Ulmus,* Apr. 1998, M.W. Sykes *SE 086208*, mixed collection with *D. loculata*, K(M) 57450(2), culture KC1365; West Sussex, Horsham, Warnham Local Nature Reserve, on logs of *Betula pubescens*, 19 Nov. 2009, V. Hodge, K(M) 168855. Wales, Carmarthenshire, vicinity of National Botanic Garden, Tywi Valley near Porthyrhyd, *Fraxinus excelsior*, 20 Apr. 2001, *STMA 01007* (M, culture CBS 113278, GenBank Acc. No. of DNA sequence AY616682, see Triebel *et al.* 2005). Ceredigon (Cardiganshire): Lampeter, Falcondale, Fern Cottage, on dead branches of *Prunus serrula*, 1 Apr. 2001, M. Rotheroe (K(M) 84463, culture KC 1687).

*Notes*: This study and other data provided by Petrini & 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

[6]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 *D. concentrica* (*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 characters and dimensions of conidiogenous structures agree with *D. concentrica*, and even molecular data are not well-suited for their discrimination (see further below in Results on molecular phylogeny). We cannot exclude that they have become degenerate in storage.

Interestingly, this species was also rather frequently encountered among the specimens in MA, derived from the Madrid area and even in the rather hot climates of Central Andalucía. Morphological studies and HPLC analyses of a specimen in CWU revealed that at least one of the records of Cesati & De Notaris (1863), indeed, corresponds with *D. concentrica sensu stricto*. Previous work (Johannesson *et al.* 2000, Wollweber & Stadler 2001) had revealed relatively few records of true *D. concentrica* from Northern, Central and Eastern Europe. Even Saccardo's concept of *D. concentrica* obviously included various taxa of *Daldinia*, as revealed from an examination of his herbarium at PAD. Some of his specimens are listed elsewhere herein. Typical stromata of *D. concentrica* are here reported from Bulgaria and the Greek isles of Crete and Rhodes. In none of these cases was *Fraxinus* reported as the host plant. These findings should give reason to evaluate the actual distribution of this species in southeast Europe and the Mediterranean. The species has been searched for in southernmost Sweden for the last decennia but still without luck. Only immature stromata of what could be *D. concentrica* have several times been found on *Fraxinus* (S.-Å. Hansson and B. Nordén, pers. comm.). 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.

***Daldinia andina*** Læssøe, J. Fourn. & M. Stadler, **sp. nov.** MycoBank MB800022. Figs 4J–L, 22.

*Diagnosis*: *A Daldinia grandis differt ascosporibus regulariter ellipsoideo-inequilaterales cum perisporibus indehiscentes, apicibus non angustatis.*

*Holotypus*: **Ecuador**, Pinchincha, Pasochoa, 00° 28' S, 78° 30' W, 2900 m alt., on cut *Alnus acuminata* trunk in *Chusquea* dominated mountain forest, 18 May. 2002, T. Læssøe *TL-9572*, (C-F-58309 - **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 spore 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 equilateral ascospores with broadly rounded ends and indehiscent perispore being the

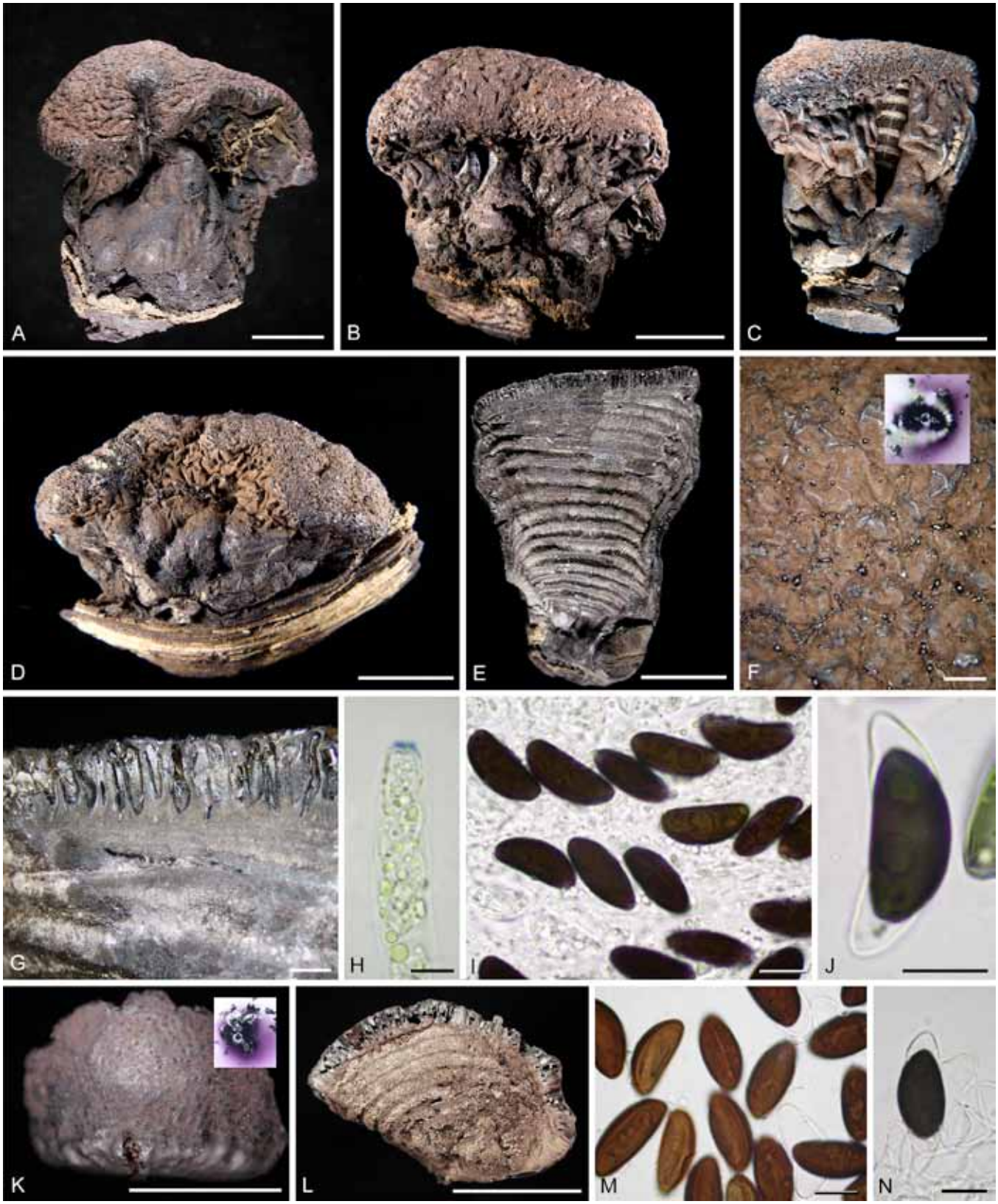



**Fig. 22.** Teleomorphic characteristics of *Daldinia andina* A–J: Holotype, C-F-58309 (Ecuador). K–N. T. Læssøe AAU 59449 (Ecuador). A–D, K. Stromatal habit (K: Inserted: Stromatal pigments in 10 % KOH). E, L. Stroma in longitudinal section showing internal concentric zones and perithecial layer. F. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). H. Ascus top in Melzer's reagent revealing amyloid apical apparatus. I, M. Ascospores in SDS, revealing germ slits and dehiscent perispore (M). J, N. Ascospore in KOH, showing dehiscing perispore. Scale bars A–E, K, L = 1 cm; F, G = 1 mm; H–J, M, N = 10 µm.

main character that members of the *vernicosa-loculata* 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.

***Daldinia dennisii*** M. Stadler, J.A. Simpson & Wollw. **var. *dennisii***, Mycol. Res. 108(9): 1027. 2004. Figs 4D, 9G, H, 23A–F.

*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).

=? *Hypoxylon simile* C. G. Lloyd, Mycol. Writings 5, Large Pyrenomycetes: 24, 1282. 1924.

*Holotypus*: **Australia**, Mid Canterbury, Christchurch, J. Mitchell ex Lloyd herb. *11354* (BPI 11354).

*Selected illustrations*: Stadler *et al.* (2004d), figs 1, 2 (stromata), 7, 8 (ascospores by EM), 23 (culture), 27, 28 (anamorphic structures).

*Known distribution/host preference of stromata*: Southern Hemisphere, in particular Australia and New Zealand; no apparent host specificity. The four identified hosts belong to *Pittosporaceae*, *Eleocarpaceae*, *Lauraceae* and *Scrophulariaceae*.

*Teleomorph*: *Stromata* semiglobose, with inconspicuous perithecial outlines, 1.5–4(–5) × 1.5–4 × 1–4 cm; surface Brown Vinaceous (84) in young conidiogenous stromata, often becoming blackish and conspicuously laccate in age; with dull reddish brown granules immediately beneath surface, with KOH-extractable pigments Purple (35), Livid Purple (81) or Violet (32), the tissue between perithecia brown, pithy to woody; tissue below the perithecial layer composed of alternating zones, narrow, darker zones dark brown, turning greyish black in mature specimens, pithy to woody, 0.2–0.4 mm thick, broad, lighter zones white or greyish white in young specimens, gelatinous when fresh, becoming loculate, 1–2 mm thick (Ratio darker/lighter zones 1:4–10). *Perithecia* lanceolate, 0.8–1.5 × 0.4–0.8 mm. *Ostioles* slightly papillate. *Asci* 190–270 × 11–14 µm, p. sp. 90–110 µm, stipes 85–110 µm, with amyloid, discoid apical apparatus, 0.75–1 × 4–4.5 µm. *Ascospores* dark brown, ellipsoid-inequilateral, with narrowly rounded ends, (13–)16–18(–19) × 6–8(–9) µm, with straight germ slit spore length on convex side; perispore dehiscent in 10 % KOH; appearing smooth by LM and SEM (10.000×).

*Cultures and anamorph*: *Colonies* on OA reaching the edge of a 9 cm Petri dish in 7–9 d, whitish, felty, zonate, with diffuse margins, aerial mycelium Greenish Olivaceous (90) in places; reverse Greenish Yellow (16) to Citrine (13), later becoming melanised. Sporulating regions at first appearing in zones near the margins of colonies, which later become tufts, later scattered over entire surface of colonies, greyish brown. Conidiogenous structure nodulisporium-like. *Conidiophores* mononematous, di- or trichotomously branched, sometimes with additional branches arising from the first level of conidiogenous regions, hyaline to yellowish, finely roughened, 150–220 × 2.5–3 µm, with 2–4 conidiogenous cells arising from each terminus. *Conidiogenous cells* intercalary or terminal, cylindrical, hyaline, finely roughened, 12–21 × 3–4 µm; conidia produced holoblastically in sympodial sequence. *Conidia* hyaline, smooth to finely roughened, dacryoid or ellipsoid, mostly with flattened base, (6.5–)7–9.5 × 4–5 µm.

*Additional specimens examined*: **Australia,** Lord Howe Island, Middle Beach, toward Valdon Guest House, on dead stump, 13 Sep. 1963, A.C. & H.M. Beauglehole *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 Ruatahuna, 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. childiae 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. childiae* (see Stadler *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.

***Daldinia dennisii*** **var. *microspora*** M. Stadler & Wollw., Mycol. Res. 108(9): 1029. 2004. Figs 4G, H, 9I, J, 23G–M.

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

*Holotypus*: **New Zealand**, Gisborne, Bay of Plenty, Urewera National Park, on fallen wood of *Beilschmiedia tawa*, 11 May 2001, E.H.C. McKenzie (PDD 73921).

= *Hypoxylon stratosum* Sacc., Syll. Fung. IX, p. 544. 1891.
≡ *Daldinia stratosa* (Sacc.) Sacc. & Trott., Syll. Fung. XXII, p. 327. 1913.

*Holotypus*: **Australia**, Gracemere, O' Shenesy (PAD).

*Selected illustrations*: Stadler *et al.* (2004d), fig. 9 (ascospores by SEM).

*Known distribution/host preference of stromata*: Southern Hemisphere, in particular Australia and New Zealand, but also occurring in Polynesia and South Africa. On various dicot hosts (with a single record from a monocot plant), without apparent host specificity.

*Teleomorph* like the typical variety except for having smaller ascospores (12–15 × 6–8 µm) and smaller ascal apical apparati (0.5–0.75 × 3.5–4 µm). *Anamorph* like the typical variety.

*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, Tataa,

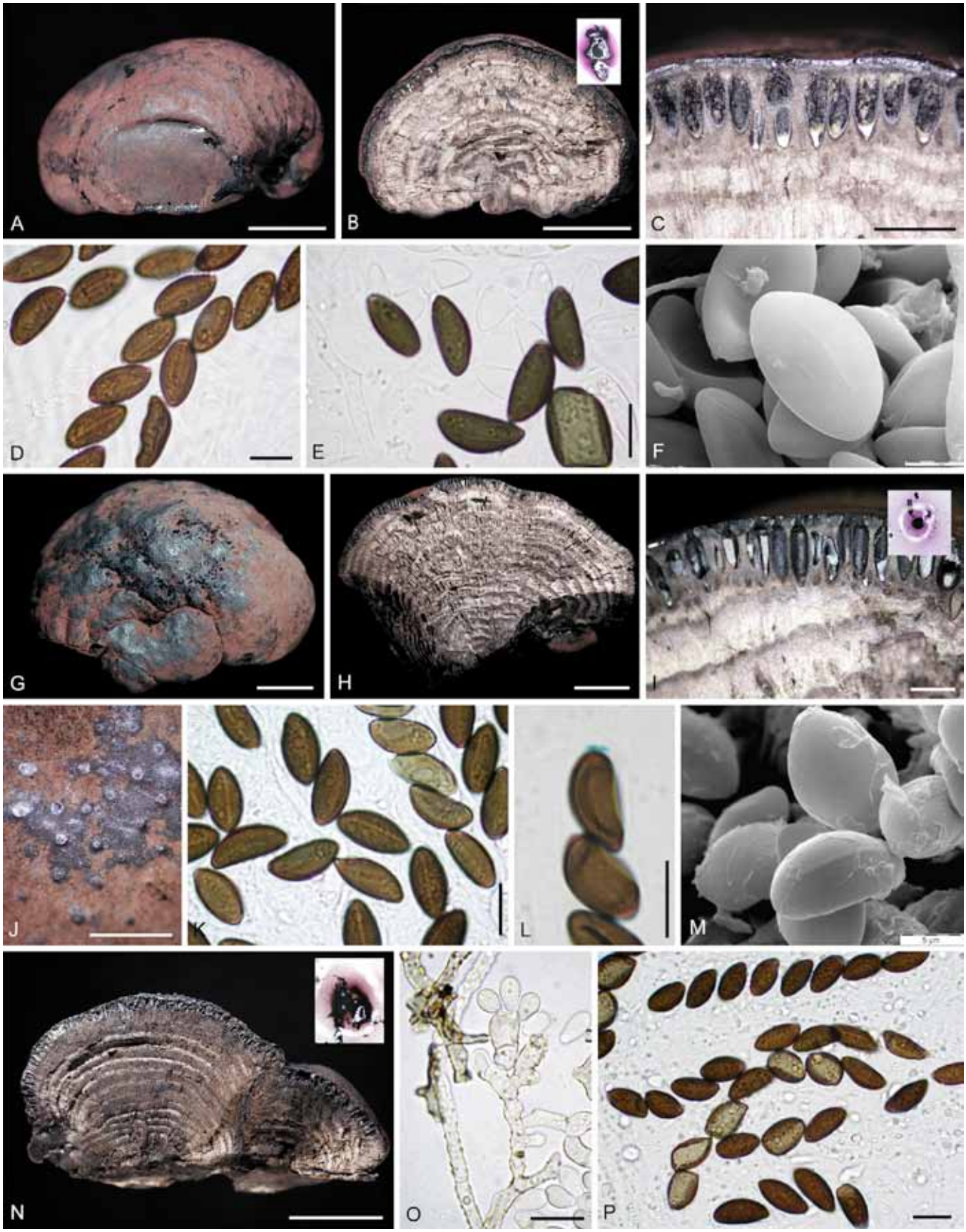



**Fig. 23.** Teleomorphic characteristics of *Daldinia dennisii* var. *dennisii* (*Ww 3953*; A–F), *D. dennisii* var. *microspora* (PDD 81346; G-M) and *Daldinia sp.* (PDD 87953; N–P). A, G. Stromatal habit. B, C, H, I, N. Stroma in longitudinal section showing internal concentric zones and perithecial 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.

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.

Mitchell ex Lloyd herb. *11759* (BPI 716962, see Child 1932 as *D. occidentalis*); Riccarton Bush, *Pittosporum eugenoides*, 19 May 1986, J.M. Dingley (PDD 52020); Chatham Islands, Hapupu Reserve, 20 Nov. 1992, P.R. Johnston & E.H.C. McKenzie *PRJ C66* (PDD 61684); Gisborne, Bay of Plenty, Te Urewera, Tarapounamu, *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, Ruatahuna, 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 18264); near Ruatahuna, Te Waiiti, 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 55130); Mid Canterbury, Govenor's Bay, Forest & Bird Arboretum, Nov. 2002, P. White *PW 92,* (PDD 76710, culture CBS 116734, ICMP 15775); Northland, Poor Knights Island, Tawhiti Rahi, The Bluffs, *Nestegis apetale*, 22 Apr. 1991, R.E. Beever *REB 1139* (PDD 59178); Wellington, Weraroa, 15 Aug. 1919, G.H. Cunningham (BPI 594616); Wellington, *Myrsine 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 3892* (KR, culture CBS 113485, MUCL 45011); Somerset East, near the Cape of Good Hope, on dead trunks, 1875–1876, MacOwan & Tuck, de Thümen, Mycotheca universalis No. *69b* as *D. concentrica* (B–70 0009631, FH 220992, M–0079882; 2 packets in NY); near Cape of Good Hope ("Kapland"), no date, Ecklon & Zegher (B70 0009598). **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.).

*Notes*: Unlike the typical variety, *D. dennisii* var. *microspora* is here shown to have a wider geographic distribution than reported by Stadler *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 3892*) 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 × (2.5–)3–6 µm in *Ww 3892 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 *69b*", which has been distributed to various herbaria, was cited by Child (1932) as *D. concentrica* from "Somerset, England". She obviously did not recognise the African origin (label reads "*promont. Bonae Spei*", *i.e.*, the Cape of Good Hope).

The ascospores of the type of *H. stratosum* also resembles those of *D. dennisii* var. *microspora*, rather than those of *D. eschscholtzii* as stated by Child (1932) and Ju *et al.* (1997). Lloyd (1919) characterised this fungus as having extraordinarily large stromata ("up to 3 inches in diameter"), but this was not confirmed by our studies on the type in PAD. That material is fragmentary and depauperate, but its HPLC profile was devoid of concentricol and cytochalasins (**8**, **9**), and the morphology of stromatal fragments (revealing slightly papillate ostioles) and ascospores (12–15 × 6–7.5 µm) with broadly to narrowly rounded ends and a dehiscent perispore and is here regarded as a synonym of *D. dennisii* var. *microspora*. In young stromata of PDD 76657 and PDD 76710, we detected traces of concentricol A (**8**) by HPLC–MS, revealing that this compound is not lacking altogether but constitutes a minor component in stromata of *D. dennisii* var. *microspora*. This confirms the relationship of *D. dennisii* to *D. concentrica*, even though stromata of the latter species may contain up to 10 % of concentricol A (**8**) and usually yield far less BNT (**1**). We suspect that terpenoids of the concentricol type are mainly produced by the anamorphs on the stromatal surface, as even samples taken from the nodulisporium-like stages of various *Daldinia* spp. of the *D. concentrica* group on woody substrates yielded large amounts of these compounds when studied by HPLC. However, in *D. dennisii*, BNT (**1**) is always the prevailing stromatal metabolite. Consequently, the stromatal pigments of *D. dennisii* are rather dense, while those of *D. concentrica* often only yield a faint purple pigment. Of course, they also differ in teleomorphic and anamorphic morphological characters (cf. Tables 3, 4).

Some specimens studied 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 reported here:

a) Two specimens from Pacific islands [**Tonga**, Vava' u, *Cocos nucifera*, 19 Feb. 1977, P.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 Olivaceous (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. *Annulata*").

However, none of the above specimens from the Pacific would serve well 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 stromata 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 twisted. The anamorph in culture and on stromata (Fig. 23O) revealed short and broad conidiogenous cells, 12–15 × 3.5–4 µm), with conidiogenous structures sporothrix- 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.

***Daldinia macaronesica*** M. Stadler, Wollw. & J.M. Castro, Mycol. Res. 108(3): 259. 2004. Figs 4I, 9E, F, 24A, G.

*Etymology*: For its area of distribution.

*Types*: **Spain,** Canary Islands, Tenerife Prov., Isla de La Palma, Cubo de La Galga, 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 brown, pithy to woody and below the perithecial layer composed of alternating zones, darker zones dark greyish brown, pithy to woody, 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). *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 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, felty, 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, dacryoid to ellipsoid, mostly with flattened base, (7.5–)8–9.5(–10) × (3.5–)4–5(–6) µm.

*Additional specimens examined*: **Portugal**, Azores, Island of São Miguel, Ponta Delgada, near Pico de Cedro, wood of cf. *Pittosporum undulatum*, Apr. 2007, E. Beltran-Tejera (TFC, MUCL 49357); Island of Madeira, Funchal, on hiking trail to Levada do Risco, on tree trunk in *Eucalyptus* plantation, *ca.* 970 m, 4 Jan. 2007, W. Jäger *et al*., *STMA 07023* (WUP, culture MUCL 52883); Fanal, laurisilva forest, *Ocotea foetens*, Dec. 2002, H.R. Glimpf & W. Jäger, *Ww 4275* (M-culture CBS 113040, MUCL 44613); Portas da Vila, near Viveros Forestais, on dead wood, 21 Jan. 2001, Sequeira & F. D. Calonge *231* (MA 50390); Santana, Fajã do Nogueira, *Ocotea foetens*, E. Beltrán-Tejera, Oct. 2006 (TFC, culture MUCL 49357); Seixal, Chao da Ribeira, P.N. da Mesa, dead wood, 16 Jan. 2001, M. Sequeira & F.D. Calonge *184* (MA 50389). **Spain**, Canarias, Gran Canaria Prov., Gran Canaria Island, Barranco de Los Tilos de Moya, *Ocotea foetens*, 14 Feb. 2006, E. Beltrán-Tejera & L. Rodriquez-Armas (TFC-Mic 15872, culture CBS 119984); same coll. data (TFC-18571, culture MUCL 53973); La Gomera Island, P.N. de Garajonay, sendero de Las Mimbreras a Meriga, near Montana de las Cuevas, 960 m, *Persea indica*, Feb. 2001, E. Beltrán (TFC-Mic 14240, CBS 119985, MUCL 47605); P.N. de Garajonay, near Cabecito Alto, 1050 m, *Laurus novocanariensis*, Nov. 2001, E. González & J. Barrera (TFC-Mic 14230, culture CBS 119986, MUCL 47607); P.N. de Garajonay, Fuensanta, on dead wood in Lauro-Perseetum indicae, 15 Apr. 2000, E. Beltrán-Tejera *et al.* (TFC-Mic 14240, culture CBS 119985); same collection data, TFC-14281 (TFC, culture MUCL 47605); vicinity of Hermigua, *Laurus novocanariensis,* 19 Feb. 1997, M. Eckel, *STMA 05060* (K(M) 130022, culture KC1698, MUCL 52884); La Palma Island, Los Tiles, *Ocotea foetens*, Mar. 2006, H. Anderson (TFC, culture MUCL 47712); Vueltas de Taganana, *Lauraceae* trunks, 26 Dec. 1971, A. Santos (MA 02315, TFC-Mic 54); same locality, on trunks of *Lauraceae*, 26 Dec. 1971, A. Santos (MA 42338 ex MUB 54); La Palma, Cubo de La Galga, *Laurus novocanariensis*, 3 Dec. 2010, W. Jaklitsch (WU, MUCL 53751).

*Notes*: *Daldinia macaronesica* appears closely related to *D. concentrica*, from which it mainly differs in its ascal and 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 martinii*** M. Stadler, Venturella & Wollw., Mycol. Res. 108(3): 263. 2004. Fig. 24H–M.

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

*Holotypus*: **Italy**, Sicily, Palermo Prov., Bosco della Ficuzza, *Quercus suber*, Jul. 2002, G. Venturella (PAL, ex-type culture CBS 113041, MUCL 44614).

*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, 1–1.5 × 0.3–0.4 mm. *Ostioles* slightly papillate. *Asci* fragmentary, size not determinable, with discoid, amyloid apical apparatus 0.5 × 4 µm. *Ascospores* variable in shape and size, brown to dark brown, ellipsoid-inequilateral, mostly with narrowly rounded ends, 14–17(–21) × 6–8(–9) µm, with straight germ

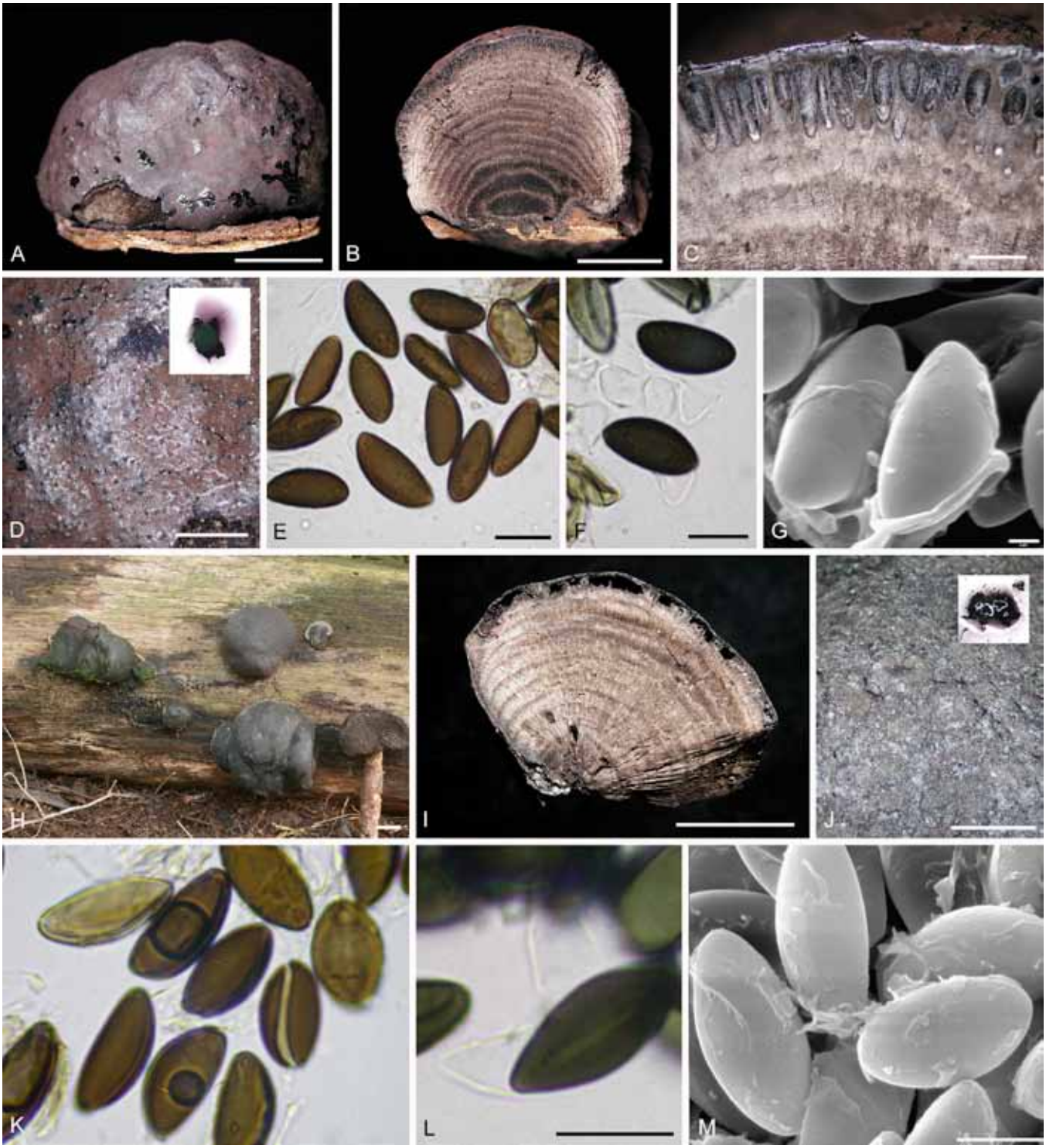



**Fig. 24.** Teleomorphic characteristics of *Daldinia macaronesica* (holotype; A–G) and *D. martinii* (*JF-10016*; H–M). A, H. Stromatal habit. B, C, I. Stroma in longitudinal section showing internal concentric zones and perithecial layer. D, J (inserted). Stromatal pigments in 10 % KOH. E, K. Ascospores 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 = 1mm; E, F, K, L = 10 µm; M = 5 µm; G = 2 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*

*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, dacryoid to ellipsoid, mostly with flattened base, 6.5–8(–8.5) × 2.5–3.5 µm.

*Additional specimens examined*: **Algeria**, vicinity of Algiers, Oct. 1889, L. Trabut in C. Roumeguère: Fungi Gallici exsiccati *7210* as *D. concentrica* var. *obovata* (NY). **India,** Himachal Pradesh, Hatoo Peak, Narkanda, Mahasu, *Quercus incana*, 16 Aug. 1971, K.S. Thind & J.S. Dargan as *D. concentrica* (BPI 594940). **Italy**, Sicily, Palermo University, Botanic Garden, on trunk of *Carya olivaeformis,* Aug. 2002, G. Venturella (PAL, culture CBS 113973, MUCL 44615); Sicily, Vulcano Island, alt. 20 m, on dead trunk of ? *Eucalyptus*, 20 Nov. 2009, H. Campos, comm. P. Roux & H. Noguere, *JF-10016* (KR, culture MUCL 52892). **Spain**, Cadiz, P.N. Grazalema, Casa del Escribano, alt. 400 m, on broadleaved wood, 18 Oct. 2003, A. Castro *698* (MA 59630); Ceuta, near town of Ceuta, burnt wood, no date, A. Marañes (MA 1810 - specimen depauperate).

*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 alone, and they were not in a particularly good shape when studied by us. Curiously, Child (1932) listed the Algerian specimen as *D. eschscholtzii*, despite its ascospores being significantly larger than allowed in her species description. *Daldinia macaronesica* and the yet 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.

***Daldinia palmensis*** M. Stadler, Wollw. & H. V. Tichy, Mycol. Res. 108(3): 265. 2004. Figs 9K, 25A–F.

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

*Typus*: **Spain**, Canary Islands, Tenerife Prov., La Palma, La Galga, freshly felled trunk of *Laurus novocanariensis* (as "*L. azorica*"), Oct. 1998, B. & M. Stadler, *Ww 3518* (M – **holotype,** KR ex WUP - **isotype**; **ex-type culture** CBS 113039, MUCL 44616).

*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 1:2–3). *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–inequilateral 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 conidiogenous regions, hyaline to yellowish, finely to coarsely roughened, 55–100 × 3–4 µm, with two to three conidiogenous 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 conidiogenous cells, hyaline, smooth to finely roughened, ellipsoid, 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. macaronesica* in having smaller ascospores bearing a conspicuously striate perispore by SEM, and from *D. dennisii* var. *microspora*, *D. eschscholtzii*, *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. macaronesica*.

***Daldinia raimundi*** M. Stadler, Venturella & Wollw., Mycol. Res. 108(3): 268. 2004. Figs 4C, 9D, 25G–L.

*Etymology*: For the Italian botanist, Francesco Maria Raimondo.

*Typus*: **Italy**, Palermo Prov., Monte Petroso, San Martino delle Scale, *Quercus ilex*, Feb. 2002, G. Venturella, *Ww 3951* (PAL-**holotype**; M-**isotype, ex-type culture** CBS 113038, MUCL 44618).

*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.


**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 = 2mm; C, I = 1 mm; D, E, K, L = 10 µm; F = 2 µm.

*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. *Asci* 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*

nodulisporium-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, 7–8.5(–9) × 4–4.5 µm.

*Additional specimens examined*: **Cyprus**, Karaman, Levante Restaurant, on wooden table, 14 Aug. 1997, D. Viney *F40* (K(M) 79707, culture KC 1691). **France**, Charente Maritime, Ile de Ré, Forét du Lizay, Petit Bec, *Quercus ilex*, 28 Apr. 2004, M. Hairaud, *JF-04043* (KR 0026341, culture MUCL 51689); same locality, St. Martin de Ré, les Saliéres, *Quercus ilex*, 28 Apr. 2004, C. Lechat, *JF-04044* (KR 0026343, culture MUCL 51680). **Italy**, Sicily, Bosco Niscemi, *Quercus ilex*, Jul. 1998, G. Venturella (M, culture CBS 113037, MUCL 44617).

*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.

***Daldinia vanderguchtiae*** M. Stadler, Wollw. & Briegert, Mycol. Res. 108(3): 268. 2004. Figs 9L, 26.

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

*Typus*: **UK**, Channel Islands, Isle of Jersey, Rozel Bay, *Acer campestre*, Aug. 1997, H. Forstinger, *Ww 3378* (M – **holotype**, KR ex WUP– isotype; **ex-type culture** CBS 113036, MUCL 44619).

*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-inequilateral 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 nodulisporium-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.

*Additional specimen examined*: **UK**, England, Surrey, Redhill, Redhill Common, *Acer pseudoplatanus*, 24 Feb. 2008, B.M. Spooner (K(M) 156281).

*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

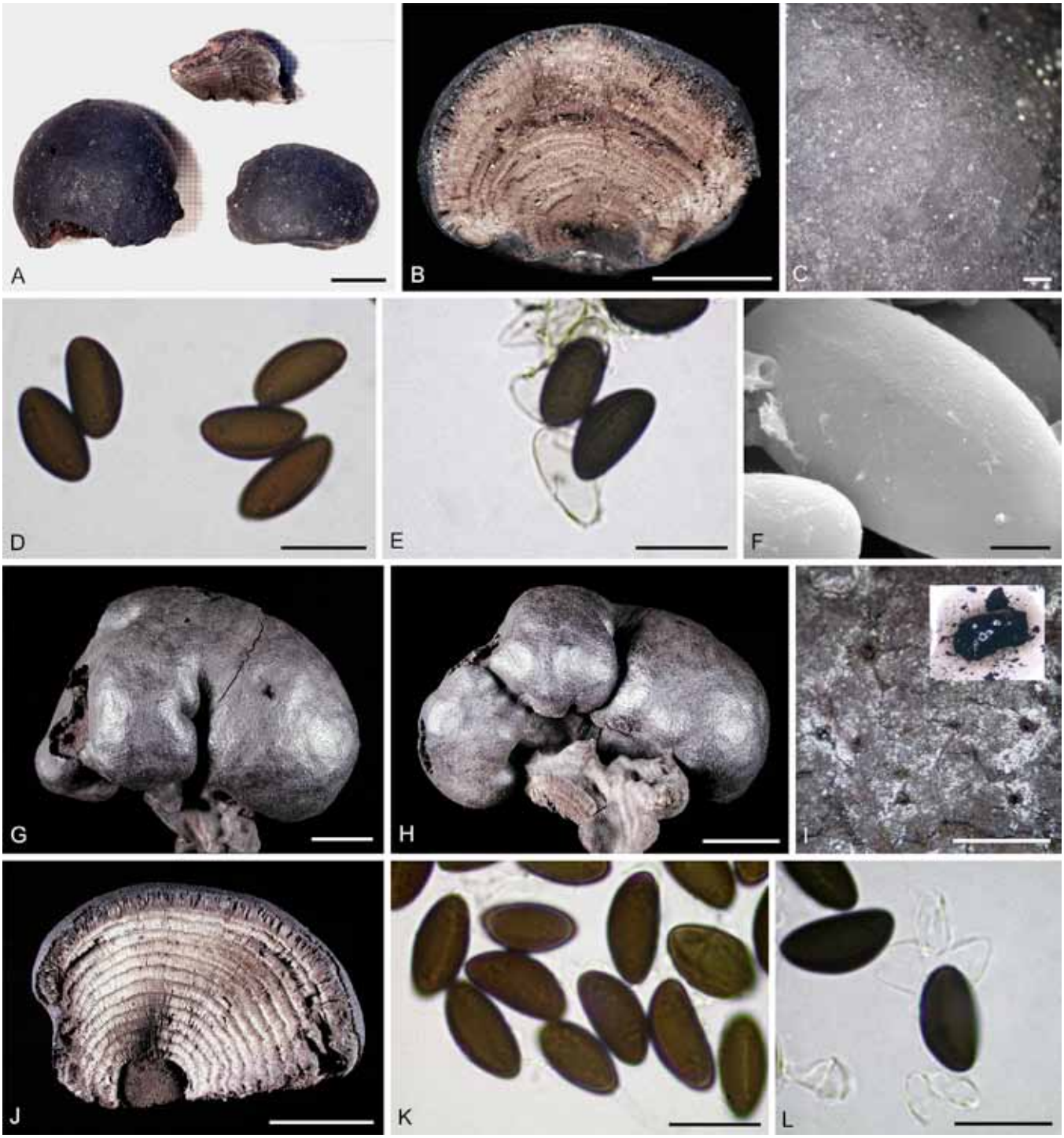



**Fig. 26.** Teleomorphic characteristics of *D. vanderguchtiae*. A–F: Holotype *Ww 3378* (UK). G–L. K(M) 156281 (UK). A, G, H. Stromatal habit. B, J. Stroma in longitudinal section showing internal concentric zones and perithecial layer. C, I. Stromatal surface. I. (inserted): Stromatal pigments in 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.

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-inequilateral 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. 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 conidiogenous 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–Myc 003525,60); same locality, 5 Nov. 1981, J. Rammeloo *7147* (BR–Myc 033526,61); same locality, 11 Nov. 1981, J. Rammeloo *7337* (BR–Myc 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 (12.000×).

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 fareastern 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 *Thamnomyces* (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 virgariella-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 eschscholzii* 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 "S*phaeria 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. eschscholtzii* 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

[7]Ehrenberg 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*".

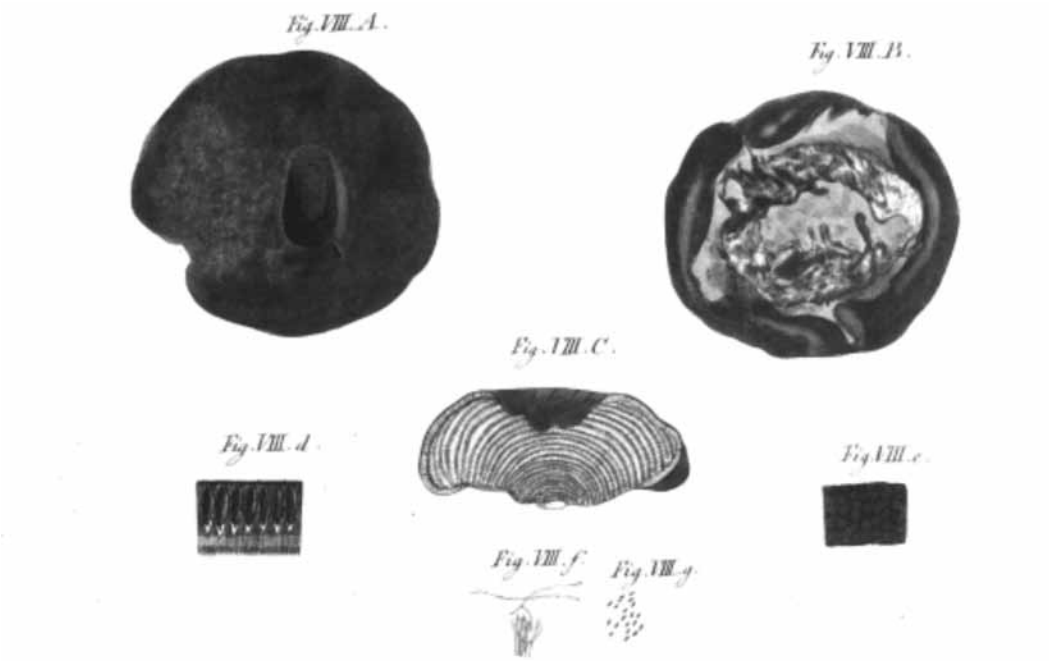



**Fig. 28.** Reproduction of original drawing by Ehrenberg (1820) of the type of *Sphaeria eschscholtzii*, showing an apparently immature *Daldinia*.

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. eschscholtzi*, and regarded *D. luzonensis* as a synonym. She mainly distinguished *D. concentrica* from *D. eschscholtzii*, based on ascospore size and morphology of perithecial 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 on 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.

| Author(s) | Size ranges (µm) | Origin of material/Remarks |
|---|---|---|
| Starbäck (1901) | 10–12.5 × 5–6 | Brazil |
| Rehm (1904) | 10–12 × 5 | USA, Texas |
| Rehm (1907) | 10–12 × 5–7 | Western Samoa |
| Theissen (1909) | 8–11.5 × 4–5 | Brazil |
| Rehm (1913) | 10 × 4–5 | *D. luzonensis*, first description |
| Miller (1930) | 12–15 × 5–7 | "Rehm' s material" of *D. eschscholtzii* (from Texas 1904 ?), and *D. luzonensis* (1913a) |
| Child (1932) | (8)–11.2(–14.4) × 4.8(–6.4) | Various specimens from around the world in tropical and subtropical climates, also including material from Europe (France, Germany (!))** |
| | Mean value = 11.2 × 4.8 | |
| | | Correspondence of materials examined to the defined subtypes not stated |
| | 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 Martín (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) |

to their production pattern of prevailing cytochalasins, one of these chemotypes is mainly comprised by specimens from Africa and America, while the other comprises mainly the specimens from Asia, Australia and the Indopacific. However, we have not been able to link this phenomenon conclusively to molecular or morphological data. It appears necessary to do preparative work on representative specimens, to isolate the prevailing cytochalasins to purity and elucidate their chemical structures by means of mass spectrometry and NMR spectroscopy. They could then be used as standards, facilitating the interpretation of the HPLC profiling data.

*Teleomorphic 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 further morphological traits such as shape and size of ostiola and perithecia.

***Daldinia eschscholtzii*** (Ehrenb.: Fr.) Rehm, Annls mycol. 2(2): 175. 1904. Figs 5A–C, 10A–J, 29.

*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° *fide* Ehrenberg, who stated that this fungus was "*very frequent in this locality*"), 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.

| Herbarium Code | Country | Ascospore size (µm) | Chemotype |
|---|---|---|---|
| **Africa: Most frequent morphochemotype** | | | |
| BR–Myc 129691,89, BR–Myc 130332,61, BR–Myc 112811.00, BR–Myc 130340,69, BR–Myc 130332,61 | Benin | (10–)11–14 × 5.5–6.5(–7) | 2 |
| JHP 00194 (C), Guissou No. 34 (C) | Burkina Faso | | |
| B70 0009593, M-0079884, Ww 4059, LB-01-157 (M) | Cameroon | | |
| BR–Myc 033523.58, BR–Myc 0993367,53, BR–Myc 033531,66, BR–Myc 033531,66, BR–Myc 033510,45, BR–Myc 033509,44´, BR–Myc 033522,57, BR–Myc 033521,56, BR–Myc 033504,39, BR–Myc 033516,51, BR–Myc 033517,52. BR–Myc 033514,49, BR–Myc 033512,47, BR–Myc 033513,48, BR–Myc 033502,37, BR–Myc 033511,46, BR–Myc 033505,40, BR–Myc 033503,38, BR–Myc 033515,50, K(M) 130243, Gillet 1901 (PAD) | D.R. Congo | | |
| K(M) 130372, K(M) 130373, K(M) 131680, K(M) 131681 | Ghana | | |
| K(M) 130374, K(M) 130375 | Kenya | | |
| K(M) 130245, K(M) 131682, K(M) 131683, Maguire (NY) | Nigeria | | |
| R 4281 (L) | Rwanda | | |
| B70 0009594, S-F 43703 | São Tomé e Príncipe | | |
| BR–Myc 003529,64 | Senegal | | |
| K(M) 130371, K(M) 131688] | Sierra Leone | | |
| K(M) 131685A & B | Sudan | | |
| K(M) 130379, K(M) 130380, K(M) 130381 | Tanzania | | |
| BPI 594955 | Uganda | | |
| **Africa: Deviating collections** | | | |
| Rammeloo 470 (Ww 3774 & Ww 3775, GENT) | D.R. Congo | (8–)9–10(–11) × 4–5(–5.5) | 2 (+ daldinone B (**3**) and other binaphthyls) |
| K(M) 130378, K(M) 130377 | Uganda | | |
| BR–Myc 129040,17, J. Rammeloo 423, 424, 428 (GENT) | D.R. Congo | 8–10 × 4–4.5(–5) | 1 |
| BR–Myc 033518,53 | D.R. Congo | 10–12 × 5–6 | 2 |
| B70 0009592 (Holst) | Tanzania | (10–)11–13 × 5–6(–7) | 2 (containing BNT (**1**) and additional binaphthyls) |
| **Americas: Most frequent morphochemotypes** | | | |
| S-F 43785 | Argentina | (10–)11–13 (–13.5) × 5–6.5 | 2 |
| BPI 594804, BPI 594759, Bononi 16, Bononi 132 and 320 (NY), Rodrigues 215, 190, and 1163 (NY), K(M) 130240, L 0275625 | Brazil | | |
| K(M) 91626 | Cayman Islands | | |
| Ww 3846, Ww 3852, STMA 04019, STMA 04020 | Cuba | | |
| TL 9833 | Ecuador | | |
| Gúzman 16304 (NY), Gúzman 10169 (NY), Gúzman 10319 (NY), Gúzman 10152 (NY), Gúzman 15557 (NY), Gúzman 15559/15571 (NY), Peréz–Silva (NY), Mojica 7 (NY), M. Eckel (K), A. Welden 4001 (NY), SM 23, 422A, 1035 (JDR) | Mexico | | |
| BPI 594808 | Nicaragua | | |
| Welden 7988 (NY) | Panama | | |
| T. Læssøe P–013. P–153 P–288 (C) | Peru | | |
| K(M) 25381 | Saint Lucia | | |
| BR–Myc 093359,45, L 0275626, L 0275627, NY 460110, Welden 2351 (NY) | Surinam | | |
| S-F 43788 (Rehm 1904) | USA | | |
| K(M) 130241, K(M) 131691, Ww 3960 (C) | Bolivia | (10–)11–13(–14) × 5–6.5 | 1 |
| S-F 38150, S–F38151, S–F38152, Samuels 751 (NY) | Brazil | | |
| S-F 43784 | | | |
| Underwood & Earle 738 (NY), Ww 3847, Ww 3850, Ww 3853 (Kr.), Ww 3591, Ww 3592 (MUCL) | Cuba | | |
| Orr No. 943 (NY), Ww 3943 | Ecuador | | |
| Le Gallo (NY) | Guadeloupe | | |

**Table 6.** (Continued).

| Herb Code/Continent/Species | Country | Ascospore size (µm) | Chemotype |
|---|---|---|---|
| BPI 594811 | Honduras | | |
| K(M) 130242, S-F 43795 | Venezuela | | |
| **Americas: Deviating collections** | | | |
| S-F 38151 and S-F 38152, Samuels *751* (NY). | Brazil | (9–)10–12 × 5–6 | 2 + daldinone B (**3**) |
| JFM 340 (KR), TL 9703 (C) | Ecuador | | |
| MUCL 45436 (*D. starbaeckii*, holotype) | French Guiana | | |
| CL–0882 (KR) | Martinique | | |
| StJ 106 StJ 187, StJ 191, F.J. Beaver *777* and *811* (NY) | US Virgin Islands (St. John) | 12–15 × 5.5–7 | 2 |
| K(M) 103863 | Venezuela | | |
| INPA 78-470 ex NY (*D. rehmii*, holotype) | Brazil | 9.5–10.5 (–11) × 4.5–5.5 | 1 |
| AAU 59501 | Ecuador | | |
| **Asia/Australia/Oceania: Most frequent morphochemotype** | | | |
| Ww 3959, Ww 3551 | Japan | (10.5–)11–13(–14) × (5–) 6–6.5) | 1 |
| M-0079883, TL-5156, TL-6173, Ww 4174 - Ww 4181 and Ww 4183 (ex AJSW) | Malaysia | | |
| K(M) 131699 | Bangla Desh | | |
| M–0079877, M–0079878 | Pakistan | | |
| BR–Myc 093358,44, BR–Myc 075661,01, BPI 594812, Ww 3781, Ww 4089 (B) | Indonesia | | |
| BPI 594760 | P.R. China | | |
| S-F 38154, BPI 594758, Saccardo 1817 (PAD), BPI 717066, BPI 717062, S-F 38156, S-F 43786, C. J. Baker 5488 (PAD), S-F 43789, S-F 43789, S-F 43790, S-F 43791, S-F 43791, Saccardo "Laguna" (PAD) | Philippines | | |
| Ww 4166 (M), Ww 4171 - Ww 4173 (ASJW), Demoulin 5405 (NY) | Thailand | | |
| K(M) 131694, Ww 4365 (K) | Sri Lanka | | |
| YMJ 264, BPI 594688 | Taiwan | | |
| STMA 07012 (KR) | Vietnam | | |
| K(M) 24537, K(M) 24521, Ww 4182/AJSW | Australia | | |
| K(M) 24568, K(M) 91622, Ww 3779 | New Guinea | | |
| K(M) 130238, Ww 3563 | Caroline Islands | | |
| BPI 594956, BPI 594761, M–0079881 | W. Samoa | | |
| PDD34954, PDD45927 | Solomon Islands | | |
| PDD36258 | Tahiti | | |
| **Asia/Australia/Oceania: Deviating collections** | | | |
| G.J. Samuels 2357a, 1939, 2035, 2052, 2230, (NY), L 0275624 | Indonesia | (9.5–)10–12 × 5–6 | 1 |
| M–0079879 | P.R. China | 9.5–12 × 4–5.5 | 2 |

**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 11206; GenBank Acc. No. of DNA sequence: HE590883).

= *Daldinia luzonensis* Rehm, Philipp. J. Sci. Bot. 8: 260. 1913.

*Lectotypus* (Ju *et al*. 1997: 266): **Philippines**, La Laguna Prov., Los Baños, C.F. Baker *516*, comm. Merrill *ex* Lloyd herb *12401* (BPI 716999).

*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 substipitate, 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

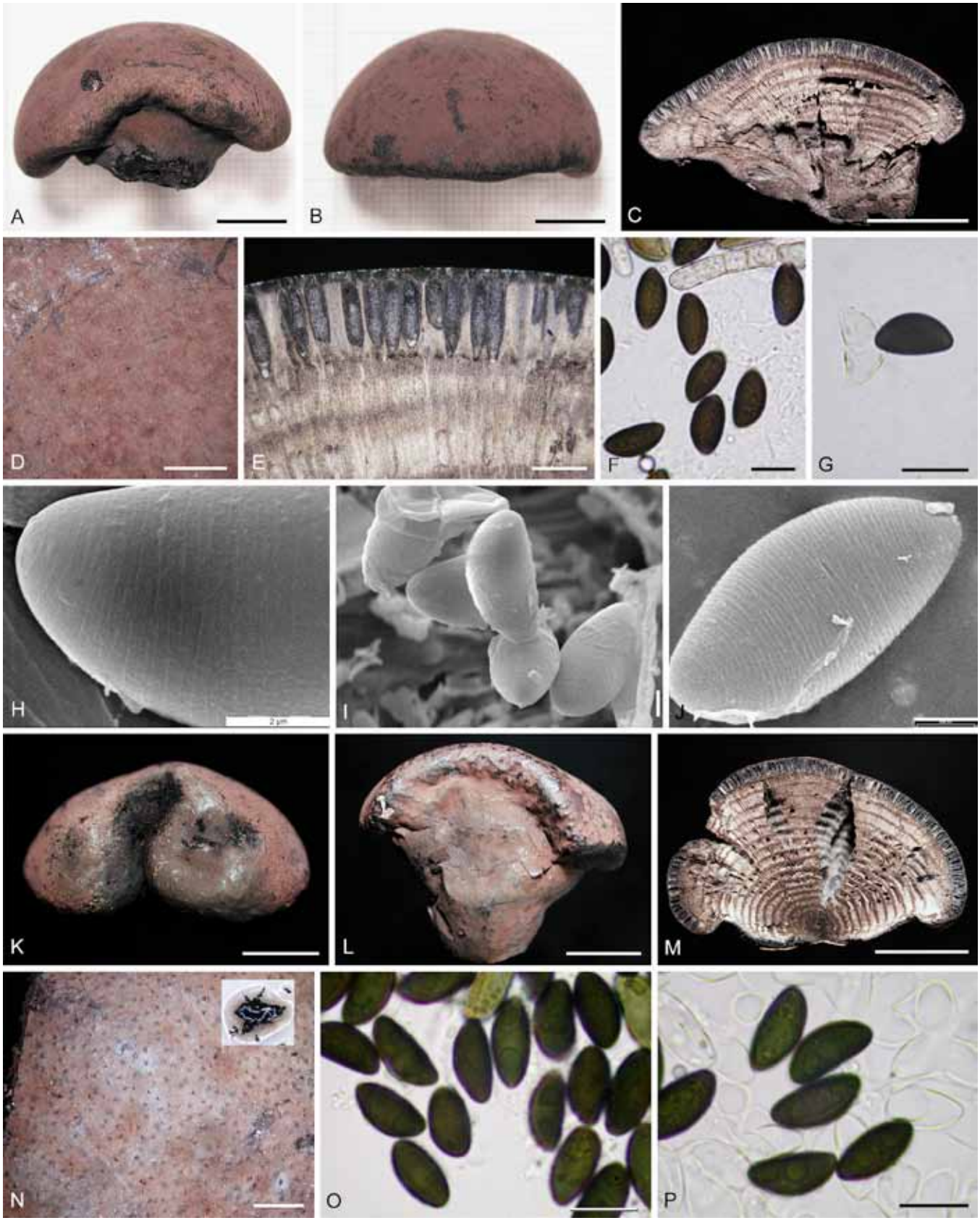



**Fig. 29.** Teleomorphic characteristics of *Daldinia eschscholtzii.* A–G. CALP 11232, KR (Philippines). H. Lectotype of *D. luzonensis* (Philippines). I. *Ww 3551* (Japan). J. *Ww 3591* (Cuba). K–P. CLL 8314 (Martinique). A, B, K, L. Stromatal habit. C, E, M. Stroma in longitudinal section showing internal concentric zones and perithecial layer. D, N. Stromatal surface showing the ostioles, (inserted (N): Stromatal pigments in 10 % KOH). F, O. Ascospores in SDS. G, P. Ascospores in KOH, showing dehiscing perispore. H, I, J. Ascospores by SEM (10.000×). Scale bars A, B, C, K, L, M = 1 cm; D, E, N = 1 mm; F, G, O, P = 10 µm; H, I, J = 2 µm.

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*

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; perispore dehiscent in 10 % KOH smooth by L.M, but showing conspicuous transverse striations by SEM (5.000×); epispore smooth.

*Stromatal metabolites*: BNT (in young stromata) and cytochalasins (often in abundance); concentricols detected tentatively in some specimens.

*Cultures and anamorph*: *Colonies* on OA reaching the edge of 9 cm Petri dish in 5–8 d, initially whitish, felty, azonate, with diffuse margins, becoming Smoke Grey (105) with slight olivaceous tone, later usually melanising; reverse at first Citrine (13), later 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 production often ceases after the cultures have been transferred repeatedly onto new culture media. *Sporulating regions* scattered over entire surfaces of colony and stromata (if present), Smoke Grey (105). *Conidiogenous structure* with nodulisporium-like branching pattern. *Conidiophores* mononematous or sometimes synnematous, di– or trichotomously branched, rarely with additional branches arising from the first level of conidiogenous regions, hyaline, finely to coarsely roughened, 55–240 × 2.5–3 µm, with two to three conidiogenous cells arising from each terminus. *Conidiogenous cells* cylindrical, hyaline, finely roughened, 8–26 × 2–3.5 µm. *Conidia* produced holoblastically in sympodial sequence, hyaline, smooth to finely roughened, ellipsoid to dacryoid, often with flattened base, 4.5–6.5 × (2–)2.5–3 µm.

*Additional specimens examined*: **Angola,** Louanda**,** Mar. 1918, J. Gossweiler, Lloyd herb. *12376*, det. J.H. Miller as *D. bakeri* and Child (1932) as *D. eschscholtzii* (BPI 716965). **Argentina**, Jujuy, Quinta near Laguna de la Boca, 10 Jun. 1901, R.E. Fries in herb. brasil. Regnell *53* (S-F43785); Misiones, Puerto Londero, 20 Feb. 1948, A.S. Colla (NY ex herb Buenos Aires 884). **Australia**, Queensland, damp fallen trunk in *Eucalyptus alba* garden, 24 Mar. 1997, A.J.S. Whalley *793* (AJSW, culture CBS 116032); Townsville, Harvey's Range, on fallen branch, 30 May 1976, D.G. Reid (K(M) 91622). Western Australia, Kimberley District, near police camp, on dead fallen log in grassland with *Eucalyptus* sp. and other trees, B.M. Spooner *AK-283* (K(M) 24568); Donkey Creek, billabong in King Leopolds Range, 9 Apr. 1988, B.M. Spooner *AK119* (K(M) 24537); Windjana gorge, on rotten log, 14 Apr. 1988, B.M. Spooner *AK199* (K(M) 24521). **Bahamas**, New Providence, 1 Nov. 1916, L.J.K. Brace *9638/9762* (NY); New Providence, 25 Oct. 1918, L.J.K. Brace *9626* (NY); same coll. data, "on pineboard", L.J.K. Brace *9628* (NY, 2 packets); New Providence, *Albizzia*, 18 Jan. 1919, L.J.K. Brace *4895* (NY); New Providence, no date, L.J.K. Brace *9669* (NY); New Providence, on dead wood, 18 Jan. 1919, L.J.K. Bruce *4899* (NY); South Bimini Island, 22 Mar. 1956, N.R. Richmond *18.348* (NY). **Bangla Desh** ("East Pakistan"), Dacca, on dead branches of *Artocarpus integrifolia*, Jan. 1968, A.Z.M. & N.A. Khan (K(M) 131699). **Benin**, Atacora, Bassila, wood, 4 Oct. 2000, Y.N. Soulemane *341* (BR–Myc 130340,69, culture MUCL 45434); same locality, 4 Oct. 2000, Y.N. Soulemane *333* (BR–Myc 130332,61); same locality, 3 Oct. 2000, A. de Kesel *2984* (BR–Myc 129691,89, culture MUCL 45435); Atlantique, Niaouli, 11 Jun. 1999, A. de Kesel *2594* (BR–Myc 112969.61); Borgou, Wari Maro, Jun. 1999, A. de Kesel *2319* (BR–Myc 112811.00). **Bolivia**, Amazonas, *ca.* 5 km W of Guayaramerin, 2 Feb. 1978, W.D. Reese *13002* (NY); La Paz, Nor. Yungas, 6 May 1998, L. Beenken *LB 1170* (M, culture CBS 113968); Liriuni, Cochabamba, decaying debris, May 1947, M. Cardenas *198* as *D. bakeri* (BPI 594759); Vaca Diez, Ivon, Beri, 3 Apr. 1956, R. Singer *B2458* (K(M) 130241). Ivon, Beri, Guayayomerin, on dead dicot trunk, 8 Mar. 1956, R. Singer *B1736* (K(M) 131693). Beri, Riberalta, on decorticated trunk, 2 Apr. 1956, R. Singer *B2426* (K(M) 131691). **Bonin Islands,** US North Pacific Exploration Expedition, 1853–1856, C. Wright (FH 220996). **Brazil**, Amazonas, 25-30 km NW of Rio Branco, along road to Serra Madureira, 25 Feb. 1978, W.D. Reese *13234* (NY); Territory of Roraima, Vic. of Auaris, on burnt logs in plantations, Jul. 1974, O. Fidalgo *et al.* (NY); Manicoré, Estrada de Estanho km 40, on dead trunk, 16 Apr. 1985, K. Rodrigues *190* (NY); Paria Grande, Inv. Botanico-Ecologico del Territoria Federal Amazonas, 23 Apr. 1978, G.E. Iturriaga *191* (F 331690); Road from Boa Vista to Venezuelan border, 2 km after Boca da Mata, Carpoeira, on dead trunk, 10 Dec. 1977, G. Samuels *et al. 751* (NY); Belem, Pará, dead wood, 31 Jul. 1957, A.F. Vital *1393* (L 0275625); same locality, A.F. Vital *1955* (BPI 594214); same locality, 16 Feb. 1955, A.F. Vital in herb. P. Martin *630* (IMI; see Martin 1969 as *D. concentrica*)*;* Minas Gerais, near Coimbra, *Citrus nobilis* var. *tangerina*, Mar. 1902, in herb. Saccardo as *D. concentrica* (PAD); Mato Grosso, Novo Aripuana, Vila do Apuy, Rod. Transamazonica, BR–230, 36 km from INRRA towards Sucunduri, on dead trunk, 2 May 1982, K.F. Rodrigues *444* (NY); Cachoeira Porteira, ca. 10 km from Camp Andrade Gutierrez, 17 Jun. 1980, V.L. Bononi *320* (NY); Oriximiná, BR 163, 30–40 km from Oriximiná City, on wood, 3 Jun. 1980, V.L. Bononi *16* and *132* (NY); Santa Catarina, Porto Novo, J. Rick (S-F43784 *ex* FH); Porto Novo, 1928, J. Rick *781* (FH 220986); São Paulo, Agua Funda, Parque Floristico of Botanical Institute, humid tropical forest, on wood, 22 Jan. 1987, K. Rodrigues *et al. 1163* (NY); same locality, Instituto de Botanica, 6 Nov. 1969, D.M. Dring *188* (K(M) 131690). **Burkina Faso**, Ouagadougou, in park, 24 Aug. 2000, J.H. Petersen *JHP 00194* (C, OUA, culture CBS 117470); Ouagadougou University grounds, 7 Jun. 1999, Guissou *34* (C, OUA); South Ouest province, F.C. de Mouhoun, 440m, forest near highway Orodara-Banfora, Jul. 2009, S. Gahrt, *STMA 09138* (M, culture MUCL 52675). **Cameroon**, South Province, Bipindi, wood in rain forest, no date, G. Zenker *1360a* (M–0079884); South West Province, Limbe, on dead stump in Botanic Garden, 2 Nov. 2001, L. Beenken & T. Franke *K212* (M, culture CBS 113969); same locality, Molire on putrefied trunk, 1 Oct. 2001, L. Beenken *K01/159* (KR, culture CBS 117735); exact locality unknown, label reading "Bibundi" (probably meaning Bipindi), Regio Kamerounensis", Apr. 1891, J.R. Jungner (B70 0009593); "near N´Congsamba", on dead wood, 15 Jul. 1946, R. Heim (UPS); Dja Biosphere reserve, near Schouam village, 12º50'E., 3º21'N, 640 m, 28 Jun. 1997, P.P. Daniels *et al.* (MA 39142). **Colombia,** Antioquia, Finca Granada, 20 May 1926, C.E. Chardon *78* (NY); near Bonda, Dec. 1908, C.F. Baker in herb. F.S. Earle (NY). **Cook Islands**, Rarotonga, Titikaveka, *Mangifera indica* (mango), 6 Oct. 1975, J.M. Dingley (PDD 34145). **Costa Rica**, Guanacaste Prov., Granadilla, 10 Feb. 1930, C.W. Dodge & W.S. Thomas *6783* (FH 220962); Heredia Prov., near Puerto Viejo, La Selva Biol. Station and Reserve, 20 Jan. 1986, C.L. Ovrebo (NY); Limon Prov., Livingston Farm near La Junta, 12 Dec. 1929, C.W. Dodge & W.S. Thomas *5884* (FH 220965); San José Prov., Potreros de Chino, 8 Nov. 1920, C.W. Dodge & W.S. Thomas *5283* (FH 220961); Potrero of Finca Sta. Rosa, north of El Alto de Cabeza de La Vaca, 14 Nov. 1929, G.W. Dodge & W.S. Thomas *5218* (FH 79494); Potrero of Finca Sta. Rosa, Rio Sucio, 14 Nov. 1929, C.W. Dodge & W.S. Thomas *5219* (FH 79491); Potreros de Rancho Redondo, Nov. 1929, C.W. Dodge & W.S. Thomas *5234* (FH 220963); exact locality unknown, Jul. 1921, P.V. Siggers, in Lloyd herb. *12178* (BPI 716980), immature, det. Child (1932) as *D. bakeri*. **Cuba**, Camaguey, La Gloria, Feb. 1908, J.A. Shafer *732* and *736* (NY); Ciego (de Avila), on dead roots in cane field, 5 Dec. 1924, J.R. Weir (FH 79475); La Habana, Estacion Central Agronomica, 6 Mar. 1904, F.S. Earle *6* (NY); Cienfuegos, Sierra de Escambray, Cumanayagua, *Sizygium jambos*, Apr. 1999, R.F. Castañeda, *Ww 3591* (MUCL, culture CRGF 150, MUCL 41778, see Stadler *et al.* 2001a,b); La Habana, Calabazar, Arroyo Pancho Simon, dead wood in semi–deciduous forest, 23 Aug. 1968, H. Kreisel & M. Rodriguez *63* (Kr.); same locality, 17 Sep. 1968, O. Oliva, H. Kreisel & M. Rodriguez *190* (Kr.); Rio Guayaibon, 1 Sep. 1968, H. Kreisel & M. Rodriguez *87* (Kr.); Matanzas, Cienaga de Zapata, *Bucida palustris*, Apr. 1999, R.F. Castañeda (MUCL, culture CRGF 150, MUCL 41778, see Stadler *et al.* 2001a,b); Jagüey Grande, Empresa Citricola, on dead stump of *Citrus* sp. (grapefruit), near the base (close to the ground) in *Citrus* orchard, 17 Aug. 2004, C. Fidalgo-Jiménez & C. Decock (MUCL, culture CRGF 152, MUCL 46087); on dead *Citrus* trunk, Sep. 2004, C. Fidalgo-Jiménez & C. Decock (MUCL, culture CRGF 153, MUCL 46088); Oriente, Juguey, Yateras, 5 May 1907, W.R. Maton *4503* (NY); Oriente, Sra. Nipe, near Woodfred, 450–550m, Dec. 1909, J.A. Shafer *3377* (NY, 2 packets); same collection data, J.A. Shafer *3757* (NY); Moa, Rio Queragua, mixed forest, 14 Nov. 1969, H. Kreisel & M. Rodriguez *1467* (Kr.); Pinar del Rio, Peninsula de Guanahacabibes, Municipio Sandino, La Bajada, Oct. 2005, C. Decock (MUCL, culture MUCL 47596); same locality, different specimen (MUCL, culture MUCL 47596); Pinar del Rio City, 17 Nov. 1968, H. Kreisel & M. Rodriguez (Kr.); Cumanayagua, *Jambosa vulgaris*, Apr. 1999, R.F. Castañeda & C. Decock (KR; MUCL; culture MUCL 41777); Parque Nacional "La Güira", *Pinus* forest, Aug. 2002, S. Herrera & C. Decock (MUCL, culture CRGF 151, MUCL 44145); San Diego de los Baños, Mar. 1904, W.A. Murrill (NY); vicinity of Los Palacios, Jan. 1912, J.A. Shafer *12050* (FH 79474, NY); Santa Clara, vicinity of Soledad, Aug.-Sep. 1933, A.G. Kevorkian (FH 79479); Exact locality unknown, no date. S.M. Underwood & F.S. Earle *738* (NY); on royal palm log (*Roystonea regia*), S.M. Underwood & F.S. Earle *152* (NY); locality not stated, 1836, M.R. de la Sagra as *Hypoxylon concentricum* (MA 21017). **D.R. Congo** (formerly Zaire), Angodia, May 1931, J. Lebrun *2961* (BR–Myc 033505,40); Bambatas region, Feb. 1910, H. Vandereyst *12* ex herb. Allard (BR–Myc 033511,46; see Dennis 1963[8]); Bumbuli, Lake Leopold II, Nov. 1932, J. Lebrun *6583* (BR–Myc 033502,37); District du

[8]Dennis referred to the specimens from D.R. Congo as "*D. concentrica* var. *eschscholzii*."

Haut Katanga, Keyberg, Base de Mukenu, "on small termite hill" (!?), 24 Feb. 1947, D. Soyer *244* (BR–Myc 033515,50; see Dennis 1963); District Forestier Central, Kisangani (Stanleyville), Feb. 1926, Ghesquire *328*, (K(M) 130243); Ipamu, 1 Feb. 1956, H. Vandereyst *8926* (BR–Myc 033531,66); Kasai, Kakenge, *Entandrophragma cylindrum*, no date, Dechamps *22* (BR–Myc 033522,57 – immature); Kisantu, 20 May 1910, H. Vandereyst ex herb. Bresadola (BR–Myc 033513,48; see Dennis 1963); same locality, 1906, H. Vandereyst (BR–Myc 033510,45; see Dennis 1963); vicinity of Kisantu, 1909, J. Gillet (BR–Myc 033509,44; see Dennis 1963); same locality, 25 Jan. 1907, H. Vandereyst (BR–Myc 033504,39 –immature); same locality, 1901, J. Gillet, det Saccardo as *D. concentrica* var. *eschscholtzii*, ex herb. Saccardo (PAD); Kivu, Panzi, Oct. 1947, Goossens–Fontana *5072* (BR–Myc 033521,56; see Dennis 1963); Mayidi, 1 Feb. 1910, H. Vandereyst (BR–Myc 033512,47); Ntindibidi, no date, H. Vandereyst *199* (BR–Myc 033503,38; see Dennis 1963); exact locality unknown, E. Bommer & M. Rousseau (BR–Myc 993367,53); 1910, H. Vandereyst ex herb. Bresadola (BR–Myc 033514,49; see Dennis 1963). **Dominican Republic**, Macoris Prov., Consuelo, Nov. 1909, N. Taylor (NY). **Ecuador**, Cotopaxi, 1 km S of Maná (0° 56' S / 79° 14' W), alt. 175 m, 10 Jun. 1985, T. Læssøe *AAU 59501* (C); Galapagos, Indefatigable Island, 29 Jan. 1964, R.T. & D.B. Orr, California Academy of Sciences Mycological Collection *943* (NY); Manabi, Puerto Lopéz, Isla de la Plata, 7 Jul. 2002, T. Læssøe *TL–9833* (C, QCA, culture CBS 116025); Orellana, Añangu, south bank of Río Napo, 95 km downstream from Coca, lowland rain forest, on large, dead and rotten dicot trunk (0° 32' S / 76° 23' W), alt. 300 m, 19 Jun. 1985, T. Læssøe *AAU 59551* (C); same locality, 23–27 Aug. 1985, T. Læssøe *AAU 59950* (C). **El Salvador**, Dpto. de Sta. Ana, Finca Las Piletas, 1975, G.A. Escobar *5200* (NY). **Ethiopia,** Gamu-Gopa region, Arba Minch, below encampment east of town, groundwater forest with *Cordia* and *Ficus*, 1250 m, on dead branches on the ground, 30 Aug. 1975, M. Thulin *2527*; in packet with *D. clavata* (UPS). **Federal States of Micronesia**, Ponape, Colonia, *Citrus* sp., 26 Jan. 1949, M.M. Ross *M–2228* (BPI 594761). **French Polynesia**, Tahiti, Faaa District, May 1922, W.A. Setchell & H.E. Parks *5019* **(**FH 79452); Tahiti, Papenu, May 1922, W.A. Setchell & H.E. Parks **(**FH 79451); Tahiti, May 1922, H.E. Parks ex Lloyd herb. *12394* (BPI 715026); "Tahiti No. 3", ex herb. Saccardo as *D. concentrica* (PAD); Tahiti, dead wood, May 1930, J.C. Neill (PDD 3500). **French Guiana,** Haute-Orénoque, ex Ellis Collection *241*, as *D. concentrica* var. *obovata* (NY); Ile du Salut, St Joseph, tropical rainforest, Mar. 2007, C. Lechat, *STMA 07011* (LIP, culture CBS 121677, MUCL 49338). **Gabon**, Estuaire Prov., Kinguélé, 00°28, 103N, 010°16,695'E, Monts de Cristal National Park, Apr. 2009, C. Decock (MUCL, culture MUCL 52252); Ogooué-Ivindo, Parc National de l'Ivindo, Réserve Intégrale d'Ipassa, Ipassa Biological Station, Apr. 2006, C. Decock, *STMA 06092* (MUCL, culture MUCL 47433); same collection data, *STMA 06093* (MUCL, culture MUCL 47434); same collection data, *STMA 06094* (MUCL, culture MUCL 47435). **Ghana** ("British Togo"), Gbadzene, Jan. 1957, Miss Hewlett (K(M) 130373); Tafo, 1955, M. Holden *GC123* K(M) 130372; Tafo, Jan. 1957, Miss Hewlett (K(M) 131681); East Region, Pusu Pusu, Miss Hewlett (K(M) 131680). **Guadeloupe**, Marie Galante Island, rotten wood of *Hippomane manchinella*, 15 Jun. 1951, C. le Gallo (NY); Monts Caraibes Basse Terre, Dec. 1988, J. Vivant (JDR, culture BCRC 34046 and CBS 122878; GenBank Acc. Nos of DNA sequences: AY951695 and AY951807; see also Ju *et al.* 1997, Stadler *et al.* 2001a; Hsieh *et al.* 2005). **Guam**, exact locality unknown, 1918, P. Nelson *472* (NY). **Guyana** ("British Guiana"), Kartabo Point, Mazaruni River, in dense forest at sea level, Mar. 1924, W.A. Murrill (NY). **Honduras,** Dept. Atlantida, Lancetilla Valley, 6 Dec. 1927, P.C. Standley *53673* (F 331681); La Ceiba, May 1923, O.M. Sutter (FH 79481); Lancetilla Valley, near Tela, 6 Dec. 1927, P.C. Standley *52949* (F 331682); same collection data, P.C. Standley *55524* (F 331683). Dept. Yoro, Quebrada Seca, Dec. 1927, P.C. Standley *53934* (BPI 594811, F 331684). **India**, Bombay, Poona, Aug. 1988, collector unknown (FH 220993); Panjab, Chandigarh, on bark of dead angiosperm log, 26 Aug. 1968, J.S. Dargan *7427* (K(M) 131695); exact locality unknown, "Glen", twigs of *Quercus*, 28 Jul. 1965, Thind *2606 & 2607* (K(M) 131696); Uttar Pradesh, Allahabad University, *Citrus limon*, Mar. 1981, Bihasi Lal (IMI 256508). **Indonesia**, Borneo, D.E. Elmer, Plants of Borneo *20579* (BR–Myc 075661,01); Kalimantan Timur, Balikpapan, on dead wood, 22 Apr. 2006, J.P. Laffont, *JF-06215* (JF); Java, Buitenzorg, Botanic Garden, 1897(–99), E. Nyman (UPS); Buitenzorg, C. Hartley in herb J.R. Weir *19661* (BPI 594812); Buitenzorg, Martii, Planta Javanica *2095* (BR–Myc 93358,44); Zandbai, 18 Jul. 1897, E. Nyman (UPS). Samosir Island, Lake Toba, 1992, E. Heinrichs ex herb. D. Benkert, *Ww 4089* (B, WUP). Sumatra, Aek Pantjar, old trunk of *Hevea*, Mar. 1956, V. Schmidt (L 0275624); Fort de Kock, Nov. 1924, E. Jacobson (FH 79453). Timor Island, 1910, M. Ferreira in Torrend: Fungi selecti Exsiccati (F 331696). **Jamaica,** Chester Vale, Dec. 1908, W.A. Murrill *366* (NY); Hope Gardens, 23 Oct. 1902, F.S. Earle *152* (NY); Morge's Gap, 200 ft., Dec. 1908 – Jan. 1909, W.A. Murrill (NY). Kingston, Dec. 1908, A.E. Wright *32200* (FH 79480); Balaclava, 4 May 1909, A.E. Wright ex herb. Farlow (FH 79478). **Japan**, Shikoku, Tokushima, *Quercus acutissima*, Jun. 1992, Y. Asakawa, *Ww 3551* (WUP, see Hashimoto & Asakawa 1998, as "*D. vernicosa*"; Stadler *et al.* 2001a); same locality, *Quercus acutissima*, Y. Asakawa, Sep. 2000, *Ww 3959* (KR). **Liberia**, Ganta, 1938, Harley (FH 79490). **Kenya,** Coastal Province, Sokoke Forest, 20 Sep. 1976, J.W. Ash *3676* (K(M) 130375); Gongoni Forest with sultanate, T.W. Maitland (K(M) 130374); Coast near Mombasa, 1914, A.J. Dawson (NY ex K); Limuru, 7000 ft, root of *Cassia floribunda*, June 1932 (IMI 10666 - immature). **Madagascar**, Ankoraka, on wood, Sep. 1891, Braun (B70 0009595 - immature). **Malaysia**, Boheng, cut logs, 27 Feb. 1993, A.J.S. Whalley, *Ww 4176* (AJSW, culture CBS 116033); Selangor, FRIM institute, 19 Feb. 1993, A.J.S. Whalley *FR1–93* (AJSW, culture CBS 116038); Gombak, Kuala Selangor, fallen trunk, 10 Sep. 1993, A.J.S. Whalley, *Ww 4175* (AJSW, culture CBS 116037); same locality, rubber plantation, 22 Oct. 1999, A.J.S. Whalley *Ww 4177* (AJSW, culture CBS 116034); Gombak, on logs, 23 Feb. 1993, A.J.S. Whalley *914–93* (AJSW, culture CBS 116041); same locality, on damp fallen trunk in shade in the middle of forest, 24 Mar. 1997, A.J.S. Whalley *637* (AJSW, culture CBS 116036); Kuala Selangor Natural Reserve, Apr. 1995, A.J.S. Whalley (AJSW, culture CBS 116035); same locality, 18 Sep. 1995, A.J.S. Whalley, *Ww 4181* (AJSW, culture CBS 116040); Rumbia Demen, on log, 21 Mar. 1997, A.J.S. Whalley *Rl.5* (AJSW, culture CBS 116039). Sabah, Kota Belud, no date, Tasselton (?), "leg. District Officer", ex herb. F. Petrak (M–0079880); "British North Borneo", Elphinstone Province, Tawao, Oct. 1922, A.D.E. Elmer (B70 0009584); Kota Kinabalu, on old *Casuarina* trees near beach, 25 Feb. 1981, E. Albertshofer as *D.* cf. *concentrica* (M–0079883); Tabin Wildlife Reserve, gregarious on partly burnt log bridge over the Lipad River, 7 Feb. 1999, T. Læssøe *TL–6156* (C, culture CBS 117741); same loc., on dicot wood in tree fall area, 9 Feb. 1999, T. Læssøe *TL-6173* (C). **Martinique**, Le Marin, Aug. 2007, C. Lechat, *STMA 07011* (LIP, culture CBS 119987, MUCL 49337); same data, Dec. 2006 (LIP, culture CBS 121676); Morne Vert, Aug. 2008, C. Lechat *CLL 8337, STMA 08190* (LIP, culture MUCL 51836); same locality, C. Lechat *CLL 8340, STMA 08191* (LIP, culture MUCL 51837); Prêcheur, Aug. 2008, C. Lechat *CLL 8314, STMA 08194* (LIP, culture MUCL 51834); same locality, C. Lechat *CLL 8315, STMA 08189* (LIP, culture MUCL 51835); same locality, C. Lechat *CLL 8354, STMA 08192* (LIP, culture MUCL 51838); Robert, Aug. 2008, C. Lechat *CLL 8304; STMA 08195* (LIP, culture MUCL 51832); same locality, C. Lechat *CLL 8305, STMA 08187* (LIP, culture MUCL 51833); Saint Esprit, Aug. 2008, C. Lechat *CLL 8423*, *STMA 08193* (LIP, culture MUCL 51840); same locality, *CLL 8424*, *STMA 08188* (LIP, culture MUCL 51841); Sainte Luce, Aug. 2008, C. Lechat *CLL 8279, STMA 08197* (LIP, culture MUCL 51829); same locality, CLL 8283; *STMA 08196* (LIP, culture MUCL 51830); same locality, C. Lechat *CLL 8288; STMA 08199* (LIP, culture MUCL 51831); Sainte Marie, Aug. 2008, C. Lechat *CLL 8383; STMA 08198* (LIP, culture MUCL 51839). **Mayotte**, Combani, Combani Gulf, on dead trunk of *Mangifera indica*, 8 Jan. 2011, comm, M. Pélissier *JF-11003* (KR, culture MUCL 53498). **Mexico,** Chiapas State, near Palenque, 1 Jan. 1973, R.E. Jackson (NY); Jalisco, Municipio de Cabo Corrientes, 9.8 km on the road from Brecha el Tuito to Aquiles Serdán, *ca.* 570 m, Sep. 2004, O. Rodríguez (GUAD, C, culture MUCL 47606, see Bitzer *et al.* 2008); Mazatlan, Dec. 1961, P. Martin *910* (NY - see Martin 1969 as as *D. occidentalis*); Mazatlan, lighthouse, Dec. 1961, P. Martin *948* (IMI - see Martin 1969 as *D. eschscholtzii*); San Blas, Dec. 1962, P. Martin *1542* (IMI - see Martin 1969 as *D. occidentalis*); Nayarit State, Tepic, Vilareal-Orbaz, 18 Jul. 1996, I. Krisai-Greilhuber & H. Voglmayr *6725* (WU-Myk. 24615); Oaxaca, A. Lopéz 485, ex herb ENCB (NY); Veracruz, Oaxaca, Hole plantation, outside of Tuxtlapec, 15 Aug. 1977, A.L. Welden & T.E. Weiss *4001* (NY); Oaxaca, in Hule Plantation outside of Tuxtepec on road to Jalapa de Diez, 3 Aug. 1976, A.L. Welden & E. Weiss *4001* (NY 460093 ex NO); Rancho Lucas Martín, between Xalapa and Banderilla, 9 Oct. 1968, G. Guzman (NY); Oaxaca, A. Lopéz 498, ex herb ENCB (NY); near Yagallo, 1963, W.S. Miller (NY ex ENCB); Tamasol, tropical vegetation, Nov. 1974, O. Mojica 7 (NY ex ENCB); Temezcal, 8 Oct. 1988, F. San Martín *1135* (JDR, see San Martín (1992) as *D. eschscholtzii*); "Tamascal" (Temezcal??), hill south-east of village, hydroelectric plant, disturbed perennial tropical forest, 6 Aug. 1976, G. Guzmán *16304* (NY ex ENCB); Quintana Roo State, Blanco municipality, Ejido La Unión, 8 Jul. 1986, P. Othón, ex herb F. San Martín *422A* (JDR, see San Martín 1992 and Ju *et al.* 1997 as *D. eschscholtzii*); Veracruz, Estación Biológica de Los Tuxtlas, road from Catemaco to Montepío, perennial tropical forest, 9 Jul. 1972, G. Guzmán *10169* (NY ex ENCB); same locality, Volcán San Martín, east side of Cerro Vaxin, deciduous forest with *Liquidambar*, 11 Jul. 1972, G. Guzmán *10319* (NY ex ENCB); San José de Gracia, road from Cordoba to Veracruz, near Rio del Medio, 8 Jul. 1972, G. Guzmán *10152* (NY ex ENCB); Uxpanapa District, south-west of Brecha 104, south-east of Campamento de Hermana Cedillo, 17 Mar. 1976, G. Guzmán *15557*, *15571* and *15559* (NY ex ENCB); Veracruz, Cordoba, 5 Dec. 1937, J.H. Faull (FH 79480); Yucatán, 10 Feb. 2004, F. Dämmrich & M. Eckel, *Ww 4450* (K(M) 130023, culture KC1699); Tamaulinapas, Gómez, Farías 14 Oct. 1986, F. San Martín *23* (JDR - see San Martín 1992). **Montserrat**, Coconut Hill, 1 Feb. 1907, J.A. Shafer (NY). **Nicaragua**, Los Amates, 20 Feb. 1907, W.A. Kellerman (BPI 594808); exact locality not given**,**1893, C.L. Smith *30* (NY); Ometepa, no date, C.L. Smith: Central American Fungi *33*, det Child (1932) as *D. concentrica* (NY); locality unknown, 1893, C.L. Smith: Central American Fungi *78* (F 331685). **Nigeria**, 1917, C.O. Fargehanon (?), no further data (NY ex K); Anambra State, Naukka, on breadfruit tree (*Artocarpus altilis*), 12 Aug. 1895, O.O. Cletus (K(M) 130245); Cross River State ("Eastern Nigeria"), Ikrigon, on log, Apr. 1967, B. Maguire (NY). **Pakistan**, Lahore, *Morus alba*, Nov. 1961, S. Ahmad, Reliquiae Petrakianae *2877* (L 0275629; M–0079877; B70 0009589); West Pakistan, Chanja Manga, *Morus alba*, Jul. 1961, S. Ahmad *23547* in herb. Petrak (L 0275628, M–0079878); Changa Manga, *Morus alba,* 19 Apr. 1969, Tariq (IMI 140190). **Panama**, Chiriquí, Puerto Armuelles, 28 Jul. 1952, G.W. Martin & A. L. Welden *7988* (K(M) 131692; NY); Dolega, Los Algarrobos, on the way to Los Gonzales, *ca.* 140 m., Sep. 2005, M. Piepenbring (M, culture MUCL 47598); Valley of Upper Rio Chiriqui, 28 Jun. 1935, G.W. Martin *2058*, det. J.H. Miller as *D. concentrica*

(NY and FH 79477, the FH specimen lacking ascospores); Barro Colorado Island, Fairchild Trail, 29 Jan. 1929, W.H. Weston *39* (FH 220987); Bocas del Toro Prov., Almirante, United Fruit Co. Farm, 20 Aug. 1925, C.W. Dodge & J.L. Permor *4137* (FH 220968); Canal zone, Corundu (?), 13 Aug. 1972, G.W. Martin & A.L. Welden *8342* (FH 79517); Kentucky Farm, Changuinola River, 1 Sep. 1925, C.W. Dodge & W.S. Thomas *4184* (FH 220969). **Papua New Guinea**, Madang, Laing Island, wood near beach, 18 Jan. 1997, R. Walleyn *670*, det. K. Van der Gucht (GENT, culture MUCL 43508); near Rempi, on branch of dikot wood in coconut plantation near beach, 31 Jul. 1997, J. Häffner *JH2810* (WUP); Kanosia, on rotten branch, no date, C.E. Carr *11*, det. Van der Gucht (1994) (K(M) 130238). **P.R. China**, Yunnan, 14 Mar. 1957, X-Lian Wang & W. Quing-Zhi *2* (FH 79489 ex HMAS 20311); Mok–Kiang, rotten wood, Jan. 1934, Y. Tsiang *422* as *D. bakeri* (BPI 594760); Xishuangbanna prefecture, in rainforest, Jul. 2005, C. Decock, *STMA 05269* (MUCL, culture MUCL 47144); same collection data, *STMA 05270* (MUCL, culture MUCL 47145); same collection data, *STMA 05271* (MUCL, culture MUCL 47186); same collection data, Sep. 2006, *STMA 06158* (MUCL, culture MUCL 47965). **Peru**, Madre de Dios, Tambopata National Reserve, on rotten dicot pole in bridge, 15 Jun. 1987, T. Læssøe *P–013* (C); Huanuco, Tingo Maria, grounds of Univ. Agraria (UNAS), on dicot. wood in association with *Neohypodiscus cerebrinus*, 4 Jul. 1987, T. Læssøe *P–153* (C, culture CBS 113042, MUCL 44612); Loreto, Iquitos, Yanomono, dicot wood in sunny position, 3 Jul. 1987, T. Læssøe *P–288* (C). **Philippines**, Cafiz, Panay, 16 Jan. 1904, E.B. Copeland (NY); Camarines Sur, Mt. Isarog, Ocampo, 20 Oct. 1980, M.M. Baldovino (CALP 9349, KR); Leyte Island, Paie, Jan. 1908, A.D.E. Elmer *7202* (NY); Batan Prov., 1 Feb. 1904, E.B. Copeland *156* (NY); Batan Prov., Lamao River, Mt. Mariveles, Dec. 1908, R.S. Williams (NY); Luzon Island, Nueva Viscaya Prov., Jan. 1913, D.C. Mignegub (NY); same locality, 19 Nov. 1909, H.M. Curran ex herb. P. Sydow (S-F43790); La Laguna Prov., Los Baños, 2 Apr. 1921, O.A. Reinking ex Lloyd herb. *12290*, see Child 1932 (BPI 717066); same locality, *Tamarindus indica*, 5 Aug. 1913, Evaristo *1568* ex herb. Rehm (S–F38156; see Rehm 1914b and Child 1932 as *D. eschscholtzii*); same locality, Forestry Campus UPLB college, college, Jul. 2001, T.H. Quimio & M.M. Baldovino (CALP 11232, KR); MBG UPLB College, Dipterocarp area, 11 Feb. 2000, T.H. Quimio & M.M. Baldovino (CALP 10878, KR); Mt. Makiling, 3 Oct. 1920, C. Serrano ex Lloyd herb *12182*, det. Child (1932) as *D. eschscholtzii* (BPI 717062); Los Baños, Mt. Makiling, near Mudspring, 5 May 1993, T.H. Quimio & M.M. Baldovino (CALP 9541; KR); Mt. Banahaw, Nagerlan, 18 Jan. 2002, T.H. Quimio & M.M. Baldovino (CALP 11408; KR); Maulawin Creek, MBG UPLB College, Jan. 2001, T.H. Quimio & M.M. Baldovino (CALP 11052, WUP –immature); Makipot creek, Cavinte, 5 May 2000, T.H. Quimio & M.M. Baldovino (CALP 10858; KR); Mindoro Oriental Prov., Pola, Jul. 1965, I.J. Dogma Jr. (CALP 3185; KR); Negros del Norte Prov., Cadiz, Sep. 1909, A. Celestino ex herb. P. Sydow (S-F43791); Rizal Prov., Antipolo, Oct. 1912, M. Ramos ex herb. P. Sydow (S-F43789); Sulu Prov., Tarawakin National Agricultural School, Tawi Tawi, Jul. 1965, D.R. Reynolds (CALP 3056, KR); Jolo, Jul. 1965, D.R. Reynolds (CALP 3001; KR); Tayabas Prov., Basilan Islands, Dec. 1916, H.S. Yates, det. J.H. Miller as *D. bakeri* (BPI 594758); Basilan Islands, Jun. 1921, G.M. Reyes, ex Phil. Nat. herb. *10012* (FH 220998); Corregidor, 18 Mar. 1846, W.L. White (FH 220997); Luzon Island, Benguet Subprov., Pauai, Jan. 1915, M. Strong Clement (FH 79449); Tayabas Prov., Basiad, Dec. 1916, H.S. Yates (BPI 594841, FH 79450, the latter listed by Child (1932) as *D. bakeri*); Stotsenberg, on fire-killed *Antidesma*, Nov. 1923, M.S. Clemens (FH 79486); Mindanao, Butuan subprov., Mar.-Jun. 1911, C.M. Weber *125* (FH 220999); Sutuan Subprov., 1911, C.M. Weber *1257* (FH 220999, F 331694, both mixed with *D. placentiformis*, and NY, only containing the *D. eschscholtzii* element); Mindoro, Mt. Yagaw, 6 Oct. 1953, M.D. Sulit & H.C. Conklin, ex Phil. Nat. herb. *19217* (FH 220990); Palawan, Jul. 1912, E. Fenix ex herb. P. Sydow (S-F43786); exact locality unknown, "in Botanic Garden", 7 Mar. 1877, ex herb. Saccardo, as *D. eschscholtzii* (PAD); C.F. Baker *2723* (S–F38154, see Rehm 1914a and Child 1932 as *D. eschscholtzii*); Leyte Island, Palo, Jan. 1906, A.D.E. Elmer *7202* (F 331695). **Puerto Rico,** Candelaria, near Batamon, W.L. Britton *et al.* (NY); Carrochales (?), rotten wood, J.A. Stevenson *2768* (NY); La Isabella, 13 Dec. 1905, J.A. Stevenson *3525* (NY); Plantago, on orange stump (*Citrus*), F.S. Earle *46* (NY); Mayaguez, College Farm, 23 Jan. 1937, A.G. Kevorkian *121* (FH 79473); Rio Piedras, La Romana, 8 Apr. 1913, J.R. Johnston (NY). **Rwanda**, Park Abujera near Lake Hima, dead wood in dry savannah, 13 Aug. 1974, J. Rammeloo *R 4281* (GENT). **Senegal**, Basse Casamance, Kafoutine, edge of mangrove region, dead wood, 15 Sep. 1985, A. Fraiture *S34* (BR–Myc 003529,64). **Saint Lucia**, Rodney Bay, Hotel Sta. Lucia, *Cordia sebastina*, 24 Nov. 1993, N.W. Legon (K(M) 25381, culture KC 1616). **Seychelles,** Mahé islands, Anse takamaka, dead wood of *Mangifera indica*, Mar. 2006, A. Hausknecht (WU, culture CBS 119994, MUCL 47713). **Sint Maarten**, Summer 1979, N. Anema–Balke (L 0275632 – immature). **São Tomé e Príncipe**, São Tomé, 1886, Quintas (B70 0009594); same locality, 1887, Möller ex herb. Bresadola (S-F43703). **Sierra Leone,** Kortright, Fourah Bay College, on rotting log, 18 Feb. 1981, S.M. Mpofu *F7* (K(M) 130371); Kari, Njala, on *Annona muricata*, 12 Feb. 1955, A.B. Katta *M 6339* (K(M) 131688); Njala, *Albizia zygia*, 3 Aug. 1949, F.C. Deighton (IMI 37538). **Singapore**, Botanic Gardens, on dead *Hevea brasilensis*, C.J. Baker *5488* ex herb. Saccardo (PAD). **Solomon Islands**, New Georgia, wood, 8 Jul. 1980, E.H.C. McKenzie (PDD 45927). **Sri Lanka,** Beruwela, dead wood near beach, 12 Feb. 2003, M. Eckel (KR ex herb *Ww 4365*, culture CBS 113486). **Sudan**, Bunyiga, 1948, Tarr (K(M) 131685B); Yambio, 1948, Tarr (K(M) 131685). **Surinam**, Commewijne District, Ost–West road, 4 Jul. 1961, A.L. Welden *384* (L 0275627); same locality, A.L. Welden *2351* (NY 461065; NY; 2 packets); Citrus Proef, La Poule, 5 Jul. 1961, A.L. Welden *2360* (NY 460110); exact locality unknown, 1827, Martii ex herb. Weigelt (BR–Myc. 93359,45); locality illegible, 1982, C. Jongkind *664* (L 0275626). **Taiwan**, Taipei[9], 10 May 1931, K. Sawada (BPI 594688); Ping–Tung Co, Najanku, 8 Oct. 1997, C.C. Wen *WAN504*, comm. Y.M. Ju (HAST; culture BCRC 34047; GenBank Acc. Nos of DNA sequences AY951696 and AY951808, see Hsieh *et al.* 2005). **Tanzania**[10], Eastern Province, Kilosa, Illonga, Matarawe, on rotten wood lying on the ground, 25 May 1968, D.N. Pegler *Tl036* (K(M) 131671); Northern Province, Arusha Ditrict, Arusha National Park, Mt. Meru, Jekukumia Ca, 30 May 1968, D.N. Pegler *T782* (K(M) 130380); Southern Highlands Province, Iringa District, Ruaha National Park, Magagwe, on burnt wood, 18 May 1968, D.N. Pegler *7941* (K(M) 130379); Mbeya Government Hospital, on dead log of cf. *Acacia* sp., 10 May 1983, R.A Nicholson *5* (K(M) 131668); Western Province, Kigomo, Lugomela, 20 Oct. 1969, K. Pyrozynski *M814* (K(M) 130381). **Thailand**, Chiangmai Province, Chiangmai, isolated from endophyte collected in 1997, artificially induced stromata, comm. A.J.S. Whalley (AJSW, culture CBS 116031); Nan Province, log pile, 7 Sep. 1994, A.J.S. Whalley (AJSW, culture no longer viable); Phuket Province, Phuket, on angiosperm wood, 2 Apr. 2002, M. Eckel, *Ww 4166* (M, WUP, culture CBS 113047, MUCL 44611, GenBank Acc. No. AY616684); Saraburi Prov., Saraburi Botanical Garden, 3 Dec. 1979, dead trunk, V. Demoulin *5405* (NY ex LG); Soratthani Prov., Khao Sok, *Ficus* (dead rubber tree), Sep. 1993, R.J. Bandoni (JDR, culture CBS 122877, see Ju *et al.* 1997, Stadler *et al.* 2001a); exact locality unknown, alt. 2100m, on dead trunk, M. Thulin & B. Mhoro *2797* (UPS). **Trinidad and Tobago,** Casparee Island, Apr. 1921, F.J. Seaver *8448* (NY); Trinidad Island, Arima Valley, 15 Jan. 1959, H. Fleming (NY); Trinidad, 1912–1913, R. Thaxter (FH 79468); same collection data, R. Thaxter *5303* (FH 79476); St. Ann's Valley, 1912–1913, R. Thaxter *6751* (FH 79482); St. Augustin, *Angelica* sp. [?[11]], Mar. 1927, H.R. Briton-Jones (IMI 10669). **Uganda**, Mulange, burnt logs, Jul. 1919, R.A. Duemmer (BPI 594955 - see Child 1932 as *D. eschscholtzii*); Kipayo, on stump, Apr. 1915, R.A. Duemmer *1442* (K(M) 131686). **USA,** California, Edwards**,** ex herb. W.A. Murrill (NY). Florida, Dade Co., Coral Gables, *Albizzia lebbek*, 14 Nov. 1942, R. Singer *1478* (F 331673); Orange Co., Winter Park, *Quercus* ("dead oak tree"), 7 Sep. 1946, P.O. Schallert *2142* (F 331661); Daytona, 1897, R. Thaxter (FH 79467); Florida, on bark of orange tree (*Citrus*), Jan. 1917, F.S. Meade *5768* (NY); Louisiana, Plaquemines Par., Edward Robert Center, Tulane Univ., 14 Nov. 1973, R.J. Bandoni & A.L. Welden *5446* (NY); St. Martinsville, 22 Jul. 1883, A.B. Langlois, Flora Ludoviciana *2166*, ex Ellis coll. (NY); St. Martinsville, 30 Aug. 1989, A.B. Langlois, Flora Ludoviciana *2282* (NY); Texas, near Sinton, Welder Wildlife Refuge, Dec. 1973, J.F. Lawrence (JDR, culture CBS 122876, see Ju *et al.* 1997, Stadler *et al.* 2001a). **US Virgin Islands,** St. Jan [St. John], American Hill, 17 Mar. 1906, 1905-06, C. Raunkiær, Plantae ex Ind. occid., *1784*, det. Ferdinandsen & Winge (UPS); St. Thomas, Mar. 1923, F.J. Seaver *778* and *805* (NY); St. Croix, Mar. 1923, F.J. Seaver *884* (NY); no exact locality given, Jan. – Apr. 1923, F.J. Seaver & C. S. Chardon *1402* (NY); Port Antonio, 1906, A.E. Wright *238* (FH 220989). **Venezuela**, Amazonas, Puerto Ayacucho, 7 Aug. 1990, F.D. Calonge (MA 53208); same locality, 10 Aug. 1990, F.D. Calonge (MA 53209); Isla Margarita, Cerro Copey, dead wood, 21 Aug. 1990, F.D. Calonge (MA 53210); Orinoco region, 1887, A. Gaillard ex herb. Bresadola, Champignons du Haut-Orénoque *241* as "*D. concentrica* var. *obovata* Nees" (S-F43795); exact locality unknown, 1970, R. Urteaga (K(M) 130242); 1915, Blakeslee (FH 79485). **Vietnam**, Ho Chi Minh City ("Saigon"), Oct. 1966, Maas Geesteranus *212* (L 0275623); Vicinity of Hanoi, Mar. 2007, D.N. Quang, *STMA 07012* (KR, culture MUCL 49359). **Western Samoa**, Mount Apia, *Citrus aurantium*, May 1905, *K. & E. Reichenberger*, comm. Dr. von Höhnel, Rehm: Ascomyceten *1718* (M–0079881); same locality, *Albizzia*, 23 Sep. 1975, E.H.C. McKenzie (PDD 39454); Upolu, *Citrus aurantifolia*, 2 Feb. 1977, E.H.C. McKenzie (PDD 36258). **Zambia**, Chowo, Nyika Plateau, on dead wood, 27 Jan. 1983, G.D. Pearce *FP 736/5* (K(M) 131686); Gwembe Valley, *Tamarindus indica*, 4 Jul. 1961, A. Angus (IMI 90087); Mt. Makulu Research Station, near Chila, 9 Jul. 1962, A. Angus (IMI 95890; label reading "southern Rhodesia"). **Central Africa**, country unknown, label reading: "Ondetei; 800–900 m NN, 0`41 N lat.", 26 Dec. 1901, F. Stuhlmann (B70 0009597). **Locality unknown**, (Philippines?) Laguna, 1885 (?)", remainder of label illegible, leg. B. Scortellini in herb. Saccardo as *D. concentrica* f. *eschscholtzii* (PAD).

*Stromatal metabolites*: BNT (1), concentricol derivatives (**2–3**; sometimes only detected in traces) and cytochalasins (*e.g.*, **4–5**; often present in large quantities); oxidised binaphthalene derivatives such as daldinones also present in some specimens.

[9]Label reads "Taihokuensis", Japanese name for Taiwanese capital, *fide* Y.–M. Ju, pers. comm.

[10]Specimens from Tanzania were det. by R.W.G. Dennis as "*D. concentrica* var. *eschscholzii*".

[11]Dubious host record, since *Angelica* is not a woody plant and no plant material was attached to the stromata of the specimen.

**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.

| Species and origin of material | Conidiogenous structures (µm) |
|---|---|
| ***D. albofibrosa*** | CC: 10–16 × 2–2.5 |
| Papua New Guinea (MUCL 38738 ex-type); Malaysia (CBS 117737) | CON: 4–6 × 2–3 (av. 5.1 × 2.4) |
| | Nodulisporium-like to periconiella-like branching pattern |
| ***D. bambusicola*** (data given in Ju *et al.* 1997 confirmed by us): | CC: 10–17 × 2.5–3.5 |
| Thailand (CBS 122872 ex-type) | CON: 3.5–4.5 × 2.5–3 (av. 4.2 × 2.7) |
| | Periconiella-like branching pattern predominant |
| ***D. caldariorum*** (current study): | CC: 10–20 × 2–3.5 |
| Cuba (MUCL 47595); France (MUCL 49217); R. South Africa (MUCL 47715); Taiwan: (BCRC34042); UK (KC1523, ATCC 36660) | CON: 4.5–6.5(–7) × 2.5–4.5 |
| ***D. caldariorum*** (Ju *et al.* 1997): | CC: 10–17 × 2–3 |
| Mexico (CBS 122874) | CON: 4.5–6.5 × 3–4.5 |
| ***D.* cf. *caldariorum***: | CC: 12 – 20 × 3.5 – 4.5 |
| Ecuador (CBS 113045) | CON: 7–8 × 4 – 5 (av. 7.4 × 4.6) |
| ***D.* cf. *eschscholtzii***: | CC: 16–21 × 3–3.5 |
| Benin (MUCL 45434, MUCL 45435); Burkina Faso (CBS 117470); Cameroon (CBS 113969, CBS 117735) | CON (5.5–)6.5–7.5(–8.5) × 3–4 |
| ***D.* cf. *eschscholtzii***: | CC: 6–12 × 2.5–3 |
| Malaysia (CBS 116036) | 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 |
| ***D.* cf. *eschscholtzii***: | CC: 14–22 × 3–4 |
| Malaysia (CBS 116040, CBS 116041) | CON: 2–2.5 (–3) × 6–7.5(–8.5) (av. 7.2 × 2.4) |
| ***D. eschscholtzii sensu stricto*** (in agreement with Ju *et al.* (1997): | CC: 8–22 × 2.5 –3 |
| 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: KC1699, MUCL 47606; Panama (MUCL 47598); P.R. China (MUCL 47144, MUCL 47186, MUCL 47965); Peru (CBS 113042); Saint Lucia: (KC 1616); Seychelles (CBS 119994); Sri Lanka (CBS 113486); Taiwan (BCRC 34047); Thailand (CBS 113047, CBS 116031, CBS 122877); USA (CBS 122876); Vietnam (MUCL 49359) | CON: 4.5–6.5 × 2–3 (av. 5.2 × 2.8) |
| ***D. starbaeckii***: | CC: 16–22 × 2.5–3.5 |
| Cayman Islands (KC 1692); Ecuador (MUCL 45438, CBS 116026); French Guyana (MUCL 45436); Martinique (MUCL 52886) | CON: 5–8 × 3–4.5 (av. 6.8 × 4.0) |
| | Virgariella-like branching pattern predominant |
| ***D. theissenii*** (= *D. clavata sensu*. Ju *et al*. (1997) | CC: 8–22 × 2.5 –3 µm |
| Argentina (CBS 113044); Peru (CBS 113043 ex-type); a culture from Mexico reported by Ju *et al*. (1997) as *D. clavata* was also studied earlier on (Stadler *et al.* 2001a, b) but is not extant anymore. | CON: 4.5–6.5 × 2–3 (av. 5.2 × 2.8) |
| | Similar to *D. eschscholtzii sensu stricto* |

*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.

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

* 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 concentricols as in the *D. concentrica* 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.

*Deviating specimens examined*: **US Virgin Islands**, St. John, Cinnamon Bay, Campground St. John, on log, 6 Jan. 1994, D.J. Lodge *StJ 106* (NY); same locality, beyond Mahoe Bay on North Shore Road, abandoned warehouse, on branch, 30 Dec. 1995, D.J. Lodge & W.J. Henderson *StJ 187* (NY); same locality, Reef Bay Trail, in gut, rotten log, 2 Jan. 1995, D.J. Lodge & W.J. Henderson *StJ 191* (NY); "St. Jan[12]", American Hill, 17 Mar. 1906, 1905-06, C. Raunkiær, Plantae ex Ind. occid. *1784*, det. Ferdinandsen & Winge (S-F43787); St. Thomas, on wood, Mar. 1923, F.J. Seaver *777* and *811* (NY). **Venezuela**, Amazonas, 100 km east of Puerto Ayacuebo, Jul. 1991, A. Ditlevsen *et al.* (K(M) 103863, culture KC 1690).

[12]St. John (= St. Jan) was a Danish protectorate at that time.

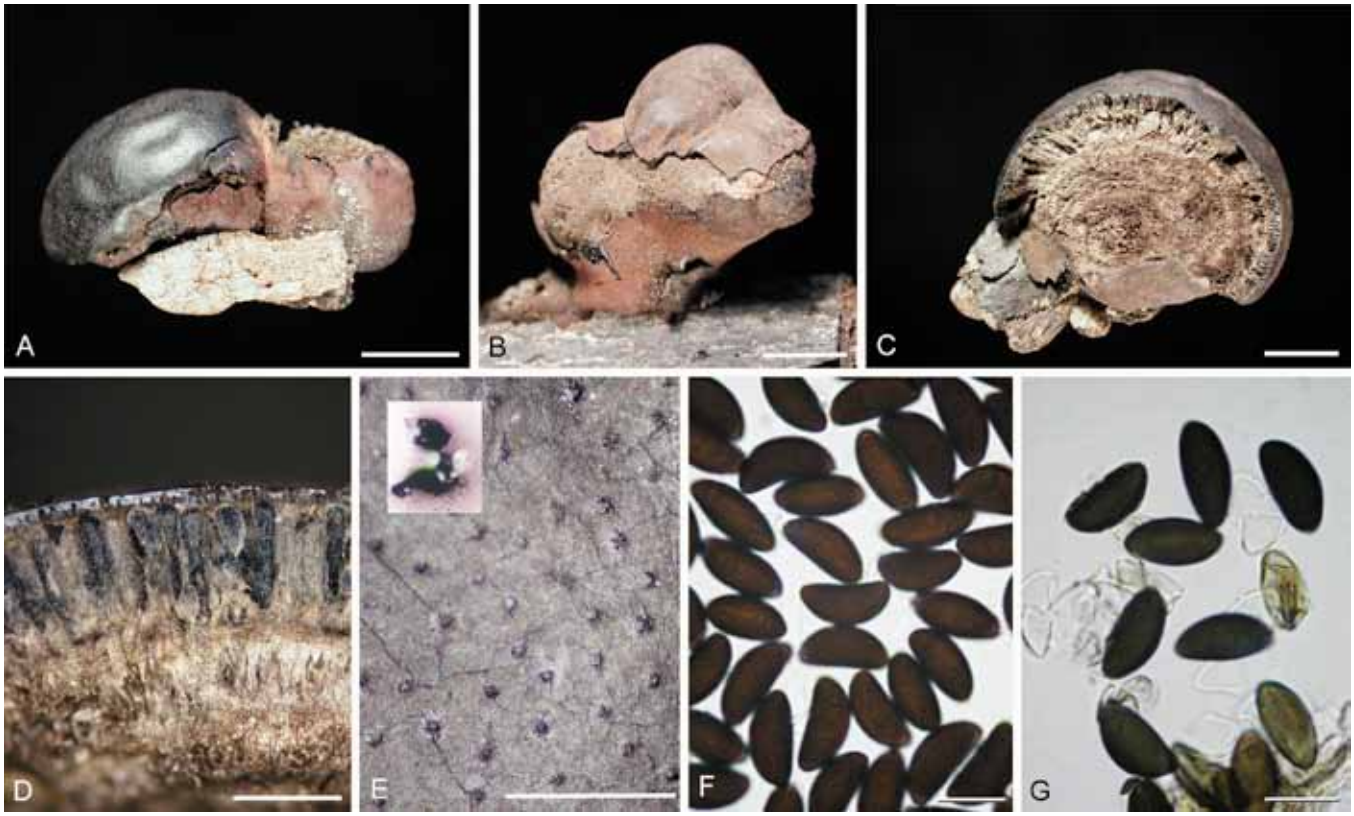



**Fig. 30**. Teleomorphic characteristics of *Daldinia* sp. (cf. *eschscholtzii*) Martin 910 (Mexico). A, B. Stromatal habit. C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). F. Ascospores in SDS. G. Ascospores in KOH, showing dehiscing perispore. Scale bars A–C = 5 mm; D, E = 1 mm; F, G = 10 µm.

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-inequilateral, 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.

*Deviating specimens examined*: **Indonesia**[13], North Sulawesi, Dumoga-Bone National Park, Sep. – Oct. 1985, G.J. Samuels *2357A* (NY); same locality, Confluence of Toraut and Tumpah Rivers, Sep. – Nov. 1985, G.J. Samuels *1939* and *2035* (NY); same locality, vicinity of Maleo Bird Nesting site and Hot Springs, in banana plantation, 22 Oct. 1985, G.J. Samuels *2230* (NY); Eastern Dumoga-Bone National Park, vicinity of Camp Edwards, 6–8 Oct. 1985, G J. Samuels *2052* (NY).

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

[13]All specimens were cited as *D.* cf. *eschscholzii* in Rogers *et al.* (1987).

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 originaly 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 conidiogenous 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 glimpse. 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.

***Daldinia albofibrosa*** M. Stadler, M. Baumgartner & Wollw., Mycotaxon 80: 186. 2001. Figs 11E–H, 31.

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

*Typus*: **Papua New Guinea**, Madang Prov., lowland rain forest, Oct. 1989, K. Van der Gucht as *D. albozonata* (GENT-**holotype***;* **ex-type cultures** MUCL 38738, obtained by Van der Gucht 1994, and MUCL 43509, obtained by Stadler *et al.* 2001c).

*Misapplied name*: *Daldinia albozonata sensu* Van der Gucht (1994, 1995).

*Selected Illustrations*: Van der Gucht (1995): figs 10a, b (teleomorph) and 11d–f (anamorph) as *D. albozonata*; Stadler *et al.* (2001c), figs 6, 7 (stromata), 14 (anamorph) and 18 (ascospores by SEM).

*Known distribution/host preference of stromata*: New Guinea and Southeast Asia; host affinities unknown.

*Teleomorph*: *Stromata* subglobose, subsessile or turbinate, (0.5–)1–2.5 × 1–2.5 cm, without visible perithecial outlines but cerebriform due to shrinkage of the internal tissues, surface greyish brown to Vinaceous Brown (84), with reddish brown granules immediately beneath surface, with KOH extractable pigments Dull Green (70), Isabelline (65), Fuscous Black (104) or Sepia (63), tissue between perithecia pithy to woody, tissue beneath the perithecial layers composed of alternating concentric zones, darker zones dark brown, pithy to woody, 0.1–0.15 mm thick, lighter zones white, pithy to woody, persistent, 0.8–1.5 mm thick (Ratio of darker/ligher zones 1:4–10). *Perithecia* lanceolate, 0.8–1 × 0.2–0.4 mm. *Ostioles* umbilicate, often inconspicuous. *Asci* 110–150 × 6–7 µm, p. sp. 60–75 µm, stipes 50–75 µm, with amyloid, discoid apical apparatus 0.5–0.75 × 2–2.5 µm. *Ascospores* brown, elongate ellipsoid-inequilateral with narrowly rounded ends to almost reniform in the material from Sabah, (8–)9–10.5 × 4–4.5 µm, with straight dorsal germ slit spore length, perispore dehiscent in 10 % KOH, smooth by LM, revealing transversal striations by SEM (5.000×); epispore smooth.

*Stromatal metabolites*: BNT and daldinone A; cytochalasins not detected.

*Cultures and anamorph*: *Colonies* on OA reaching the edge of a 9 cm petri dish in 10 d, felty, zonate, with diffuse margins, at first whitish to pale yellow, becoming floccose and greyish brown when sporulating, reverse Herbage Green (17) to Citrine (13), blackening with age, releasing greenish to brownish exudates into the agar, developing a sweet odour. Sporulating regions at first appearing in the centre of the colony, later scattered over entire surface of the colony. *Conidiophores* up to 210 µm × 2.5–3 µm, mononematous, dichotomously or (sometimes) trichotomously branched, hyaline, smooth or finely roughened, with 1–3(–4) conidiogenous cells arising from each terminus, showing a nodulisporium-like, to less frequently, a periconiella-like branching pattern. *Conidiogenous cells* terminal or intercalary, cylindrical, hyaline, smooth, 10–16 × 2–2.5 µm. *Conidia* produced holoblastically from sympodially proliferating conidiogenous cells, hyaline, obovoid, smooth or finely roughened, 4–6 × 2–3 µm.

*Additional specimens examined*: **Papua New Guinea**, Madang Prov., lowland rain forest, forest border, on small log, 6. Sep. 1990, P. Van der Veken *90-687*, det. K. Van der Gucht (1994) as *D. albozonata* (GENT). **Malaysia,** Sabah, Danum Valley, nature trail at field centre, on (dicot.) stick in sunny spot, 29 Jun. 1999, T. Læssøe *TL-6011* (C, culture CBS 117737)[14].

*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 Thalland, 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.

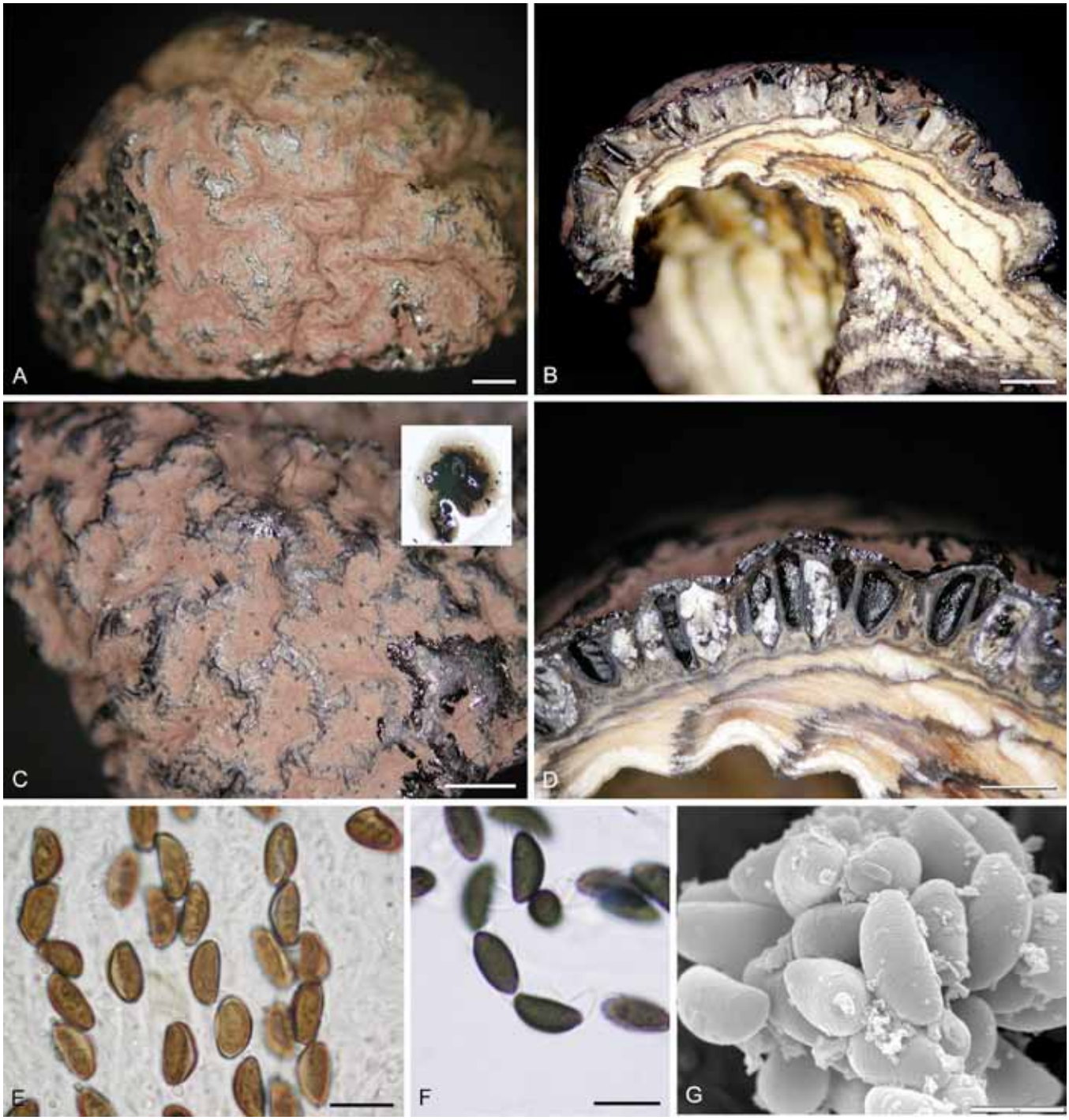



**Fig. 31.** Teleomorphic characteristics of *Daldinia albofibrosa.* Holotype (Papua New Guinea). A. Stromatal habit. B, D, E. Stroma in longitudinal section showing hollow interior, internal concentric zones and perithecial layer. C. Stromatal surface with ostioles, and stromatal pigments in 10 % KOH 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.

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 xylariaceaous 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. 32.** Teleomorphic characteristics of *Daldinia albozonata* (Holotype, Cameroon). A, D. Stromatal habit of mature stromata. B. Stromatal habit of immature stroma. C, E. Stroma in longitudinal section showing internal concentric zones and perithecial layer; inserted stromatal pigments in 10 % KOH. F. Ascospores in SDS. G. Ascospores in KOH, showing dehiscing perispore. H. Ascospores by SEM (10.000×). Scale bars A, C = 5 mm; B, D, E = 1 mm; F, G = 10 µm; H = 2 µm.

*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 *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 *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 *D. albozonata* (K(M) 120968). **Cameroon**, Bipindi, W. Zenker ex herb. Petrak as *D. albozonata* (M-0079887, probably part of **type**).

*Notes*: Ju *et al.* (1997) treated this name as a synonym of *D. clavata.* However, we prefer to accept it *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 *Daldinia* aside from *D. brachysperma*. Their stromatal habit also differs from that of typical *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 *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 *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 Martín, Mycotaxon 61: 253. 1997. Fig. 33.

*Etymology*: For the host plants.

*Holotypus*: **Thailand**, Chiangmai Prov., Doi Inthanon National Park, Education Centre, on bamboo, 23 Sep. 1994, R.J. Bandoni & T.W. Flegel (WSP 69652; **ex-type culture** CBS 122872; GenBank Acc. Nos of DNA sequences: AY951800, AY951688 and AB376692; see Hsieh *et al*. 2005).

*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.

*Additional specimen examined*: **USA**, Washington D.C., *Bambusa* sp., 12 Oct. 1912, G.R. Lyman (BPI 594887, see Ju *et al.* 1997).

*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 8.5–11 × 4–5 µm. The darker, more solid and zonate internal tissues reported by Ju *et al.* (1997) were probably encountered in other cited collections that include another Thai collection and two Philippine collections previously labelled *D. gollani*. This is why a full description is not given here.

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 Martín, 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 Martín *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). *Perithecia* obovoid 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 Martín 1992 as *D. albozonata* affin.) 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.

***Daldinia caldariorum*** Henn., Verhandlungen des Botanischen Vereins der Provinz Brandenburg 40: 158. 1898. Figs 5F, G, 11I–L, 35.

*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).

*Isolectotypus* (selected here): MBT177381; **Germany**, Berlin, fern house in Botanic Garden, Nov. 1887, H. Sydow ex herb. Rehm, label reading "*Hypoxylon concentricum*/*Daldinia berolinensis*" (S–F38120).

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

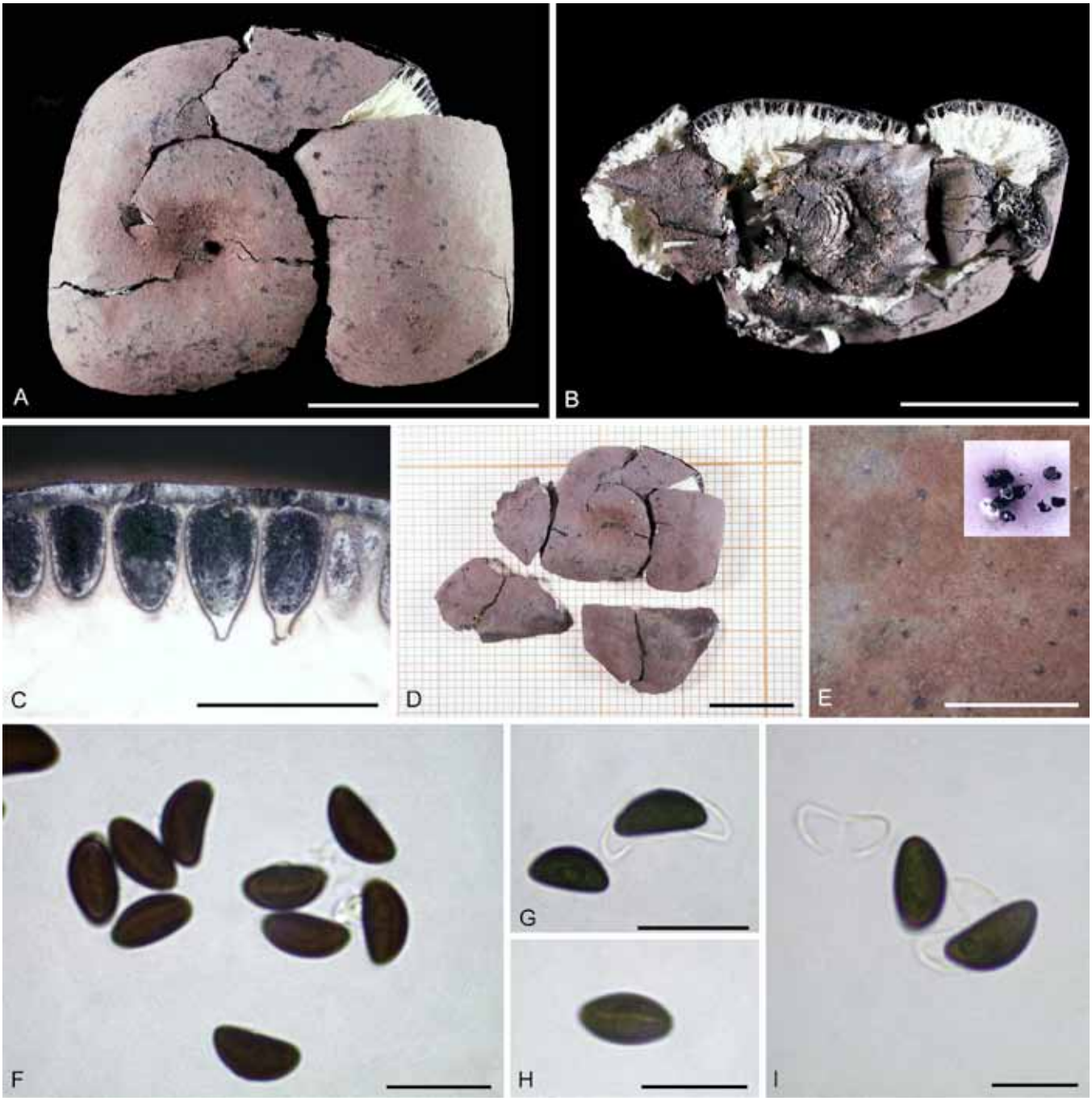



**Fig. 33.** Teleomorphic characteristics of *Daldinia bambusicola.* Holotype, WSP 69652 (Thailand). A, B, D. Stromatal habit. C. Part of stroma in longitudinal section showing perithecial layer. E. Stromatal surface showing the ostioles (inserted: Stromatal pigments in 10 % KOH). F. Ascospores in SDS. 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.

= *Daldinia cognata* Har. & Pat., J. Bot. (Paris) 17: 15. 1903.

*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*: **Philippines**, on dead stem of *Hibiscus rosa-sinensis*, E.D. Merrill *4115* (BPI 716950 ex Lloyd herb. *12408* (K - **lectotype**; NY - **isolectotypes**, selected by Ju *et al.* 1997.

= *Daldinia platensis* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 19: 345. 1909.

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

= *? Daldinia gollani* Henn., Hedwigia 40: 339. 1901.

*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).

= *? Daldinia aparaphysata* Saccas, J. Agric. Trop. Bot. Appl. 1: 190. 1954.

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

= *? Daldinia corrugata* Pat. & Har., Bull. Soc. mycol. France 22: 120. 1906.

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

= *Daldinia concentrica* var. *minuta* Waraitch, Indian J. Mycol. Pl. Path. 7: 16. 1977.

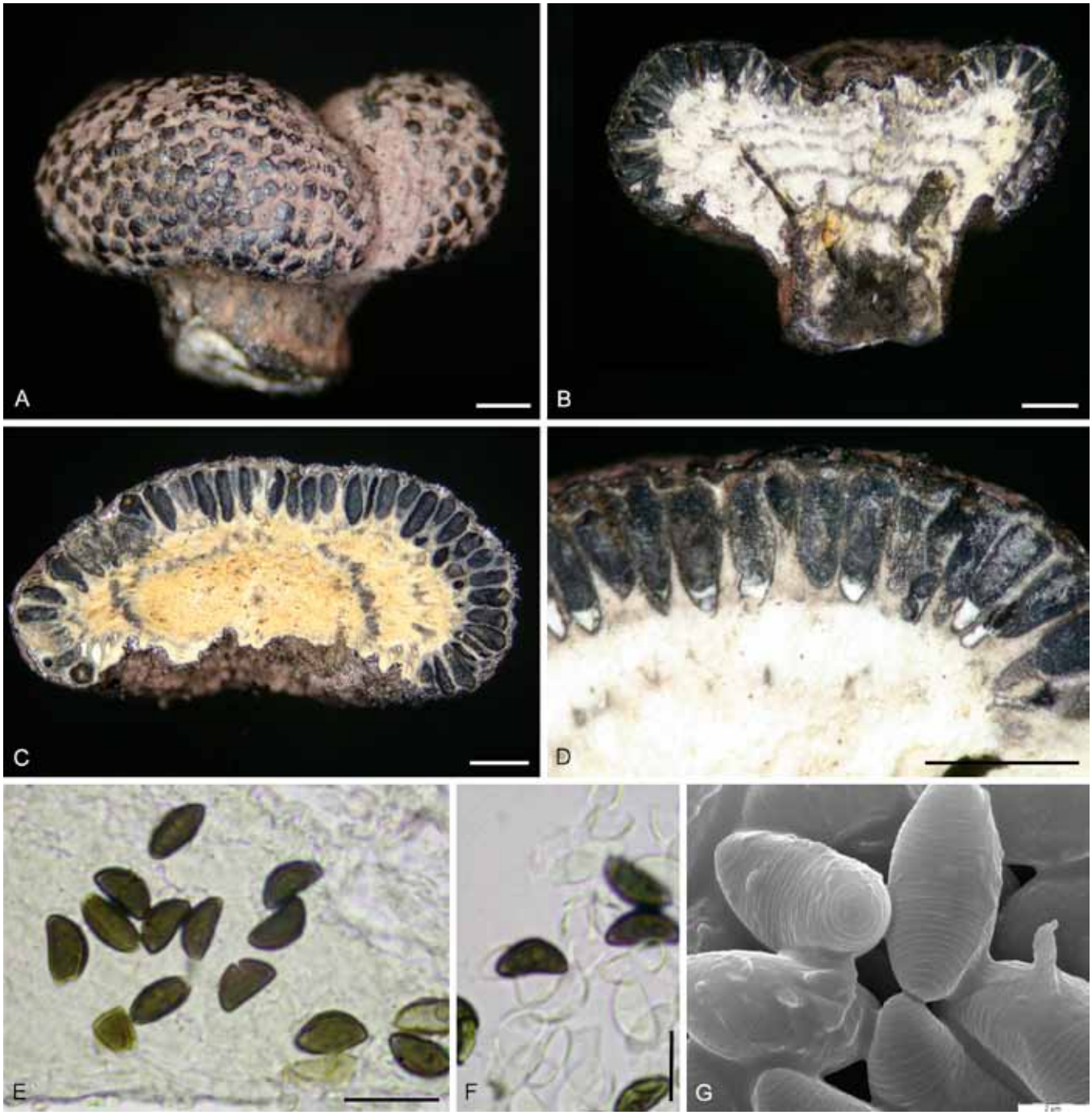



**Fig. 34.** Teleomorphic characteristics of *Daldinia brachysperma* (isotype, Mexico). A. Stromatal habit. B, C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Ascospores in SDS. F. Ascospores in KOH, showing dehiscing perispore. G. Ascospores by SEM (10.000×).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

*Typus*: **India**, Himachal Pradesh, Glen, Simla, bark of *Quercus*, 28 Jul.1965, K.S. Waraitch (BPI 594922 - **isotype**; **holotype** in PAN *fide* Waraitch 1977, n. v.).

*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

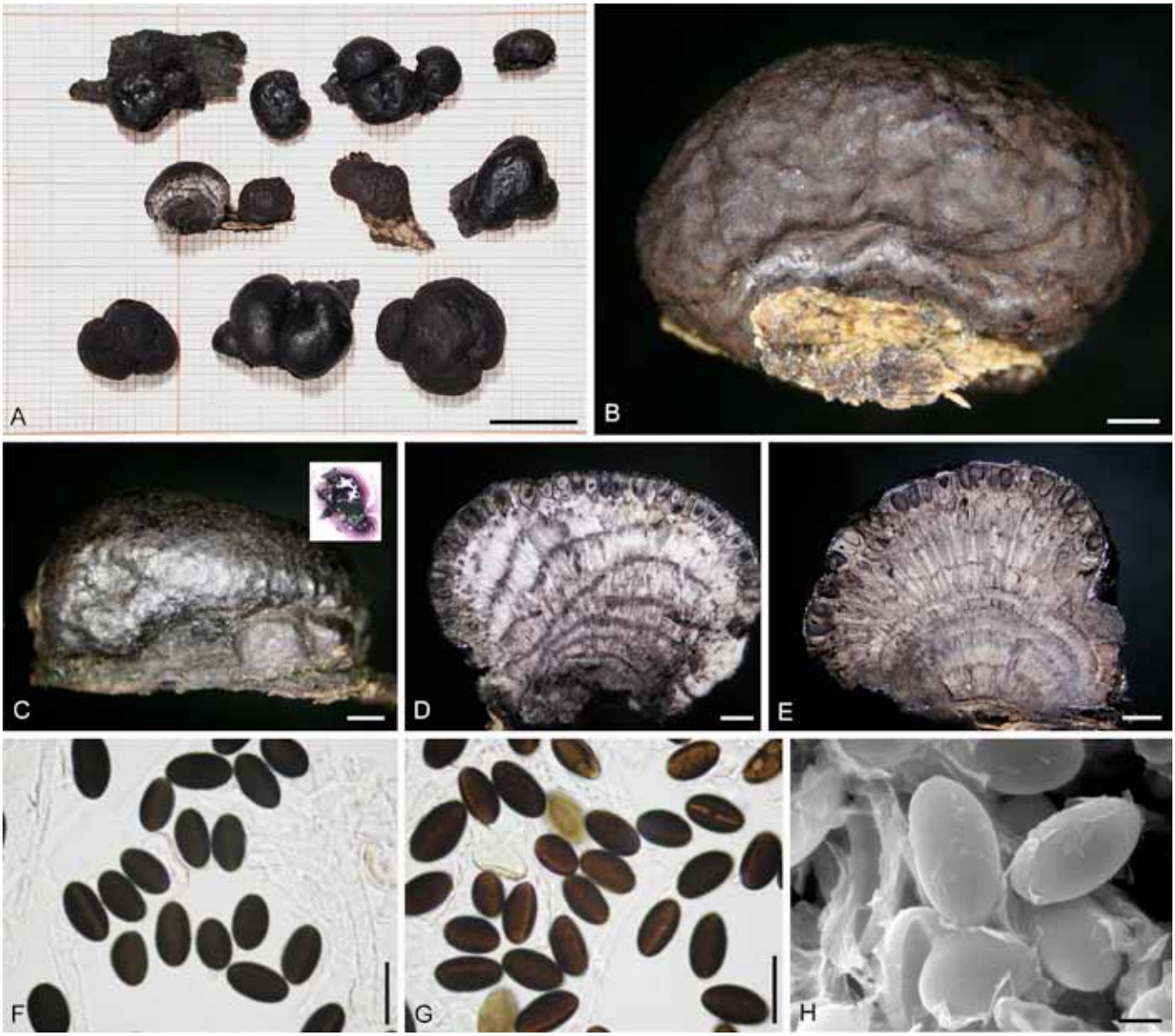



**Fig. 35.** Teleomorphic characteristics of *Daldinia caldariorum* (A–G: *JF-07045*, *Ulex*, France; H: K(M) 47140, *Ulex,* UK). A–C. Stromatal habit (C: Inserted: Stromatal pigments in 10 % KOH). D, E. Stroma in longitudinal section showing internal concentric zones, locules and perithecial layer. F. Ascospores in KOH. G. Ascospores in SDS, showing germ slits. H. Ascospore by SEM (10.000×). Scale bars A = 1 cm; B–E = 1mm; 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. *Asci* 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 funiculose; reverse uncoloured. Sporulating regions preferentially at edge of colony, Hazel (88). Conidiogenous structures nodulisporium-like. *Conidiophores* di- 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. *Conidia* produced holoblastically in sympodial sequence, hyaline, smooth, ellipsoid, with flattened base, 4.5–6.5(–7) × 2.5–4.5 µm.

*Additional specimens examined*: **Australia,** Queensland, Macpherson Range, Mount Ballow, 44 miles S of Ipswich, on bark of dead tree, 3 Apr. 1953, R. Melville & T.E. Hunt *3595* (K(M) 120962). **Brazil**, Rio Grande do Sul, Parcey Novo, 1928, J. Rick as *D. corrugata* (FH 79477); Sebastopol, on *Baccharis*, J. Rick (FH 79463). **Cuba**, Pinar del Río, Peninsula de Guanahacabibes, Oct. 2005, C. Decock (specimen and culture MUCL 47595). **Cameroon,** South West Province, Mt. Cameroon, 900 ft, on dead, burnt stems of *Adenocarpus manii*, Jan. 1931 (collector's name illegible) *108* (K(M) 131689). **Canada**, British Columbia, Koreai Creek, Jan. 1924, D.H. Linder (FH 79471). **Colombia**, Buga, Granja Agricola, 5 May 1938, C. Garces *114* (BPI 594193). **Ecuador**, Napo, Añangu, lowland rain forest, on felled logs in plantation, 19 Jun.–4 Jul. 1985, T. Læssøe *AAU 59759* (C, culture CBS 113045, MUCL 44607). **France,** Manche, Vauville, Vallée du Petit Doué, burnt *Ulex europaeus*, 7 May 2007, M. Basley-Gallis (*JF-07045*); Morbihan, St. Congard, Nazareth, burnt *Ulex europaeus*, 24 Nov. 2006, J.P. Priou *JPP 26211*

(JF, culture MUCL 49217; GenBank Acc. No. AM749934, see Bitzer *et al.* 2008). **Mexico**, Chiapas state, La Trinitaria municipality, Montebello Lagoons, 24 May 1988, F. San Martín (JDR, see Ju *et al.* 1997; Hsieh *et al.* 2005; culture CBS 122874; BCRC34041; GenBank Acc. Nos of DNA sequences: AY951689 and AY951801). **New Zealand**, Chatham Islands, Te One Stream, near Owenga, *Olearia traversii*, 9 Jan. 1970, B.G. Hamlin *BGH 2041* (PDD 39243); **Niue**, on wood of unknown plant, Jun. 1975, R.A. Fullerton (PDD 38443). **Philippines**, Luzon Island, Manila, Wack Wack Country Club, *Lantana camara*, 16 Sep. 1945, C.T. Rogerson *667*, det. J.H. Miller as *D. vernicosa* (NY). **Republic of South Africa**, Natal (Kwazulu), St. Lucia, Sugarloaf campingsite, Feb. 2006, V. Kummer (B, culture MUCL 47715). **Spain,** Galicia, Vigo Prov., Barra, on *Cytisus*, 19 Nov. 1988, F. Martinez Campos ex herb. F. Candoussau *FC 195* (S-F38127, ZT). **Portugal,** Azores, São Miguel Island, vic. of Sete Cidades, Lagoa Azul, *Ulex europaeus*, 14 Aug. 1998, B. & M. Stadler *STMA 98247* (WUP). **Taiwan,** Taiwan Prov., Taitung Co., Lan-yuh, 25 Oct. 1999, S.Z. Chen *957* (HAST, BCRC34042, see Hsieh *et al.* 2005; GenBank Acc. Nos AY951690, AY951802, EF026144). **UK**, England, Cornwall, Padstow, *Ulex europaeus*, Apr. 1993, M.C. Clark (K(M) 47140, culture KC1523, see Stadler *et al.* 2001b); Northern Wales, Glynwood, Bangor, burnt *Ulex*, 24 Dec.1975, A.J.S. Whalley, mixed with *D. vernicosa* (AJSW, culture ATCC 36660; GenBank Acc. No. of ITS nrDNA sequence AM749933, see Bitzer *et al.* 2008, treated as *Ww 3753* by Wollweber & Stadler 2001). For further specimens of this species from the personal herbarium of A.J.S. Whalley collected in Britain see Wollweber & Stadler (2001).

*Notes*: The holotype of *D. caldariorum*, originally collected by P. Sydow in a fern greenhouse in the Berlin Botanical Garden and held at B, was lost in WW II, and Ju *et al*. (1997) only reported on a mixed collection containing small fragmented stromata to be extant in S that was chosen as lectotype. A diligent search by the curators of S for *Xylariaceae* specimens from the Rehm herbarium produced S–F38120*,* along with further materials that are treated elsewhere herein. This specimen is clearly part of the original collection and in much better condition than the lectotype studied by Ju *et al.* (1997). We confirmed their results and identified the elements treated as "*D. concentrica*" in Ju *et al.* (1997) as *D. childiae*. The newly discovered specimen (S–F38120) is regarded as isolectotype. The name "*D. berolinensis*" as stated on the label was apparently never published. The ascospores of *D. caldariorum* are peculiar in having ventral germ slits (Ju *et al.* 1997) and appear smooth by SEM (Stadler *et al.* 2002). Hennings (1901) described *D. gollani* from material collected from *Ficus carica* in India, which was not located. He emphasised the small stromata (0.5–1 cm diam), small perithecia (0.6–0.8 × 0.3–0.4 mm) and reported ascospores 5–9 × 3.5–4 µm, without giving any reference to shape or dehiscence of the perispore. He further stated that this species "differed from all known species of *Daldinia*" in having smaller ascospores, and this obviously included *D. caldariorum*, which was described some years earlier by the same author. This implies that Hennings may have noted differences among the two taxa. Ju *et al.* (1997) reported that Child's concept of this species was ill-defined but failed to mention that Child had reported the ascospores of this taxon to have "conspicuously acute ends", a feature that applies to none of the specimens listed by her sub *D. gollani* that we have studied. Other specimens she studied may actually belong to *D. brachysperma*, which has ascospores with narrowly rounded ends that are in about the same size range. The synonymy of *D. gollani* and *D. caldariorum* is questionable, because Child's data, which could have been a reliable source of information on this matter, are contradictory and the type specimen of *D. gollani* will probably never turn up again. On the other hand, we agree with Ju *et al.* (1997) that the types of *H. hibisci* and *D. cognata* are conspecific with *D. caldariorum*.

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 only 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 122674 *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 cleistothecious tropical genera *Phylacia* and *Rhopalostroma*, and also to *Thamnomyces*. 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 possssing conidiophores of the nodulisporium-type with relatively small conidia.

Tropical collections of *D. caldariorum* are hard to tell from *D. clavata* (the only distinguishing teleomorphic microscopic features being the indehiscent perispore 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 ex-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 5I, J, 36.

*Etymology*: For the stromatal shape.

≡ *Daldinia concentrica* f. *clavata* (Henn.) Theiss., Ann. Mycol. 7: 4. 1909.

*Lectotypus* (selected by Ju *et al.* 1997): **Brazil,** Sta. Catarina, Blumenau, wood, 1892, A. Möller (S–F11855).

= *Daldinia vernicosa* f. *microspora* Starbäck, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 27, 3: 6. 1901.

*Holotypus*: **Brazil**, Matto Grosso, Guia, *ad truncum mucidum in* "capoeira" *vatusta*, 13 May 1894, G. Malme *595* (S-F40196).

= *Daldinia argentinensis* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 8: 68. 1902.

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

= *Daldinia barbata* Rick, Brotería 5: 50. 1906.

(*Lecto)typus*: **Brazil,** Sta. Catarina, Lageado, J. Rick as *D. clavata* in Lloyd herb. *12393* (BPI 716338, "**type**" *fide* Ju *et al.* 1997; officially lectotypified here), MBT177382.

= *Daldinia argentinensis* Speg. var. *sessilis* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 19: 345. 1909.

**Lectotypus** (selected by Child 1932): **Argentina**, Jujuy, Bobadal, Río Pescado, Mar. 1905, C. Spegazzini (LPS 158).

*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 (perithecia of type of *D. vernicosa* 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, 1–3.5 × 1–5.5 cm, the stipe up to 2.5 cm long × 0.5–1.5 cm diam; surface Brown Vinaceous (84) to Sepia (63), blackened and varnished 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 mm thick (Ratio darker/lighter zones 1:3–6). *Perithecia* obovoid, 0.6–1 × 0.3–0.5 mm. *Ostioles* slightly papillate, inconspicuous. *Asci* 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 µm. *Ascospores* brown to dark brown, ellipsoid-inequilateral, with narrowly rounded ends, 8–11.5 × (3.5–)4–5.5 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.

*Cultures*: *Colonies* on OA reaching the edge of 9 cm Petri dish in 8–10 d, at first whitish, felty, 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 Hazel (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 conidiogenous structures observed on either OA or YMG agar.

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

*Additional specimens examined*: **Angola**, Huilla, Lake Svantala, on bark of old tree, Mar. 1860, E. Welwitsch *137* ( K(M) 120964). **Brazil,** Sta. Catarina, Sao Leopoldo, 1904, de Thümen in herb. J. Rick *629*, label reading "*D. barbata & concentrica*" (FH 220985 – could be part of *D. barbata* type); same locality, 1904, J. Rick (two packets, BPI 594762, BPI 715030[15] - possibly part of the type of *D. barbata*); same locality, 1904, de Thümen (FH 220984); same locality, 1904, J. Rick ex herb. Theissen *623* (FH 79475); Rio Grande do Sul, Novo Petropolis, 1923, J. Rick (FH 79473); Rio Grande do Sul, Parecy Novo, 1928, J. Rick (FH 79474); Rio Grande do Sul, J. Rick in Lloyd herb. *12383*, det. Van der Gucht (1994) as *D. albozonata* (BPI 716960). **Cuba**, Oriente, Nicaro, Sierra Christel, 3 Mar. 1970, H. Kreisel *1839* (KR); Calabazar, 9 Feb. 1970, H. Kreisel *1637* (KR); Arroyo Pardo, 1 Mar. 1971, H. Kreisel, *Ww 3857* (KR). **Colombia,** Dept**.** Cundinamarca, *ca.* 7 miles from Tocaima, 1200 feet, 14 Jan. 1976, K.P. Dumont *et al.* (NY). **D.R. Congo,** Djuma, Parc National Albert, Riviere Ngitte, on a tree in ombrophile forest, 27 Jan. 1954, G.F. De Witte *9784*, det. Dennis (1963) as *D. cuprea* (BR–Myc 102737,14); Kisantu-Kwango, Goa, Mission Agronomique, H. Vandereyst *15494* (K(M) 130244). **Ecuador,** Galapagos Islands, Isla Sta. Cruz, 21 Feb. 1964, I. Wiggins (NY). **El Salvador,** Dpto. de Sta. Ana, Hacienda San José, 7 Jul. 1973, G.A. Escobar *5094* (NY). **Ethiopia,** Gamu-Gopa region, Arba Minch, below encampment east of town, groundwater forest with *Cordia* and *Ficus*, 1250 m, on dead branches on the ground, 30 Aug. 1975, M. Thulin *2527* (UPS - partial specimen, in packet with *D. eschscholtzii*). **Gabon**, Ogooué-Ivindo, Parc National de l'Ivindo, Réserve Intégrale d'Ipassa, Ipassa Biological Station, dead fallen trunk, Apr. 2006, C. Decock (specimen and culture MUCL 47436). **Liberia**, Ganta, 21 Nov. 1939, G.W. Harley *331* (FH 79472, JDR, see Ju *et al.* 1997). **Mexico,** Veracruz, 3 km S of Monterfe, region "Las Tuxtlas", 22 Jun. 1969, G. Guzman (NY); Uxpanaba, SW of Brecha 104, Campamento Hermanos Cedillo, 17 Mar. 1976, G. Guzman (NY); Xuchiles, near Cordoba, Rio Blanco, 17 Jan. 1910, W.A. & E.L. Murrill *1084* (NY). **Peru**, Lima, J.J. Sonkap ex herb. F. Petrak (M-0079886). **Surinam**, no data and collector, as *Sphaeria concentrica* (M-0079885). **Tanzania**, Eastern Province, Kilosa, Matarawe river, on fallen dead branches, 25 May 1968, D.N. Pegler *T l061* (K(M) 131668). **USA**, Florida, Dade Co., Hammocks, Caesar's Rock, 10 Mar. 1915, J.K. Small & C.A. Mosier *6867* (NY).

*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. vernicosa* var. *microspora* have been studied for comparison, including HPLC (Fig. 17) and SEM analyses. Only the types of *D. barbata*, *D. vernicosa* 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

[15]The former specimen was selected as "lectotype" of *D. barbata* by Ju *et al.* 1997, despite a holotype of the same name is mentioned in the same paper from another locality; the latter is filed as "*D. concentrica*" Lloyd herb. 12304 (BPI).


**Fig. 36.** Teleomorphic characteristics of *Daldinia clavata*. A–C, I: *Ww 3856* (Cuba). D–F, J. Wiggins (Ecuador, Galapagos). G, H. BR-Myc 102737,14 (Congo). K. BPI 716338, type of *D. barbata* (Brazil). A, F, G. Stromatal habit (inserted A, F: Stromatal pigments in 10 % KOH). B–E, H. Stroma in longitudinal section showing internal concentric zones and perithecial layer. I. Ascospores in SDS. J. Ascospores in KOH, showing dehiscing perispore. K. Ascospores by SEM (10.000×). Scale bars A, B, E–H = 1 cm; C, D = 1 mm; I, J = 10 µm; K = 2 µm.

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 *Daldinia* 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 obovoid, 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 (dehiscence of perispore, position of the germ slit). Unfortunately, material of *D. clavata* 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 *D. albofibrosa* can be easily segregated by a comparison of stromatal pigments in KOH.

Theissen (1909) lumped *D. vernicosa* var. *microspora* and *D. clavata* with *D. barbata* and *D. eschscholtzii* as "*D. concentrica* var. *microspora*", but his conclusion appears to be mainly based on the type of *D. barbata* (here, indeed, regarded as a synonym of *D. clavata*). Theissen even added *D. caldariorum* and *D. cognata* as further probable synonyms and segregated *D. clavata*, *D. argentinensis*, and *D. cuprea* under *D. concentrica* var. *microspora* as "*forma clavata*". His inclusion of *D. eschscholtzii* was based on Starbäck´s specimens (*i.e.*, *D. starbaeckii* as understood here), which, indeed, have a similar ascospore size range as the remaining species in Theissen's list of synonyms. The type specimen of *D. vernicosa* var. *microspora* bears the annotation "Malme *595*", but this may have been added by another mycologist who studied the material subsequently. The remainder of the collection data are in agreement with the protologue (if translated from Swedish into Latin). A specimen "Malme *595*" with different collection data was actually treated by Starbäck (1901) as *D. eschscholtzii*, and is here listed as *D. starbaeckii*. As stated by Ju *et al.* (1997), the specimen package of *D. argentinensis* var. *sessilis* also contains *D. placentiformis* and a largely immature stroma of *D. childiae*. The specimens were separated by Child (1932). Specimen BR–Myc 102737,14, cited as *D. cuprea* in Dennis (1963) has purple stromatal pigments, and its surface lacks conspicuous perithecial outlines, thus it is listed here under *D. clavata* as well. On the other hand, some specimens with anamorphic and SEM characteristics described previously (Ju *et al*. 1997, Stadler *et al.* 2001a, 2002) as *D. clavata* are listed here under *D. theissenii*.

***Daldinia cuprea*** Starbäck, Bihang till Kungliga Svenska Vetenskaps-Akademiens Handlingar 27(9): 5. 1901. Fig. 37.

*Etymology*: For the copper-coloured stromatal surface.

*Lectotypus* (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 (isolectotype) is stored in S as S-F11856).

= ***Daldinia granulosa*** Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 19: 345. 1909.

*Holotypus*: **Argentina**, Jujuy, Bobadal, Río Pescado, Mar. 1905, C. Spegazzini (LPS 157).

*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. argentiniensis*) 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. *Asci* fragmentary, p. sp. 65–80 µm, with amyloid, discoid apical apparatus, 0.5 × 2.5 µm. *Ascospores* brown to dark brown, ellipsoid-inequilateral, 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 naphthoquinones as inferred from HPLC-DAD/MS data.

*Additional specimen examined*: **D.R. Congo**, Kivu, Nngungura "Madiwe", secondary forest on *Ficus*, Oct. 1938, P. Gille *161* (BR-Myc 033523,58).

*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* (synonymous *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,

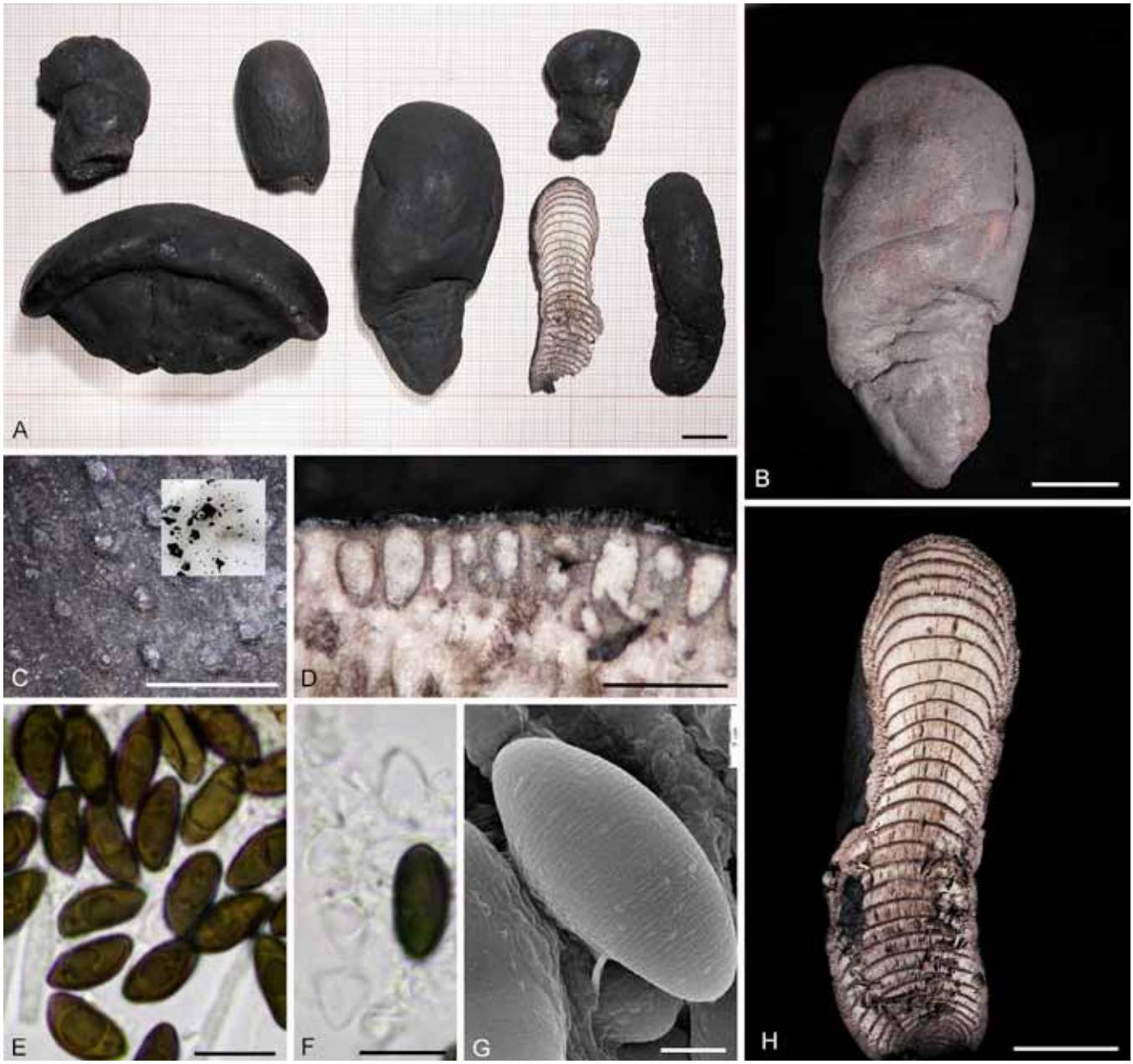



**Fig. 37.** Teleomorphic characteristics of *Daldinia cuprea*. A–F, H. BR-Myc 033523,58 (Congo). G. S-F11856, S-F11857, lectotype of *D. cuprea* (Paraguay). A, B. Stromatal habit. C. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). D, H. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Ascospores in SDS. F. Ascospores in KOH, showing dehiscing perispore. J. Ascospores by SEM (10.000×). Scale bars A, B, H = 1 cm; C, D = 1 mm; E, F = 10 µm; G = 2 µm.

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 daldinone 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, nevertheless, 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 eschscholtziae differt in ascosporae minorae, 9.5–10.5(–11) × 4.5–5.5 µm vel granulis violaceis obscuris in KOH dissolutis.*

*Holotypus*: **Brazil**, Roraima, Boa Vista-Venezuela road, 2 km after Boca da Mata. Capoeira, on dead trunk, 19 Dec. 1977, K. P. 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. *Ostioles* 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-inequilateral 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 perhaps present in traces.

*Additional specimen 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. rehmii* because of strong morphological resemblance and similar HPLC profiles, but deviates by slightly larger ascospores 10–11(–12) × 5.5–6.5 µm.

***Daldinia starbaeckii*** M. Stadler & Læssøe, **sp. nov.** MycoBank MB512385. Figs 5B, 11A–D, 39.

*Etymology*: Named for the Swedish mycologist Karl Starbäck.

*A Daldinia eschscholtziae differt in ascosporibus minoribus, ellpsoidae-inequilaterales vel equilaterales, (9–)10–12 × 5–6(–6.5) µm, in stromata cum zonis interiores albis et in statu anamorphosis Virgariellam similis. Granulis stromatibus olivaceis in KOH dissolutis. Cellulae conidiogenae cylindricae 16–24 × 2.5–3.5 µm; conidia guttiforma vel ellipsoidea, apices basales frequenter applanatae, 5–9 × (2.5–)3–4.5 µm.*

*Types*: **French Guiana**, Cacao, Roura, Rue Nationale 2, near Auberge des Orpailleurs (4°N0'71"N–52°21'06"W), dead stump in a burnt forest, 29 Jun. 2002, C. Decock, *Ww 4190* (MUCL - **holotype**, KR – **isotype**; **ex-type culture** MUCL 45436).

*Misapplied name*: *Daldinia concentrica* var. *eschscholtzii sensu.* Starbäck, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 27, 3: 5. 1901.

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

*Teleomorph and anamorph*: This species differs from *D. eschscholtzii* in having smaller ascospores, ellipsoid–inequilateral with broadly to narrowly rounded rounded ends, (9–)10–12(–13) × 5–6(–6.5) µm, in having relatively dense yelllowish-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* cylindriform, 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 daldinone B as major component.

*Additional specimens examined*: **Brazil**, Amazonas, road from Boa Vista to Venezuelan border, 2 km after Boca da Mata, Carpoerra, on dead trunk, 10 Dec. 1977, G. Samuels *et al. 751* (NY); Bahia, Mar. 1915, C. Torrend ex herb. J.R. Weir *15811* (BPI 594804; see. Child 1932 as *D. eschscholtzii*); Matto Grosso, Cuiaba, Guia, in forest near Coxipo Guassú, 12 May 1894, G. Malme *No. 595* (2 packets, S-F38151 and S-F38152); Serra de Chapado, Buriti, 20 Jun. 1894, G. Malme, (S-F38150; see Starbäck 1901); Rio Grande do Sul, Serra Azul, 1925, J. Rick (BPI 594809). **Cayman Islands**, Grand Cayman, Button Tree Road, W. Kings No. *F 63*, det. B.M. Spooner & T. Læssøe as *D. eschscholtzii* (K(M) 91626, culture KC 1692). **Ecuador**, Napo, vicinity of Tena, unknown dicot wood in rain forest, 22 Jul. 2003, J.F. Magni *JFM 340* (KR, culture CBS 116727, MUCL 45438); Orellana, east of Añangu, south side of Rio Napo (La Selva trails 5), 12 Jun. 2002, T. Læssøe *TL-9703* (C, QCA, culture CBS 116026). **French Guiana**, Piste de Saint Leodate, on rotting log, 24 Feb. 1988, A.Y. Rossman & C. Feuillet *3318* (BPI 1107335). **Martinique**, Case Pilote, wood, 5 Sep. 2003, C. Lechat *CL–0882* (KR, culture MUCL 52886). **USA**, Texas, 1901, on putrified wood, Long Jr., comm. Atkinson (S-F43788 ex B, see Rehm 1904 as *D. eschscholtzii*).

*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 spores 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. rehmii* in that daldinone 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*. Daldinone 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 daldinone 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

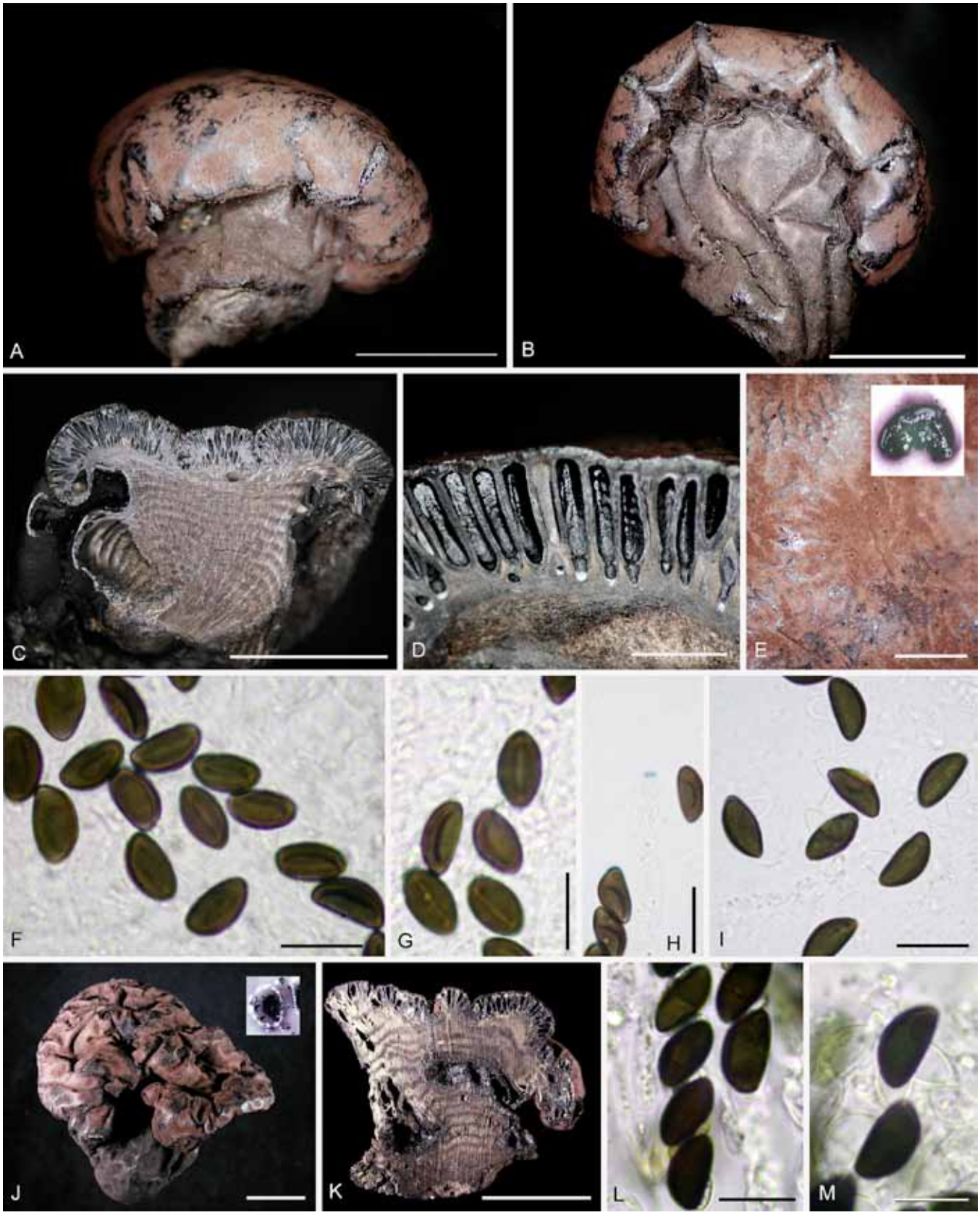



**Fig. 38.** Teleomorphic characteristics of *Daldinia rehmii* (A–I: Holotype, Brazil) and *D.* cf. *rehmii* (J–M: AAU 59501, Ecuador). A, B, J. Stromatal habit (J: Inserted: Stromatal pigments in 10 % KOH). C, D, K. Stroma in longitudinal section showing internal concentric zones and perithecial layer. 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.

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. 39.** Teleomorphic characteristics of *Daldinia starbaeckii* (A–D, G–I: *Ww 4190*, Holotype, French Guiana; E, F: CLL 0882, Martinique). A, E. Stromatal habit (E: inserted: Stromatal pigments in 10 % KOH). B, D, F. Stroma in longitudinal section showing internal concentric zones and perithecial layer. C. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). G. Ascospores in SDS. H. Ascospores in KOH, showing dehiscing perispores. I. Ascospores by SEM (10.000×). Scale bars A, B, E = 1 cm; F = 5 mm; C, D = 1 mm; G, H = 10 µm; I = 2 µm.

morphology and anatomy. In addition to daldinone 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 ×

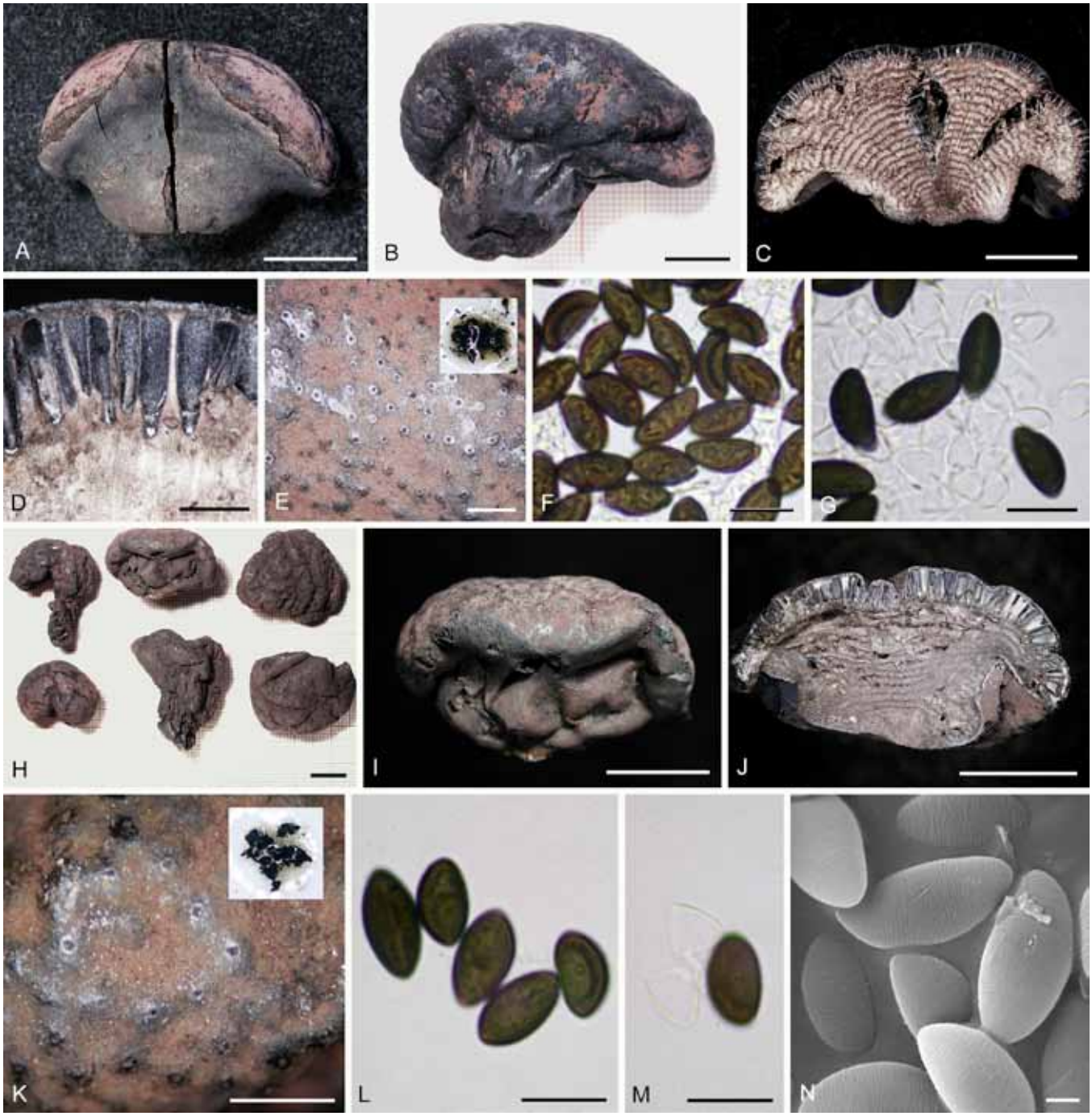



**Fig. 40.** Teleomorphic characteristics of *Daldinia* cf. *starbaeckii* JRZ 470 (D.R. Congo). (A–G: *Ww 3775*; H–N: *Ww 3774*). A, B, H, I. Stromatal habit. C, D, J. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E, K. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). F, L. Ascospores in SDS. G, M. Ascospores in KOH, showing dehiscing perispore. N. Ascospores by SEM (10.000×). Scale bars A–C, H–J = 1 cm; D, E, K = 1 mm; F, G, L, M = 10 µm; N = 2 µm.

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).

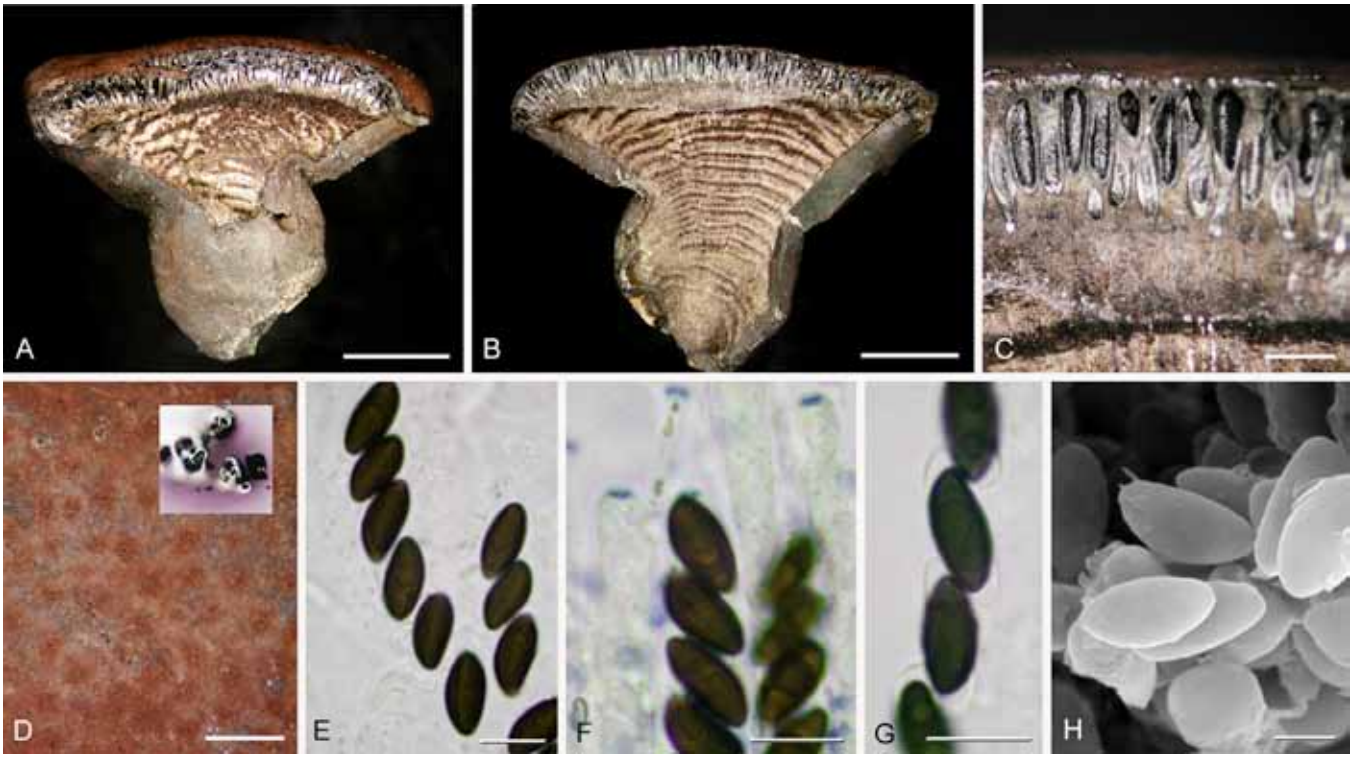



**Fig. 41.** Teleomorphic characteristics of *Daldinia theissenii.* Holotype (Peru) A. Stromatal habit. B, C. Stroma in longitudinal section showing internal concentric zones and perithecial layer. D. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). E. Ascospores in SDS. F. Ascal tops in Melzer's reagent showing apical apparati. 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.

*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 Farías town, Mar.1988, Flores 2 & San Martín 1024 (ICTV, culture BCRC34045, CBS 122875; GenBank Acc. Nos AY951805 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.

**Table 9.** Major discriminative characters of the species in the *D. childiae* 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).

| Species (*Daldinia*) | Ascospore size (µm) | Ascal apical apparatus (µm) | Stromatal pigments (KOH) | Ratio darker/ lighter concentric zones | Anamorphic structures (µm) |
|---|---|---|---|---|---|
| *australis* | 13.5–18(–19) × 7–8.5 | 0.8–1 × 3.5–4 | Cinnamon (62) to Fulvous (43) | 1–2: 1 | CC: 10–21 × 3–4.5<br>CON: 7.5–9.5(–11) × 4.5–6.5<br>(S, V) |
| *childiae* | 12–16(–17) × 5.5–7.5 | 0.5 × 3 | Mostly Umber (9) or Cinnamon (62) | 1:1–2 | CC: 10–25 × 3–4<br>CON: 7–9 (–10.5) × 4.5–5.5<br>(N) |
| *pyenaica* | 13–17(–20) × 6.5–8(–9) | 1.5 × 4 | Fulvous (43), Apricot (42), Umber (9), or Honey (64) | 1:1–2 | CC: 10–25 × 2.5–3<br>CON: 6.5–7(–8) × 4–5<br>(S, N) |
| *steglichii* | (13–)14 –15.5(–17.5) × 7–8<br>Often Rugby-ball shaped | 0.8–1 × 3–3.5 | Sepia (63), Umber (9), Fuscous Black (104) | 1:1–2 | CC: 12–20 × 2.5–3.5<br>CON: (5.5–)6–7.5(–8) × 3.5–4.5(–5)<br>(P, N) |

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

The *D. childiae* group comprises species that have yellowish brown stromatal pigments, owing to the presence of daldinals (**7**) and daldinins C (**6**). 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 lighter 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 perispores in KOH (generally showing transversely striation by SEM). The anamorphs exclusively show a holoblastic conidiogenesis and stromatic structures are always produced in culture. This species complex appears to be predominant in warmer climates, an exception being the northern part of Eastern Asia, where *D. childiae* has been found as far north as Central Japan and the Primorsky Territory in line with many other exceptionally northern occurrences of various groups of organisms in this region. In North America, *D. childiae* is rather frequent, and has been found all over the USA, as well as southeastern Canada. In Europe, it appears to be frequent only in southwestern France and the Black Sea area. Only recently has it been found in central Europe, and our results indicate that it is absent in northern Scandinavia and the British Isles.

Other species of this group have a tropical distribution and are apparently rare. Our knowledge on the distribution of this species complex in the Southern Hemisphere is still insufficient, even though a fungus very closely related to *D. childiae* has been found in Hawaii and New Zealand.

***Daldinia childiae*** J.D. Rogers & Y.M. Ju, Mycotaxon 72: 512. 1999. Figs 6A, B, 12D, E, 42.

*Etymology*: After the American mycologist Marion Child.

*Holotypus*: France, Pyrenées Atlantiques, Forêt de Bugangue, Aug. 1990, J.D. Rogers (WSP; **ex-type culture** CBS 122881).

= *Daldinia concentrica* f. *intermedia* Lloyd, Mycol. Writings 5, Large Pyrenomycetes: 25. 1919.

*Lectotypus* (selected here): **USA**, Wisconsin, Cleveland, C. Goessel in Lloyd herb. *12405* as *D. intermedia* (BPI 716996; Lloyd mentioned two collections in his very brief description, the other being from Ohio).

*Selected illustrations* (notably, none of those was made from the holotype specimen): Petrini & Müller (1986) as *Daldinia* (cf.) *eschscholtzii*, fig. 41 (ascospores, anamorph); Ju *et al.* (1997) as *D. concentrica*, figs 6 (ascospores), 27–29 (stromata) and 72 (anamorph); Wollweber & Stadler (2001) Abb. 5 (stromata); Stadler *et al.* (2002), fig. 7 (ascospores by SEM).

*Known distribution/host preference of stromata*: Widely distributed, with preference for warmer climates; especially frequent in USA. Without apparent host preference and even recorded on a conifer (*Cryptomeria*).

*Teleomorph*: *Stromata* spherical, depressed-spherical to turbinate, sessile or with short, stout stipe, mostly with inconspicuous perithecial outlines, 0.5–5 × 0.5–5 × 0.8–4 cm, but mostly not measuring over 2.5 cm in diameter, surface Brown Vinaceous (84), Chestnut (40), or Grayish Sepia (106), melanised and dull in age; dull orange brown or dull reddish brown granules immediately beneath surface, with KOH-extractable pigments Isabelline (65), Hazel (88), Honey (64), Amber (47) (*fide* Ju *et al. 1*997, but mostly Umber (9) or Cinnamon (62) in the specimens studied by us), tissue between perithecia brown, pithy to woody; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2–0.6 mm thick, lighter zones brown, pithy to woody, persistent, 0.6–1 mm thick (Ratio of darker/lighter zones 1:1–3). *Perithecia* obovoid to lanceolate, 0.7–1.5 × 0.3–0.5 mm. *Ostioles* slightly papillate to papillate. *Asci* 180–220 × 8–12 µm, p. sp. 85–95 µm, stipes 85–130 µm, with amyloid, discoid apical apparatus 0.5 × 3 µm. *Ascospores* brown to dark brown, ellipsoid-

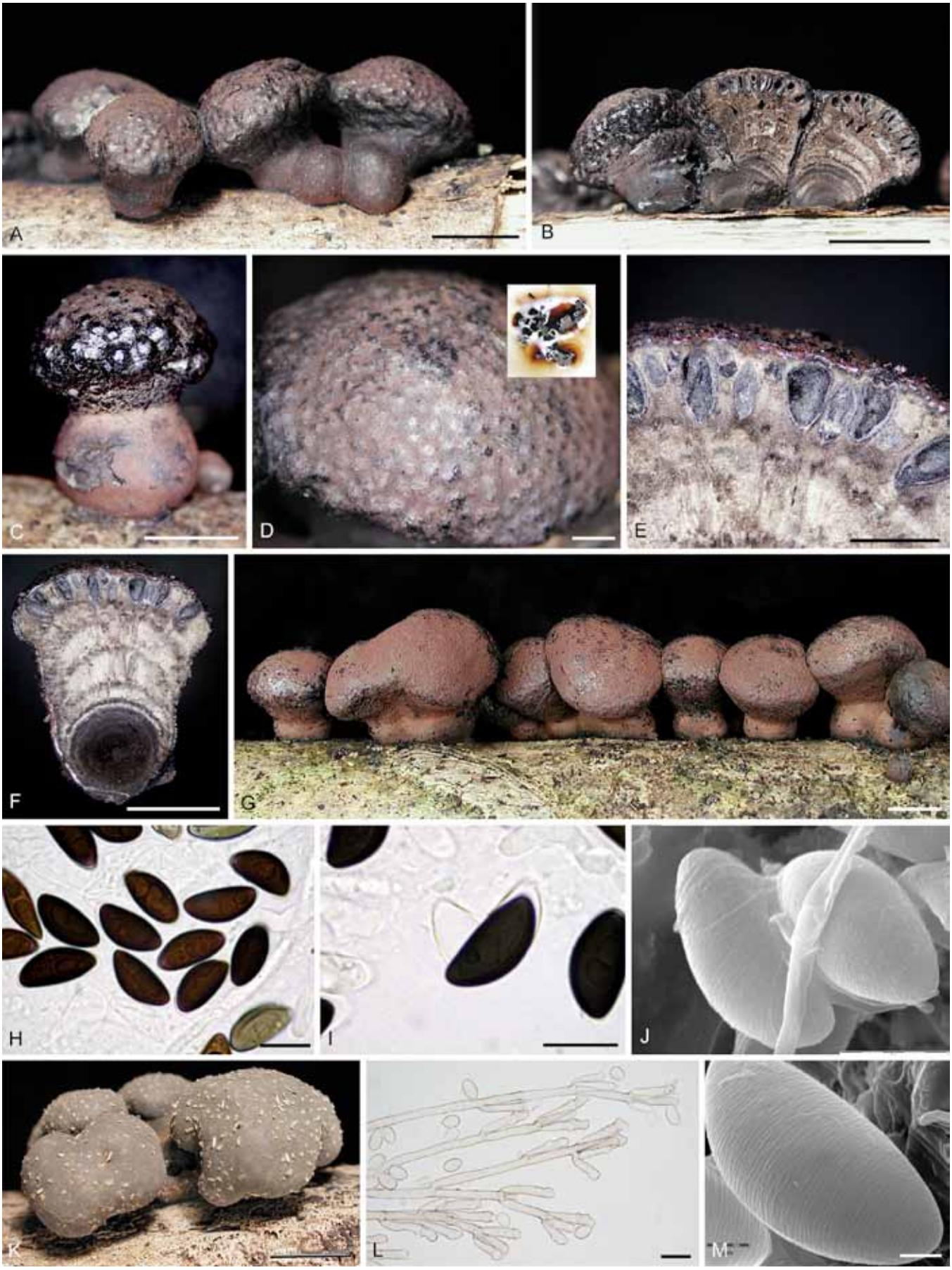



**Fig. 42.** Teleomorphic and anamorphic characteristics of *Daldinia childiae*. A–F, H, I. *JF-99243* (France). B. *JF-08182* (France). J. Holotype (France). K, L. Anamorphic state and anamorph, *JF-00064* (France). M. TL-9493 (Ecuador). A, C, G, K. Stromatal habit. B, E, F. Stroma in longitudinal section showing internal concentric zones and perithecial layer. D. Stromatal surface, with stromatal pigments in 10 % KOH inserted. H. Ascospores in SDS. I. Ascospores in KOH, showing dehiscing perispore. J, M. Ascospores by SEM (5.000–10.000×). L. Conidiogenous structure and conidia in SDS. Scale bars K = 1 cm; A–C, F, G = 5 mm; D, E = 1 mm; H, I, L = 10 µm; J = 5 µm; M = 2 µm.

inequilateral, with narrowly rounded ends, 12–16(–17) × 5.5–7.5 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.

*Cultures and anamorph*: Colonies on OA reaching the edge of 9 cm Petri dish in 6–8 d, at first whitish, felty, azonate, with diffuse margins, becoming Honey (64), sometimes with grey concentric zones, with Fulvous (43) exudates; reverse Citrine (13) to Dull Green (70). Sporulating regions scattered over entire surface of colony but with more abundant sporulation on tufts of hyphae at edge of colony, Buff (45) to Honey (64). Conidiogenous structures with nodulisporium-like branching pattern. *Conidiophores* 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. *Conidia* produced holoblastically in sympodial sequence, hyaline, smooth to finely roughened, ellipsoid, with flattened base, 7–9(–10.5) × 4.5–5.5 µm. Conidiogenesis in cultures often ceases after several consecutive transfers to new culture media, and in some cultures, no conidiogenous structures appeared.

*Additional specimens examined*: **Brazil**, Rio Grande do Sul, Lageado, 1921, J. Rick ex herb. J.R. Weir 19811 (BPI 594807). **Canada**, Ottawa, no date, Macoun *189* ex Ellis collection (NY). **Chile**, Rio Puelo, Llanguihue, dead trunks, Jan. 1916, M.R. Espinosa ex herb. J.R. Weir *16378* (BPI 594803). **Czech Republic**, Moravia, Lanžhot near Břeclav, forest "Ranspurk", on fallen trunk of *Acer campestre*, 29 Oct. 1987, F. Kotlaba & Z. Pouzar as *D. concentrica* (PRM 853136). **Denmark**, Sjælland, Slagelse Lystskov, on *Betula*, 24 Oct.1975, L. Hansen (C 46195). **Ecuador,** Napo Prov., Cuyuja, S of river, pasture with *Alnus* along river (alt. 2400 m), on bark and wood of *Alnus acuminata*, 4 May 2002, T. Læssøe *TL–9493* (C, QCA); same data, T. Læssøe *TL–9494* (C, QCA). **France**, Ariège, Rimont, Las Muros, *Acer campestre*, 3 Nov. 1999, *JF-99243* (KR 0029395); same locality, *Prunus spinosa*, 26 May 2000, *JF-00064* (KR 0029396; immature, with anamorph); same locality, *Fraxinus excelsior*, 21 Sep. 2008, *JF-08182* (KR 0029397); Landes, Bois de la Barthe, *Alnus glutinosa*, 1 Sep. 1995, G. Gilles (ZT, KR); Pyrenées Atlantiques, Auterrive, Ile du Gave d'Oleron, *Acer negundo*, 2 Jun. 2004, J. F. & M. S., *STMA 04076* (KR, JF, culture CBS 116725); Itxassou, Pas de Roland, *Fraxinus*, 30 Jun. 1999, M. S., *Ww 3587* (KR 0026334, see Wollweber & Stadler 2001); Oloron-Ste. Marie, *Fraxinus,* Oct. 1981 (ZT, Petrini & Müller 1986 as *D.* cf. *eschscholtzii*); Tartas, Aug. 1990, J.D. Rogers (WSP, culture CBS 122882). **Germany**, Badenia–Württemberg, Breisgau, Rheinauen near Breisach, *Carpinus betulus*, 3 Aug. 2004, W. Jaklitsch *WJ-2672* (WU, culture CBS 116992); same locality, *Salix alba*, 3 Aug. 2004, W. Jaklitsch *WJ-2673* (WU, culture CBS 116993); Karlsruhe City, Naturkundemuseum, on wood stem of *Malus* in the terrarium, 14 Jul. 2005, M. Scholler (KR 0014221); Karlsruhe–Daxlanden, Upper Rhine Valley, Rappenwört, *Prunus avium*, 15 Nov. 2003, M. Scholler (KR 0005129, culture MUCL 45437); same locality, on dead thick branch of cf. *Carpinus betulus*, 26 Sep. 2004, M. Scholler (KR 0010710); same data, *Carpinus betulus*, M. Scholler (KR 0010710); Karlsruhe-Grötzingen, Brennenwiese, *Fagus sylvatica*, 3 Feb. 2008, D. Matalla (KR 0020603); Grötzinger Baggersee, *Robinia pseudacacia*, 31 Aug. 2008, M. Ziegmann (KR 0002284); vic. of Karlsruhe, Oberwald, mixed deciduous forest, on strongly decayed felled tree trunk, 14 Sep. 2008, P. & R. Matalla (KR 0001692); District Emmendingen, Sasbach, Limberg, 30 Apr. 2002, H. Waldschütz *Ww 4188* (KR, culture CBS 113484); Mannheim, Neckarau, LSG Waldpark, lying stem of *Populus* sp., 12 May 2003, U. Sauter & H. Staub (KR 0012097); Neckarau, NSG Silberpappel, flood plain, deciduous wood branch on ground (initial deterioration stage), 26 Feb. 2000, H. Staub & U. Sauter (KR 0012098); same locality, *Acer pseudoplatanus*, 30. Sep. 2004, M. Scholler (KR 0010745 & KR 0010746); Neckarau, Reißinsel, on stem in flood plain, *Acer*, 30 Nov. 1996, H. Staub (KR 0012099) ; Hessen, Frankfurt, Stadtwald, Oberschweinsteige, 24 Aug. 2009, W. Pohl & M. Meusers (KR 0026247, culture MUCL 52674); Berlin, fern house in Botanic Garden, Nov. 1885, P. Sydow (S-F38115A, *D. childiae* element contained in the lectotype specimen of *D. caldariorum*, see Ju *et al.* 1997); Rheinland-Pfalz, Berghausen, Altrhein, trunk of *Alnus glutinosa,* 1 May 2010, B. & M. Stadler, *STMA 10037* (KR). **Georgia** (label reading "Russia"), Caucasus, Abkhazia, Gagri, *Acer*, 3 Aug. 1912, V.P. Savin, ex herb St. Petersburg (NY). **Guadeloupe**, Basse-Lieu, *Lespedeza manniana*, 1903, P. Duss *90* (NY). **Hungary**, exact locality unknown, F.A. Hazslinszky von Hazslin *1279* (F 331692); same data, F.A. Hazslinszky von Hazslin s.n. (F 331693). **India**, West Bengal, Darjeeling Town, logs of *Cryptomeria japonica*, 14 Aug. 1914, M.K. Maity (BPI 594902); West Himalaya, Himachal Pradesh, Manali, Solang Nullah, *Populus*, 7 Sep. 1983, P.F. Cannon (IMI 355417 – largely immature); Jagat Sukh, Kulu, K.S. Waraitch (BPI 594881); Uttar Pradesh, Sat Tal, Naini Tal, 7 Aug. 1968, K.S. Waraitch (BPI 594885). **Italy**, Vercelli, Cesati, in Rabenhorst Herb. Mycol. Ed. II, No. *500* (NY). **Japan**, Hokkaido, Sapporo, 15 May 1914, T. Hirumi *43* ex herb. Agr. Dep. Imp. Kyoto (NY); Shikoku, vicinity of Tokushima, 10 Jun. 1998, T. Hashimoto, *Ww 3597* (WUP); Kamiyama-cho, *Quercus*, 11 Oct. 1999, M. Stadler & Y. Asakawa, *Ww 3643* (WUP). **Kenya**, Limuru (alt. 7000 ft.), 1946, R.W. Rayner (K(M) 131684). **Latvia**, Prov. Vidzeme, Distr. Madona, Vestiena, *Alnus incana*, 25 Aug. 1935, K. Starcs (B70 0009624). **Malaysia**, on trunk in heath forest, Sep.1966, D. Hou *743* (L 0275631). **Nepal** (as "India" on label), Kathmandu, Cokarna, Sanctuary, 29 Aug. 1969, K.S. Waraitch (BPI 594878). **New Zealand**, Auckland, Tauranga, *Quercus rubra*, May 1954, J.D. Atkinson as *D. occidentalis* (IMI 69629 - immature with typical anamorph); Kermadec Islands, *Metrosideros kermadecensis*, 22 Sep.1988, E.H.C. McKenzie (PDD 54733). **Nicaragua**, "Winter 1893", C.L. Smith as *Xylaria* (NY). **P.R. China**, Heilongjiang Prov., Shengli State Farm, *Acer* sp., 6 Aug. 2004, E. Bulakh (VLA, culture CBS 117001, MUCL 46176); Hulin, Dongfanghong. Sep. 2003, L. Vasilyeva (VLA, culture CBS 116998, MUCL 48174); Kianhzi, near Yellow Dragon Temple, 8 Oct.1929, H.W. Chung *4355* (FH 79487); Kwangsi Prov., Ling Yuin Hsien, Loh Hoh Tsuen, 30 Mar. 1933, S.Y. Cheo *1759* (FH 220995); Jianxi, Sep. 1936, D. Xiang-Kun (FH 220994ex HMAS 17358). **Republic of South Africa**, Pretoria, Aug. 1918, J.M. Sim in Lloyd herb. *10824* (BPI 715045, see Child 1932 as *D. bakeri*); Natal, no date, A.J.T. Janse in Lloyd herb. *10870* (BPI 715081). **La Réunion**, Bras des Demoiselles, Cirque de Salazie, 16 Apr. 1980, F. Billiet & F. Jadin *771* (BR-Myc 003519,54). **Romania**, Mantenia near Bucharest, *Acer campestre*, 18 May 1933, Savulescu (M - largely immature). **Russia**, NW Caucasus, *ca.* 70km SSE of Maikop, so called Eichberg, *ca*. 2 km from Nowoprochladnoje. Aug. 2003, V. Kummer (B, culture MUCL 46170); same data (B, culture MUCL 46171); Kharbarovsk Territory, Big Khekhtsir Nature Reserve, Sosninsky brook, Oct. 1981, L. Vasilyeva (VLA, culture CBS 117002, MUCL 46177); Primorsky Territory, Vladivostok, *Prunus padus*, Oct. 2000, L. Vasilyeva (VLA, culture CBS 116995, MUCL 46176); Khabarovskiy krai, Petropavlovka lake; 48°38'N, 135°33'E, unburnt *Acer*, 14 Aug. 1998, H. Knudsen, *TL–5133* (C); same locality, Khrebet Khekhtsir (loc. 1), 48°15'N, 135°01'E, *Tilia*, 8 Aug.1998, T. Læssøe *TL–5044* (C); same province, Khrebet Khekhtsir (loc. 2), 48°14'N, 134°58'E, *Alnus*, 8 Aug.1998, T. Læssøe *TL-5061* (C); Rostov District, near Veshenskaya, Semenovskaya beam, *Quercus robur*, 6 Oct. 2006, A. Akulov (CWU-Myc 2046: KR). **Slovenia**, Llubljana (label reading "Laibach"), Carniolia (?), 1892, Prof. P. Voß *31* in herb. Saccardo (PAD). **Slovakia,** Prov. Sáros (formerly Hungary), Eperies, F. Hazslinszky (B70 0009607). **Switzerland**, Aargau, Bremgarten-Zopfhau, *Fagus,* Jul. 1999, R. de Marchi, comm. B. Senn-Irlet, *Ww 3714* (BERN, see Wollweber & Stadler 2001). **Ukraine**, Donetsk district, Drobyshevo forest, Svajatie Gory National Park, near Prishib, Jul. 2008, A. Akulov (CWU-AS 2799, culture MUCL 51699); Kharkov City, Forst park, *Quercus robur*, 12 Sep. 2006, A. Akulov (CWU-Myc 2068, KR); same locality, on fallen trunk of broadleaved tree, A. Akulov (CWU-Myc AS2069, KR); vicinity of Kharkov, Sargin Jar, *Acer negundo*, Jul. 2004, A. Akulov (CWU, M, culture MUCL 47222). **USA**[16], Alabama, Lee Co., Auburn, Jan. 1896, F.S. Earle & L.M. Underwood (NY, 2 packets); Auburn, 22 Feb. 1896, F.S. Earle (NY); Auburn, Nov. 1895, L.M. Underwood (NY); Lee Co., *Salix* ("on willow"), 25 Jan. 1897, F.S. Baker (NY); California, Humboldt Co., Arcata, *Acer*, Jun. 1961, P. Martin *874* (NY); same data, P. Martin *873* (NY); San Francisco, Golden Gate Park, Nov. 1911, W.A. Murrill *1108* (NY); Colorado, Boulder, Aug. 1923, J.D.A. Crockwell (NY); Connecticut, Ditchfield, Summer 1900, ex herb. Underwood *1929* (NY); Litschfield Co., woods of White Memorial Foundation, 6 Sep. 1980, C.T. Rogerson (NY); Roaring Break, 23 Jul. 1893, collector unknown (NY); Willimantic Area, log of *Acer*, 25 Aug. 1979, M.E. Bigelow *6579* (NY); Florida, 1889, M.A. Russell (NY); Georgia, Athens, Mitchell Bridge, on *Betula nigra*, 14 Dec. 1928, J.H. Miller (S-F43794 ex GAM 1533); Illinois, Jackson Co., 1 mile W of Glenn, 22 Oct. 1956, D. Stone & C.R. Shoop (NY 00460112); McLean Co., Univ. Illinois timber woods, Funks Grove, 13 Aug. 1965, C.T. Rogerson (NY); Cook Co., Eggers Grove, 23 Aug. 2002, Bioblitz *016* (F 331698); DuPage, Churchill Woods Forest Preserve, Glen Ellyn, 15 Jul. 1995, J. Murphy *2575* (F 331700); Lake Co., Wright Woods, 29 Jul. 1995, E. Schutte *2* (F 331699); Peoria, Forest Park South Nature Preserve, Peoria Heights, mixed deciduous hardwood forest, 15 Nov. 1990, H.L. Monoson *244* (F 87892); Indiana, Scottsburg, 1907, J.R. Weir (BPI 594813); Marion Co., J.O. Cottingham ex herb. V.H. Welch (NY); Putnam Co., Greencastle, Fountain Park woods, 1 mile N of Remington, 11 Jun. 1935, V.H. Welch *33622* (NY); Putnam Co., 7 miles SW of Greencastle, 23 Aug. 1958, S. Shushan *F-3443* (NY); Putnam Co., vicinity of Greencastle, 9 Oct. 1935, H. Youse *23* ex herb. V.H. Welch (NY) Putnam Co., Greencastle, 1932-1933, F. Shuttleworth *3352* (NY); Putnam Co., Greencastle, DePauw Arboretum, 25 Oct. 1945, E.G. Simmons *1131* (NY, 2 packets); same data, E.G. Simmons *1130* (NY); Putnam Co., Fern, *Fagus*, 12 Oct. 1945, E.G. Simmons *1132* (NY, 2 packets); same data, fallen *Ulmus* log, 12 Oct. 1945, E.G. Simmons *1133* (NY, 2 packets), Putnam Co., Hooster Highlands, 16 Sep. 1941, E.G. Simmons *1134* (NY, 2 packets); same locality, along

[16]About 30 further specimens with incomplete collection data in NY are not listed here; mostly labelled as *D. concentrica* prior to our revision.

Mill Creek, 3 Jun. 1936, V.H. Welch *2249*; near Vincennes, on bark in apple orchard, 20 Oct. 1934, M.A. Eyers (NY); Scottsburg, *Hickoria ovata*, May 1901, J.R. Weir (NY); Tippecanoe Co., West Lafayette, Happy Hollow Park, 12 Nov. 2000, M. Scholler (KR 0000085); Iowa, exact locality unknown, 8 Dec. 1935, G.W. Martin (NY); Iowa City, 18 Nov. 1932, G.W. Martin (NY); Kansas, Louisvlle, 9 Oct. 1893, E. Bartholomew *1164* (NY); Riley Co., Manhattan, 16 Sep. 1889, W.A. Kellerman & W.T. Swingle *876* (NY); Riley Co., Manhattan, 2 Oct. 1958, C.T. Rogerson (NY); Riley Co., Ravine NW Country club, Manhattan, on *Ulmus*, 25 Aug. 1957, C.T. Rogerson (NY); Louisiana, Iberia Parish, Lake Dautine near Caroline, 14 Oct. 1956, A.L. Welden (NY 00460092); Jefferson Parish, under Huey Long Bridge, 4 Mar. 1957, A.L. Welden (NY 004600103); Baton Rouge, 12 Dec. 1961, B. Lowy ex herb. P. Martin *642* as *D. eschscholtzii* (IMI); Maine, Penobscot Co., Norcross, 29 Aug. 1962, H.E. & M.E. Bigelow *3715* (NY); same locality, Birch Camp No. 1, Aug. 1905, W.A. Murrill (NY); Maryland, Frederick Co., Cunningham Falls State Park, near Thurmont, 13 Aug. 1966, C.T. Rogerson (NY); Massachusetts, Amherst, 18 Apr. 1917, P.J. Andersen (NY); Greenfield, Shattuch Park, Jul. 1950, H.E. Bigelow *134* (NY); Manchester, *Betula lutea*, Sep. 1889, W.C. Sturgis (NY, 2 packets); Mt. Toby, 4 Oct. 1958, H.E. & M.E. Bigelow *2529* (NY); Mt. Toby, Sunderland, 10 Aug. 1967, H.E. & M.E. Bigelow *5024* (NY); Pelhem, *Populus deltoides*, 15 Apr. 1917, F.J. Anderson *2122* (NY); Michigan, Emmet Co., Pelleton Falls, 30 Jul. 1953, J. Zucker *1151*, det. M.E. Bigelow as *D. concentrica* (NY); Emmet Co., Burt Lake, *Betula*, 6 Sep. 1969, H.E. & M.E. Bigelow *5290* (NY); Lower Taquamamnon Falls, fallen beech (*Fagus*), 29 Jun. 1953, M.E. Bigelow (NY); Washtenaw Co., SW of Ann Arbor, Aug. 1948, E.G. Simmons *2296* (NY); Washtenaw Co., Univ. Michigan School of Forestry, 8 Aug. 1946, E.G. Simmons *1275* (NY); Michigan, Baraga, Ford Forestry Center, Alberta, on hardwoods, 16 Sep. 1978, A.H. Smith (F 80908); Benzie, Frankfort, Sep. 1908, E.T. & S.A. Harper (F 93909); Mackinac, Mackinac Island, *Betula* (on birch tree) 20 Jul. 1899, E.T. & S.A. Harper (F 93911); same locality, Sailors Encampment, Sep. 1899, E.T. & S.A. Harper (F 93908); same locality, Aug. 1897, E.T. Harper (F 93910); same locality, *Ulmus*, 8 Aug. 1899, E.T. & S.A. Harper (F 93907); Missisippi, Grenada Co., Holcomb, 10 Jun. 1939, G.T. Johnson & H.N. Andrews (NY); Missouri, St. Louis, Forest Park, on dead wood in oak forest, Aug. 1999, M. Stadler *et al. Ww 3608* (KR 0026320, see Wollweber & Stadler 2001); Castlewood State Park, on trunk of *Quercus* sp., Jul. 1999, D. Triebel *et al*., *Ww 3609* (M, KR, culture MUCL 51679, see Wollweber & Stadler 2001); Meremac Park, dead wood, 3 Oct. 1926, Overholts & Shope, ex herb P. Shope *102(66232)* (COLO-F1370); New Hampshire, White Mountains National forest, *Betula*, 30 Jul. 1963, H.E. & M.E. Bigelow (NY); New Jersey, Long Island, Cold Spring Harbor, 20 Jul. 1921, M. Bronchard (NY); Morris Co., Jockey Hollow State Park, 15 Oct. 1974, S.T. Garey *74-17* (NY); New York, Adirondacks, Lake Placid, *Acer*, 17-29 Jun. 1912, W.A. Murrill *321* (NY); same locality, Upper St. Regis, Camp Kanosa, Aug. 1915, W.A. Murrill *32* (NY); Barnes Point, Aug. 1921, D.R. Sumstine (NY); New York City, Bronx Park, 1908, ex Underwood collection (NY); Catehill (?), on elm tree (*Ulmus*), ex Underwood collection *525* (NY); Chataugua Co., Jul. 1911, D.R. Sumstine *4640* (NY); Delaware Co., Arkville, 7–17 Aug. 1916, W.A. Murrill (NY); Genesee Co., Bergen Swamp. *Betula lutea*, 11 Jun. 1949, C.T. Rogerson *3072* (NY); Jamesville, 1 Mar. 1890, L.M. Underwood *27* (NY); Rockland Co., Nyack Village, Jul. 1963, P. Martin *1634* (NY); same collection data, P. Martin *1636* (NY); Scansdale, 30 Sep. 1905, W.A. Murrill *2691* (NY); Tomkins Co., Ithaca, Stewart Park, no date, C.T. Rogerson *607* (NY); Tompkins Co., Ithaca, Labrador Lake, Jun. 1919, F.J. Seaver *et al.* (NY); Tompkins Co., near Ithaca, Cornell Plantations, 17 Sep. 1947, C.T. Rogerson (NY); Warren Co., East side of Schroon river, near Chestertown, 14 Oct. 1972, C.T. Rogerson (NY); Orient, *Quercus*, 19 Aug. 1921, R. Lantham (BPI 715014); North Carolina, Macon Co., Nantahala National Forest, west of Franklin, Wine spring Bald, west of Wayah Bald, 26 Sep. 1989, G.J. Samuels *et al.* (NY); Great Smoky Mountains, Highlands, Ilges Cottage, 9 Aug. 1951, E.P. Goldsmith (NY); Cranberry, Aug. 1896, R. Thaxter (FH 79464); Yadkin, Line Rock, 7 Aug. 1938, P.O. Schallert *13658* (F 331675); same collection data (F 331675); Ohio, Aberlin, 22 Sep. 1929, C. Davis (NY); near Cashocton, 28 Sep. 1942, H.N. Moldeake *13816* (NY); near Oxford, 17 Oct. 1940, B. Fink *1048* (NY); Ross Co., Long Branch Hollow, Scioto Trail State forest, 31 Aug. 1968, C.T. Rogerson (NY); Cincinnati, Hazelwood Nature reserve, *Fagus*, 28 Oct. 1948, S. Braunstein ex herb. W.L. Culberson (F 331663); Coshocton, North Appalachian Experimental Watershed, 1942, L.J. King (F 331663); Hamilton Co., California Nature preserve, 28 Oct. 1948, W.L. Culberson (F 331662); Oregon, along Chetco River, on log, 4 Jul. 1944, T.P. Maslin *6229* (NY); Pennsylvania, Allegheny Co., 10 Sep. 1934, L.K. Henry (NY); Allegheny Co., 10 Sep. 1940, D.R. Sumstine (NY); Allegheny Co., 13 Jul. 1906, D.R. Sumstine (NY); Allegheny Co., 2 miles S of Moon along RT 978, 29 Sep. 1949, L.K. Henry (NY, 2 packets); Allegheny Co., 26 May 1926, D.R. Sumstine (NY); Allegheny Co., 5 Aug. 1946, L.K. Henry (NY); same locality, 9 Sep. 1943, F. Napier (NY); Allegheny Co., Crafton, 1 Aug. 1945, L.K. Henry *13726* (NY); same locality, Edgewood, A. Koenig (NY); New Alhambra, 12 Oct. 1937, D.R. Sumstine *11472* (NY); Panther Hollows, 16 Aug. 1922, M.L. Bombard (NY); upper part of Powers Run, 5 Apr. 1919, O.E. Hennings (NY); Wildwood, 30 Sep. 1928, C.K. Henter (NY); Armstrong Co., 1902, D.R. Sumstine (NY); Armstrong Co., 22 Oct. 1938, D.R. Sunstine (NY); same locality, Kattawang, *Carya* ("Hickory"), Sep. 1901, D.R. Sumstine *1874* (NY); same locality, Jul. 1904, D.R. Sumstine *2661* (NY); Bedford Co., 25 Nov. 1934, L.K. Henry (NY); Blair Co., 3-4 miles SE of Williamsburg, 10 Aug. 1957, L. K. Henry *5176* (NY); Buck Hill Falls, Sep. 1920, Mrs. Delafield (NY); Cambria Co., Aug. 1916, D.R. Sumstine (NY); Crawford Co., on birch stumps (*Betula* sp.) 30 Jun. 1936, L.K. Henry *106* as *D. grandis* (NY); Erie Co., Burgess Gulf, 8-18 Sep. 1948, H. Roslund, det. L.K. Henry as *D. concentrica* (NY); near Erie, Jul.-August 1927, O.E. Jennings (NY); Fayette Co., near Sharpsburg (?), 11 Sep. 1906, O.E. Jennings (NY); Fayette Co., Ohio Pyle, 16 Sep. 1906, D. Sumstine (NY); same locality, *Acer*, 12 Aug. 1908, D. Sumstine (NY); same locality, *Acer*, 15 Aug. 1922, O.E. Jennings (NY); Ohio Pyle, 3-8 Jul. 1905, W.A. Murrill *1215* (NY); Somerset Co., Buck Swamp, 25 miles W of Shanksville, 7 Aug. 1948, L.K. Henry (NY); 2.5 miles N of Thomas Mills, 21 Sep. 1960, L.K. Henry (NY); same locality, 5 Oct. 1944, D.R. Sumstine (NY); Somerset Co., 8 Jul. 1906, D.R. Sumstine (NY); Venango Co., 3 miles NE of Enderton, 3 Aug. 1941, L.K. Henry (NY); Washington Co., Woodsat Distillery near New Eagle, 9 Sep. 1947, L.K. Henry *5176* (NY); Westmoreland Co., Derry, 10 Nov. 1906, D.R. Sumstine (NY); Rock Rim-Lynn Rim-Sector, on dead *Betula lenta*, Sep. 1927, O.E. & G.K. Jennings (NY, 2 packets); Philadelphia, Jenkintown, vicinity of railway station, J.L. Surault, comm. J. Fournier, *STMA04133* (WUP, culture MUCL 46172); Texas, Hardin, Big Thicket National Preserve, Jack Gore Baygall Unit, 28 Nov. 1980, D.P. Lewis *2458* (F 83563); Vermont, Lamoille Co., Stowe, *Betula*, 22 Jul. 1964, H.E. & M.E. Bigelow (NY); same locality, *Betula*, 13 Aug. 1964, H.E. & M.E. Bigelow *4513* (NY); Windsor Co., vicinity of Ascutney, 29 Aug. 1996, S. Sheine *82* (NY); Virginia, Blacksburg, Jul.–Aug. 1904, W.A. Murrill *340* (NY); Blue Ridge Mountains, 18 miles N of Bydford, Apple Orchard Mountain, Oct. 1916, W.A. Murrill (NY); Germantown, 1889, T.H. Gentry ex Ellis coll. (NY); West Virginia, Pocahontas Co., Durbin, 28 Aug. 1902, W.A. Kellerman (BPI 594814); Durbin, 31 Aug. 1974, L.K. Henry *6052* (NY); Durbin, 18 Nov. 1895, L.W. Nuttall *26* (F 331657); Wisconsin, vicinity of Madison, *Acer rubrum*, 10 Oct. 1926, J.R. Hansburgh (NY); Bayfield, Herbster, F.B. Lucas *296* (F 93914); Walworth, Lake Geneva, Linn Township, 3 Jul. 1988, E.O. Farwell (F 93912); Waukesha, Bishop's Woods, Brookfield, 16 Nov. 1978, A.D. Parker (F 331702); same locality, Brookfield, Aug. 1978, A.D. Parker (F 331703). **Exact locality unknown**: No *31*, as "*Hypoxylon concentricum* (Bolt.) Grev.", in herb Saccardo (PAD), possibly another part of the above cited Slovenian material; " *ad lignum*.., ..22 Jun., remainder of label illegible, as *H. concentricum* Fr. in herb Saccardo (PAD).

*Further, authentic cultures* (corresponding stromata not studied, but nrDNA 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. Untereiner (MUCL 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 HPLC 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 childiae* 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 childiae* 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. childiae* 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 confusion occurred with *D. eschscholtzii*.

Applying the concept of Child (1932) to European material, Petrini & 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* Petrini & 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. petriniae*). 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 Xi 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.

***Daldinia australis*** M. Stadler & J. Fourn., **sp. nov.**, MycoBank MB563696. Figs 6C, 13A–D, 44.

*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.

*Holotypus*: **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. *Ostioles* papillate-discoid. *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-inequilateral, 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.

*Additional specimens examined*: **New Zealand,** Auckland, Three Kings, *Pittosporum crassifolium*, Jul. 1956, F.J. Newhook (PDD PDD 78322); Kaikoura, Puhipuhi reserve, 29 May 1983, G. Stevenson *GS 83/161* (PDD 90458); Nelson, Woodstock, near Murchison, Hancock's Bush, *Nothofagus* sp., 14 May 1982, G.J. Samuels *et al.* (NY, PDD 43170, see Ju *et al.* 1997 as *D. concentrica*); Wairarapa, Cobden Road, Fensham Reserve, 8 May 2007, L. Fischer (PDD 92573, culture ICMP 18263). **USA**, Hawaii, Puukapu, 1 Jan. 1947, H.S. Cowan *439*, det. J.H. Miller as *D. concentrica* (NY, 2 packets).

*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 *090328G* ex herb JF (KR, culture STMA09063, MUCL 53761) featured substipitate, 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.

***Daldinia pyrenaica*** M. Stadler & Wollw., Mycotaxon 80: 180. 2001. Figs 6D, E, 12A–C, 13E–G, 45.

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

*Typus*: **Spain**, Navarra, Señorio de Bertiz, 29. Jun. 1999, *Quercus petraea*, B. & M. Stadler, *Ww 3585* (M-**holotype**; KR ex WUP - **isotype**; **ex-type culture** MUCL 43507, GenBank Acc. No. of DNA sequence AM749927).


**Fig. 43.** Teleomorphic characteristics of *Daldinia* aff. *childiae* CH 08-539 (P.R. China). A, B. Stromatal habit. C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface, with stromatal pigments in 10 % KOH inserted. F, G. Ascospores in SDS, showing short germ slit. H. Ascospores and asci in Melzer's reagent, revealing amyloid apical apparati. I. Ascospores in KOH, showing dehiscing perispore. Scale bars A, B = 1 cm; C–E = 1 mm; F–I = 10 µm.

*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 fuscous, 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. *Asci* 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-inequilateral with narrowly rounded ends, 13–17(–20) × 6.5–8(–9) µm, germ slit straight, on


**Fig. 44.** Teleomorphic and anamorphic characteristics of *Daldinia australis* (holotype, New Zealand). A, C. Stromatal habit. B, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface, with stromatal pigments in 10 % KOH inserted. F. Ascospores in SDS. G. Ascospores in KOH, showing dehiscing perispore. H. Conidiogenous structure. I. Ascospore by SEM (10.000×). Scale bars A–C = 1 cm; D = 5 mm; E = 1 mm; F–H = 10 µm; I = 2 µm.

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 dacryoid, 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**.**

*Additional specimens examined*: **France**, Hautes Pyrénées, Gerde, Castet, 31 Jul. 2011, on dead wood, G. Corriol *GC 11073110* in herb. JF (KR, culture MUCL 53969); Pyrénées Atlantiques, Nay, Saligues-les-Bourdettes, 12 Oct. 1981, L. Petrini & F. Candoussau (ZT, see Petrini & Müller 1986, as *D.* cf. *loculata*); Oloron, Forét de Bugangues, Oct. 1981, L. Petrini & F. Candoussau, *Ww 3291* (ZT, see Petrini & Müller 1986 as *D.* cf. *loculata*). **Germany**, Badenia–Württemberg, Rhine Valley, 1 Apr. 1979, Waßmuth ex herb. G. Krieglsteiner (ST); "Württemberg", exact locality not recorded, *Salix*, 5 Nov. 1986, *L. Krieglsteiner* as *D. vernicosa*, ex herb. G. Krieglsteiner *Kri 1200/86* (ST). **Spain**, Burgos, Valle de Mena, 11 Oct. 1983, M.T. Tellería (MA 13418); Oviedo, Mieres, on branch of dead tree, 19 Oct. 1994, F.D.Calonge (MA 33166). **Ukraine**, Donetsk District, Drobyshevo Forest, Svajatie Gory NP, vicinity of Prishib village, on stub of *Acer campestre*, 22 Jul. 2008, A. Akulov (CWU-AS2799, MUCL 51700). Kharkov, Gomolshansky Nature Park, unidentified angiosperm wood, 7 Jul. 2005, A. Akulov (CWU-AS 1406; M, culture MUCL 47219); same locality and date, *Populus tremula*, A. Akulov (CWU-AS 1404; M; culture MUCL 47220); Kharkov Forest Park, *Quercus robur*, Jul. 2005, A. Akulov (CWU-AS 1402, M, culture MUCL 47221); Kharkov city, 50°00.706N, 036° 12.719E, fallen trunk of *Aesculus hippocastanum*, 19 Sep. 2007, A. Ordynets (CWU-AS-2506, culture MUCL 51701); same locality, *Quercus robur*, 12 Sep. 2006, A. Akulov (CWU-AS 2067; KR); Yalta Mountain-Forest Reserve, Mountain Crimea, "*Fagus sylvestris*", 8 Sep. 2003, I.A. Dudka, comm. A. Akulov as *D. childiae, STMA 05107* (KW, culture CBS 117736).

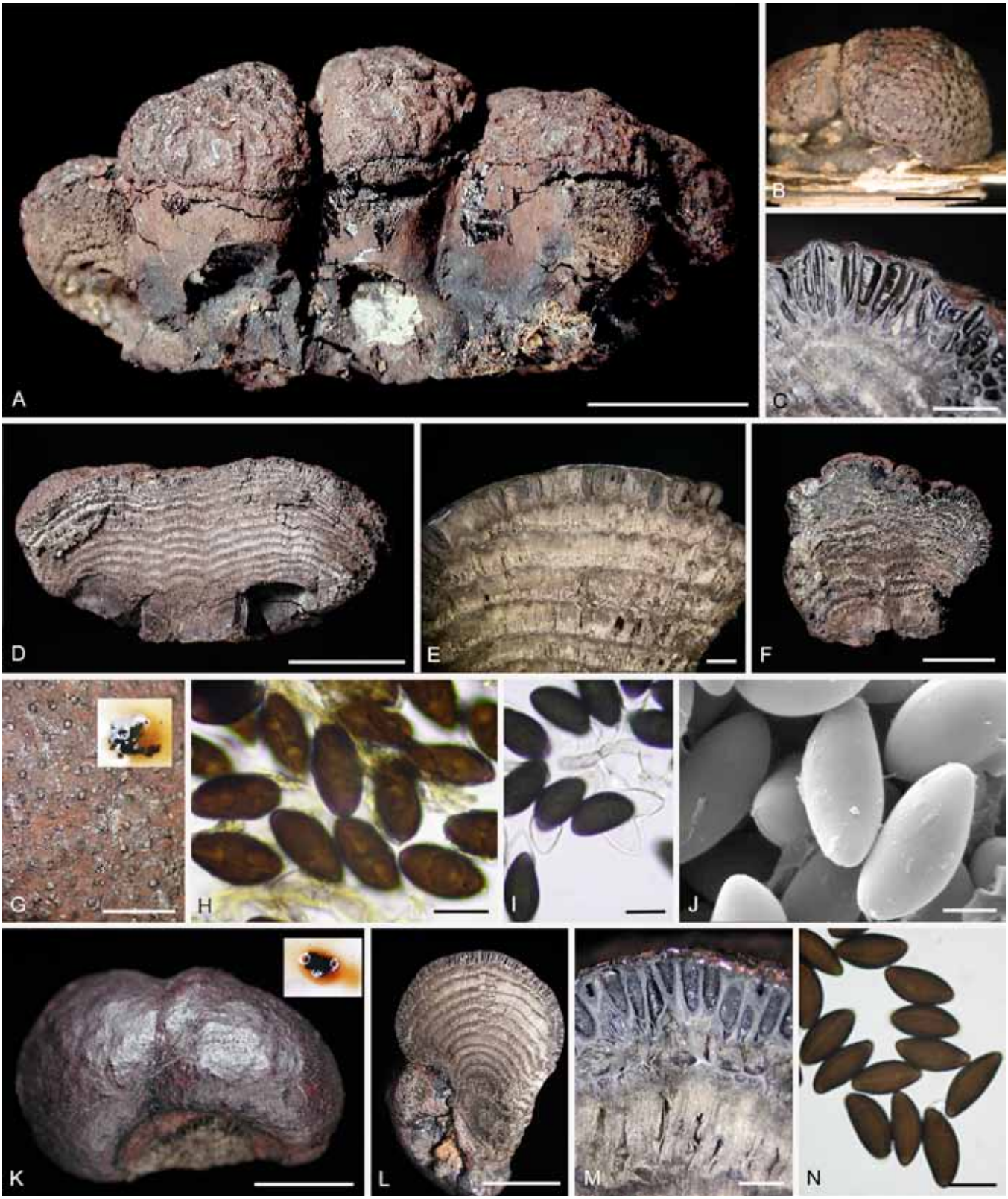



**Fig. 45.** Teleomorphic characteristics of *Daldinia pyrenaica*. A, C–J. Holotype (Spain). B. *Ww 3291* (France). K–N. CWU-AS 2506 (Ukraine). A, B, K. Stromatal habit with stromatal pigments in 10 % KOH inserted (K). C–F, L, M. Stroma in longitudinal section showing internal concentric zones and perithecial layer. G. Stromatal surface, with stromatal pigments in 10 % KOH inserted. H, N. Ascospores in SDS. I. Ascospores in KOH, showing dehiscing perispore. J. Ascospores by SEM (10.000×). Scale bars A, B, D, F, K, L = 1 cm; C, E, G, M = 1 mm; H, I, N = 10 µm; J = 5 µm.

*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,

see Figs 6E, 13E–G). Its conidiophores appeared only at the centre of colonies and showed slightly larger conidiogenous cells (15–28 × 2.5–3 µm) compared to the type strain. The conidia deviated by being subglobose to almost globose, 5.5–7 × 4.5–6 µm. However, since the specimens of *D. childiae*, we studied concurrently showed smaller ascospores as compared to *D. pyrenaica*, wherever it was found, and the anamorphic structures seem to be more similar to *D. pyrenaica* than to *D. childiae*, it appears suitable to refer the Ukrainian collections to *D. pyrenaica*.

***Daldinia steglichii*** M. Stadler, M. Baumgartner & Wollw., Mycotaxon 80: 183. 2001. Figs 6F, 12F–I, 46.

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

*Holotypus*: **India**, West Bengal, Chattari 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, 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 rounded ends, (13–)14–15.5(–17.5) × 7–8 µm, germ slit straight, on the convex side of the spore in case of inequilateral spores, perispore dehiscent with 10 % KOH, smooth by LM, but with faint transversal striations by SEM; epispore smooth.

*Cultures and anamorph*: *Colonies* on OA reaching the edge of a 9 cm petri dish in 7–8 d, felty, zonate, with diffuse margins, at first whitish to pale yellow, becoming floccose and brown when sporulating, reverse yellow-greenish, blackening with age, releasing orange-brownish exudates into the agar, developing a sweet odour. Sporulating regions at first appearing on the margins of the colony, later scattered over entire surface of the colony. *Conidiophores* up to 180 × 2.5–3 µm, mostly clustered together in synnematous structures (less frequently mononematous), dichotomously or (sometimes) trichotomously branched, hyaline, smooth or finely roughened, with one conidiogenous cell arising from each terminus, showing a periconiella-like or, less frequently, a nodulisporium-like branching pattern. *Conidiogenous cells* cylindrical, smooth, 12–20 × 2.5–3.5 µm. *Conidia* produced holoblastically from sympodially proliferating conidiogenous cells, hyaline, obovoid, smooth or finely roughened, (5.5–)6–7.5(–8) × 3.5–4.5(–5) µm.

*Additional specimens examined*: **India**, Himachal Pradesh, Narkanda, Mahasu, bark of *Juglans regia*, 18 Aug. 1971, J.S. Dargan, det. Thind & Dargan 1978 as *D. concentrica* (BPI 594920); Uttar Pradesh, Magra, Mussoorie, 30 Aug. 1968, K.S. Thind & K.S. Waraitch as *D. concentrica* (BPI 594882); same locality, trunk of *Quercus* (alt. 1800 m), 29 Sep. 1965, C.L. Malhotra *274* (L 0275630); Ranikhet, Nainital, 9 Aug. 1968, K.S. Thind & K.S. Waraitch as *D. concentrica* (BPI 594886). **Papua New Guinea**, Western Highlands Prov., Kubor range, Uinba, on old fence in native garden, wood unknown, 23 Aug. 1994, W. Vink 163355, *Ww 3944* (L, cultures MUCL 38739 and 43512, see Van der Gucht (1994, 1995) as *D.* cf. *grandis*). **Philippines**, Benguet Prov., Mt. Data, 20 Dec. 1980, M.M. Baldovino (CALP 9707). **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 98a/11* (KR 0029401, WU, culture MUCL 53886).

*Notes*: *Daldinia steglichii* shows a HPLC profile similar to that of *D. childiae*, 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. *grande*" 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. childiae* 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 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. childiae* 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

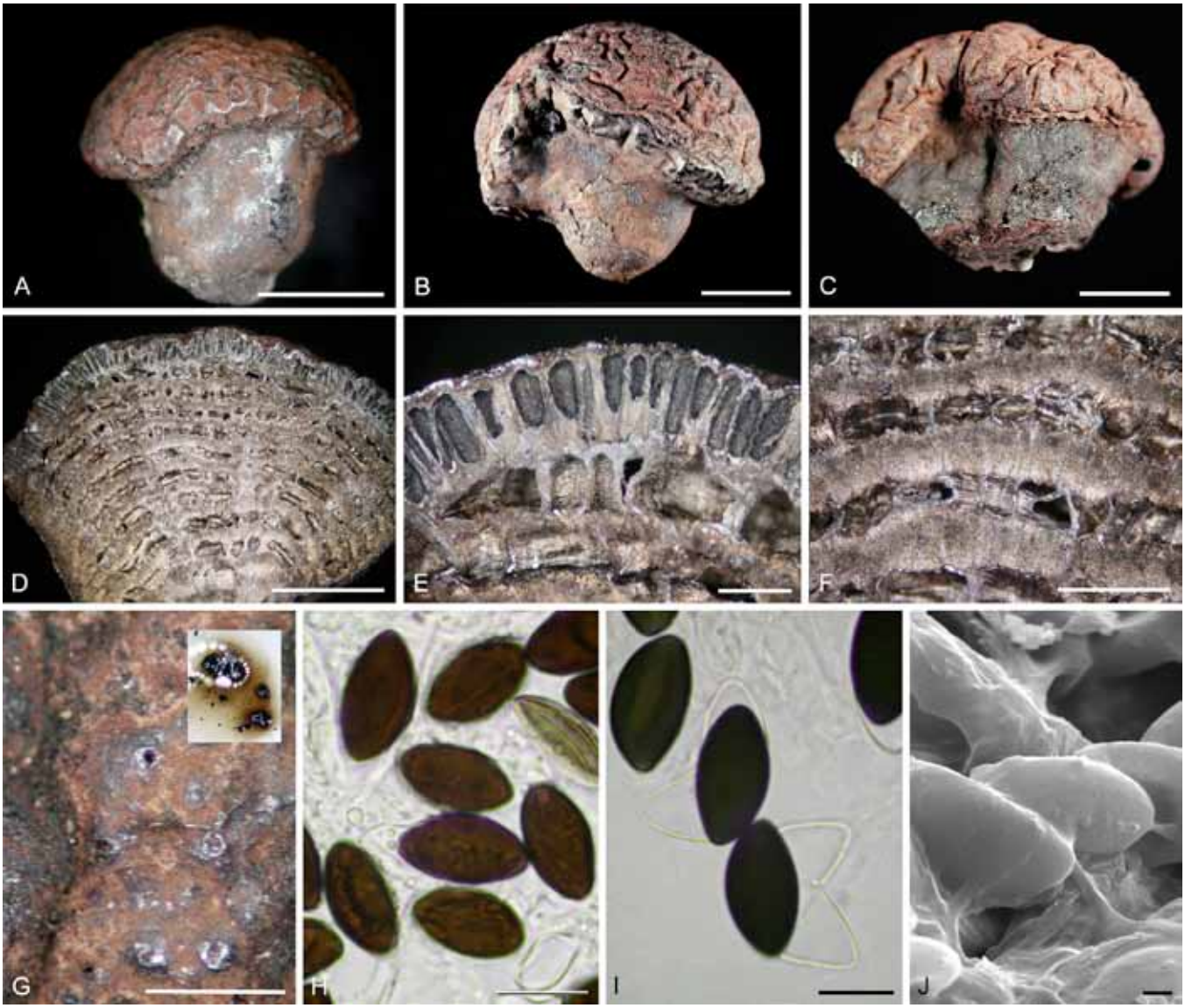



**Fig. 46.** Teleomorphic characteristics of *Daldinia steglichii* A–B, D–J. Holotype (India). C: *Ww 3944* (GENT, Papua New Guinea). A–C. Stromatal habit. D–F. Stroma in longitudinal section showing internal concentric zones and perithecial layer. G. Stromatal surface, with stromatal pigments in 10 % KOH inserted. H. Ascospores in SDS. I. Ascospores in KOH, showing dehiscing perispore. J. Ascospores by SEM (10.000×). Scale bars A–D = 5 mm; E–G = 1 mm; H, I = 10 µm; J = 2 µm.

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.

***Daldinia vernicosa*** Ces. & De Not., Comment. Soc. Crittog. Ital. 1: 198. 1863 - nom.nov. for *Sphaeria vernicosa* Schwein. 1825 non *S. vernicosa* DC. & Lam. 1815. Figs 7A, 14B, C, 47, 48.

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

≡ *Sphaeria vernicosa* Schwein., J. Acad. Nat. Sci. Philadelphia 5: 9. 1825; *non* DC. & Lam. [: Fr.]. 1815; *nec* Fée, 1834.
≡ *Hypoxylon vernicosum* (Schwein.) Berk. & M.A. Curtis in Berk., J. Linn. Soc., Bot. 10: 384. 1869, *non* Ellis & Everh., 1897.

*Holotypus*: **USA**, North Carolina, Salem, *Syn. 1175* (PH). **Epitype** (here selected): MBT177384; **Germany**, North Rhine, Westphalia, Wuppertal, burnt *Fagus sylvatica*, 31 Aug. 1996, H. Wollweber, *Ww 2899* (KR 0026318, duplicates in K and herb JDR, culture BCRC 34048, GenBank Acc. Nos of DNA sequences: AY951697, AY951809, and EF026146; see Ju *et al.* 1999 and Hsieh *et al.* 2005).

= *Lycoperdon atrum* Schaeff., Fung. Bavar. Palat. 4: 131. 1774. - nom. inval. (another valid name cited as synonym).
= *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.

| Species (*Daldinia*) | Ascospore size (µm) | Ascal apical apparatus (µm) | Stromatal pigments (KOH) | Ratio darker/lighter concentric zones / Significant stromatal features | Anamorphic structures (µm) |
|---|---|---|---|---|---|
| *bakeri* | 14.5–16 × 8–8.5 | 0.5–0.75 × 3–3.5 | Purple or absent | 1:5–40<br>Lighter zones greyish white | Unknown |
| *cahuchucosa* | 13–17(–18) × 7.5–9(–10) | 0.5–0.75 × 3–5.4 | Purple | Only faint zonation in otherwise homogeneous context | Unknown |
| *gelatinoides* | (11–)12–13(–14) × 6–8 | 0.5–0.75 × 3 | Purple or absent | STR entirely hollow at maturity | CC: 10–21 × 3–4.5<br>CON: 7.5–9.5(–11) × 4.5–6.5<br>(S, V) |
| *grandis* | (14–)17–22(–25) × 7–10(–11), highly irregular | 1–1.5 × 4.5–5 | Purple | 1:3–4 | Unknown |
| *hausknechtii* | 13–16 × 7–8, regular | Unknown | Purple | Lighter zones light brown | Not produced in culture |
| *novae–zelandiae* | (14–)16–23 × 8–13(–14), highly regular, ovoid | 0.75–1 × 3.5–4.5 | Dense purple | 1:3–6<br>Lighter zones greyish white | CC: 10–22 × 2–3.<br>CON: (6.5–)7–9.5 × 2–4.5<br>(V) |
| *loculata* | 11–14(–15) × 6–8 | 0.75–1 × 3–3.5 | Dense purple | Lighter zones light brown | CC: 11–20 × 3.5–4.4<br>CON: 6–7.5 × 4.5–5<br>(N) |
| *loculatoides* | 15–19(–21) × 7–9(–10) | 0.75–1 × 4 –4.5 | Dense purple | Lighter zone light brown | CC: 12–1 6 × 3–3.5(–4)<br>CON: 4.5–7.5 × 3–5.5<br>(S) |

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

= ? *Sphaeria concentrica* var. *pedicellata* Pers., Syn. meth. fung. (Göttingen) 1: 8. 1801, *fide* Ju *et al.* (1997). *Typus*: not located/selected.
= *? Daldinia concentrica* var. *obovata* (Fr.) Sacc., Syll. fung. (Abellini) 1: 394.1882.
≡ *Sphaeria concentrica* var. *obovata* Fr., Syst. mycol. (Lundae) 2(2): 331.1823. *Typus*: Not located/selected.
= *Daldinia simulans* Child, Ann. Missouri Bot. Gard. 19: 453. 1932.

*Holotypus*: **USA**, Missouri, Valley Park, Sep. 1929, D.H. Linder (FH).

*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. *Asci* 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 indehiscent 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

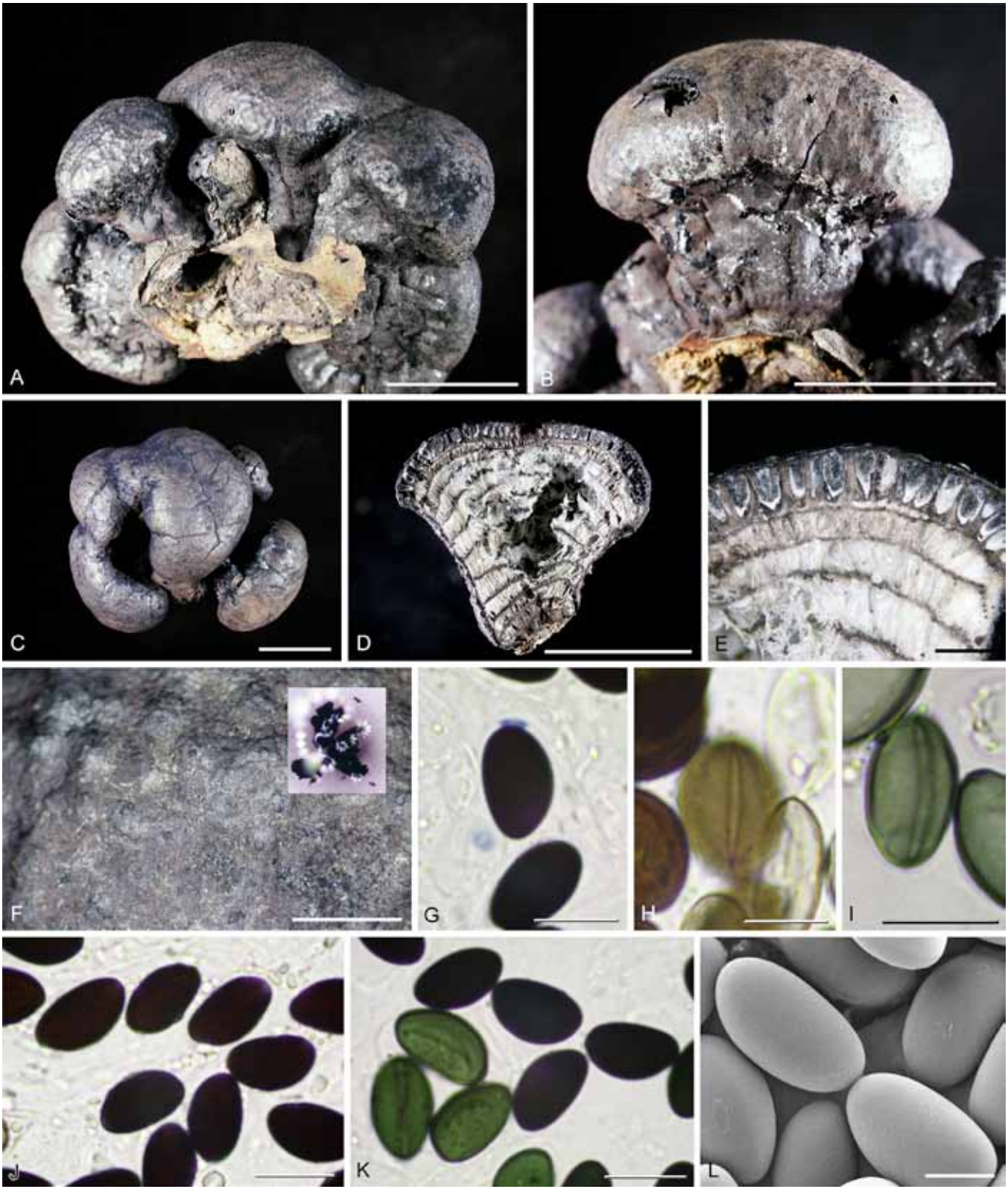



**Fig. 47.** Teleomorphic characteristics of *Daldinia vernicosa.* Epitype *Ww 2899* (Germany). A–C. Stromatal habit, reverse, side and top view respectively. D, E. Stroma in longitudinal section showing internal concentric zones and perithecial layer. F. Stromatal surface (inserted: Stromatal pigments in 10 % KOH). G. Ascus top in Melzer's reagent revealing amyloid apical apparatus. H, J. Ascospores in SDS. I, K. Ascospores in KOH, showing germ slit and non-dehiscing perispore. L. Ascospores by SEM (10.000×). Scale bars A–D = 1 cm; E, F = 1 mm; G–K = 10 µm; L = 5 µm.

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, Mühlleiten: 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,

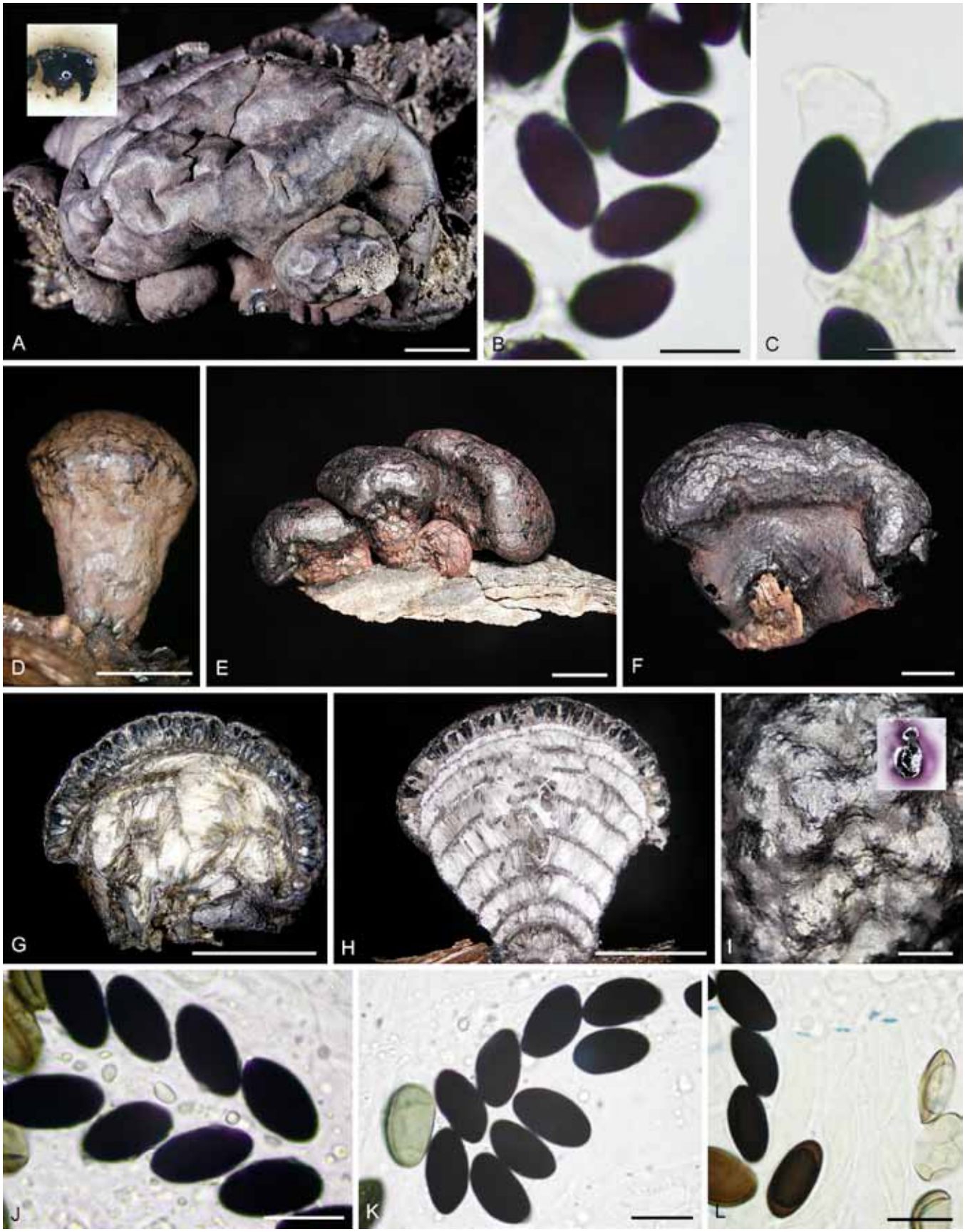



**Fig. 48.** Teleomorphic characteristics of *Daldinia vernicosa*. A–C. Holotype of *D. fissa* BPI 716013 (USA) and *D. vernicosa.* D, G, H, J–L. *JF-02217* (France). E. *Ww 2042* (UK). F, I. *JF-96112* (France). A, E, F. Stromatal habit (mature) (A: Stromatal pigments in 10 % KOH inserted). D: Stromatal habit (immature). G, H. Stroma in longitudinal section showing loculate to hollow interior, internal concentric zones and perithecial layer. I. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). B, J. Ascospores in SDS. C, K. Ascospores in KOH, showing non-dehiscing perispore. L. Ascospores and asci in Melzer's reagent, revealing amyloid apical apparati. Scale bars A = 1 cm; D–H = 5 mm; I = 1 mm; J–L = 10 µm.

*Betula verrucosa*, A. Kerner, Flora Exs. Austr.-Hungarica *2370* (UPS). Styria, Voitsberg, on *Crataegus*, *Acer*, *Alnus*, *Corylus*, no date, Niessl (von Mayendorff?) as *Hypoxylon concentricum*, in herb Saccardo (PAD). **Bulgaria**, Sozopol near Burgas, harbour, on dying trunk of *Celtis* cf. *australis*, 4 Sep. 1985, F. Kotlaba (PRM 837919); same locality, 3 Sep. 1984, F. Kotlaba (PRM 836179). **Canada**, Ontario, London, Jul. 1904, J. Dearness in Ellis & Everharts' Fungi columbiani *2013* (NY, UPS); Muskoka, Lake Rosseau, Harraby, Aug. 1903, E.T. Harper (F 331677); Ottawa, 1887, ex Ellis coll., as *D. concentrica* (NY); Toronto, Humber river, 11 Sep. 1935, G.D. Darker *5445* (FH 79496, duplicate in M ex herb. Petrak); Quebec, Montreal, Oct. 1902, J. Brunel (NY); Duchenay, 24 Aug. 1092, L.K. & E.S. Henry (NY, two packets numbered *2515* and *2029*). **Czech Republic**, Bohemia, vicinity of Prague, Pruhonický park, near fishing lake "Podzámecký rybník", on burnt wood of *Ulmus laevis*, 15 Sep. 1992, F. Kotlaba (PRM 876449); Moravia, Tisnov, *Acer campestre,* 6 Aug. 1926, E. Baudys (NY). **Denmark,** Sjælland, Vrangeskov near Haraldsted/ Ringsted, on fence post, 14 Sep. 1990, L. Olsen (C-F-52668). **Estonia**, Distr. Saaremaa, Viidu; on branches of *Betula pubescens*, 16 Aug. 1962, P. Pôldmaa as *D. concentrica* (B70 0009638). **France,** Ariège, Rimont, Las Muros, on fire-damaged trunk of *Ulmus minor*, 2 Sep. 1996, *JF-96112* (KR 0029399); Rimont, Le Touron, on fire-damaged stem of *Crataegus* sp. in a hedge, 14 Nov. 2002, *JF-02217* (KR 0029400); Marne-et-Loire, Chaumont, Bois de Chaumont, *Betula pendula*, 14 Jul. 1977, T.R. Lohmeyer & J. Mornand ex herb. H. Wollweber *Ww 3683* (WUP)**;** Seine-et-Oise, *Fagus*, F. Sarrazin in C. Romeguere: Fungi Gallici exsiccati *2040* (NY). **Germany**, Bavaria, Tegemheim near Regensburg, *Carpinus betulus*, 9 Sep. 1987, A. Bresinsky, *Ww 3822* (WUP ex R); Berlin, on tree trunks ("an Baumstuempfen"), 1890/91, P. Sydow, Mycotheca marchica *9469* (NY); Brandenburg, Eberswalde *Carpinus betulus*, Mar. 1959, J. Endtmann (Kr); Neuruppin, *Fagus sylvatica*, 16 Aug. 1960, H. Fischer (Kr.); Oderberg, *Quercus petraea*, 27 Oct. 1957, H. Kreisel (Kr.); Hessen, Nassau, Hattenheim, *Fagus*, Fuckel, Fungi rhenani *2468* as *D. concentrica* var. *obovata* (NY ex herb. Barbey-Boissier); same locality, 1894, K.W.G. Fuckel *305* (F 331691); Mecklenburg-Vorpommern, Rostock, *Carpinus betulus*, J. Duty (Kr, 2 collections dated 21 Aug. and 26 Nov. 1961); Woldeyck, *Fraxinus excelsior*, 19 Nov. 1958, H. Kreisel (Kr); North Rhine, Westphalia, burnt *Fagus sylvatica*, 31 Aug. 1996, same locality as epitype specimen, H. Wollweber *Ww 2885* (WUP); same locality and substrate, Oct. 1997, H. Wollweber, *Ww 3186 & Ww 3187* (KR 0026316, culture CBS 119316, see Bitzer *et al.* 2008); same locality, burnt *Carpinus betulus*, H. Wollweber *Ww 3189* (KR 0026315; culture CBS 119314, see Bitzer *et al.* 2008); same locality, burnt *Corylus avellana*, H. Wollweber *Ww 3191* (CBS 119315, see Bitzer *et al.* 2008); same locality, *Fagus sylvatica*, 6 Apr. 1997, H. Wollweber, *Ww 3102* (WUP, atypical stromata featuring compact internal concentric zones, due to abnormal development in the dry autumn of 1996); Thuringia, Jena, Thalbürgel, near Laupmalsmühle, *Quercus*, Aug. 1965, H. Kreisel (Kr). **Hungary**, Hanság. "Wieselburger Comitat" (Hansagán Mosony megye), Nov. 1882, Linhart, Fungi Hungariensi *180* in herb. Saccardo (PAD); Kecskemet, Pußzta Bugac, burnt *Betula*, 27 Oct. 1957, H. Kreisel (Kr). **Italy**, Piemont, Verbano-Cusio-Ossola, near Cannero, Lago Maggiore, on burnt wood of *Fagus*, Autumn 1865, Gibelli, det. de Notaris as *D. vernicosa* (B70 0009586). **Japan**, Shikoku Island, *Quercus*, Oct. 2002, T. Hashimoto (KR 0026333 ex herb. STMA). **Mexico**, Xalapa, 5000 ft, 12–20 Dec. 1909, W.A. & E.L. Murrill *292* (NY); El Chico National Park, Cerca de Las Ventanas, 7 Mar. 1975, Hidalgo (BPI 594223). **Netherlands**, Limburg, Mook, fire-scorched trunk of *Quercus robur*, 26 Oct. 1960, R.A. Maas Geesteranus *13500* (UPS). **P.R. China**, Anhwei Prov., Kuan Ying Lung, Ching Young Hsien, 13 Oct. 1932, S.Y. Chen *1214* (FH 79498); Kwangsi Prov., No Kang, Link Yung Hsien, 16 May 1933, S.Y. Cheo *2113* (FH 79511). **Poland**, Gdansk, *Fraxinus* (burnt), 29 Aug. 1980, E. Paechnetz *4084* ex herb D. Benkert (B, duplicate in herb Kr.); "Myschinjetz", fence post (branches of *Betula*), summer 1918, Laubert (B70 0009615). **Romania**, "Transsylvania", Valea Lunga (Langenthal), putrified wood of *Quercus*, 1873, C. Barth, comm, de Thümen as *D. concentrica* (B70 0009635); same locality, Dec. 1872, ex herb de Thümen in herb Saccardo (PAD; doplicates in B70 0009628, B70 0009629, 2 packets). **Russia**, "Przasnysg"(?), burnt *Aesculus hippocastanum*, Sep. 1915, *Laubert* (B70 0009614); Khabarovsk Territory, Khrebet Khekhtsir, 48°18'N, 135°03'E, 11. Aug. 1998, H. Knudsen, *TL-5099 (C)*; same locality, fire-damaged *Tilia*, 11. Aug.1998, H. Knudsen, *TL-5098* (C). **Sweden**, Norrbotten, Älsby, Älvsbyn, Sep. 1943, A. Berglund (UPS); Öland, Algutsrum, Holmeterparken, *Lauraceae* wood lying on the ground, 12 Aug. 2005, B. Nordén (GB, culture CBS 119002). **Switzerland**: Ticino, Castensago, Oct. 1992, *Fagus sylvatica*, *Ww 3601* (WUP ex MCT 8110, see Lucchini, 1997). **UK**, Cornwall, Scilly Isles, St. Mary's, between coast guard station and Halangy Point, burnt *Ulex*, 15 Aug. 1963, R. Santesson *16193* (UPS, 2 packets); East Sussex, Brighton, Moulsecombe National Park, 12 Sep. 1948, J.A. Nannfeldt (UPS); Wales, Glynwood, Bangor, burnt *Ulex*, 4 Oct.1975, mixed with *D. caldariorum*, A.J.S. Whalley *AJSW 378*, see Whalley & Watling (1980) as *D. vernicosa* (AJSW, part of the *D. vernicosa* element also deposited in KR 0026326). **USA**, Arkansas, *Quercus*, 25 Sep. 1908, E. Bartholomew *3962* (FH 79514); California, on *Salix*, 1945, ex Ellis collection (NY); Connecticut, Plainfield, 22 Sep. 1919, E. Bartholomew *6885* (FH 79501); Georgia, Atlanta City, Aug. 1887, ex Underwood collection (NY); Tallulah Falls Park, ex Underwood collection (NY); vicinity of Tallulah Falls, Hickorynut Mountain, 22 Aug. 1901, A.B. Seymour, det. Child 1932 as *D. vernicosa* (FH 79510); Indiana, Greencastle, Jul. 1890, G. Wilson, ex Underwood coll. (NY); vic. of Greencastle, on *Acer*, Oct. 1891, L.M. Underwood (NY, 2 packets); Kansas, Leavenworth Co., 26 Jul. 1958, C.L. Cramer (NY; duplicate in IMI labelled "P. Martin *1829*"; see Martin 1969 as *D. vernicosa*); Fort Riley, *Quercus* ("on oak poles"), Oct. 1917, J.F. Brenckle (B70 0009585/B70 0009587; 2 packets; FH 79516; PAD ex herb Saccardo); Rooks Co., *Celtis occidentalis,* 6 Dec. 1893, E. Bartholomew *2466* (FH 79513); same locality, *Ulmus* ("old elm stump"), 7 Dec. 1893, E. Bartholomew *1296* (FH 79512); Louisiana, Lafayette, Sep. 1932, Bro. Neon (?), *1746* (FH 79497); Maine, Piscataquis Co., Camp Balsam, two miles W of Sebec Village, *Betula*, 8 Sep. 1905, W.A. Murrill (NY); Piscataquis Co., Boerstone Camp. Dec. 1905, W.A. Murrill *2460* (NY); Maryland, Prince Georges Co., Patuxent Wildlife Refuge, 12 Aug. 1996, MSA Foray (NY); Massachusetts, Amherst, 17 Sep. 1916, D. White (NY); Canton, *Nyssa sylvatica* ("on tupela"), C.W. Cooke, 19 Oct. 1924 (FH 79519); same data, Dodge *3033* ex herb. C.W. Cooke (FH 79520); Hadley, 16 Nov. 1889, Halsted *886* (NY); Pride's Co, Apr. 1888, K. Miyabe & A.B. Seymour (NY); same locality, *Laurus*, Apr. 1888, K. Miyabe & A.B. Seymour (NY); same locality, *Quercus*, 10 Apr. 1888, K. Miyabe & A.B. Seymour (NY, 2 packets); Enfield, *Pinus rigida* (no substrate attached for verification), 2 Oct. 1932, A.V. Osmun in herb M.E. Bigelow *3920* (NY); Waverley, *Quercus alba*, G.D. Darker *4833* (FH 79502); Cambridge, Sep. 1915, A.P.D. Piquet (UPS ex FH); Michigan, Whitmore Lake, 14 Aug. 1932, Smith, det. J.H. Miller as *D. vernicosa* (F 93919); Washtenaw, Schoolgirls Glen, Ann Arbor, on limbs of *Quercus*, 31 Mar. 1893, L.N. Johnson (F 93920); Missouri, Center Co., on burnt spot on oak tree (*Quercus*), Sep. 1940, C.M. Tucker & J.B. Routien *1646* (NY); Dean Springs, on live poison ivy (*Toxicodendron radicans*), 14 Sep. 1944, Miss S. Bark (NY); *Ulmus* (?), ex herb. Ellis as *D. concentrica* (NY); Arcadia, Pilot Knob, on charred wood, 9 Nov. 1926, Overholts & Shope, ex herb. P. Shope *115* (Note on label: "see Rhoads: Mycologia 10:177-284, 1918") (COLO-F1373); Montana, Perryville Junction, 4 Mar. 1915, L.O. Overholts & R.A. Studhalter *2680* (NY); Créve Coeur, Oct. 1916, Dodge *708* ex herb. C.W. Cooke (FH 79521); New Jersey, on dead shrubs and limbs", Ellis. North American Fungi *166* (NY, 3 packets; PAD, 2 packets, one of the PAD specimens rev. as *D. vernicosa* by Saccardo); Newfield, 1899, in herb. Farlow ex herb. Ellis (FH 79518); Newfield, *Quercus*, 17 Nov. 1892, J.B. Ellis (FH 79506); same locality and host, 23 Nov. 1892, J.B. Ellis (FH 79505); New York, Palham Park, 17 Oct. 1909, H.J. Banker *397* (NY); New York City, 12 Oct. 1891, H.J. Banker *593* (NY); Bellport, *Betula papyrifera*, Nov. 1984 (NY); Berne Park, Jul. 1916, D.R. Sumstine *5163* as *D. concentrica* (NY); New York City, Bronx, Eastern Van Cortland Park, *Fraxinus*, Oct. 1959, C.T. Rogerson (NY); Buffalo, Jun. 1892, G.W. Clinton (NY, 2 packets); Huntington Forest, 29 Jun. 1957, H.E. & M.E. Bigelow (NY); Staten Island, *Betula*, Jul. 1886, ex Ellis Coll. (NY); Ulster Co., Trout river area, near Rondont Reservoir, 23 Sep. 1995, S. Sheine (NY); North Carolina, Wilmington, *Carya*, 10 Dec. 1899, H. Commons *1241* (NY); same locality, on hollow charred trunk of living *Celtis*, Aug. 27, 1899, H. Commons *943* ex Ellis collection (NY); Henderson Co., vicinity of Camp Green Cove, S of Tuxedo, on log, 20 Sep. 1980, J. Turner (NY); Ohio, Highland Co., 3 Apr. 1933, W.B. Cooke *2195* (NY); Pennsylvania, Allegheny Co., 22 Aug. 1984, A.E. Ortmann (NY); Bridgewell State Park, 16 Aug. 1932, L.K. Henry *2280* (NY); Erie Co., Waldamees Park, *Acer*, 30 Jul. 1930, C.K. Kenlon (NY); Lawrence Co., Muddy Creek Falls, 10 Jul. 1937, L.K. Henry *1958* (NY); Monroe Co., 5 Aug. 1937, D.R. Sumstine (NY); Tennessee, Burbank, 1896, R. Thaxter *3931* (FH 79509); Virginia, Richmond, *Quercus,* Aug. 1939, (FH 79499); West Virginia, Fayette Co., Mar. 1895, L.W. Nutall (FH 79507); Allegheny Ridge, E of Horton, *Fagus ferruginea*, 17 Sep. 1904, A.H. Moore (FH 79508, see Child 1932 as *D. vernicosa*). **Locality unknown**: as *D. concentrica*, *No. 17B*, in herb Saccardo (PAD); V. Wimmer as *D. concentrica* in herb Saccardo (PAD).

*Additional cultures* (from Child 1932, stromata not studied): **USA**: Missouri, Dixon, M. Child *5332* as *D. vernicosa* (culture CBS 157.32, GenBank Acc. No. of ITS nrDNA sequence AF163022); origin unclear, CBS 161.31, probably ex-paratype culture of *D. simulans*).

These cultures resembled those reported by Ju *et al.* (1999) with regard to their ITS rRNA gene sequences and their secondary metabolite production in YMG medium, but did not produce any conidiogenous structures when studied by us. The *D. vernicosa* culture in CBS is probably derived from *Acer rubrum,* since Child (1932) listed only one specimen from Dixon, Missouri in her monograph sub *D. vernicosa* from that host. The origin of the *D. simulans* culture remains unclear. Martin (1969) also reported on a culture of *D. vernicosa* "ex CBS, 1961", but this strain is not available according to the current catalogue.

*Notes*: Ju *et al.* (1997) revised the nomenclatural history of this taxon, and proposed to use the name *D. fissa f*or the fungus called "*D. vernicosa*" in most taxonomic papers that have been published ever since Cesati & De Notaris (1863) erected *Daldinia*. Their

rationale was that Lloyd´s name was the oldest available, since the basionym of *D. vernicosa, Sphaeria vernicosa* Schweinitz, a later homonym of *Sphaeria vernicosa* DC & Lam., was invalidly published. Here we, based on advice from Paul Kirk, treat the Cesati & De Notaris name as a *nomen novum* for *S. vernicosa* Schwein. in order to save this long established name. Wollweber & Stadler (2001), already pointed out the strong similarities of *Lycoperdon atrum*, a fungus originally described by Schaeffer (1774) from Germany and *D. vernicosa*. This taxon had been regarded as a synonym of *D. concentrica* by other authors, including Fries (1823) that used a broad species concept within this group of fungi. However, the species depicted by Schaeffer shows several features that actually match *D. vernicosa sensu* Cesati & De Notaris (1863), and conspecificity with *D. concentrica* can easily be excluded based on the Schaeffer plate. Unfortunately, Schaeffer (1774) cited an earlier valid name, *Valsa tuberosa* Scop. 1772, as a synomym thus making his own superfluous. The epitype we have selected for *D. vernicosa* is derived from Germany, rather than the type locality in eastern USA. However, it is highly similar to the holotype in every respect. In addition, the first permanently preserved culture and the first DNA sequences of this taxon were made from this specimen.

Nevertheless, the name *D. fissa* adapted by Ju *et al.* (1997) evidently refers to an aberrant form, featuring gregarious and luxuriant, unusually compressed stromata (Fig. 48A), with hollow interior apparently damaged by insect larvae, releasing Hazel (88) pigments in 10 % KOH, which even deviates in its micromophological characters in having some ascospores with perispore dehiscing in 10 % KOH (Fig. 48C), as revealed from a re-examination of the type specimen. However, SEM and HPLC characteristics of this specimen agree with those of other 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, indistiguishable 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. *obovata*" 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. *obovata* as an obligate 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 heterogeneic 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 Isabelline (65) in the type specimen, due to artifacts, cf. Stadler *et al*. 2004a[17], 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). *Perithecia* 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 narrowly rounded ends, 13–16(–17) × 7.5–9(–10) µm, with straight germ slit spore length on more convex side of inequilateral spores; perispore indehiscent in 10 % KOH; perispore/epispore smooth both by LM and SEM (10.000×).

*Cultures and anamorph*: Unknown.

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

*Additional specimens examined*: **Chile**, Chaparro, Limache, *Eucalyptus*, 23 Sep. 1927, Garaventa ex herb. Looserianum (FH 79470). **Costa Rica,** San José Prov., C.W. Dodge & W.S. Thomas *5086* (FH 220970). **New Zealand**, Wellington, Palmerston North, *Ulex europaeus,* Aug. 1956, E.C.S. Little (PDD 16383). **Thailand**, Payab, Doi Sutep, in evergreen forest, alt. 1100 m, Aug. 30, 1958, [comm.] G. Carrol (IMI, label reading "Martin *1839*", see Martin 1969 as *D. vernicosa*[18].

[17]Dilute isabelline in the type specimen, due to artifacts, cf. Stadler *et al.* 2004a.
[18]The specimen in IMI 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).

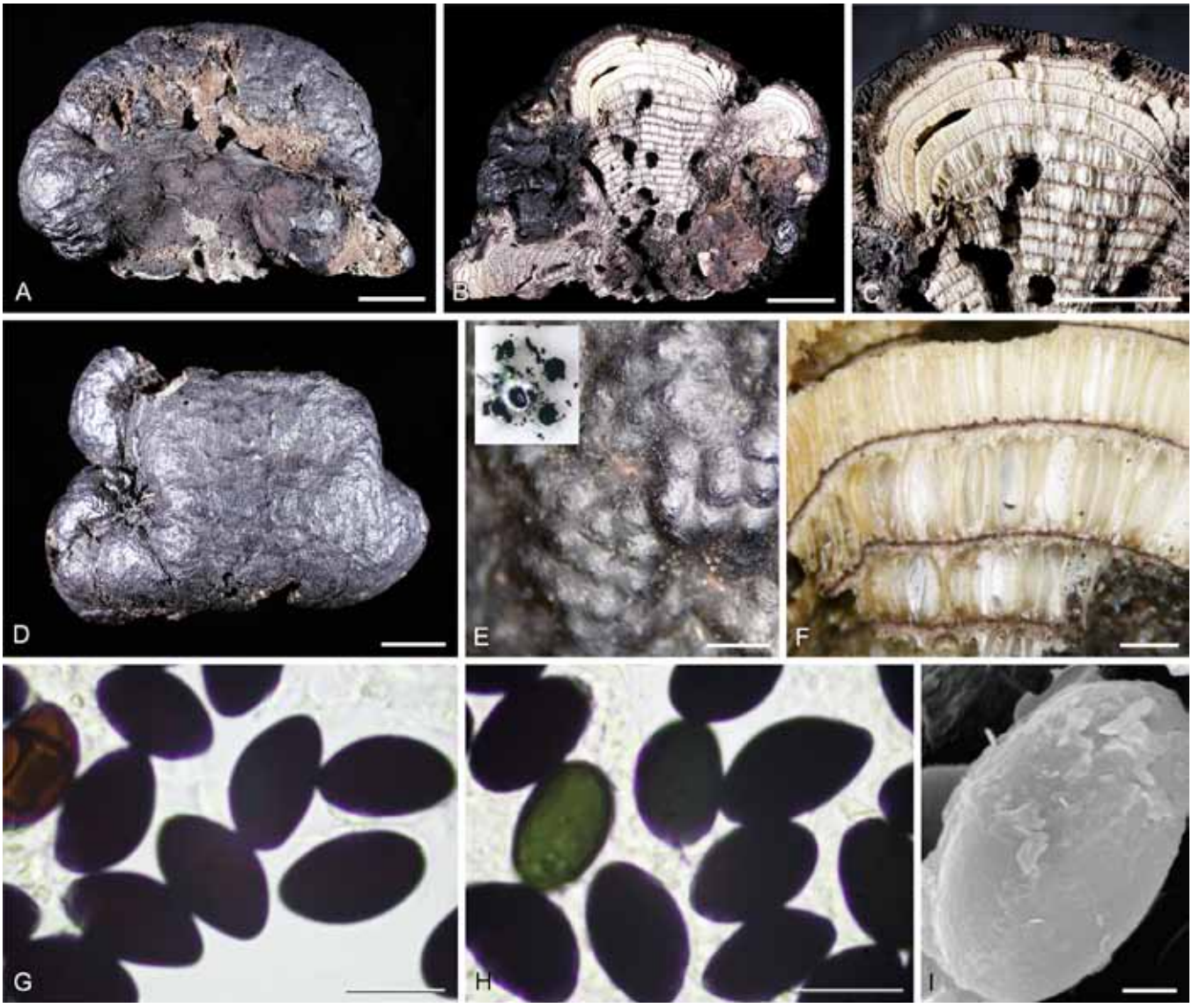



**Fig. 49.** Teleomorphic characteristics of *Daldinia bakeri.* Holotype, BPI 716970 (Australia). A, D. Stromatal habit in side (A) and top (D) view. B, C. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface with ostioles and perithecial outlines (inserted: Stromatal pigments in 10 % KOH). F. Close-up of internal concentric layers. G. Ascospores in SDS. H. Ascospores in KOH, showing non-dehiscing perispore. I. Ascospore by SEM (10.000×). Scale bars A–D = 1 cm; E, F = 1 mm; G, H = 10 µm; I = 2 µm.

*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. steglichii*) 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. vernicosa* 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* obovoid, 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-equilateral 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 *vernicosa* 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, obovoid 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 asci 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 hemispherical 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 Fuscous (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* lanceolate, 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. hausknechtii* 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 *vernicosa*-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. loculatoides* 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 cahuchucosa*** (Whalley & Watling) M. Stadler & Læssøe, **comb. nov.**, MycoBank MB807746.

*Etymology*: From the Carib Indian word "cahuchu", "rubbery".

*Basionym*: *Versiomyces cahuchucosus* Whalley & Watling, Notes R. bot. Gdn Edinb. 45(2): 401. 1989 [1988].

*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 iregularly 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 indihescent 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 cahuchucosus* was already discussed as a possible synonym of *D. vernicosa* (as *fissa*) by Ju *et al.* (1997), and we confirm the affinities to the *D. vernicosa*/*D. loculata* group

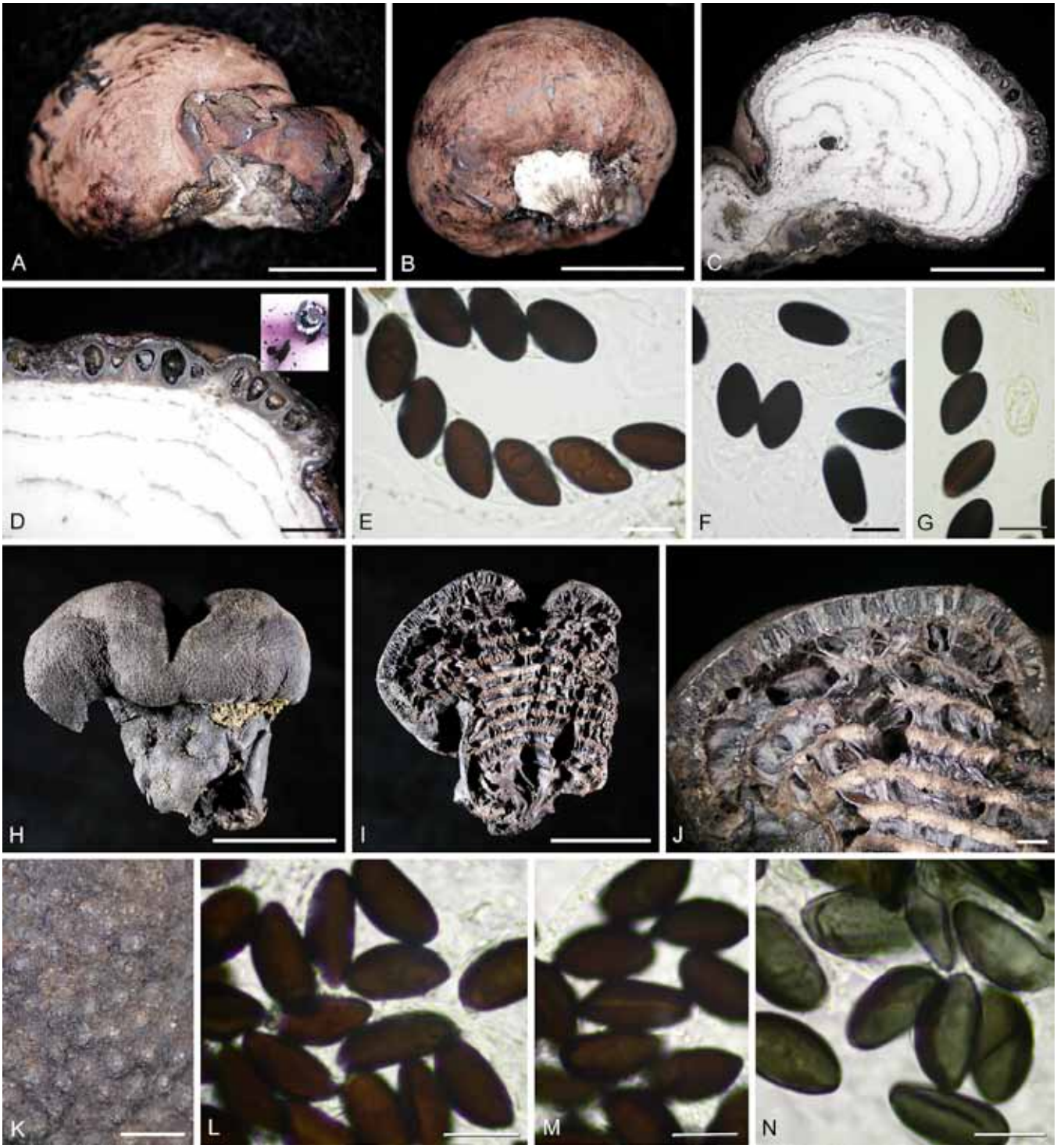



**Fig. 50.** Teleomorphic characteristics of *Daldinia* spp. (cf. *D. bakeri)*. A–G. BR-Myc 033528,63 (Sénégal). H–N. K (M) 130378 (Tanzania). A, B, H. Stromatal habit. C, D, I, J. Stroma in longitudinal section showing internal concentric zones and perithecial layer (D: Stromatal pigments in 10 % KOH inserted). E, L, M. Ascospores in SDS. F, N. Ascospores in KOH, showing non-dehiscing perispore. G. ascus top in Melzer's reagent, showing absence of bluing. K. Stromatal surface with ostioles and perithecial outlines. Scale bars A–C = 5 mm; H, I = 1 cm; D, J, K = 1 mm; E–G, L–N = 10 µm.

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.

***Daldinia gelatinoides*** Lar. N. Vassiljeva, *Nizshie Rasteniya, Griby i Mokhoobraznye Dalnego Vostoka Rossii*, Griby. Tom 4. Pirenomitsety i Lokuloaskomitsety (Sankt-Peterburg): 177. 1998. Figs 7B, 51.

*Etymology*: For the gelatinous interior, and for being like *D. gelatinosa* (a species which does actually not 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 dicotyledoneous angiosperms.

*Teleomorph*: *Stromata* turbinate or peltate, subsessile 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* obovoid to lanceolate, 1–1.3 × 0.35–0.5 mm. *Ostioles* 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 broadly to narrowly rounded ends, (11–)12–13(–14) × 6–8 µm, with straight germ slit spore length on more convex side; perispore indehiscent 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, and simple, unbranched sporothrix-like conidiophores are prevailing. Conidiophores up to 90 µm long, conidiogenous cells 10–21 × 3–4.5 µm. *Conidia* ellipsoid to elongate-elllipsoid, hyaline, with flattened base, 7.5–9.5(–11) × 4.5–6.5 µm.

*Specimens examined*: **Japan**, Kobe, J.E.A. Lewis ex Lloyd herb. *11793* as *D. vernicosa* (BPI 715095). **P.R. China**, Hebei, 27 May 1950, Z. Ji-Ding, *HMAS 17360* (FH 79522). **Russia**, Primorsky Territory, vicinity of Vladivostok, Sirenevka, on *Kalopanax septemlobus*, 26 Sep. 1999, *L. Vasilyeva* (VLA, culture CBS 116996, MUCL 46173, GenBank Acc. No. of DNA sequence FN428829); same locality, on living *Fraxinus* sp., 12 Sep. 1996, L. Vasilyeva (VLA); Spassk-Dalny, Khanka Lake, W of Gayvoron, 44°46'N, 132°40'E, fire-damaged *Ulmus*, 25. Aug. 1998, H. Knudsen, *TL–5235* (C, culture CBS 116991).

*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. 51C) 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 hypoxyloid *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.

***Daldinia grandis*** Child, Ann. Mo. bot. Gdn 19: 456. 1932. Figs 7E, 52.

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

*Lectotypus* (selected here): MBT177385; fig. 8 of Plate 29 in Child (1932) representing: **USA**, California, San Bernardino, on *Salix*, 24 May 1920, E. Bethel - *fide* Child 1932 deposited in the "Paul Shope herbarium, Boulder, Colorado", now COLO, but not located there in 2008.

= *Daldinia concentrica* f. *californica* Lloyd, Mycol. Writings 5, Large Pyrenomycetes: 24. 1919.

*Holotypus*: **USA**, Washington, Sequim, J.M. Grant, Lloyd herb. *12378* (BPI 716340).


**Fig. 51.** Teleomorphic characteristics of *Daldinia gelatinoides*. TL-5235 (Russia). A, B. Stromatal habit. C. Stroma in longitudinal section showing hollow interior, perithecial layer and remnants of internal concentric zones at base. D. Close-up on dissected perithecial layer. E. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). F. Asci tops in Melzer's reagent revealing amyloid apical apparati. G. Ascospores in SDS. H. Ascospores in KOH, showing non-dehiscing perispore and germ slit. Scale bars A–C = 5 mm; D, E = 1 mm; F–H = 10 µm.

*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 dicotyledoneous 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.

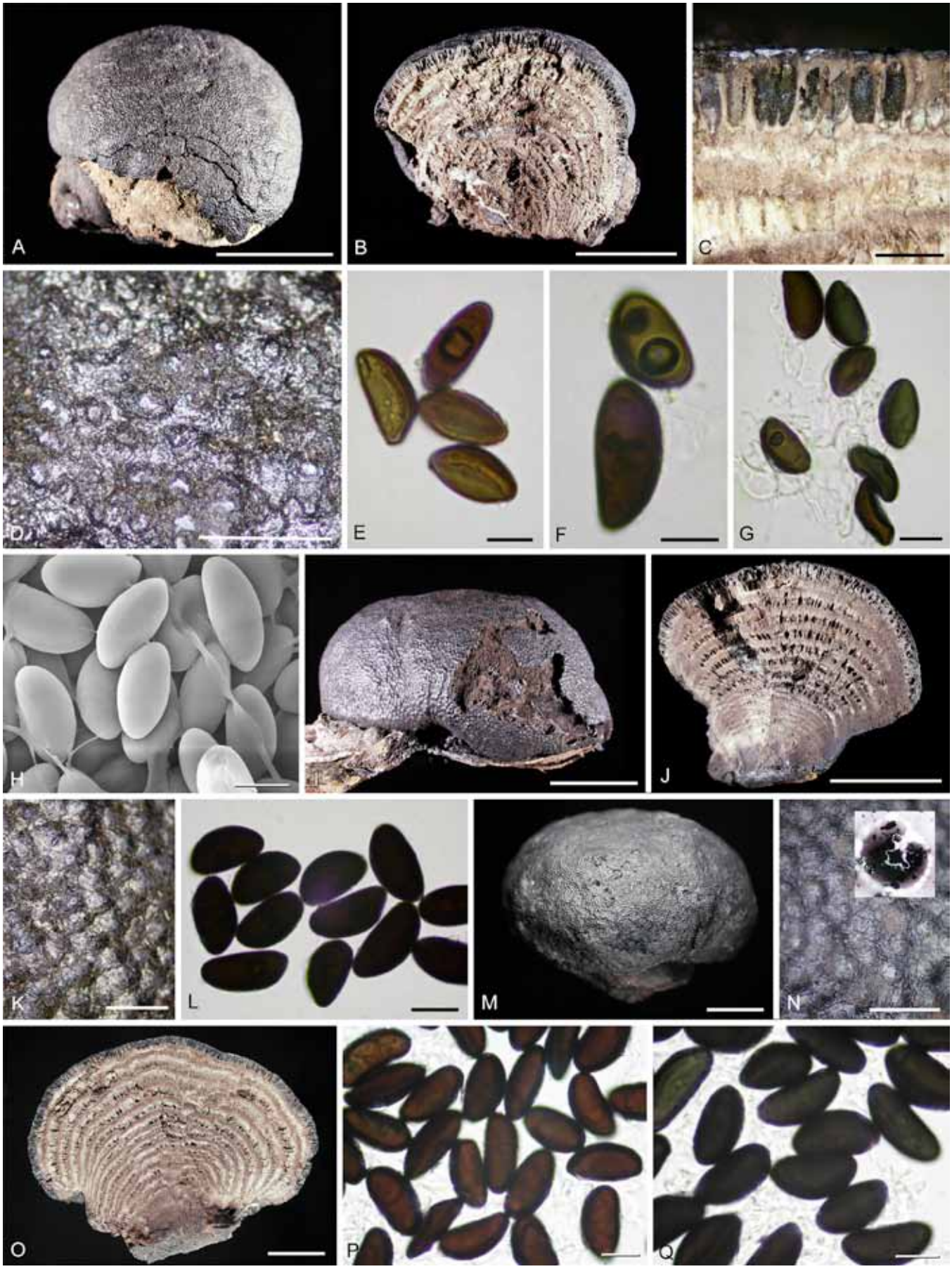



**Fig. 52.** Teleomorphic characteristics of *Daldinia grandis*. A–H. Paratype, BPI 716988 (USA). I–L. Holotype of *D. concentrica* var. *californica* BPI 716340 (USA). M–Q. *Daldinia* cf. *grandis*, as *D. concentrica* PDD 90478 (New Zealand). A, I, M. Stromatal habit. B, C, J, O. Stroma in longitudinal section showing internal concentric zones and perithecial layer. D, K, N. Stromatal surface with ostioles (N: Inserted: Stromatal pigments in 10 % KOH). E, P. Ascospores in SDS. F, G, L, Q. Ascospores in KOH, showing non-dehiscing perispore. H. Ascospores by SEM (10.000×). Scale bars A, B, I, J, M, O = 1 cm; C, D, K, N = 1 mm; E–H, L, P, Q = 10 µm.

*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).

*Additional specimens examined*: **Brazil**, Bahia, Municip. Abaira, Catolés Campo de Ouro, Mata E of Catolés trail, on standing, dead dicot. tree, 7 Mar. 1992, T. Læssøe & P.T. Sano ex herb Harley *52699* (K, SP). **Costa Rica**, San José Prov., Rancho Redondo (alt. 2200–2600 m, 9 Nov. 1920, C.W. Dodge & W.S. Thomas *5280* (FH 220971). **Ecuador**, Chimborazo Prov., Vicinity of Hoigra, Hacienda de Licay, Aug. 1918, J.N. Rose *23724* (NY). **Mexico**, Nueva Leon State, San Roque, wood in oak forest, R.F. Jorge (WSP, see Ju *et al.* 1997). **USA**, California, Alameda Co., *Umbellularia californica*, May 1924, H.E. Parks, Calif. Fungi *303* (B70 0009610; BR–Myc 075656,93; NY; S-F43793; UPS); San Bernardino, ex Underwood collection as *D. thouarsiana* (NY); near Sacramento, on *Gossypium hirsutum* (cottonwood stump), Apr. 1909, Ms. Sutliff in Lloyd herb. *10941* (BPI 716988 – **paratype** of *D. grandis*, see Child 1932); S Washington, 1923, Langley, as *D. concentrica* (BR–Myc 075659,96); Sumner, Apr. 1906, E.T. Harper (F 331670).

*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 hypoxyloid *Xylariaceae*), we propose, to avoid such ambiguous results, to test the perispore dehiscence by addition of a drop of 10 % KOH to the edge of a water mount of ascopores and to observe under the microscope what happens when the KOH reaches the ascospores. Even if some of the perispores were already released and were floating free (which occurs sometimes in weathered stromata), the ones that are still in place will show the typical dehiscence that is typical of a positive reaction.

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 misfiled. 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 IMCP 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 hausknechtii*** J. Fourn. & M. Stadler, **sp. nov.** MycoBank MB488678. Fig. 53.

*Etymology*: For the collector, the Austrian mycologist Anton Hausknecht.

*A Daldinia loculata differt in ascosporae maiorae, angustiorae, irregulariter ellipsoidae-inequilaterales, apicibus angustatis vel rotundatis, usque at 13–16 × 7–8 µm. A Daldinia loculatoides differt ascosporae minorae.*

*Holotypus*: **France**, La Réunion (Indian Ocean), Saint Paul, le Maïdo, 2200 m alt., substrate not documented, 27 Mar. 2005, A. Hausknecht (WU 26501, ex-type culture CBS119995, GenBank Acc. No. JX658521).

*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 gray, 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, felty, 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. hausknechtii*, *D. bakeri*, *D. loculata*, *D. loculatoides* or *D.grandis*. *Daldinia hausknechtii* 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

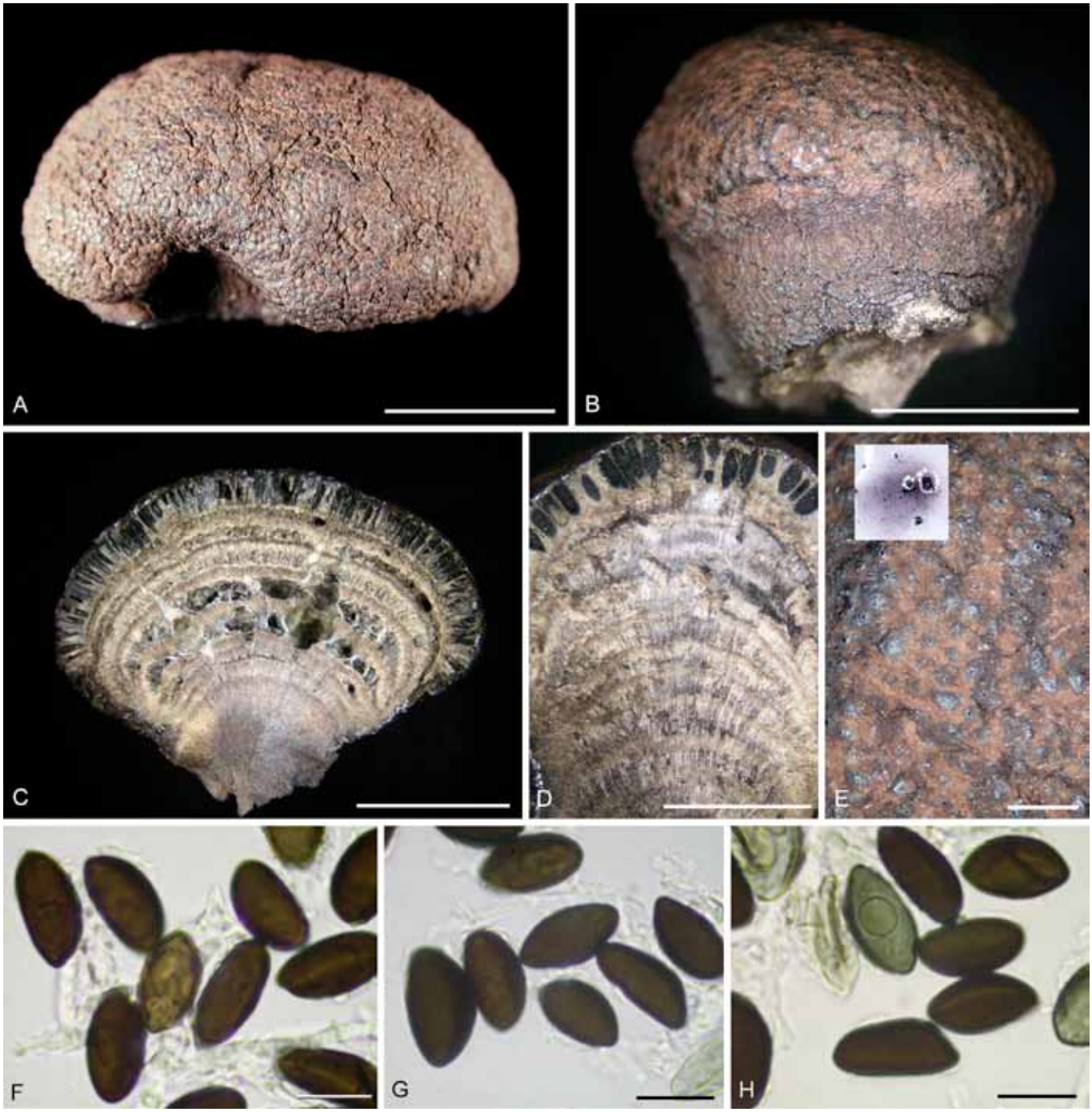



**Fig. 53.** Teleomorphic characteristics of *D. hausknechtii.* Holotype WU 26501 (La Réunion). A, B. Stromatal habit. C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). F. Ascospores in SDS. G, H. Ascospores in KOH, showing non-dehiscing perispore and germ slit. Scale bars A = 1 cm; B–D = 5 mm; E = 1 mm; F–H = 10 µm

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.

***Daldinia loculata*** (Lév.) Sacc., Syll. fung. (Abellini) 1: 394. 1882. Figs 7C, 14A, 54.

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

≡ *Sphaeria loculata* Lév., Ann. Sci. Nat. Bot., sér. III, 3: 47. 1845.

*Holotypus*: **USA**, locality unknown, ex herb. Léveillé (PC). **Epitype** (selected here): MBT177386; UK, Scotland, Kincardinshire, Devilly Forest, *Betula*, B.J. & G.J. Coppins *10274* (E; culture CBS 114738; GenBank Acc. No. AF176965, see Johannesson *et al.* 2000).

= *Hypoxylon durissimum* Fr., Summa veg. Scand., Section Post. (Stockholm): 384. 1849.

≡ *Daldinia durissima* (Fr.) Sacc., Syll. fung. (Abellini) 1: 394. 1882.

*Lectotypus* (selected here): **Sweden**, Uppland, Uppsala, Fries (K(M) 120970, ex herb. Berkeley).

= *Daldinia occidentalis* Child, Ann. Missouri Bot. Gard. 19: 453. 1932.

*Holotypus*: **USA**, South Dakota, Black Hills, 1903, H. Schrenk (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 perithecial 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. *Ostioles* papillate. *Asci* 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 ends, 11–14(–15) × 6–8 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*: Colonies on OA reaching the edge of 9 cm Petri dish in 10–12 d, at first whitish, felty, azonate, with diffuse margins, becoming grayish with sporulation after 3–4 wk. Reverse after 1–2 wk turning Green Olivaceous (70), blackening with age. Sporulating regions sparsely scattered over entire surface of colony. Conidiogenous structure with nodulisporium-like branching pattern. *Conidiophores* stout, mostly dichotomously branched, hyaline, coarsely roughened, up to 100 × 3.5–4.5 µm, with 1–3 conidiogenous cells arising from each terminus. *Conidiogenous cells* terminal or intercalary, cylindrical, hyaline, with apical scars, 11–20 × 3.5–4.4 µm. *Conidia* produced from sympodially proliferating conidiogenous cells, hyaline, smooth, subglobose to globose, 6–7.5 × 4.5–5 µm.

*Additional specimens examined*: **Austria**, Lower Austria, Weißenbach, Eichberg, *Betula*, 23 Apr. 1994, A. Hausknecht (WU-Myk. 10538). **Canada**, Ontario, Limprise Lake, *Betula*, 5 Aug. 1919, O.E. Jennings *et al.* (NY); same locality, *Betula*, 23 Apr. 1918, O.E. Jennings *et al.* (NY); same locality, on dead white birch (*Betula alba*), 10 Jul. 1919, O.E. Jennings *et al. 4902* (NY); Porphyr Island, *Betula*, 24 Jul. 1913, O.E. Jennings *3902* (NY). **Finland**, P.A. Karsten, ex Ellis collection (NY). **Germany,** Brandenburg, Bad Liebenwerden, NSG Loben, *Betula*, 16 Aug. 1987, Günther *et al.* ex herb. D. Benkert, *Ww 4093* (B, WUP); Luckau, *Betula*, Jul. 1976. H. Illig ex herb. D. Benkert, *Ww 4097* (B, WUP); Perleberg, *Betula*, 14 Jul. 1984, H. Kossak ex herb. D. Benkert, *Ww 4095* (B, WUP); Potsdam, trunk of dedicous wood, 13 Nov. 1977, D. Benkert, *Ww 4083* (B, WUP); Zossen, SSW Klausdorf, *Betula*, 28 Jul. 1987, R. Hanke ex herb. D. Benkert, *Ww 4096* (B, WUP); exact locality unknown, *Betula*, Jun. 1977, *Ww 3888* (WUP, Kr); Lower Saxony, Elsfloth, Strohauser Plate, on burnt stem of *Alnus*, 15 Jul. 1998, J. Albers & B. Grauwinkel, *Ww 3891* (KR, culture CBS 114737); Steller Heide, SE of Delmenhorst, *Sorbus aucuparia,* 1 Sep. 1978, B. Grauwinkel ex herb Wollweber (KR 0026319); North Rhine Westphalia, Altenberge near Münster, Jun. 1965, H. Wollweber, *Ww 3078* (WUP); Gruiten, Grube 7, *Betula*, 22 Feb. 1997, H. Wollweber *Ww 3087* (WUP); Hilden, Nature Reserve Hildener Heide, Taubenberge, *Betula*, 6 Oct. 1971, H. Wollweber *Ww 3096* (WUP); Schwarze Berge (Senne), *Betula*, 9 Mar. 1991, I. & W. Sonneborn, *Ww 2991* (KR 0026332); Wuppertal, In der Beek, *Betula*, 3 Sep. 1969, H. Wollweber, *Ww 2886* (WUP); Mecklenburg-Vorpommern, Neukloster, *Betula*, 27 Aug. 1961, *Ww 3838* (WUP, Kr). **India**, Uttarkashi, Rudugaira Kharek Valley, Uttaranchal, *ca.* 3250 m, half distance between Gangotri and Delhi, *Betula*, 29 Sep. 2002, K. Vincennecova (PRM 900706, culture CBS 116030). **Latvia,** Livland, Riga District, Pabbasch, near farm "Lilaste", *Betula pubescens*, 30 Aug. 1942, J. Smarods (B70 0009633). **Norway**, Oppland, Vang, Krok, *Betula*, 4 Sep. 1969, L. Ryvarden (NY); Troms, Municipal Hallbad, Grytoya, Hallevika, burnt *Betula*, O. Abelsen, 8 Oct. 2000 (TROM, culture CBS 113970); Lenvik, burnt *Betula*, O.H. Werle, 30 Aug. 1999 (TROM, culture CBS 113971); Municipial Nordreisa, Rendalen, Vinnelys, on dead branch of *Betula*, 1 Jul. 2000, O. Abelsen (TROM); Lulle, Skibotdalen, Storfjord, on *Betula*, 19 Aug. 1992, P. Marstad (TROM 6830). **Russia**, Caucasus, near Gagri, *Carpinus betulus*, 2 Feb. 1910, F.H. Meyer, ex Ellis collection (NY); Kamchatka*, Salix (?)*[19], 1 Aug. 1997, T. Læssøe *TL-4630* (C, culture MUCL 51686, GenBank Acc. No. AF176960, see Johanneson *et al.* 2000); vicinity of Vladivostok, Natural Reserve Cedrovaya Pad, on indet. angiosperm wood, 22 Aug. 2005, E. Popov (CWU-Myc AS 205, KR). **Sweden**, Bohuslän, Torsby, Överön, *Sorbus aucuparia*, 30 Mar. 1985, I. Nordin (UPS); Darlarna, Orsa, Berget, *Betula*, 8 Jan. 1985, D. Broström *341* (UPS); Säter parish, Säterdalen, *Alnus incana*, 3 Jun. 1972, G. Lohammar (UPS); Gotland, Kräklingbo, Nygårds Myr, near Fornbogen, *Sorbus hybrida*, 3 Oct. 2001, I. Nordin (UPS); Lappmark, Åsele (or Lycksele), trunk of *Betula*, 1903, G. von Post (UPS); Björkvattnet, 1874, A.N. Lundström (UPS); Medelpad, Alnö, dead *Alnus*, 17 May 1983, H. Lindström in herb. J.O. Tedebrand *1033* (UPS); Närke, Snavlunda, Långsbergs trädgård, *Malus* ("äppleträd"), 13 Aug. 1898, R. Sernander (UPS); Villingsbergs skjutfält, Lövbråten, *Betula*, 7 May 1967, I. Nordin *4300* (UPS); Norrbotten, Övertorneå, between Hiriioja and Korpilombolovägen, in swamp forest, 9 May 1959, O. Lönnequist *586* (UPS); Tärendö, 17 Jul. 1958, E.R. Julin (UPS); Öland, Persnäs Parish, between Persnäs Railway St. and Legenäs, trunk of *Betula*, 24 Aug. 1953, J.A. Nannfeldt *13132* (UPS); Östergotland, Omberg, Väversunda, *Sorbus aucuparia*, 16 Apr. 1967, I. Nordin *4233* (UPS, 2 packets); Småland, Femsjö, 1854, M.A. Lindblad (UPS); Torne Lappmark, Jukkusjärvi, Luopakte, *Betula*, 11 Jul. 1964, E. Kankainen (UPS); Uppland, Almunge, near Uppsala, *Betula,* comm. H. Johannesson *HJ 105* (UPS, culture MUCL 51688, GenBank Acc. No. AF176967, see Johanneson *et al.* 2000); Vaksala, Jälla, Hassellund, SW from agricultural school, *Betula*, 19 Mar. 1967, I. Nordin (UPS); Västergötland, Töreboda, Gastorg, *Betula,* 1 Jun. 1958, J. Lundberg (UPS); Västra Frölunda, vicinity of Göteborg, Ekebäcks fritidsgård, *Sorbus aucuparia*, 19 Oct. 1969, I. Nordin (UPS); exact locality unknown, dead trunk of *Populus tremuloides*, 19 Jul. 1894, Grandall *47* ex Ellis collection (NY); no detailed data, ex Ellis collection, det. Everhart as *D. concentrica*, label inside reading "*Hypoxylon durissimum*" (NY). **Ukraine**, Donetsk District, Drobyshevo Forest, Svajatie Gory National Park, near the village of Bogorodichnoe, *Betula pendula*, Jul. 2008, A. Akulov (CWU Myc AS2801, culture MUCL 51702); Kharkov-City, Forest Park, *Betula pendula*, 27 Aug. 2006, A. Akulov & A. Ordynets (CWU-Myc AS 1979, KR). **UK**, England, Devon, Slapton Ley Nature Reserve, *Crataegus*, 2 Nov. 1973, D.L. Hawksworth (IMI 180155); Cobham, Fairmile Co., charred *Betula*, 30 Jul. 1958,

[19]The host of this specimen was given as *Betula* in Johannesson *et al.* (2000) but acc. to Notebook T. L. derived from *Salix (?)* and immature. In any case the resulting culture shows the typical morphology of *D. loculata* and can be considered as genuine.

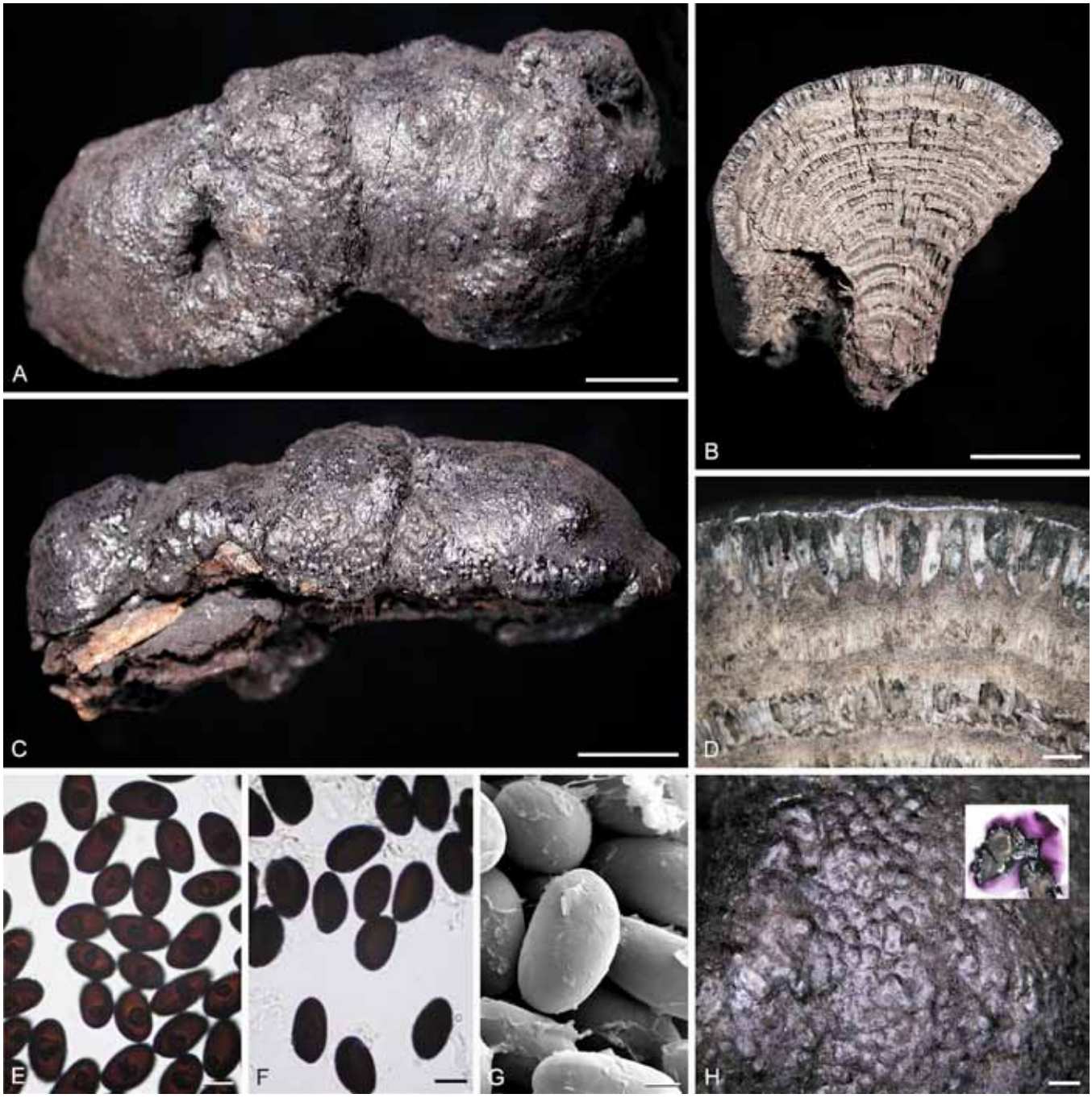



**Fig. 54.** Teleomorphic characteristics of *Daldinia loculata. Ww 2886* (Germany). A, C. Stromatal habit. B, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Ascospores in SDS. F. Ascospores in KOH, showing non-dehiscing perispore. G. Ascospores by SEM (10.000x). 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.

F.C. Deighton (IMI 72453); Surrey, Pirbright, *Betula pendula* (burnt), Nov. 1991, G. Butterfill, mixed with *D. concentrica* (K(M) 18694; culture KC1522 - see Stadler *et al.* 2001a); Esher, West End Co., *Fagus*, Oct. 1993, P.M. Kirk (K(M) 24541, culture KC1525, BCRC34117; GenBank Acc. Nos of DNA sequences AY951698 and AY951810, see Hsieh *et al.* 2005). **USA**, California, Kern Co., Bakersfield, Oct. 1961, P. Martin *897* as *D. occidentalis* (NY); Humboldt Co., Trinidad, *Alnus*, 6 Jun. 1931, H.E. Parks (M; F 331668); Colorado, Gilpin Co., Ellsworth Gulch, bark of dead *Populus tremuloides*, 12 Jul. 1964, H.G. Rodeck as *D. grandis* (UPS F12,456 ex COLO); exact locality not stated, Bethel *487* (NY); Grand Mesa, on dead aspen (*Populus tremuloides*), 14 Sep. 1929, P.F. Shope & M.O. Jung *824*; (COLO), same data, Seaver & Shope *567*; ex herb. P. Shope *102-66138* (COLO-F1369, see Child (1932) as *D. occidentalis*); Huerfano Co., 0.5 miles N of Pass Creek Pass, no substr. and date, H.R. Simms *Sf-50* (NY); Idaho, Bonner Co., Priest River, in branches of uprooted trunk of *Betula papyrifera*, 5 Aug. 1920, A.S. Rhoads (NY); Massachusetts, Cambridge, Sep. 1915, A.P.D. Piquet, Rel. Farlowianae *10* (NY); Michigan, Cheboygan Co., Wolf's Hog, *Betula*, 26 Jun. 1953, M.E. Bigelow *790* (NY); Utah, Garfield Co., Henry Mountains, *Populus tremuloides*, 10 Sep. 1992, C.T. Rogerson *92-27* (NY); loc. cit., along Slate Creek, *Populus tremuloides*, 30 Jul. 1992, C.T. Rogerson as *D. occidentalis* (NY); Garfield Co., Sevier Plateau, Dixie National Forest, *Populus tremuloides*, 20 Aug. 1992, C.T. Rogerson (NY); Weber Co., North Odgen Pass, Wasatch Mountains, Cache National forest, *Acer grandidentum*, 8 Sep. 1993, C.T. Rogerson (NY); Virginia, Mountain Lake, 8–14 Jul. 1908, W.A. Murrill *445* (NY); Washington, Oreille Co., Metelina Falls, fire killed *Betula papyrifera*, 27 Aug. 1920, A.S. Rhoads *16865* (NY); New Boundary, *Betula alba-occidentalis*, 1 Aug. 1933, G.C. Hedgcock (BPI 594597, BPI 594598, two packets); Northport, *Betula alba-occidentalis*, no date, G.C. Hedgcock *54613* (UPS).

*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

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 loculatoides* appears to be its closest relative, only differing from *D. loculata* in ascospore size and morphology and in the dimensions of its conidiogenous structures,

***Daldinia loculatoides*** Wollw. & M. Stadler, Mycol. Res. 108(9): 1030. 2004. Figs 7F, 14D, E, 55.

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

*Holotypus*: **UK**, Scotland, Alva, Silver Glen, *Fagus*, exposed trunk, old tree, stromata occuring 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 stromata*: 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 binaphthalene derivatives prevailing.

*Additional specimens examined*: **Canada:** British Columbia, Vancouver, on *Acer*, 27 Jul. 1970, S.A. Redhead *45* as *D. grandis* (BPI 594973, NY). **Czech Republic**, Moravia, vicinity of Hodonín, Ratíškovice,"Mokrý háj", on burnt living trunk of *Betula pendula*, 17 Jun. 1995, C. Kosina as *D. concentrica* (PRM 885050, culture CBS 116729, GenBank Acc. No. AM407726). **Russia**, Caucasus Mountains, Dombaj near Teberda, Amanauska dolina, alt. *ca.* 2.200 m, on root of *Salix caprea* near road, 8 Aug. 1986, J. Houda, det. F. Kotlaba as *D. concentrica* (PRM 842320). **UK**, England**,** Norfolk, Ringstead, ex herb. C.B. Plowright (K(M) 91739). **USA**, Illinois, Cook Co., Chicago, Lincoln Park, between Montrose and Foster Beach, on trunk wounds of *Gleditzia triacanthos*, 12 Sep. 1990, S. Huhndorf (NY, specimen largely immature); Oregon, East side of Willamette River, 29 May 1916, C.H. Bryant *27,043* (NY ex Oregon State Univ.).

*Notes*: This species has now also been found on *Betula*, and is here recorded for the first time from the Czech Republic, England, Russia, 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. loculatoides* 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. loculatoides* has been transferred to *D. andina*. This leaves the ascospore morphology (highly variable in *D. grandis vs.* rather homogeneous and often Rugby ball shaped in *D. loculatoides*) as major discriminative characters, but *D. loculatoides* 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 conclustion about the status of these closely related taxa can be reached.

## Tropical relatives of *Daldinia loculata* and *Daldinia loculatoides*

Some specimens of tropical origin show affinities to *D. loculata* with ascospores of intermediate size range between those given above for *D. loculatoides* 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. *loculata/loculatoides***: Germany**, Hamburg**,** storage facilities of wood–import company "Müller", on tree trunk (of presumably tropical origin), Oct. 1935, Liese, det. W. Kirschstein as "*D. angolensis*" (B70 009590). **Kenya,** Central Prov**.,** Nanyuki distr., Naro Moro River Lodge, alt. *ca.* 2.000 m, 1 Mar. 1972, J. A. Nannfeldt *22089* (S). **Rwanda**, Route Cyangugu–Butase, Rurasenkoko Park, dead wood, 6 Mar. 1972, P. Van der Veken *9689* (GENT).

## Notes on *Daldinia nemorosa* (syn. *Annellosporium nemorosum*)

The anamorphic genus and species *Annellosporium 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 the *D. petriniae* complex. Despite the author described an anamorph showing annellidic 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. loculatoides*, 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. nemorosum* (*D. nemorosa* herein).

*Specimens examined (of D.* cf. *nemorosa)*: **Canada**, Alberta, Calmar, *Populus tremelloides*, 21 Aug. 1997, S.P. Abbott *SA 1256,* as *D. grandis* (UAMH, culture UAMH 9035 - stromata largely immature); Edmonton, Devon, UADBG (University of Alberta Devonian Botanic Garden), *Malus*, 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).

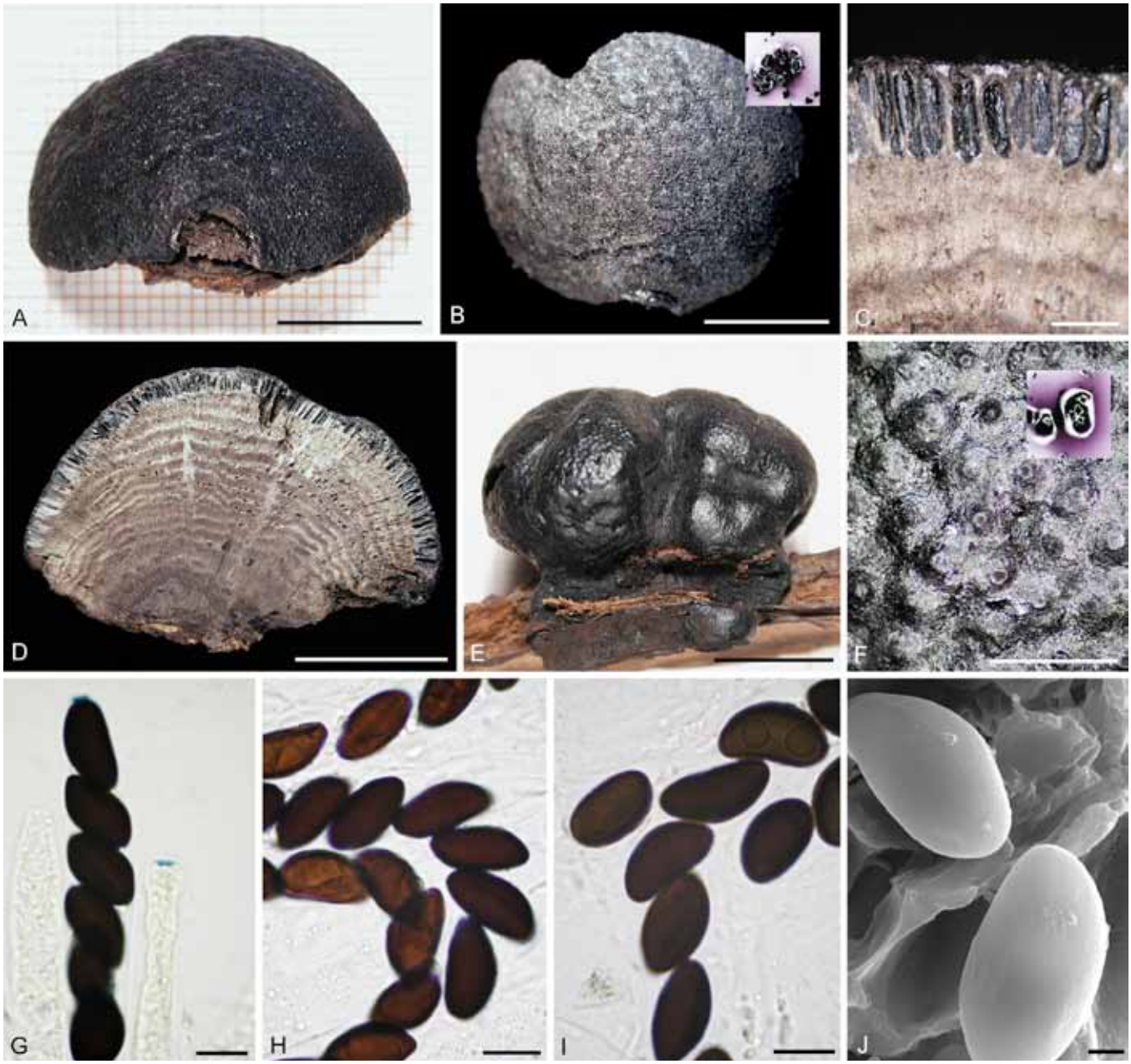



**Fig. 55.** Teleomorphic characteristics of *Daldinia loculatoides*. A–D, G–J. Holotype (UK); E, F. BPI 594973 (Canada). A, B, E. Stromatal habit (A, E: Side view; B: Top view, with stromatal pigments in 10 % KOH inserted). C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. F. Stromatal surface (stromatal pigments in 10 % KOH inserted). G. Asci 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.

***Daldinia novae-zelandiae*** Wollw. & M. Stadler, Mycol. Res. 108(9): 1031. 2004. Figs 7F, 14F, G, 56.

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

*Holotypus*: **New Zealand**, Mid Canterbury, vicinity of Springfield, Kowai Bush, wood of *Nothofagus*, 15 May 2000, P.R. Johnston & R.E. Beever *PRJ H513* (PDD 72010).

*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

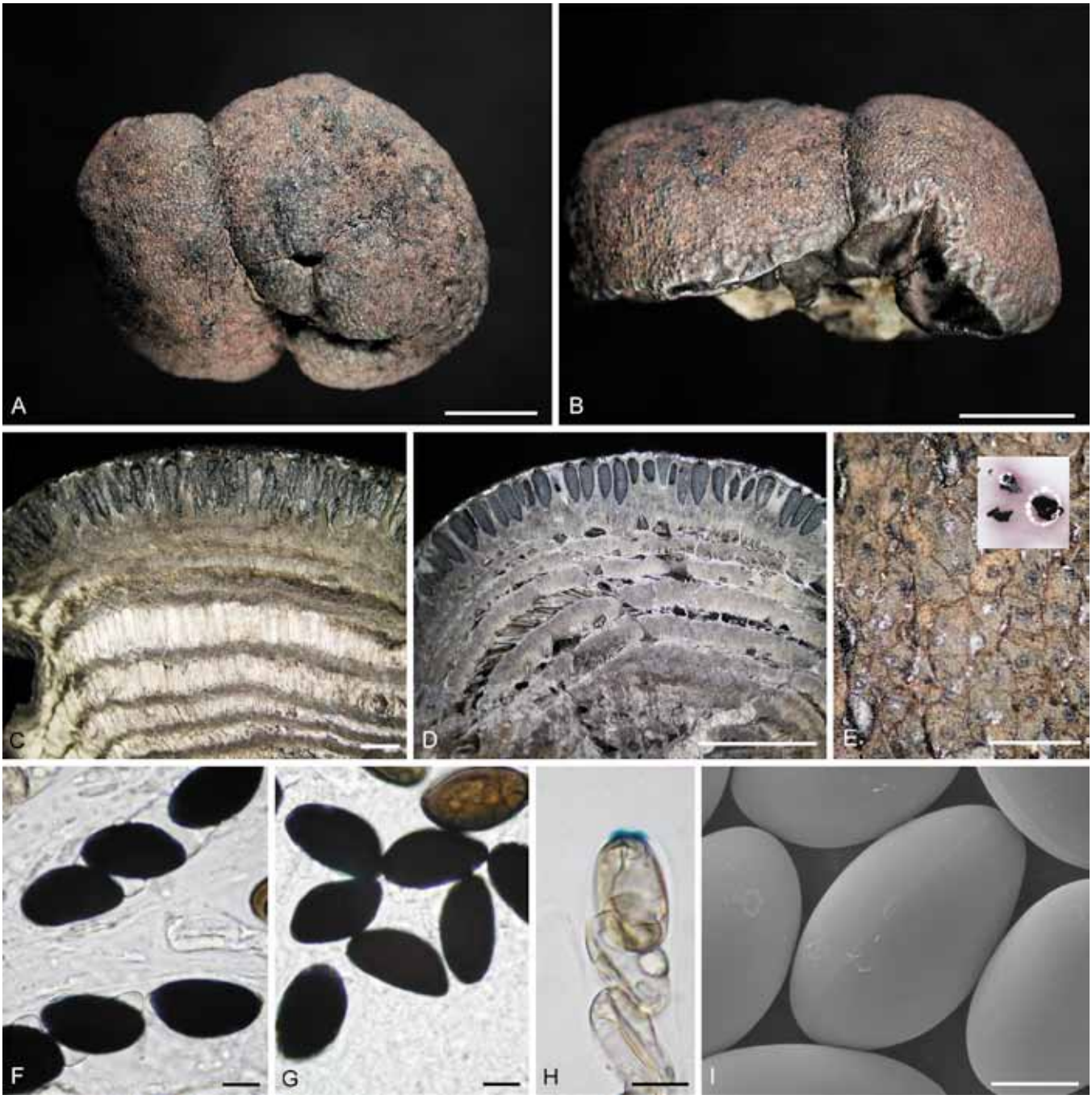



**Fig. 56.** Teleomorphic characteristics of *Daldinia novae-zelandiae*. A–C, E–H. PDD 82745. D. PDD 82155. I. Holotype, PDD 72010 (all from New Zealand). A, B. Stromatal habit. C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). F. Ascospores in SDS. G. Ascospores in KOH, showing non-dehiscing perispore. H. Ascus top in Melzer's reagent revealing amyloid apical apparatus. I. Ascospores by SEM (10.000×). Scale bars A, B = 1 cm; D = 5 mm; C, E = 1 mm; F–H = 10 µm; I = 5 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.

*Additional specimens examined*: **New Zealand**, Auckland, Papakura, Kirks Bush, wood, "late summer" (no year), C. Shirley *CS AK079* (PDD 81217); Bay of Plenty, Te Urewera, Tarapounamu, 15 Oct. 2003, P.R. Johnston (PDD 81343, culture CBS 119014, ICMP 16538); Chatham Islands, Nikau Bush, 18 Nov. 1992, P.R. Johnston & E.H.C. McKenzie *C25* (PDD 61834, culture CBS 114739 and ICMP 15489, see Stadler *et al.* 2004c, and CBS 122873; see Ju *et al.* 1997 as *D. grandis);* Gisborne, Urewera National Park, Lake Waikareiti, 10 May 2001, R. Leschen *RL 849* (PDD 74313); Mid Canterbury, Alford Forest, Mt. Somers, 30 Dec. 2003, J.A. Cooper *8766* (PDD 79933); Nelson, McKee Reserve, 3 Feb. 2002, P. Leonard *PL41202* (PDD 75987, culture CBS 114740, ICMP 15470); South Island, Harmer State forest, *Nothofagus*, 12 Sep. 1981, W.R. Buck *6910* (NY); Wellington, Papaitonga, *Myoporum laetum*, Oct. 1930, G.H. Cunningham (PDD 3715); Rimutaka Range, Orongorongo Valley Field Station, 22 Jan. 2005, M. Efford (PDD 82155, culture ICMP 18258); Taupo, Tongariro, Mangaehuehu Scenic Reserve, 5 Apr. 2005, S. Mortimer (PDD 82745, culture ICMP 18259). **Philippines**, Luzon Island, Beuguet Prov., *Quercus*, Nov. 1905, E.D. Merrill as "*D. concentrica* var. *obovata*" (NY).

*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, dehiscent 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 Petrini & 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 equilateral, obovoid ascospores with indehiscent 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. childiae* 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 concentricols 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 perithecial 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. carpinicola*, 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 stromatal 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 stromatal 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, *Annellosporium*, 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 homogeneous 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.

***Daldinia petriniae*** Y.M. Ju, J.D. Rogers & F. San Martín, Mycotaxon 61: 275.1997. Figs 8A, B, 15A, B, 57.

*Etymology*: For the Swiss mycologist, Liliane Petrini, 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**).

= *? Daldinia concentrica* f. *confluens* C.G. Lloyd, Mycol. Writings 5, Large Pyrenomycetes: 25. 1919.

*Holotypus*: **USA**, Idaho, Priest River, *Alnus*, J.R. Weir ex Lloyd herb. *12379* (BPI 716987).

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

| Species (*Daldinia*) | Ascospore size [µm] | Ascal apical apparatus (µm) | Stromatal pigments (KOH) | Ratio darker/lighter concentric zones + significant stromatal features | Anamorphic structures (µm) |
|---|---|---|---|---|---|
| *asphalatum* | 12.5–16.5(–19.5) × 6–8 | 0.5–0.75 × 3–3.5 | Purple or absent | 1:1.5–9 | CC:14–22 × 4 |
| | | | | STR: long stipitate, zones extending into the stipe | CON: 6–8 × 3.5–5 |
| *barkalovii* | 12–14(–15) × 6–7(–7.5) | 0.75–1 × 2.5–3 | Purplish-gray | 1:1–1.5 | CC: 10–25 × 3–5 |
| | | | | STR: turbinate, with characteristic brownish-yellow striate surface stripes (surface not reticulate!) | CON: 7–10 × 5.5–7 |
| *carpinicola* | (13–)14–16.5 × (6.5)7–8(–10) | 0.5 × 3–3.5 | Purplish-gray | 1:0.75–2 | CC: 10–12(–14) × 3–3.5 |
| | | | | STR: mostly clavate | CON: 6–7.5 × 4.5–5.5 |
| *decipiens* | (13–)14–18(–20) × 6.5–10(–11) | 0.5–0.8 × 4.5–5 | Purplish-gray | 1:0.75–2 | CC: 13–22 × 2.5–4 |
| | | | | STR: mostly semiglobose-substiptitate | CON: 7–8 × 4.5–5.5 |
| *gelatinosa* | 12.5–16(–17) × 6–8(–10) | 0.5–1 × 3.5–4 | Purplish-gray | 1:1–4 | CC: 10–12(–14) × 3–3.5 |
| | | | | STR: mostly turbinate | CON: 6–7.5 × 4.5–5.5 |
| | | | | | Stromata in OA culture |
| *govorovae* | (15–)16–18(–20) × 8–10 | Not seen | Greenish brown | 1:1–4 | CC: 12–15 × 3–5 |
| | | | | STR: pulvinate | CON: (7–)8–11 × 6–7.5) |
| *lloydii* | (11–)12–18 × 6–8(–9) | 0.5–0.75 × 4–5 | Olivaceous | 1:2–3 | CC: 18–35 × 3.5–5 |
| | | | | STR: hemispherical to pulvinate, basal parts often vertically zonate, surface of young STR reticulate | CON: 6–8 × 3–4 |
| *macrospora* | 22.5–30 × 8.5–10.5 | 1 × 4 | None | 1:1–5 | Unknown |
| | | | | STR: mostly turbinate | |
| *mexicana* | 12.5–15.5 × 6.5–7.5 | 1 × 3.5–4 | Weakly isabelline | 1:1–2 | CC: 14–34 × 4–5 |
| | | | | STR: mostly turbinate | CON: 6–7 × 4–5.5 |
| | | | | | (to be confirmed based on fresh material) |
| *petriniae* | 12.5–16.5 × (6–)6.5–7.5 | 0.75–1 × 3.5–4 | Purplish-grey, sometimes isabelline, often with colour changes | 1:1–3 | CC: 10–24 × 3–5 |
| | | | | STR: initially hemispherical to almost clavate, later often pulvinate or placentiform | CON: (5.5–)7–9 × (4.5–)5–6(–7) |
| *singularis* | 9–11 × 4.5–5.5 | Inamyloid, reduced or absent | Weakly purple | 1:1–1.5 | CC: 10–20 × 2.5–3.5 |
| | Perispore very easily detached in KOH | | | STR: tiny, max 5 mm diam | CON: 5.5–8 × 3.5–4.5 |
| | | | | | Fertile stromata on OA culture *fide* Ju *et al.* (1999) |

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

*Selected illustrations*: Petrini & 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, 1–5.8 × 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, 0.3–0.7 mm thick, lighter zones 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, amyloid apical apparatus, 0.75–1 × 3.5–4 µm. *Ascospores* brown to dark brown, ellipsoid-inequilateral, 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.

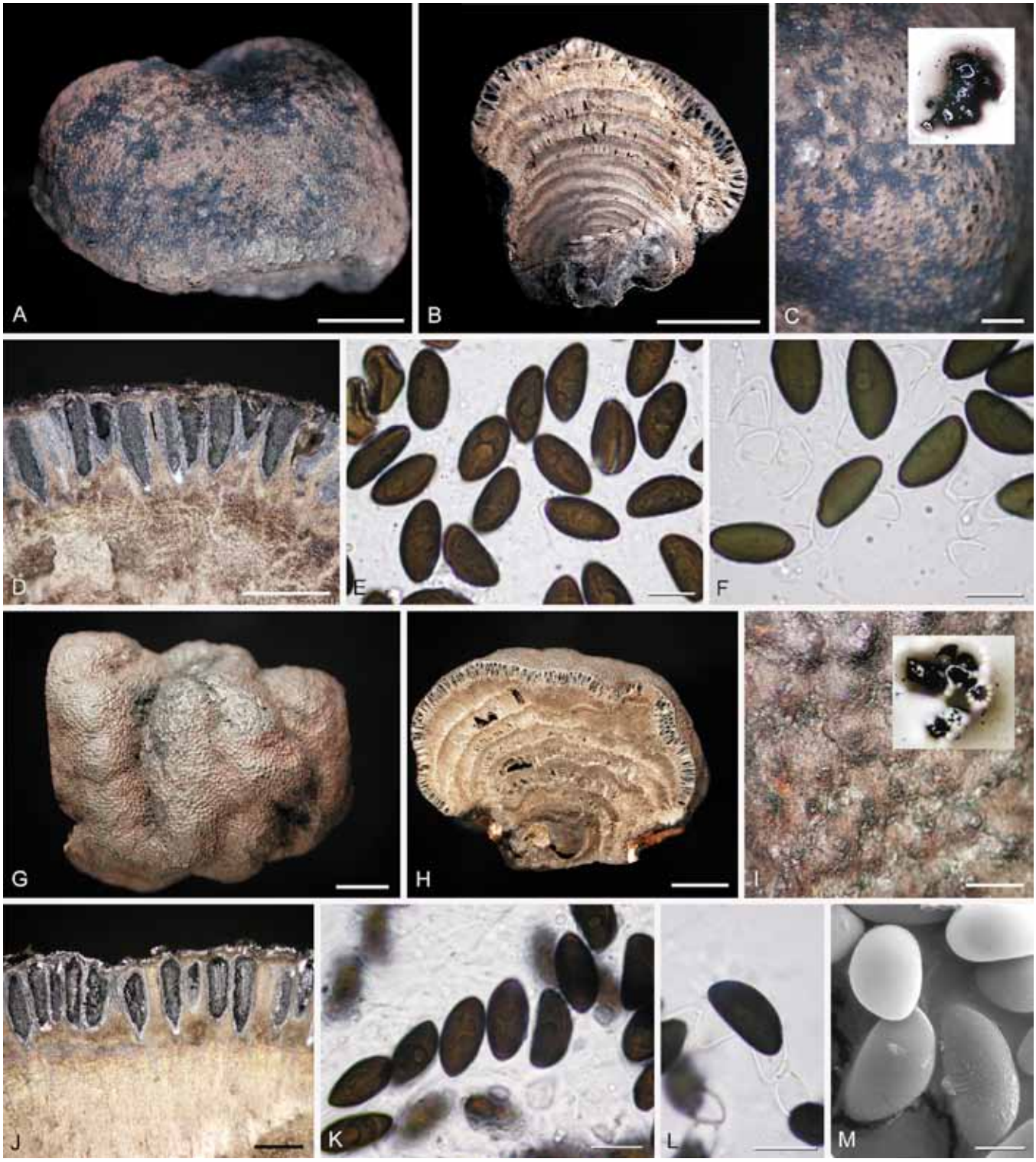



**Fig. 57.** Teleomorphic characteristics of *Daldinia petriniae.* A–F. *Ww 3298* (Switzerland). G–L. Isotype (Switzerland). M. *Ww 3393* (Austria) A, G. Stromatal habit. B, D, H, J. Stroma in longitudinal section showing internal concentric zones and perithecial layer. C, I. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). E, K. Ascospores in SDS. F, L. Ascospores in KOH, showing dehiscing perispore. M. Ascospores by SEM (10.000×). Scale bars A, B, G, H = 5 mm; C, D, I, J = 1 mm; E, F, K, L = 10 µm; M = 5 µm.

*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 sporothrix-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) conidiogenous cells arising from each terminus. *Conidiogenous cells* clavate, hyaline, roughened, 10–24 × 3–5 µm. *Conidia* produced from percurrently proliferating conidiogenous cells or, infrequently, from sympodially proliferating conidiogenous cells, hyaline, smooth, subglobose to obovoid, usually with an attenuated flattened base, (5.5–)7–9 × (4.5–)5–6(–7) µm.

*Additional specimens examined*: **Austria**, Burgenland, Forchtenstein, Weißes Kreuz, Hofleiten, 9 Nov. 2001, G. Koller (WU-Myk. 21289); Carinthia, Seebach near Spittal, *Alnus glutinosa*, Aug. 2000, Niessl von Mayendorf (M); Lower Austria, Diendorf, Dienbachtal, Seewiese, *Betula*, 25 Mar. 1984, A. Hausknecht (WU-Myk. 3143); Weißenbach, Eichberg, *Betula*, 23 Apr. 1992, A. Hausknecht (WU-Myk. 10546); Salzburg, Irlacher Au, *Alnus*, Oct. 1987, T.R. Lohmeyer *87/69* (WUP); Millstädter See, *Alnus incana*, 6 Sep. 2002, H. Wollweber *Ww 3814* (WUP); Hinterglemm near Saalbach, Alnus incana, 18 Mar. 196, H. Wollweber *Ww 3823* (WUP); Pinzgau, Kapruner Tal, A. glutinosa, 13 Sep. 1991, H. Wollweber *Ww 3316* (WUP); Styria, *Alnus*, 23 Sep. 1986, "AMO" ex herb Krieglsteiner *KR 842/86*, *Ww 4123* (STU, WUP); Tyrollia, Rotholz, Inn-Aue, *Alnus incana*, 27 Aug. 1998, E. Wollweber, *Ww 3393* (KR, WUP); Hochpillberg, Zillertal, *Alnus incana*, 30 Aug. 1998, U. Helm, *Ww 3391* (WUP); same collection data, J. Keller, *Ww 3392* (WUP, KR, culture CBS 119988, MUCL 49214, GenBank Acc. No. of ITS nrDNA sequence AM749937, see Bitzer *et al.* 2008); Vorarlberg, Feldkirch, "an Buchen" (*Fagus*), J. Rick as *D. concentrica* in herb. Saccardo (PAD); Feldkirch, *Fagus*, Winter 1848, J. Rick in Rehm: Ascomyceten *1228* (NY). **Canada**, Ontario, Toronto, *Alnus incana*, Oct. 1902, J.L. Paull as *D. vernicosa* (FH 79500). **Czech Republic**, Bohemia, Novy Hradec Králové, near Birička, on branch of still living ("semivivum") *Alnus incana*, 22 Sep. 1985, Z. Pouzar as *D. concentrica* (PRM 869448); Moravia, Hranice ("Mährisch Weisskirchen"), *Carpinus*, Sep. 1928, F. Petrak (M). **Denmark**, Fyn, Nov. 1962, G. Carrol in herb. P. Martin *1764* as *D. concentrica* (IMI, see Martin 1969). **Estonia**, Lahema National Park, *Alnus* cf. *glutinosa*, 22 Aug. 1989, *TL-52577* (C). **Finland,** Mustiala, 24 Oct. 1866, *P.A. Karsten* (UPS). **Germany**, Badenia-Württemberg, Allgäu, *Alnus*, 28 Mar. 1977, H.-O. Baral ex herb. Krieglsteiner *KR 278/77, Ww 4109* (STU, WUP); Wangen, *Alnus incana*, W. Pohl, Aug. 1998, *Ww 3394* (WUP); Weingartener Moor, *Alnus glutinosa*, 28 Aug. 1987, W. Winterhoff (M); Oberschwaben, *Sorbus aucuparia*, 22 Mar. 1978, Finkenzeller ex herb Krieglsteiner s/n, *Ww 4145* (STU, WUP); Württemberg, *Betula*, Jul. 1977,G.J. Krieglsteiner *KR 304/77*, *Ww 4111* (STU, WUP); Württemberg, *Quercus*, 18 Jan. 1975, Payerl ex herb. Krieglsteiner *KR 550/75* (STU, WUP); Bavaria, Füssing, Innauen, *Alnus glutinosa*, 29 Oct. 1994, H. Wollweber, *Ww 3889* (WUP); Oberammergau, Graswangthal, *Alnus incana*, Aug. 1889, Schnabel as *D. vernicosa* in herb Saccardo (PAD; duplicate in NY and M, for the latter see Wollweber & Stadler 2001); *Alnus*, Oct. 1972, H. Marschner *397* (M); Wertach-Auen near Augsburg, *Alnus incana*, Jul. 1974, J. Stangl (M 51915, ST); same locality, St. Erasmus, *Alnus incana*, Apr. 1978, H. Marschner *628* (M); exact locality unknown, *Alnus*, 20 Mar. 1994, Paulus *et al*. ex herb Krieglsteiner *KR 163/94* (STU); exact locality unknown, *Betula pubescens* May 1992, G. Seeger ex herb Krieglsteiner *KR 550/92* (STU); Volkach, *Alnus glutinosa*. 29 Oct. 1994, L. Krieglsteiner *WU 2855*, *Ww 3819* (KR, WUP). Brandenburg, Havelland district, Brieselang, *Alnus glutinosa,* 10 Jan. 1915, W. Kirschstein (B70 0009613); Fürstenwalde/Spree, NSG Lochnitztal, Liebenwerden, *Betula*, 30 Feb. 1990, D. Benkert, *Ww 4094* (B, WUP); Potsdam, *Alnus*, 12 Nov. 1975, D. Benkert, *Ww 4087* (B, WUP); Saxony, Sächsische Schweiz, Pastor Michelis, det. Nitschke as *D. concentrica* (B70 0009608). **Hungary**, Heviz, cf. *Alnus incana*, Aug. 1984, H. Werner ex herb. D. Benkert, *Ww 4085* (B, WUP). **Latvia**, "Kurland, Libau, Kriegshafengebiet", on dead branch of *Alnus glutinosa*, 7 Jun. 1917, A. Ludwig as *D. concentrica* (B70 0009619). **Liechtenstein**, Triesenberg near Vaduz, 1500 m alt., dead branch of *Alnus incana*, 5 Oct. 1995, F. Kotlaba as *D. concentrica* (PRM 886101, culture CBS 116728). **P.R. China**, Heilongjiang Prov., Shengli State Farm, 6 Aug. 2004, *Acer* sp., E. Bulakh, comm. L. Vasilyeya (VLA, culture CBS 117125); vicinity of Sanjiang, Nature reserve, 3-5 km from Donxing con, *Betula*, 5 Aug. 2004, L. Vasilyeva (VLA, culture CBS 117126). **Poland**, Mikaszowka near Augustów, virgin forest "Starozyn", standing dead trunk of *Alnus glutinosa*, 12 Sep. 1974, Z. Pouzar as *D. concentrica* (PRM 813788). **Russia**, Sakhalin Island, Proonayskiy District, Vozvrazscheniye, on *Betula*, 3 Aug. 2000, leg. A. Bogacheva, comm. L. Vasilyeva (VLA, culture CBS 116994). **Sweden**, Ångermannland, Nordingrån, Halaviksravinen, *Alnus incana*, 26 Jul. 1977, S. Olofsson ex herb. I. Nordin (UPS); Ullånger, Håll, eastern slope of Mt. Moberget, *Alnus incana*, 28 Jul. 1973, R. Moberg *2034* (UPS); Gästrikland, Gävle, Arboretum "Vallsbage", *Alnus incana*, 29 Jan. 1971, J.A. Nannfeldt *23011* (UPS); same collection data and host, 7 Aug. 1973, J.A. Nannfeldt *23085* (UPS); Hälsingland, Harmanger, Strömsbruk, fallen trunk of *Alnus*, 22 Jun. 1949, B. & J. Eriksson (UPS); Medelpad, Sundsvall, Indal Stige, dead *Alnus*, 30 Aug. 1977, R. Lidberg (UPS); Norrbotten, Övertorneå, near Hirvivaaras, in swamp forest, 21 May 1959, O. Lönnequist *591* (UPS). Östergötland, Gryt, Foreham, *Betula alba*, 18 Aug. 1958, J.A. Nannfeldt *15359* (UPS); Gryt, Säterön, dead branches of *Alnus*, 23 Apr. 1946, J.A. Nannfeldt *8298*, immature, but with typical anamorph on stromata and characteristic HPLC profile (UPS); Linköping, Nykvernparken, *Alnus glutinosa*, 6 Apr. 1968, H. Carlstedt *581* (UPS); Småland, Växjö, Oseby säteri, non-burnt *Betula*, 8 Aug. 2003, K. Bergelin (C, culture CBS 116730). Södermanland, Gyt, Natängsåns eastern beach, *Alnus* ("på fallen alstam"), 9 Oct. 1955, S. Lundell, largely immature (UPS); Stängnäs, near hospital on beach, *Alnus glutinosa*, 12 Aug. 1931, J.A. Nannfeldt *et al. 4295* (UPS); Uppland, Hacksta, near Hagslätta, *Alnus glutinosa*, 27 Oct. 1975, G. Eriksson ex herb I. Nordin (UPS); Uppsala, Vårdsätra Naturpark, *Alnus*, 8 Nov. 1929, S. Lundell, immature (UPS); Västerbotten, Lövänger, *Alnus incana*, 12 Feb. 1945, L. Holm (UPS). Västergötland, Göteborg, St. Ängården, nature park, *Alnus* trunks, 14 Sep. 1942, T. Nathorst-Windahl *3376*, largely immature (UPS); Västmannland, Skinskattebeggs, near Lindbo, *Alnus incana*, 5 Aug. 1972, I. Nordin *5292* (UPS). **Switzerland**, Bern, Grindelwald, Grund, Lütschinenufer, *Alnus incana*, 18 Jan. 2000, H. Wollweber *Ww 3713* (WUP, culture MUCL 51850); Graubünden, Filisur, *Alnus incana*, 16 Sep. 1983, H. Wollweber *Ww3718* (WUP); St. Domenica, Boga, on dead trunk of *Alnus* stil standing, 5 Aug. 1983, G. Lucchini (WUP ex Museo Cantonale Ticino); Untervaz, *Alnus incana*, Aug. 1982, L. Petrini & A.J.S. Whalley (ZT, see Petrini & Müller 1986 as *D. occidentalis*); Obwalden, Alpnach, *Alnus incana*, 9 Jul. 1978, J. Breitenbach *2807-80* ex herb Krieglsteiner *KR 025/78* (STU, see Breitenbach & Kränzlin 1981, fig. 346 as *D. concentrica*); Tessin, Sonvico-Pairolo, *Alnus viridis*, alt. 1260 m, 15 Feb. 2000, R. De Marchi, *Ww 3752* (BERN, WUP, cultured, but culture did not survive). **USA**, California, Humboldt Co., Trinidad, *Alnus rubra*, May-Jul. 1931, H.E. Parks *3727* as *D. occidentalis* (F 331667; NY, 2 packets; UPS); Idaho, Priest River, *Alnus tenuifolia,* Oct. 1915, J.R. Weir *363* and *349* (NY); Massachusetts, Berkshire Co., Savoy State Forest Aug. 1963, P. Martin *1721* (NY); Michigan, Washington Harbour, Isle Royal, 11 Jul. 1904, E.T. & S.A. Harper (F 93906); New Hampshire, Grafton Co., Hanover, *Betula*, Fall 1950, E.G. Simmons *2397* (NY); New York, Greene Co., woods below Kasterskill Falls, *Betula lutea* (on yellow birch), 11 Oct. 1963, C.T. Rogerson (NY); Rockland Co., Stony Brook, Harriman State Park, *Betula* ("on grey birch"), 4 Oct. 1963, C.T. Rogerson (NY); Indiana, Putnam Co., Greencastle, DePauw Arboretum, 25 Oct. 1945, E.G. Simmons *1130* (NY); St. Regis Mountains, 6 Aug. 1951 (NY), C.T. Rogerson (NY); New Hampshire, Intervale, *Alnus*, Sep. 1901, R. Thaxter (FH 79465); Oregon, Waldport, *Alnus*, Aug. 1929, S.M. Zeller as *D. occidentalis* (NY); Pennsylvania, Potter Co., 3 miles S of Chorry Springs, (substrate identified as *Betula*), 4 Aug. 1956, L.K. Henry *17971* (NY); Beaver Co., Rock Bowl, 8 Jul. 1909, D.R. Sumstine *3474* (NY); Rhode Island, Exeter Co., Beach Pond State Forest, 22 Jul. 1965, M.E. Bigelow *4757* (NY); Tennessee, Great Smoky Mountains Nature Park, Seiverville Co., SE of Gatlinburg, 26 Jul. 1996, I. Krisai, J. Greilhuber & H. Voglmayr *6854* as *D. concentrica* (WU-Myk. 24614); Washington, Newman Lake, *Alnus rhombifolia* Aug. 1935, C.R. Stillinger as *D. occidentalis* (M).

Numerous further specimens from Central Europe are cited in Wollweber & Stadler (2001).

*Further cultures of D. petriniae extant in public collections*: **Sweden**, Dalarna, *Alnus*, comm. H. Johannesson *HJ 103* (see Johannesson *et al.* 2000; deposited by us as MUCL 49213; GenBank Acc. No. of DNA sequence AF176975). **Switzerland**, Graubünden, Domat/Ems, *Alnus incana*, 8 Apr. 1987, B. Griesser as *D. occidentalis sensu* Petrini & Müller 1986 (CBS 527.90 ex ETH 17007).

*Notes*: This species, first identified by Petrini & 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*, *A. alnobetula*, and *A. rhombifolia* 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

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 such a specimen was made from conidia of immature stromata and resembled those of *D. petriniae*, rather than that of *D. lloydii* with respect to the morphology of its conidiophore and conidia.

*Specimens examined* (of *D.* cf. *petriniae* with olivaceous pigments in KOH and ascospores up to 19 µm long): **Germany**, Badenia-Württemberg, Black Forest, 14 May 1974, Laber & Haas ex herb. Krieglsteiner *1000413, Ww4156* (STU, WUP); Württemberg, *Betula pendula*, 3 Jan. 1975, Payerl ex herb. Krieglsteiner, *KR 555/75, Ww 4128a* (STU, WUP); Württemberg, *Populus*, 2 Sep. 1976, H. Seemann ex herb. Krieglsteiner *KR 332/76*, *Ww 4117* (STU, WUP); Württemberg, *Fraxinus excelsior*, 30 Aug. 1981, S. Philippi ex herb. Krieglsteiner s/n., *Ww 4149* (STU, WUP); Württemberg, on wood, 1976, G.J. Krieglsteiner *1000588*, *Ww 4157*(STU, WUP); Württemberg, *Alnus glutinosa*, 20 May 1978, R. Strödel ex herb. Krieglsteiner *KR 050/78*, *Ww 4125* (STU, WUP); Württemberg, *Alnus glutinosa*,10 Dec. 1979, L. Krieglsteiner. ex herb. Krieglsteiner *KR 1013/79, Ww 4129* (STU, WUP); Württemberg, *Alnus glutinosa*, 30 Jan. 1993, K. Neff ex herb. Krieglsteiner *KR 540/93, Ww 4131* (STU, WUP); Württemberg, *Alnus glutinosa*, 27 Mar.1985, O. Gruber *et al*. ex herb. Krieglsteiner *KR 212/85, Ww 4134* (STU, WUP); Bavaria, "*Alnus* or *Fraxinus*", Apr. 77, J. Stangl ex herb. Krieglsteiner s/n., *Ww 4162* (STU, WUP); Berlin, *Betula*, 2 Aug. 1987, P. Mohr ex herb. D. Benkert, *Ww 4090* (B, WUP); Brandenburg, Seelow, *Alnus*, 8 Oct. 1993, D. Benkert, *Ww 4088* (B, WUP); Saxony-Anhalt, Grockstädt**,** Nature Reserve Schönauer Börde, corticated branches of *Betula pendula*, 15 Jan. 2005, P. Rönsch *et al*., *STMA 05064* (culture MUCL 52699), stromata largely immature, culture obtained from conidia. **USA**, Massachusetts, Conway State forest, fallen sugar maple (*Acer saccharum*), 15 Sep. 1978, M.E. Bigelow *6485* as *D. grandis* (NY).

Some other specimens resembled the above ones, but had even larger ascospores up to 23 × 10 µm, with conspicuous striations by SEM, and olivaceous pigments in KOH (Fig. 58). However, the larger spores were not particularly frequent, and were never observed in an octosporous ascus. They could have arisen from abnormal ascal development, hence their significance appears to be limited. However, we neither observed intact asci nor were we able to culture these specimens. Searching for fresh material that corresponds to this putative taxon should be encouraged.

*Specimens examined* (of *D.* cf. *petriniae* with olivaceous pigments in KOH and ascospores up to 23 µm long): **Germany**, Saxony, Sächsische Schweiz, Griesegrund, südliche Wehlen, *Betula*, 13 Oct. 1979, R. Conrad ex herb. D. Benkert, *Ww 4092* (B, WUP); Saxony-Anhalt, Harz Mountains, Selketal near Meisdorf, *Sorbus,* Oct. 1970, M. Huth ex herb. D. Benkert, *Ww 4078* (B, WUP). **Sweden**, *Uppland*, Uppsala, N. Gottsunda, *Betula*, 12 Sep. 1970, B. Andersson (UPS).

A similar apparently host specific variability of ascospore sizes as described above for *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* (Granmo 1999) and *H. fuscoides* (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 cudonia* Berk. & M.A. Curtis apud Berk., Grevillea 4: 47. 1875.
≡ *Daldinia cudonia* (Berk. & M.A. Curtis) Lloyd, Mycol. Writings 7: 1255. 1924.

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

= *Daldinia murrillii* Lloyd, Mycol. Writings 6: 901. 1919.

*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 asci); 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. cudonia*.

*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 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 ×


**Fig. 58.** Teleomorphic characteristics of *Daldinia* cf. *petriniae*. A–G. *Ww 4078* (Germany). H–M. *Ww 4092* (Germany). A, H. Stromatal habit. C, D, I. Stroma in longitudinal section showing internal concentric zones and perithecial layer. B, J. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). E, K. Ascospores in SDS, revealing the wide range of variation in shape and dimensions. F, L. Ascospores in KOH, showing dehiscing perispore. G, M. Ascospores by SEM (10.000×). Scale bars A, C, H, I = 5 mm; B, D, J = 1 mm; E, F, K, L = 10 µm; G, M = 5 µm.

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, Atlipan, San Andres, 3 Jul. 1975, F. Ventura *11566* (NY); Esquilon, Jilotepec, 20 Jul. 1972, F. Ventura *5767* (NY); Veracruz, El Esquilon, Jilotepec, 7 Dec. 1970, *F. Ventura* 2943 (BPI 594610; NY); Xalapa, Lucas Martín, 27 Aug. 1954, E. Perez-Silva 1002 (NY); near Banderilla, Cerro La Martinica,


**Fig. 59.** Teleomorphic characteristics of *Daldinia asphalatum* 1. A, B. Lectotype S-F 44597 (Brazil); C–H. Holotype of *X. cudonia* K(M) 120965 (USA). A, C. Stromatal habit. B, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Close-up on stromatal surface with ostioles. F. Ascospores by SEM (10.000×). G. Ascospores in SDS. H. Ascospore in KOH, showing dehiscing perispore. Scale bars A = 1 cm; B–D = 5 mm; E = 1 mm; G, H = 10 µm; F = 2 µm

14 Sep. 1983, S. Chacon (NY); same locality, 25 Sep. 1975, G. Guzman *12459* (NY); exact locality unknown, W.A. Murrill ex Lloyd herb. *12392*, det. Child (1932) as *D. loculata* (BPI 716959). **P.R. China**, Liaoning, Kuandian County, Tianhua Mountains, Aug. 2006, C. Decock *CH06/248* (MUCL 47964 plus culture); same collection data, C. Decock *CH06/252* (MUCL 47964 plus culture). **USA**, Maryland, Laurel, Patuxent Wildlife Research Center, 18 Aug. 1966, MSA Foray (NY); Ohio, Akron, G.D. Smith ex Lloyd herb. *12404* as *D. intermedia*, see Child (1932) as *D. loculata* (BPI 7169992); Indiana, Scott Co., Scottsburg, *Quercus alba,* 1908, J.S. Weir *21070* (NY); exact locality unknown, on *Carpinus*, ex Ellis collection *1132* (NY); on dead branches of *Ostrya virginia* ex herb. Ellis, Ravenel: Fungi Caroliniani exsiccati Fasc. 3, *No 40* as *Hypoxylon concentricum* (NY).

*Notes*: *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

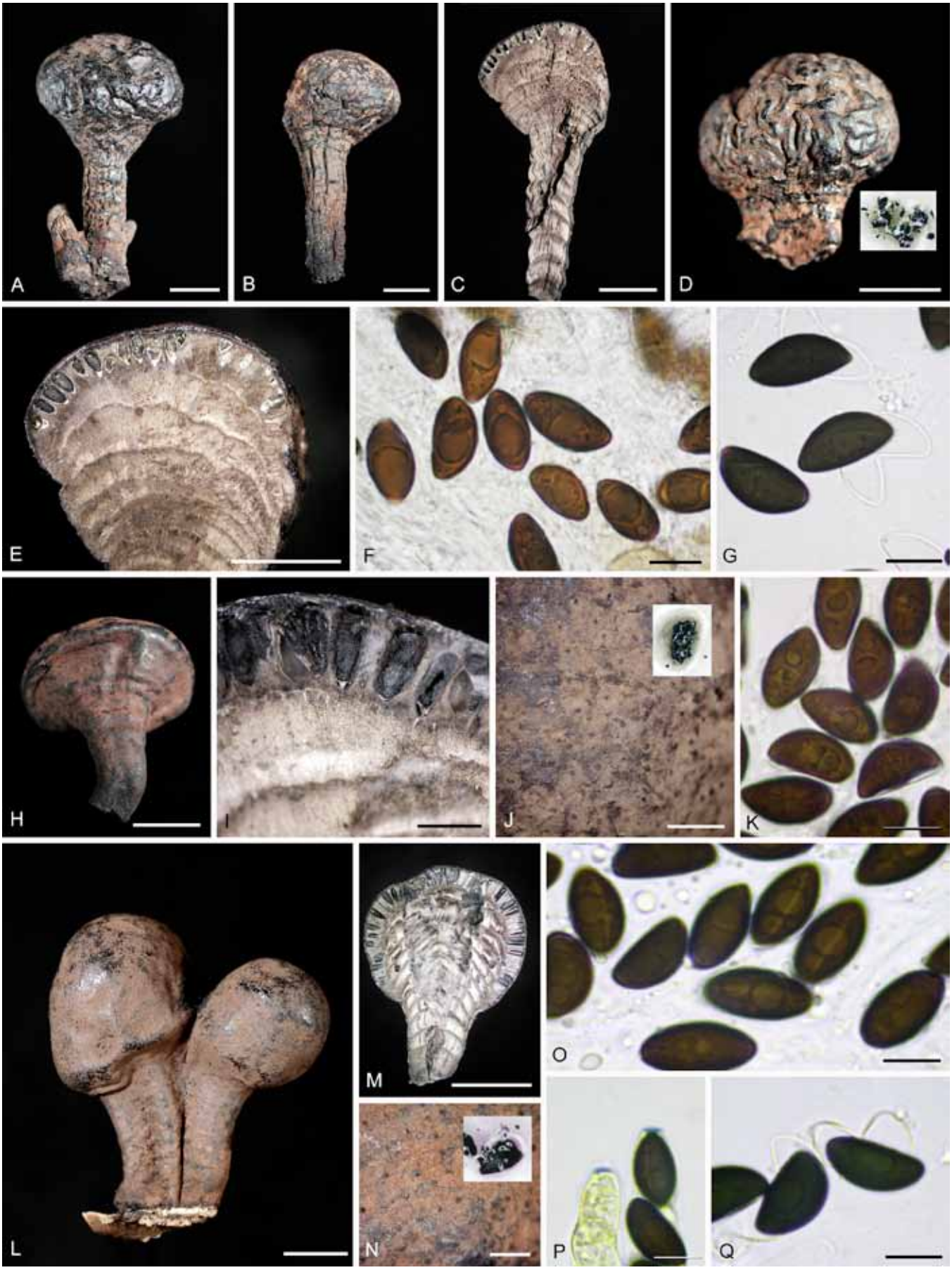



**Fig. 60.** Teleomorphic characteristics of *Daldinia asphalatum* 2. A–G. Murill 295 (Mexico). H–K. Chacon (Mexico). L, N–Q. Decock CH 06/248 (P.R. China). M. Decock CH 06/252 (P.R. China). A, B, D, H, L. Stromatal habit (D: Stromatal pigments in 10 % KOH inserted). C, E, I, M. Stroma in longitudinal section showing internal concentric zones and perithecial layer. J, N. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). F, K, O. Ascospores in SDS. G, Q. Ascospores in KOH, showing dehiscing perispore. P. Ascal tops in Melzer's reagent, revealing amyloid apical apparati. Scale bars A–E, H, L, M = 5 mm; I, J, N = 1 mm; F, G, K, O–Q = 10 µm.

attempting to conserve *D. cudonia*. Link (in Fries 1830) described the stromata as "*globosa difformis, crusta atra nitida discrete obducta, intus fuliginoso-atra obsolete zonata, perithecia linearibus peripherico-immersis*." 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[20]. 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 ascospores, 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. Ascospores were not found in the type of *D. murrillli* 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 recognisable *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 striations 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 annellidic 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. carpinicola*" and *D. decipiens.*

***Daldinia barkalovii*** Lar.N. Vassiljeva & M. Stadler, Mycotaxon 104: 291. 2008.

*Etymology*: 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**, ex-type culture** CBS 116999).

[20]The respective material of *Hypoxylon asphalatum sensu* Montagne in PC was examined and, indeed, corresponds to *D. placentiformis sensu lato.* It has nothing in common with the material in S. (M.S. unpubl.)

*Selected illustrations*: Vasilyeva & 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 Vasilyeva & 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 ascospores, 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 ascospore 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 Vasilyeva & Stadler (2008) can be provided here.

***Daldinia carpinicola*** Lar.N. Vassiljeva & M. Stadler, Mycotaxon 104: 290. 2008.

*Etymology*: For the host plant.

*Types*: **Russia**, Primorsky territory, near Vladivostok, *Carpinus cordata*, L. 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 (ascospores) 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. carpinicola*, 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 ascospores (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 binaphthalene 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 micromorphology 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,* which has also been reported from hornbeam, albeit not from *Carpinus cordata.* However, we prefer to keep it separate for the time being, until additional material has been encountered and examined.

***Daldinia decipiens*** Wollw. & M. Stadler, Mycotaxon 80: 168. 2001. Figs 8D, 15C, 61.

*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 carpatica*, 5 Oct. 2000, H. Wollweber *Ww 3811* (M).
Treated as "*Daldinia* sp. from Denmark" by Ju *et al.* 1999).

*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 *Betulaceae*; only one proven record from *Fagus*. Anamorph is associated with *Xiphydria* woodwasps, which may act as dispersal vectors (Srůtka *et al.* 2007).

*Teleomorph*: *Stromata* semiglobose 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 1:0.75–2), 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 µm. *Ascospores* light brown to dark brown, ellipsoid-inequilateral 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; perispore 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 binaphthalene derivatives prevailing.

*Cultures and anamorph*: Colonies on OA reaching the edge of 9 cm Petri dish 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 × 2.5–4 µm. Conidia produced from percurrently proliferating conidiogenous cells or, infrequently, from sympodially proliferating conidiogenous cells. *Conidia* hyaline, smooth, subglobose to obovoid, frequently with an attenuated base, 7–8 × 4.5–5.5 µm.

*Additional specimens examined*: **Denmark**, Sjælland, Petersværft, Stensby Skov, *Corylus*, 21 Oct. 1997, H. Knudsen, treated by Johannesson *et al.* (2000) as *D.* cf. *petriniae* (C; culture obtained in the present study CBS 113046, MUCL 44610; GenBank Acc. No. of DNA sequence deposited by Johannesson *et al.* 2000: AF176970). **France**, Ariége, Montségur, *Betula*, 21 Apr. 2000, *JF-00042* (KR); Rimont, *Alnus glutinosa*, 6 Aug. 2003, *JF-03133* (KR, culture MUCL 53762); Rimont, Peyrau, 6 Aug. 2003, dead trunk of *Alnus glutinosa*, J. Fournier (KR 0029398). **Germany**, Badenia-Württemberg, Reichertshofen, *Betula*, 24 Jan. 1975, Payerl ex herb. G. Krieglsteiner *557/75* (STU); Vordersteinenberg, *Betula*, 4 Aug. 1975, G. Krieglsteiner *551/77* (STU); Brandenburg, Krausnick, 16 Sep. 1995, *Betula*, V. Kummer, *Ww 3896* (WUP); Fresdorfer Moor, *Fagus*, 15 Feb. 1974, D. Benkert (B); Lower Saxony, Buxtehude, Estetal, *Betula*, 7 Mar. 1998, J. Albers & B. Grauwinkel, *Ww 3864* (KR, culture MUCL 51690); Minsener Oog, near Wangerooge Island, *Betula*, 30. Sep. 1981, B. Grauwinkel, *Ww 3863* (WUP); Mecklenburg-Vorpommern, Jeeser Moor between Greifswald and Stralsund, on *Betula*, 12 Apr. 2003, N. Amelang, *Ww 4328* (WUP); Mecklenburg-Vorpommern, north of Wöbbelin, *Betula pendula*, 2 Aug. 2007, B. Schürig, comm. N. Amelang, *STMA 10005* (KR, culture MUCL 52699); North Rhine Westphalia, Warstein, Hamorsbruch, 11 Oct. 2001, H. Wollweber *Ww 4015* (KR); Wuppertal-Dornap, 24 Jan. 1999, aged specimens on twigs of *Betula pendula*, M.S., *Ww 3542* (WUP); Saxony, Cunewalde, on *Betula*, 4 Jan. 1988, I. Dunger (GLM 18780); Markranstädt, Kulkwitzer See, on branch of *Betula*, 16 Mar. 1990, Rödel as *D. concentrica* (GLM); same locality, Chemnitz, Wasserwerkpark, on bark of *Betula*, 11 Nov. 1995, D. Schulz (GLM); Saxony-Anhalt, Albersroda, Michelholz Forest, western part, *Betula*, 15 Aug. 2010, P. Rönsch, *STMA 10256* (culture MUCL 53318); Schleswig-Holstein, near Hamburg-Harburg, Fischbeckerheide, 21 Mar. 1998, *Betula*, S. Kriese, J. Albers & B. Grauwinkel, *Ww 3865* (WUP). **P.R. China,** Heilongjiang Prov., Donxing cun, *Alnus hirsuta*, 5 Aug. 2004, L. Vasilyeva (VLA, culture CBS 116997); Vicinity of Raohe, *Alnus hirsuta*, 5 Aug. 2004, L. Vasilyeva (VLA, culture CBS 117000, MUCL 46175). **Spain**, Guipuzcoa, near Donostia (San Sebastian), on log, 15 Oct. 1988, S. Sheine (NY). **Sweden**, Scania, Kropp near Helsingborg, *Betula pendula*, 31 Dec. 1994, S.-Å. Hanson, see Ju *et al*. (1999) as "*Daldinia* sp. from Denmark" and Hsieh *et al*. (2005) for molecular phylogeny (JDR, culture CBS 122879, GenBank Acc. Nos AY951694; AY951806); Södermanland, Malmbryggshaven near Sjösa, on dead branch of *Corylus*, stromata largely immature but bearing typical anamorph, 14 Aug. 2000, H. Rydberg *HRY-Myc2000-019* (S- F15371); Uppland, Dalby, forest edge, 200 m ESE of Jerusalem, *Betula*, 10 Jan. 1980, K. & I. Holm *1899c* – depauperate (UPS); same collection site, 16 May 1979, K. & I. Holm *1650*, immature (UPS). **UK**, England, Norfolk, Castle Rising, herb. C.B. Plowright as *Hypoxylon concentricum*, det. T. Læssøe & B.M. Spooner (K(M) 91738). **USA**, Pennsylvania, Venango, Cherrytree run, 6 miles N of Oil City, 18 Mar. 1948, L.K. Henry (NY). **Locality unknown**: wood, as "*Sphaeria concentrica* Tode & *Sphaeria fraxinea* Sibth." (L 910, 270–370 ex PC; Persoon herb. 271).


**Fig. 61.** Teleomorphic characteristics of *Daldinia decipiens*. A–C, E–H. *JF-03133* (France). D. *Ww 3864* (Germany). I. Holotype, *Ww 3811* (Germany). A, D, E. Stromatal habit. C, F. Stroma in longitudinal section showing internal concentric zones and perithecial layer. B. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). G. Ascospores in SDS. H. Ascospores in KOH, showing dehiscing perispore. I. Ascospores by SEM (10.000×). Scale bars A, D–F = 5 mm; B, C = 1 mm; G–H = 10 µm; I = 2 µm.

*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").

***Daldinia gelatinosa*** Y.M. Ju, J.D. Rogers & F. San Martín, Mycotaxon 61: 269. 1997. Figs 8E, F, 15D–F, 62.

*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 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-inequilateral, 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-62770, 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 show similar microscopic features as the ex-type culture of *D. carpinicola*, 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. 62I). *Daldinia gelatinosa* differs from *D. decipiens and D. carpinicola* 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. govorovae* 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 substipitate, deeply shrivelled, without visible perithecial outlines, 0.7–1.4 × 0.5–0.8 cm; surface shiny black with remnants of a Dark Brick (60) pruina in places and orange-red resin-like droplets, with dull 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.

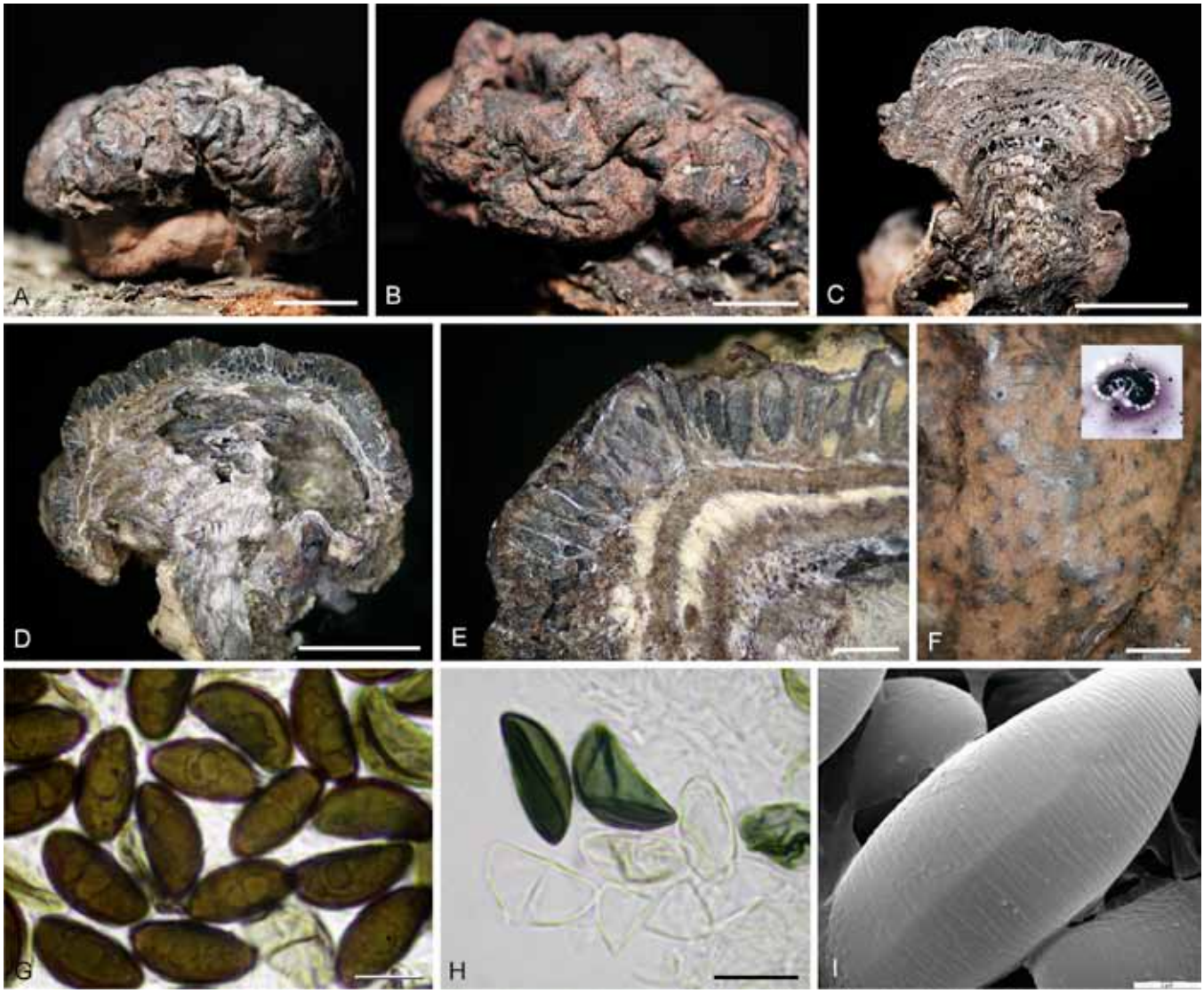



**Fig. 62.** Teleomorphic characteristics of *Daldinia gelatinosa*. Holotype, WSP 69649 (USA). A, B. Stromatal habit. C, D, E. Stroma in longitudinal section showing internal concentric zones, loculate interior and perithecial layer. F. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). G. Ascospores in SDS. H. Ascospores in KOH, showing dehiscing perispore. I. Ascospores by SEM (10.000×). Scale bars A–D = 5 mm; E, F = 1 mm; G–H = 10 µm; I = 2 µm.

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 *vernicosa-loculata* 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.

***Daldinia govorovae*** Lar.N. Vassiljeva & M. Stadler, Mycotaxon 104: 292. 2008.

*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

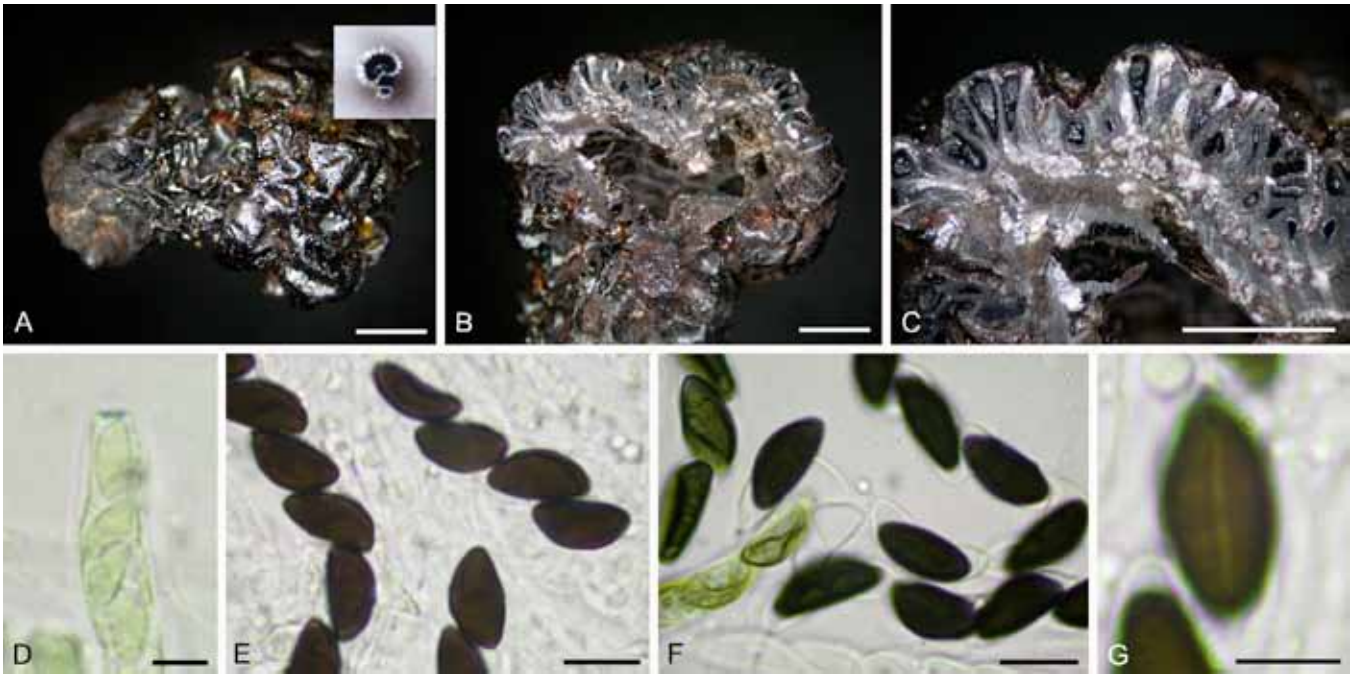



**Fig. 63.** Teleomorphic characteristics of *Daldinia* sp. K(M) 131669 (Tanzania). A. Stromatal habit (inserted: Stromatal pigments in 10 % KOH). B, C. Stroma in longitudinal section showing internal concentric zones and perithecial layer. D. Immature ascus top in Melzer's reagent, showing bluing of apical apparatus. E. Ascospores in SDS. F, G. Ascospores in KOH, showing dehiscing perispore and germ slit (G). Scale bars A–C = 3 mm; D, G = 5 µm; E, F = 10 µm.

(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 *Daldinia*. 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 daldinal and daldinins. 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.

***Daldinia lloydii*** Y.M. Ju, J.D. Rogers & F. San Martín, Mycotaxon 61: 273. 1997. Figs 8C, 15G–I, 64.

*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 perithecial layer composed of alternating zones, darker zones dark brown, pithy to woody, 0.2–0.3 mm thick, lighter zones white 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 stroma, which are composed of fibrous, woody tissue and vertically, rather than horizontally zonate. *Perithecia* obovoid 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-inequilateral, with narrowly to, less frequently, broadly rounded ends, occasionally pinched (11–)12–18 × 6–8(–9) µm, with straight to slightly undulate 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.

*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 YMG 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 µm) were observed (Fig. 64C). *Conidia* are produced exclusively in an annellidic 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.

*Additional specimens examined*: **Austria**, Carinthia, Spittal (Drau), *Betula*, "prior to 1930", G. Niessl von Mayendorf - immature (M 171 -9818). **Czech Republic**, Bartelsdort', Mährisch-Weißkirchen (Hranice na Moravě), *Betula pendula,* Sep. 1938, F. Petrak *1824* - immature (M 17 1-9817). **Denmark,** Jylland, Fjeld Skov, Klemstrup Skov, 24 Sep. 1970, J.A. Nannfeldt *21503*, immature (UPS); Northern Sjælland, Hornbæk, Hornbæk Plantage, *Betula*, Sep. 1952, B.E.F. Boots (C-71601); western Sjælland, Slagelse Lystskov, *Betula*, 24 Oct. 1975, L. Hansen (C-46195). **Italy**, "Vercellis", Rabenhorst ex Cesati, Herbarium mycologicum Ed. II, *600* (BR–Myc 0993361,47). **France** (?), on burnt wood of *Betula*, F. Fautrey in C. Roumeguère: Fungi selecti exsiccati *7210* (NY, 2 packets, both immature). **Germany**, Badenia-Württemberg, locality not recorded, *Corylus avellana*, 1 Aug. 1977, Payerl in herb. Krieglsteiner *Kri 291/77* (STU); *Betula*, 11 Apr. 1981, K. Neff in herb. Krieglsteiner *Kri 038/81* (STU); Brandenburg, Neuendorf am See, 9 Jul. 1995, *Betula*, V. Kummer; largely immature stromata bearing characteristic anamorph structures, *Ww 3893* (KR, culture CBS 113483 and MUCL 51687); Mecklenburg-Vorpommern, Anklam near Pinnow, *Betula,* 30. Aug. 1974. H. Kreisel (KR, Kr.); Stralsund, *Betula,* 6 Aug. 1962, L. Scheidemann, immature, *Ww 3829* (KR, Kr.); Saxony, Kreis Weißwasser, Walddorf bei Daubitz, *Pinus*, 5 Sep. 1977, I. Dunger (GLM); same collection site and date, on *Betula*, immature stromata (GLM); Weißwasser, Naturschutzgebiet Altteicher Moor und Große Jeseritzen, *Myrtilla-Pinetum typicum*, 20 Oct. 1977, I. Dunger, immature (GLM); Lömischau, Alt-Dubinteich, *Betula*, 27 Jul. 1977, K.F. Günther (GLM); Wellaune near Leipzig, *Betula,* 5 Aug. 1965, H. Kreisel (Kr); Schleswig–Holstein, Kiel. Botanical Garden, 1880, Engler as *D. concentrica* (B70 0009591). **Hungary**, Hanság, Wieselburger Comitat (today Győr-Moson-Sopron), Nov. 1882, *Betula alba*, Fungi hungarici *180* (NY). **Poland**, Myschinjetz, *Betula* sp. ("on birch fence posts"), Summer 1918, Laubert (B70 0009615). **Romania**, Transsylvania ("Siebenbürgen"), Aug. 1883, on branches of *Betula*, Linhart: Fungi hungarici (M, NY, PAD); "Bad Zaizon bei Kronstadt", *Betula alba*, 8. Jan. 1883, Römer (M. 17 11986). **Russia**, NW Caucasus, Camp Taiwan, Kl Bambak, cf. *Alnus*, 15 Sep. 1998, V. Kummer (WUP, B, culture CBS 117125). **Slovenia**, Llubljana (Laibach. "Craniola"), 25 Mar. 1877, W. Voss (B70 0009623). **Slovakia**, vicinity of Levice, forest on western slope of the hill "Smutný vrch" (480 m alt.), towards Čajkov, on decaying trunk of *Betula pendula*, 6 Aug. 1975, V. Holubová–Jechóvá (PRM 875256). **Sweden**, Bohuslän, Västerlanda, near Helgesjön, dead stem of *Betula*, 18 Oct. 1969, B. Gilsenius ex herb. I. Nordin, immature (UPS); Uppland, Torsvi, Ytterholmen in Mälaren Lake, trunk of *Betula* in swamp on island, 7 Aug. 1971, I. Nordin *5075*, immature (UPS); Hacksta, Prästtorpet, on dead trunk of *Betula*, 28 Dec. 1972, G. Eriksson ex herb I. Nordin (UPS); Uppsala, Gamla Uppsala Parish, Fullerö, in a grove at the Fyris river, decaying, fallen trunk of *Betula*, 8 Apr. 1973, N. Lundquist *8359*, largely immature (UPS). **UK**, England, King's Lynn, on *Betula alba*, Nov. 1874, C.B. Plowright in herb. Saccardo as *Hypoxylon concentricum* (PAD); Wales, Flintshire, Hawarden, Gladstone estate, Broughton brook, *Betula*, 9 Sep. 1972, J.A. Nannfeldt, immature (UPS). **USA,** Idaho, bottom of Squaw Creek, *Betula papyrifera*, 12 Jul. 1967, H. Goree - immature (WSP 57303); Maine, Bar Harbor, trunk of white birch (*Betula alba*), 17 Jul. 1936, A.E. Brown (NY); New Hampshire, White Mountains National forest, Howker ridge Trail, *Betula*, 31 Jul. 1963, M.E. Bigelow *4018* (NY); Chevry Mountains, *Betula lutea*, 1 Jul. 1928 G. Spaulding (M); North Carolina, Jackson Co., Whiteside, 6 Dec. 1934, P.O. Schallert *2142* (F 331659); same locality, 26 Feb. 1932, P.O. Schallert (F 331660); Pennsylvania, 21 Aug. 1947, D.R. Sumstine *14270* (NY); Fayette Co, Ohio Pyle, 20, Jun. 1937, O.E. Jennings *11471* (NY); Sugar Run, 10 miles SW of Bradford, Jun. 1948, N.D. Richmond, largely immature (NY); Vermont, Lamoille Co., Johnson, *Betula*, 2 Sep. 1964, M.E. Bigelow *4625* (NY); Stowe, Bingham Falls Trail, *Betula*, 9 Jul. 1964, M.E. Bigelow *4259* - young immature stromata (NY).

*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 *Betulaceae*). 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 macrospora*** F. San Martín, Y.M. Ju & J.D. Rogers, Mycotaxon 61: 274. 1997. Fig. 65.

*Etymology*: For the large ascospores.

*Types*: **Mexico**, Jalisco State, Colima's Volcano, wood of *Quercus,* 21 Jun. 1987, L. Villaseñor (IBUG - **holotype**, n.v., WSP 69651 – **isotype**).

*Selected illustrations*: Ju *et al.* (1997, all from isotype), figs 15 (ascospores) and 53–55 (stromata).

*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 perithecial 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, 1–1.3 mm thick (Ratio darker/lighter zones 1:1–5). *Perithecia* 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

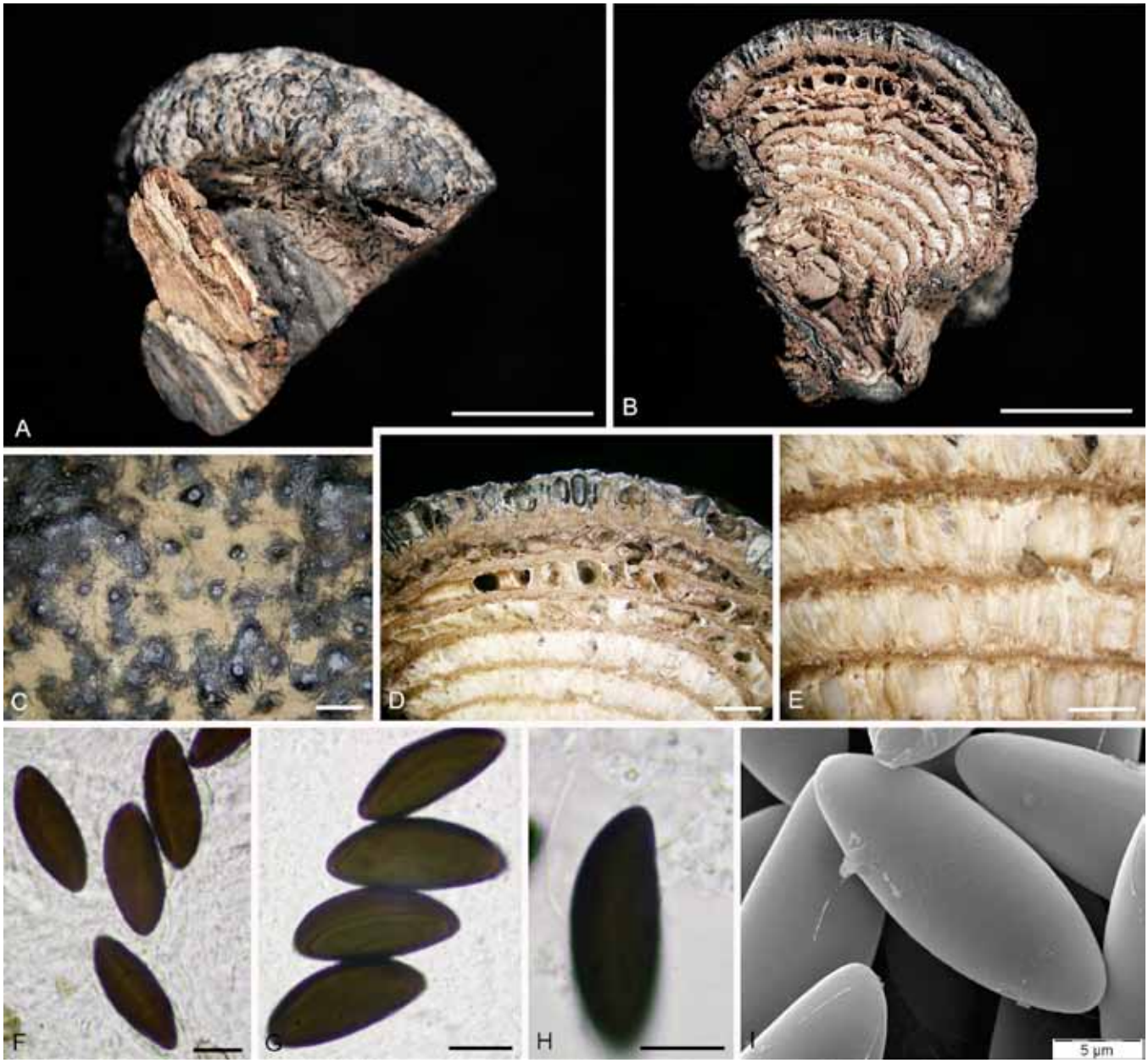



**Fig. 65.** Teleomorphic characteristics of *Daldinia macrospora.* Isotype, WSP 69651 (Mexico). A. Stromatal habit. B, D, E. Stroma in longitudinal section showing internal concentric zones and perithecial layer. C. Stromatal surface with ostioles. F. Ascospores in SDS. G, H. Ascospores in KOH, showing dehiscing perispore. I. Ascospores by SEM (10.000×). Scale bars A, B = 1 cm; C–E = 1 mm; F–H = 10 µm; I = 5 µm.

apparatus, 1 × 4 µm. *Ascospores* brown, ellipsoid-inequilateral 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.

***Daldinia mexicana*** F. San Martín, Y.M. Ju & J.D. Rogers, , Mycotaxon 61: 275. 1997. Figs 15K, 66.

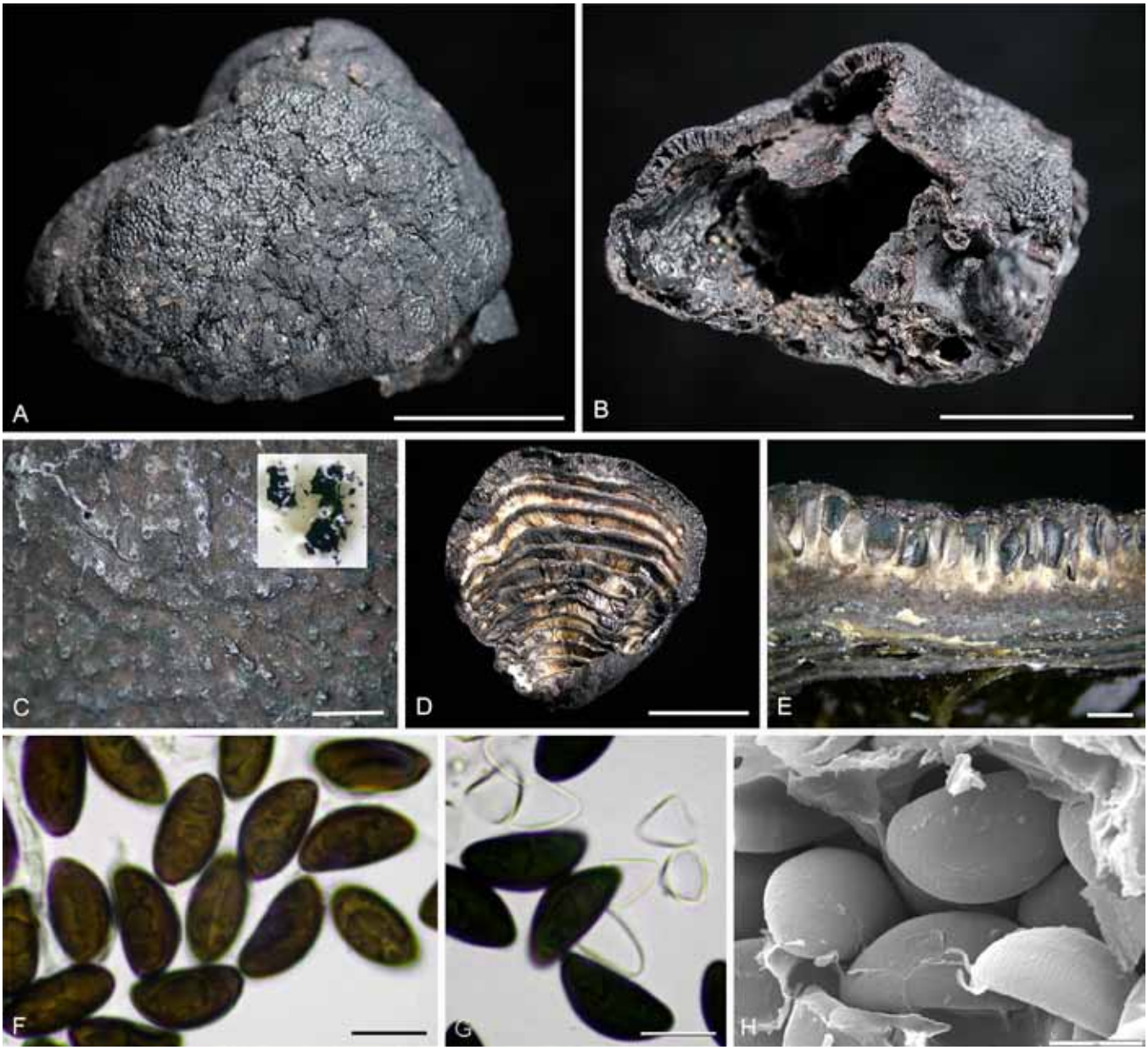



**Fig. 66.** Teleomorphic characteristics of *Daldinia mexicana*. Isotype (Mexico). A. Stromatal habit. B, D, E. Stroma in longitudinal section showing internal concentric zones and perithecial layer. C. Stromatal surface, with stromatal pigments in 10 % KOH inserted. F. Ascospores in SDS. G. Ascospores in KOH, showing dehiscing perispore. H. Ascospores by SEM (10.000×). Scale bars A, B, D = 1 cm; C, E = 1 mm; F, G = 10 µm; H = 5 µm.

*Etymology*: For Mexico.

*Types*: **Mexico**, Nuevo León State, Zaragoza municipality, "La Encantada", wood of *Quercus*, no date, Cázares *600A* (IBUG**–holotype**, *fide* Ju *et al.* (1997) n.v.; WSP 69650 - **isotype**). Culture made from perithecial contents of the specimen in 2000, *Ww 3843*, in pers. coll. STMA, recently deposited with MUCL.

*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-inequilateral 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×); epispore 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 ascospores 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. childiae* 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, 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. childiae* 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 annellidic 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. Vasilyeva (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 descrition 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 reduced ascal apical apparati, and ellipsoid-equilateral to reniform ascospores. Moreover, it produces intercalary coil-like twists in culture and has an annellidic 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.* poaceaeous, host.

*Typus*: **India**, Punjab (Union Territory), Chandigarh, on burnt stems of *Saccharum*, 20 Aug. 1966, H.S. Chahal *69* (PAN - **holotype,** n.v., K(M) 36396 - **isotype).**

*Selected illustrations*: Dargan & Thind (1984, from holotype), Plate II, figs 8–15; Ju *et al*. (1997, from isotype), figs 65–68 (stromata and ascospores).

*Known distribution/host preference of stromata*: Only known from the type; from sugarcane in India.


**Fig. 67.** Teleomorphic characteristics of *Daldinia singularis* (WSP 69958 - isotype, *Carpinus cordata,* Russia). A. Stromatal habit (inserted: Stromatal pigments in 10 % KOH). B, C. Stroma in longitudinal section showing internal concentric zones and perithecial layer (B from culture, C from natural substrate). D. Ascospores in SDS. E, F, G. Ascospores in KOH, showing short germ slit (E) and dehiscing perispore (F, G). Scale bars A = 5 mm; B, C = 1 mm; D–G = 10 µm.

*Teleomorph*: *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 teleomorphic 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.

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

* 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 perithecial 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 whitish, pithy; tissue below perithecial layer composed of alternating zones, darker zones dark brown, pithy, 0.1–0.3 mm thick, lighter zones


**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.

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. *Asci* 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 ascal apical apparatus.

Stadler *et al.* (2004d) reported a specimen from Pakistan, Punjab, Ladhar, Sheikhupura, 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.*

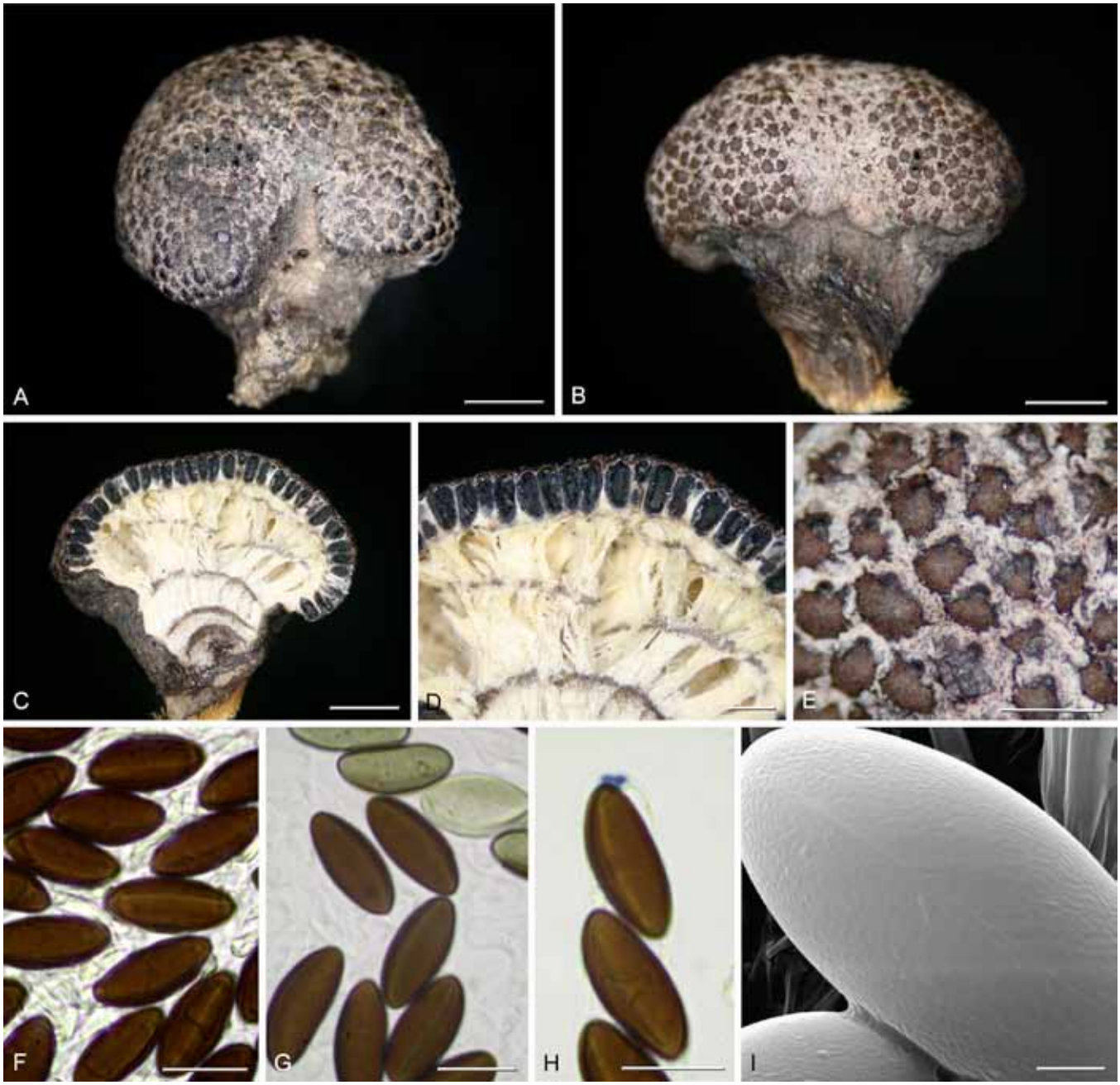



**Fig. 69.** Teleomorphic characteristics of *Daldinia sacchari.* Isotype, K(M) 36398 (India). A, B. Stromatal habit. C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface with perithecial contours. F. Ascospores in SDS, showing germ slits. G. Ascospores in KOH, showing non-dehiscing perispore. H. Ascus top in Melzer's reagent revealing amyloid apical apparatus. I. Ascospore by SEM (10.000×). Scale bars A–C = 2 mm; D = 1 mm; E = 0.5 mm; F–H = 10 µm; I = 2 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 disctinctly 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 Livid 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 bumpy 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 teleomophic 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*: *Stroma* 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. *Ostioles* umbilicate to slightly papillate, often at the centre of a low raised tubercle 0.12–0.2 mm diam. *Asci* 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 *Ruwenzoria pseudoannulata*).

*Notes*: As stated earlier (Stadler *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 daldinoid ascomycete that represents the new genus and species *Ruwenzoria pseudoannulata*. Thus, it is difficult to reasess 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.

*Basionym*: *Hypoxylon placentiforme* Berk. & M. A. Curtis, J. Linn. Soc., Bot. 10: 383. 1869.

≡ *Hypoxylon placentiforme* Berk. & M.A. Curtis, J. Linn. Soc., Bot. 10: 383. 1869.

≡ *Nummularia placentiformis* (Berk. & M.A. Curtis) Sacc., Syll. Fung. I, p. 399. 1882.

≡ *Hypodiscus placentiformis* (Berk. & M. A. Curtis) Rick, Brotéria, sér. Bot., 25: 34. 1931.

*Holotypus*: **Cuba**: *Wright* 492 ex herb. Berkeley (K(M) 125651), lectotype, selected by Ju & Rogers (1996).
For synonyms, which, however, need to be revised according to the current concept, see Ju & Rogers (1996), sub *H. placentiforme* and Hladki & 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 peltate, base broadly attached to substrate or constricted, often coalescent, with inconspicuous perithecial outlines, 0.6–2 x 0.4–0.5 cm; surface Vinaceous Grey (116) (immature) to Brown Vinaceous (84), pruinose, wrinkled to slightly nodulose, underside blackish, cracked, 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. *Ostioles* umbilicate to slightly raised discoid. *Asci* 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 condidiogenous strucures closely resemble those of *D. eschscholtzii.*

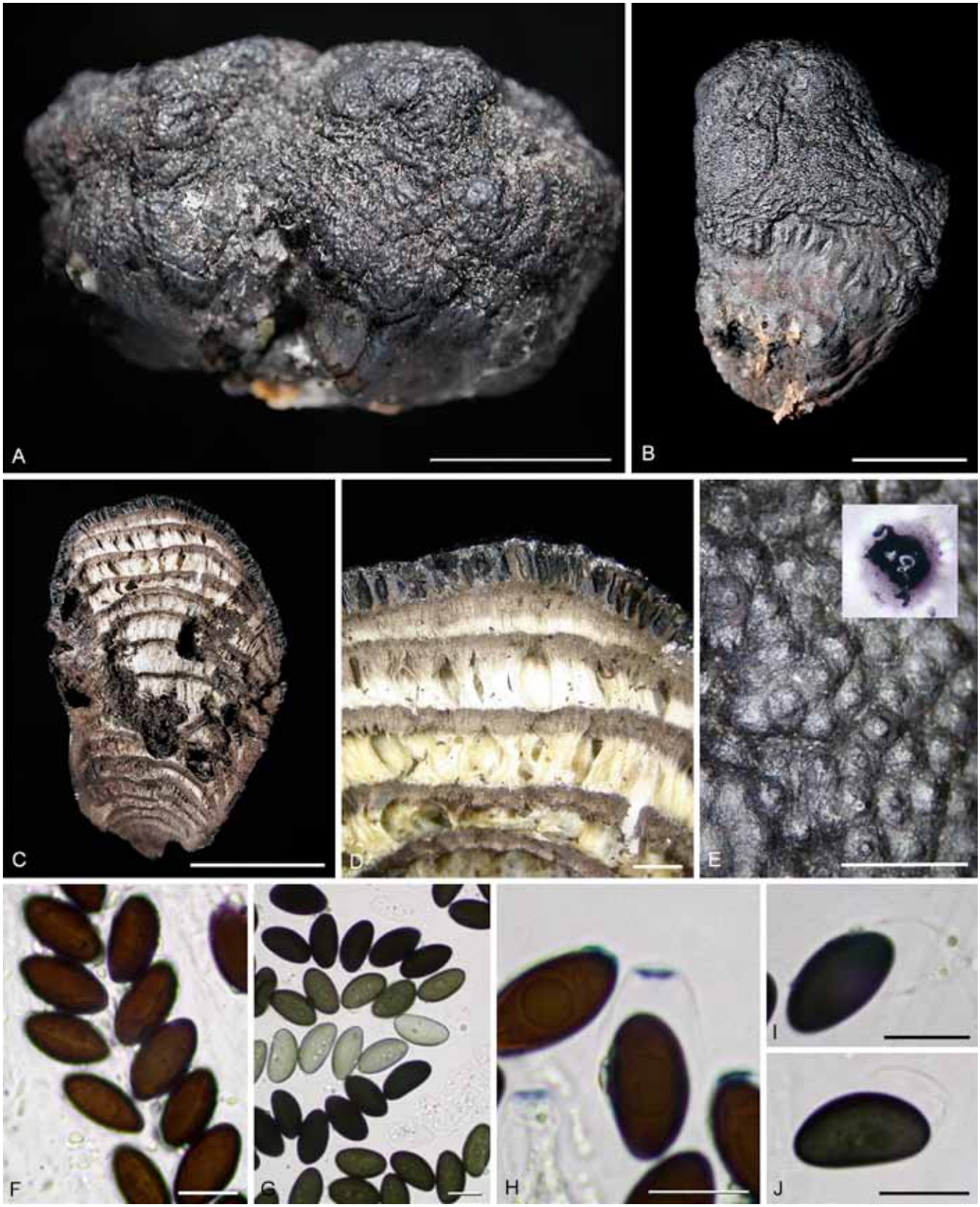



**Fig. 70.** Teleomorphic characteristics of *Daldinia* sp. WSP54679 (USA). A, B. Stromatal habit. C, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. E. Stromatal surface with ostioles (inserted: Stromatal pigments in 10 % KOH). F. Ascospores in SDS, showing 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.

*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 594122); 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 Auraucanía, Sector Collimallín, on burnt stems and branches of *Ulex europeaus* (dead wood), 7 Sep.1996,

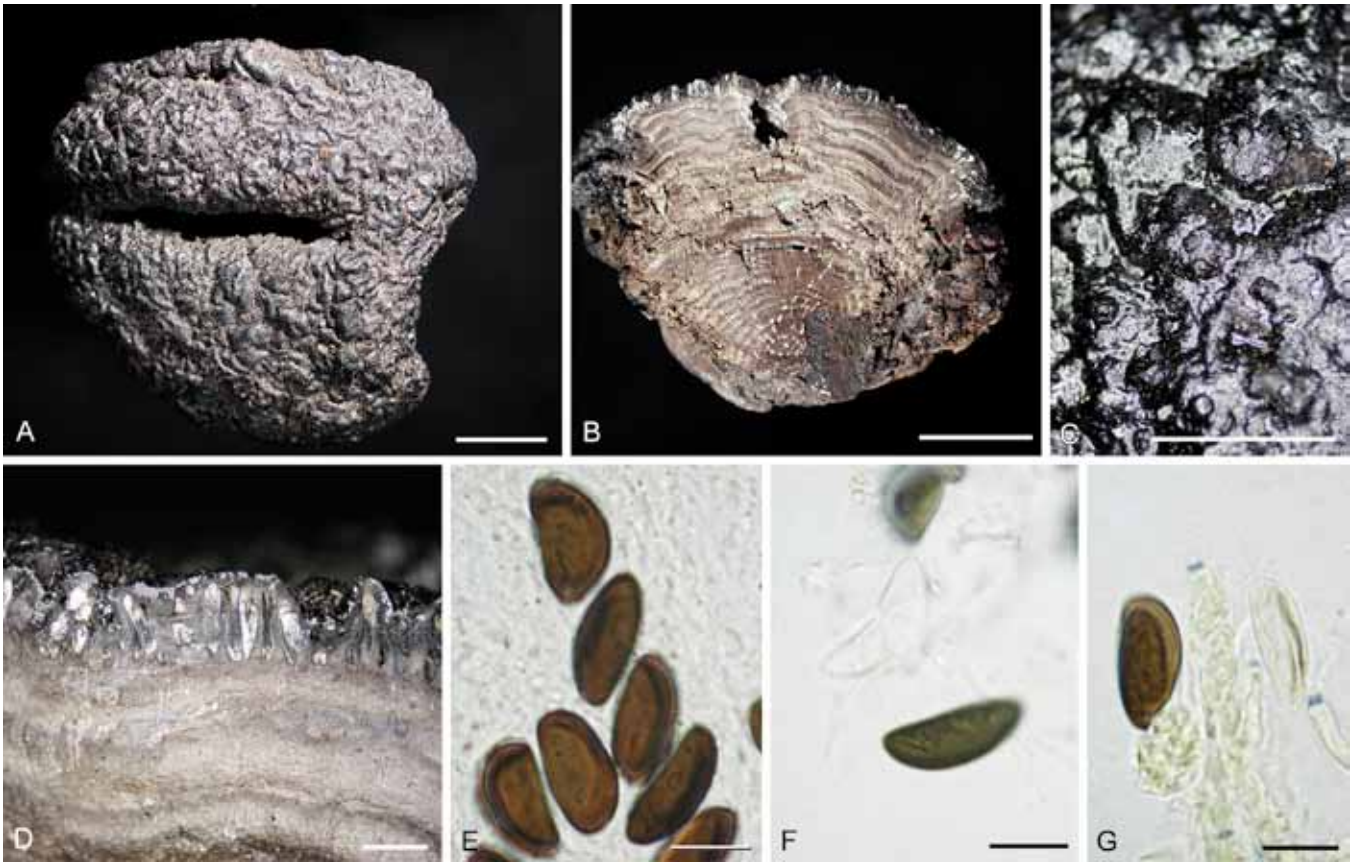



**Fig. 71.** Teleomorphic characteristics of *Daldinia* "*bakeri*" BR-Myc 103067,62 (Congo). A. Stromatal habit. B, D. Stroma in longitudinal section showing internal concentric zones and perithecial layer. C. Stromatal surface with ostioles. E. Ascospores in SDS. F. Ascospore in KOH, showing dehiscing perispore. G. Ascal tops in Melzer's reagent revealing amyloid apical apparati. Scale bars A, B = 1 cm; C, D = 1 mm; E–G = 10 µm.

S. Garnica (M). **Ecuador**, Galapagos, Sta. Cruz, Mt. Crocker, dead branch of *Scalesia*, 6 June 1976, Evans & Cronshaw *84* as *H. sclerophaeum* (K(M) 140186 - immature). **Mexico**, Jalisco, Municipio de Zapopan, Bosque de Colomos, Nov. 13, 1993, M. Gutierrez *30*, comm. L. Guzmán-Davalos (C, GUAD). **New Zealand**, Buller, Lake Rotoiti, 2.000 ft, on wood of *Nothofagus solandri* var. *cliffortioides*, Apr. 1956, S. D. & P. J. Brook, see Ju & Rogers (1996) as *H. placentiforme* (PDD 16236). **Nicaragua**, decorticated wood, C. L. Smith *57*, det. Miller (1961) as *H. papillatum*, rev. Ju & Rogers (1996) as *H. placentiforme* (NY – syntype of *H. papillatum sensu* Ellis & Everhart in Smith 1893). **Panama**, Renacimiento, Santa Clara, corticated wood, 26 Oct. 2006, AC 25, A. Carmona (M); Chiriqui, Highlands of Boquete, Bajo Mono, Finca Lérida, 1700 m, corticated wood, 4 Nov. 2008,, M. Piepenbring *MP 4573* (M). **Puerto Rico**, Las Vegas, corticated wood, 19 June 1929, A. S. Muller 3130, rev. Ju & Rogers (1996) as *H. placentiforme* (GAM 6618 – holotype of *H. mulleri*). **USA**, Florida, Orlando, *Magnolia* sp., 23 Dec. 1939, C.L. Shear 4512 (BPI 591418); Indiana, New Albany, 23 Sep. 1891, A.B. Seymour (BPI 592774); Kansas, Topeka, decorticated wood, winter of 1884, F. W. Cragin 140, det. Miller (1961) as *H. papillatum*, rev. Ju & Rogers (1996) as *H. placentiforme* (NY, 2 packets); Missouri, Emma, *Ulmus americana*, 14 Nov. 1921, C.H. Demetrio in Lloyd herb. 13043 (BPI 716671); Liberty, Clay Co. Old Pond, William Jewell College campus, *Ulmus*, 18 Jul. 1955 (BPI 592796).

*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 perithecia.

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.

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**
**1** Perispore dehiscent in 10 % KOH ..... **2**

**2** KOH-extractable pigments violaceous, purple or absent ..... **II**
**2** KOH-extractable pigments differently coloured ..... **3**

**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**
**1** 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** Ascospores13–16 × 6.8–7 µm, with perispore infrequently dehiscent; reported as “on the ground” . ***Daldinia* 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. loculatoides***[21] (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. cahuchucosa*** (p. 90)
**13** Stromatal interior grey brown, woody to fibrous; ascospores 13–16 × 7–8 µm. Known from La Réunion ..... ***D. hausknechtii*** (p. 95)

[21]In case the identity of the UAMH specimens with *D. nemorosa* were proven, this species would also key out here, but differs from *D. loculatoides* in its annellidic conidiogenesis.

**II** - KOH-extractable pigments violaceous, purple or absent

**1** Stromata very small, rarely over 1 cm in greatest dimension ..... **2**
**1** Stromata larger ..... **5**
**2** Perithecia lanceolate; ascospores 9.5–11.5 × 4.5–6 µm. Known from Tanzania ..... ***Daldinia* sp.** K(M) 131669 (p. 113)
**2** Perithecia obovoid ..... **3**

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

**4** 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)
**4** 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)

**5** Stromata upright, distinctly stipitate ..... **6**
**5** Stromata turbinate to hemispherical ..... **9**

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

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

**8** Ascospores 8–11.5 × 4–5.5 µm; ostioles inconspicuous ..... ***D. clavata*** (p. 65)
**8** Ascospores 10–11.5 × 4.5–5.5 µm; ostioles discoid-papillate ..... ***D. cuprea*** (p. 67)

**9** KOH-extractable pigments absent or appearing with delay (several minutes) ..... **10**
**9** KOH-extractable pigments present, at least in mature stromata ..... **12**

**10** 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)
**10** KOH-extractable pigments absent ..... **11**

**11** Ascospores 14.5–17 × 7–8.5 µm. Known from D.R. Congo ..... ***D.* "*bakeri*" taxon B** (p. 125)
**11** Ascospores 22.5–30 × 8.5–10.5 µm. Known from Mexico and Ecuador ..... ***D. macrospora*** (p. 117)

**12** Species known from Northern Hemisphere, with temperate to warm temperate distribution ..... **13**
**12** Species with tropical distribution ..... **23**

**13** Species occurring on *Betulaceae* ..... **14**
**13** Species occurring on other hosts ..... **18**

**14** KOH-extractable pigments vinaceous grey to pale violet ..... **15**
**14** KOH-extractable pigments dense violet ..... **16**

**15** Stromatal surface wrinkled with ochre wavy stripes; ascospores 12–14 × 6–7 µm. Known from Far Eastern Russia ..... ***D. barkalovii*** (p. 110)
**15** 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)

**16** Stromata almost sessile. Ascospores 12.5–16 × 6–8 µm ..... ***D. gelatinosa*** (p. 113)
**16** Stromata usually distinctly stipitate. Ascospores averaging longer ..... **17**

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

**18** Ascospores 13–17.5 µm long ..... **19***
**18** Ascospores 10–14 µm long ..... **21**

**19** Widespread in Europe; ascospores 13–17.5 × 6–7.5 µm ..... ***D. concentrica*** (p. 28)
**19** Known from southern Europe, North Africa and the Macaronesian Islands ..... **20**

**20** Known from the Macaronesian Islands; ascospores 14–17 × 6–8 µm ..... ***D. macaronesica*** (p. 38)
**20** Known from southern Europe and North Africa; ascospores 13–17 × 5–7 µm ..... ***D. martinii*** ( p. 38)

**21** Known from Canary Islands, on *Laurus*. Ascospores 11–13 × 5.5–6.5 µm …….. ..... ***D. palmensis*** (p. 40)
**21** Not known from *Laurus* nor the Canary Islands ..... **22**

**22** Known from UK, on *Acer*. Ascospores 10–14 × 5–7 µm ..... ***D. vanderguchtiae*** (p. 42)
**22** Known from Mediterranean and Western Europe, on *Quercus ilex*. Ascospores 12–14 × 6–7 µm ..... ***D. raimundi*** (p. 40)

**23** On bamboo; ascospores 8.5–11 × 4–5 µm. Known from Thailand ..... ***D. bambusicola*** (p. 60)
**23** On dicot. wood; ascospores larger ..... **24**

**24** Stromata hemispherical to depressed-spherical, sessile ..... **25**
**24** Stromata turbinate, more or less stipitate ..... **28**

**25** Ascospores 12.5–15.5 × 6–6.8 µm with short germ slit. Known from D.R. Congo ..... ***Daldinia* sp.** (MUCL51268) (p. 43)
**25** Ascospores with germ slit spore length ..... **26**

**26** Ostiles papillate. Ascospores 12–14.5 × 6–6.5 µm. Known from Mexico ……. ..... ***Daldinia* sp.** Martin 910 (NY) (p. 55)
**26** Ostioles inconspicuous to slightly papillate. Known from Australia and New Zealand ..... **27**

**27** Ascospores 16–18 × 6–8 µm ..... ***D. dennisii*** (P. 35)
**27** Ascospores 12–15 × 6–8 µm ..... ***D. dennisii* var. *microspora*** (p. 35)

**28** Ascospores 9–12 µm long ..... **29**
**28** Ascospores 16–21.5 µm long ..... **30**

**29** Ascospores 9.5–10.5 × 4.5–5.5 µm ..... ***D. rehmii*** (p. 68)
**29** Ascospores 9–12 × 5–6 µm, relatively more slender ..... ***D. theissenii*** (p. 72)

**30** Ascospores 16–18 × 7–8 µm. Known from Malawi ..... ***Daldinia* sp.** Rammeloo (p. 45)
**30** Ascospores 17.5–21.5 × 7–10 µm. Known from Ecuador ..... ***D. andina*** (p. 33)

* 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

**1** KOH-extractable pigments umber or sepia (in shades of brown) ..... **2**
**1** KOH-extractable pigments olivaceous to greenish ..... **3**

**2** Interior gelatinous-loculate; ascospores 16–18 × 8–10 µm. Known from Far Eastern Russia ..... ***D. govorovae*** (p. 114)
**2** Interior fibrous-loculate; ascospores 14–15.5 × 7–8 µm. Known from tropical and subtropical regions of South and East Asia and Australasia ..... ***D. steglichii*** (p. 82)

**3** Stromata erect, distinctly stipitate; ascospores 12.5–16.5 × 6–8 µm. Known from tropical and subtropical North and South America, P.R. China ..... ***D. asphalatum*** (p. 106)
**3** Stromata turbinate to hemispherical ..... **4**

**4** Ascospores 9–12 µm long ..... **5**
**4** Ascospores 12–23 µm long ..... **7**

**5** Stromatal interior predominantly white. Ascospores 9–10.5 × 4–4.5 µm. Known from New Guinea and South East Asia ..... ***D. albofibrosa*** (p. 57)
**5** Stromatal interior predominantly brown. Known from neotropics ..... **6**

**6** Ostioles inconspicuous. Ascospores 10–12 × 5–6 µm ..... ***D. starbaeckii*** (p. 69)
**6** Ostioles discoid-papillate. Ascospores 9.5–11 × 5–6 µm ..... ***D.* cf. *starbaeckii*** (p. 71)

**7** Stromatal interior gelatinous, hollow. Ascospores 12.5–15.5 × 6.5–7.5 µm. Known from Mexico ..... ***D. mexicana*** (p. 118)
**7** Stromatal interior woody-fibrous, solid. Known from North temperate Hemisphere ..... **8**

**8** Stromatal surface with persistent tan coating, cracking into large scales, not nodulose. Ascospores 12–18 × 6–8 µm .... ***D. lloydii*** (p. 115)
**8** Stromatal surface without tan scales, slightly nodulose ..... **9**

**9** Ascospores 12.5–16.5 × 6.5–7.5 µm ..... ***D. petriniae*** (p. 103)
**9** Ascospores up to 23 × 10 µm ..... ***D.* cf. *petriniae*** (p. 105)

**IV** - KOH-extractable pigments cinnamon or orange brown

**1** Stromatal surface smooth, even; ascospores with germ slit less than spore length ..... ***D.* cf. *childiae*** CH 08-539 (p. 78)
**1** Stromatal surface slightly roughened by ostioles and perithecial outlines; ascospores with germ slit spore length ..... **2**

**2** Stromata distinctly stipitate; ascospores 12–16 × 5.5–7.5 µm. Widespread ..... ***D. childiae*** (p. 74)
**2** Stromata more broadly attached to the substrate; ascospores larger ..... **3**

**3** Ascospores 13–17 × 6.5–8 µm. Known from warm temperate Europe ……..... ***D. pyrenaica*** (p. 78)
**3** Ascospores 13.5–18 × 7–8.5 µm. Known from New Zealand, Hawaii ..... ***D. australis*** (p. 78)

## Molecular phylogeny (Figs 73, 74, for correspondng 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 (9–44 %). 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 hypoxyloid *Xylariaceae* by Ju & Rogers (1996). For instance, *H. monticulosum* and *H. submonticulosum* appeared basal in this clade. However, as in previous phylogenies based on ITS nrDNA 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. gibraicense* (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 *Thuemenella 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 *Entonaema*, *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 pseudoannulata*, *Entonaema 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 daldiniod taxa, allowing for more informative reliably alignable characters to be included in the phylogenetic analyses (data not shown). According to this analysis, *D. albofibrosa* 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. steglichii* studied cluster within clade A despite the highly similar morphology and secondary metabolite profiles of *D. steglichii* 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. loculatoides* and the type material of *D. grandis*.

Group **D**, comprising sequences of members of the *D. vernicosa*/*D. loculata* group, appears as a sister group to *D. concentrica* and allies. This clade is separated into three major lineages, comprising (D1) *D. vernicosa*/*D. gelatinoides*, (D2) *D. novae-zelandiae* and (D3) *D. hausknechtii*/*D. loculata*/*D. loculatoides*, respectively. *Annellosporium 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. vernicosa*/*loculata* group is the presence of annellidic conidiogenesis. The anamorphic morphology of *A. nemorosum* (*D. nemorosa* comb. nov.) is similar to that of members of the *D. petriniae* group, but such an annellidic conidiogenesis also occurs in *D. palmensis* (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 *Daldinia* 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 *Daldinia.* 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 *Daldinia*, 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 *Daldinia* 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-zonate *Daldinia* species included in this monograph have essentially the same specific metabolites in their stromata and cultures, their spores are indistinguishable from those of true *Daldinia* spp., and their DNA sequences, where available, appear nested inside monophyletic clades comprising *Daldinia* (cf. phylogenetic tree in Fig. 73).

A problem for some taxonomists may arise from the fact that in molecular phylogenies *Hypoxylon* appears paraphyletic when *Daldinia* is included. Preliminary results on *Entonaema* (Triebel *et al.* 2005), *Phylacia* (Bitzer *et al.* 2008), *Rhopalostroma* (Stadler *et al*. 2010a) and *Thamnomyces* (Stadler *et al.* 2010b) revealed that even *Daldinia* 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 *Daldinia* 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 *Annulohypoxylon* 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 nomenclatual 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 *Daldinia.* 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 *Daldinia*. 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 *Daldinia* (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 *Daldinia* 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 *Daldinia* 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 insuffficiantly known taxa included in the present study, so the picture of global biodiversity in *Daldinia* 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

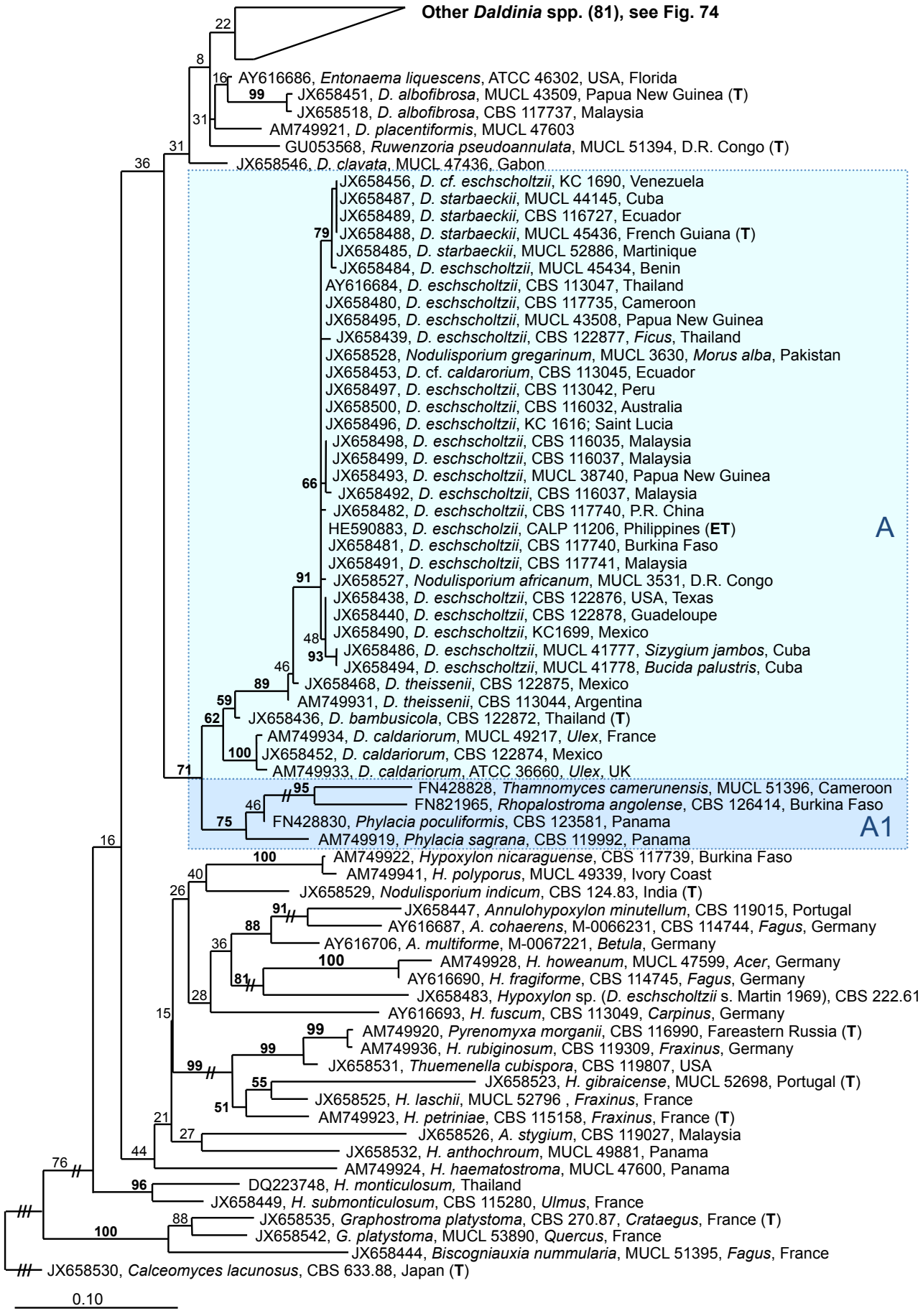



**Fig. 73.** Phylogenetic relationships among *Daldinia* spp. and selected *Xylariaceae* as inferred from ITS nrDNArRNA sequence data. The most likely tree topology found by RAxML is shown. Bootstrap support values, calculated independently from 500 RAxML replicates, are assigned to the respective branches. Selected long branches were bisected once (//) or twice (///)in length. The GenBank Acc. No. of each sequence is followed by the taxon name. Culture collection and herbarium accession numbers, as well as country and substrate of origin are noted for the analysed strains (if available). "**T**" indicates type strains, "**PT**" paratypes, and "**ET**" epitypes. The clade including 81 sequences of *D. concentrica*, *D. childiae*, *D. vernicosalloculata*, *D. petriniae* and their respective allies is shown separately (Fig. 74).

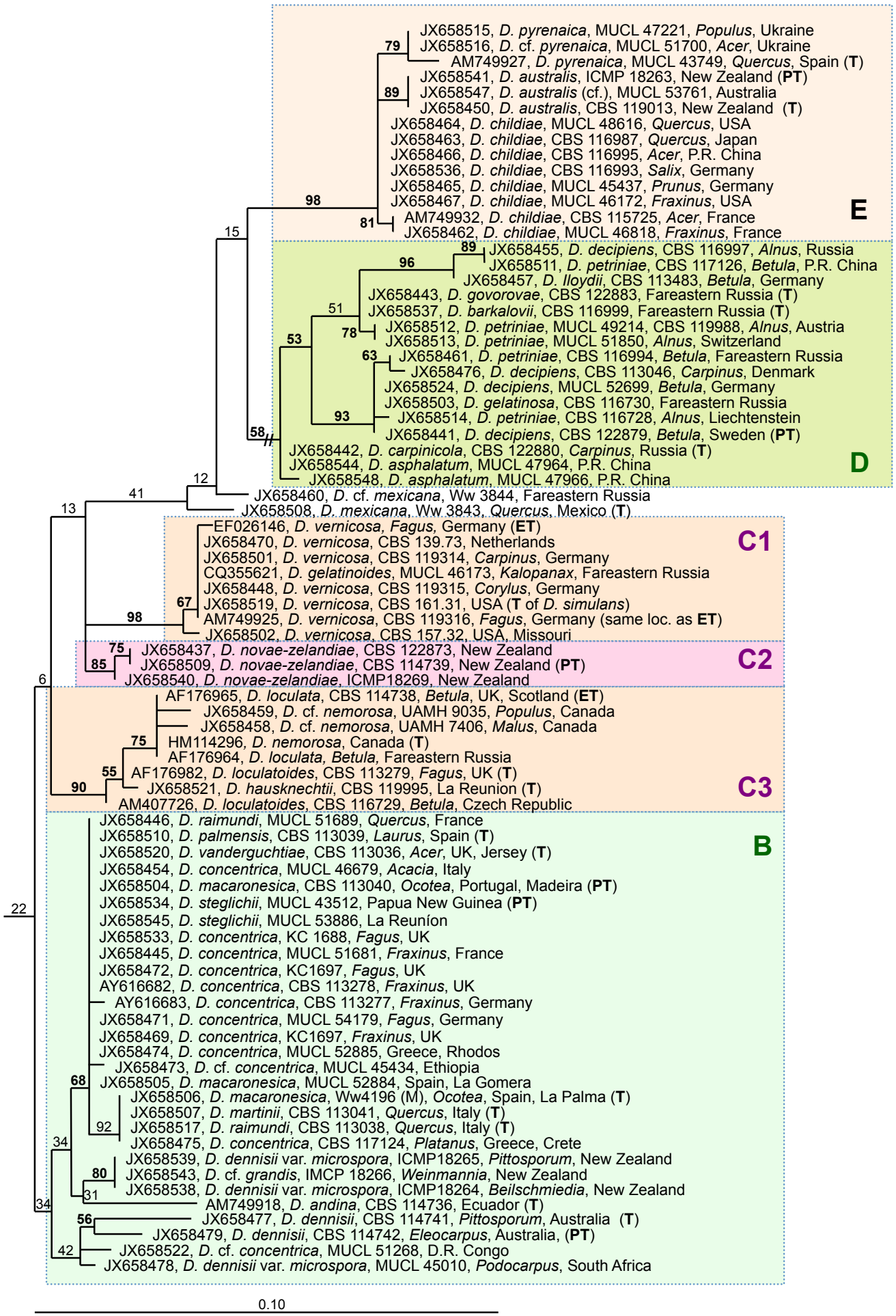



**Fig. 74.** Phylogenetic relationships among *D. concentrica*, *D. childiae*, *D. vernicosa*/*loculata*, *D. petriniae* and their respective allies. Section from Fig. 73.

**Table 13.** List of all taxa and corresponding DNA sequences selected for the molecular phylogeny, including information on the origin of the corresponding specimens. "T" indicates type strains, "PT" paratypes, and "ET" epitypes. Several of these sequence data have also been used in the phylogenies by Stadler *et. al.* (2013) and Kuhnert *et. al.* (2014).

| Species | Acc. No. (GenBank) | Specimen/ Strain No. | References | Host/Country |
|---|---|---|---|---|
| *Annulohypoxylon cohaerens* | AY616687 | M-0066231 (CBS 114744) | Triebel *et al*. (2005) | *Fagus*, Germany |
| *Annulohypoxylon minutellum* | JX658447 | CBS 119015 | Bitzer *et al*. (2008), Stadler *et al*. (2013) | *Castanea*, Portugal |
| *Annulohypoxylon multiforme* | AY616706 | M-0067221 | Triebel *et al*. (2005) | *Betula*, Germany |
| *Annulohypoxylon stygium* | JX658526 | CBS 119027 | Bitzer *et al*. (2008) | Malaysia |
| *Biscogniauxia nummularia* | JX658444 | MUCL 51395 | Bitzer *et al*. (2008) | *Fagus*, France |
| *Calceomyces lacunosus* | JX658530 | CBS 633.88 | Present study | Japan (**T**) |
| *Daldinia albofibrosa* | JX658518 | CBS 117737 | Present study | Malaysia |
| | JX658451 | MUCL 43509 | Stadler *et al*. (2001c) | Papua New Guinea (**T**) |
| *Daldinia andina* | AM749918 | CBS 114736 | Bitzer *et al*. (2008) as *D. grandis* | Ecuador |
| *Daldinia asphalatum* | JX658544 | MUCL 47964 | Present study | P.R. China |
| | JX658548 | MUCL 47966 | Present study | P.R. China |
| *Daldinia australis* | JX658541 | ICMP 18263 | Present study | New Zealand (**PT**) |
| | JX658450 | CBS 119013 | Present study | New Zealand (**T**) |
| *Daldinia bambusicola* | JX658436 | CBS 122872 | Ju *et al*. (1997) | Thailand (**T**) |
| *Daldinia barkalovii* | JX658537 | CBS 116999 | Vasilyeva & Stadler (2008) | Russia (**T**) |
| *Daldinia caldariorum* | AM749933 | ATCC 36660 | Whalley & Watling (1981) as *D. vernicosa*; Bitzer *et al*. (2008) | *Ulex*, UK |
| | JX658452 | CBS 122874 | Ju *et al*. (1997), Stadler *et al*. (2001a, b), Hsieh *et al*. (2005) | Mexico |
| | AM749934 | MUCL 49217 | Bitzer *et al*. (2008) | *Ulex*, France |
| *Daldinia carpinicola* | JX658442 | CBS 122880 | Vasilyeva & Stadler (2008), Ju *et al*. (1999) | *Carpinus,* Russia (**T**) |
| *Daldinia* cf. *australis* | JX658547 | MUCL 53761 | Present study | Australia |
| *Daldinia* cf. *concentrica* | JX658473 | MUCL 45434 | Present study | Ethiopia |
| *Daldinia* cf. *dennisii* var. *microspora* | JX658539 | ICMP 18265 | Present study | New Zealand |
| *Daldinia* cf. *eschscholtzii* | JX658456 | KC 1690 | Bitzer *et al*. (2008) | Venezuela |
| *Daldinia* cf. *grandis* | JX658543 | IMCP 18266 | Present study | *Weinmannia*, New Zealand |
| *Daldinia* cf. mexicana | JX658460 | Ww 3844/MUCL | Ju *et al*. (1999) | Far Eastern Russia |
| *Daldinia* cf. *pyrenaica* | JX658515 | MUCL 47221 | Present study | *Populus*, Ukraine |
| | JX658516 | MUCL 51700 | Present study | *Acer*, Ukraine |
| *Daldinia* cf. *caldariorum* | JX658453 | CBS 113045 | Present study | Ecuador |
| *Daldinia childiae* | AM749932 | CBS 116725 | Bitzer *et al*. (2008) | *Acer*, France |
| | JX658536 | CBS 116993 | Bitzer *et al*. (2008) | *Salix*, Germany |
| | JX658463 | CBS 116987 | Bitzer *et al*. (2008) | *Quercus*, Japan |
| | JX658466 | CBS 116995 | Bitzer *et al*. (2008) | *Acer*, P.R. China |
| | JX658465 | MUCL 45437 | Bitzer *et al*. (2008) | *Prunus*, Germany |
| | JX658467 | MUCL 46172 | Bitzer *et al*. (2008) | *Fraxinus*, USA |
| | JX658462 | MUCL 46818 | Bitzer *et al*. (2008), Kuhnert *et al*. (2014) | *Fraxinus*, France |
| | JX658464 | MUCL 48616 | Stadler *et al*. (2001a, b) | *Quercus*, USA |
| *Daldinia clavata* | JX658546 | MUCL 47436 | Present study | Gabon |
| *Daldinia concentrica* | AY616683 | CBS 113277 | Triebel *et al*. (2005) | *Fraxinus*, Germany |
| | AY616682 | CBS 113278 | Triebel *et al*. (2005) | *Fraxinus*, UK |
| | JX658475 | CBS 117124 | Present study | *Platanus*, Greece, Crete |
| | JX658533 | KC 1693 | Present study | *Quercus*, UK |
| | JX658469 | KC1697 | Present study | *Fraxinus*, UK |
| | JX658472 | KC1697 | Present study | *Fagus*, UK |
| | JX658454 | MUCL 46679 | Present study | *Acacia*, Italy |
| | JX658445 | MUCL 51681 | Present study | *Fraxinus*, France |
| | JX658471 | MUCL 54179 | Bitzer *et al*. (2008) | *Fagus*, Germany |
| | JX658474 | MUCL 52885 | Present study | Greece, Rhodes |

**Table 13.** (Continued).

| Species | Acc. No. (GenBank) | Specimen/ Strain No. | References | Host/Country |
|---|---|---|---|---|
| *Daldinia decipiens* | JX658455 | CBS 116997 | Present study | *Alnus*, Russia |
| | JX658441 | CBS 122879 | Ju *et al.* (1999), Stadler *et al.* (2001d) | *Betula*, Sweden (**PT**) |
| | JX658476 | MUCL 44610, CBS 113046 | Stadler *et al.* (2004d), Bitzer *et al.* (2008) | *Carpinus*, Denmark |
| | JX658524 | MUCL 52699 | Present study | *Betula*, Germany |
| *Daldinia dennisii* | JX658477 | CBS 114741 | Stadler *et al.* (2004c), Bitzer *et al.* (2008) | *Pittosporum*, Australia (**T**) |
| | JX658479 | CBS 114742 | Stadler *et al.* (2004c), Bitzer *et al.* (2008) | *Eleocarpus*, Australia (**PT**) |
| *Daldinia dennisii* var. *microspora* | JX658478 | MUCL 45010 | Bitzer *et al.* (2008) | *Podocarpus*, South Africa |
| | JX658538 | ICMP18264 | Present study | *Beilschmiedia,* New Zealand |
| *Daldinia eschscholtzii* | HE590883 | CALP 11206 | Present study | Philippines (**ET**) |
| | JX658497 | CBS 113042 | Bitzer *et al.* (2008) | Peru |
| | AY616684 | CBS 113047 | Triebel *et al.* (2005) | Thailand |
| | JX658500 | CBS 116032 | Bitzer *et al.* (2008) | Australia |
| | JX658498 | CBS 116035 | Bitzer *et al.* (2008) | Malaysia |
| | JX658492 | CBS 116037 | Bitzer *et al.* (2008) | Malaysia |
| | JX658499 | CBS 116037 | Bitzer *et al.* (2008) | Malaysia |
| | JX658480 | CBS 117735 | Bitzer *et al.* (2008) | Cameroon |
| | JX658481 | CBS 117740 | Bitzer *et al.* (2008) | Burkina Faso |
| | JX658491 | CBS 117741 | Bitzer *et al.* (2008) | Malaysia |
| | JX658438 | CBS 122876 | Ju *et al.* (1997) | USA, Texas |
| | JX658439 | CBS 122877 | Ju *et al.* (1997) | *Ficus*, Thailand |
| | JX658440 | CBS 122878 | Ju *et al.* (1997) | Guadeloupe |
| | JX658496 | KC 1616 | Bitzer *et al.* (2008) | Saint Lucia |
| | JX658490 | KC1699 | Bitzer *et al.* (2008) | Mexico |
| | JX658493 | MUCL 38740 | Bitzer *et al.* (2008) | Papua New Guinea |
| | JX658486 | MUCL 41777 | Bitzer *et al.* (2008) | *Sizygium jambos*, Cuba |
| | JX658494 | MUCL 41778 | Bitzer *et al.* (2008) | *Bucida palustris*, Cuba |
| | JX658495 | MUCL 43508 | Bitzer *et al.* (2008) | Papua New Guinea |
| | JX658484 | MUCL 45434 | Bitzer *et al.* (2008) | Benin |
| | JX658482 | MUCL 47965 | Bitzer *et al.* (2008) | P.R. China |
| *Daldinia gelatinoides* | GQ355621 | MUCL 46173 | Bitzer *et al.* (2008), Stadler *et al.* (2008a) | *Kalopanax*, Far Eastern Russia |
| *Daldinia gelatinosa* | JX658458 | UAMH 7406 | Present study | *Malus*, Canada |
| | JX658503 | CBS 116730 | Present study | Far Eastern Russia |
| *Daldinia govorovae* | JX658443 | CBS 122883 | Vasilyeva & Stadler (2008) | Far Eastern Russia (**T**) |
| *Daldinia hausknechtii* | JX658521 | CBS 119995 | Present study | La Réunion (**T**) |
| *Daldinia lloydii* | JX658457 | CBS 113483 | Bitzer *et al.* (2008) | *Betula*, Germany |
| *Daldinia loculata* | AF176965 | CBS 114738 | Johannesson *et al.* (2000) | *Betula,* UK (**ET**) |
| | AF176964 | TL 4613 (C) | Johannesson *et al.* (2000) | *Betula*, Far Eastern Russia |
| *Daldinia loculatoides* | AF176982 | CBS 113279 | Johannesson *et al.* (2000) as *D. grandis* | *Fagus*, UK (**T**) |
| | AM407726 | CBS 116729 | Bitzer *et al.* (2008), sequenced by S. Pazoutova | Czech Republic, *Betula* |
| | JX658459 | UAMH 9035 | Present study | *Populus*, Canada |
| *Daldinia macaronesica* | JX658505 | MUCL 52884 | Stadler *et al.* (2004c) | La Gomera |
| | JX658504 | CBS 113040 | Stadler *et al.* (2004c) | *Ocotea*, Madeira (**PT**) |
| | JX658506 | Ww4196 (M) | Stadler *et al.* (2004c) | *Ocotea*, La Palma (**T**) |
| *Daldinia martinii* | JX658507 | CBS 113041 | Stadler *et al.* (2004c) | *Quercus*, Italy (**T**) |
| *Daldinia mexicana* | JX658508 | Ww 3843/MUCL | Ju *et al.* (1997) | *Quercus*, Mexico (**T**) |
| *Daldinia nemorosa* | HM114296 | UAMH 11227 | Davey (2010) as *Annellosporium* | Soil, Canada |
| *Daldinia novae-zelandiae* | JX658437 | CBS 122873 | Present study | New Zealand |
| | JX658540 | ICMP18269 | Present study | New Zealand |
| | JX658509 | CBS 114739 | Stadler *et al.* (2004d) | New Zealand (**PT**) |

**Table 13.** (Continued).

| Species | Acc. No. (GenBank) | Specimen/ Strain No. | References | Host/Country |
|---|---|---|---|---|
| *Daldinia palmensis* | JX658510 | CBS 113039, MUCL 44616 | Stadler *et al*. (2004c) | *Laurus*, La Palma (**T**) |
| *Daldinia petriniae* | JX658512 | MUCL 49214, CBS 119988 | Bitzer *et al*. (2008) | *Alnus incana*, Austria |
| | JX658514 | CBS 116728 | Bitzer *et al*. (2008) | *Alnus*, Liechtenstein |
| | JX658461 | CBS 116994 | Present study | *Betula*, Far Eastern Russia |
| | JX658511 | CBS 117126 | Present study | *Betula*, P.R. China |
| | JX658513 | MUCL 51850 | Bitzer *et al*. (2008) | *Alnus*, Switzerland |
| *Daldinia placentiformis* | AM749921 | MUCL 47603 | Bitzer *et al*. (2008) | South Africa |
| *Daldinia pyrenaica* | AM749927 | MUCL 43749 | Bitzer *et al*. (2008) | *Quercus*, Spain (**T**) |
| *Daldinia raimundi* | JX658517 | CBS 113038 | Stadler *et al*. (2004c) | *Quercus*, Italy (**T**) |
| | JX658446 | MUCL 51689 | Present study | *Quercus*, France |
| *Daldinia sp. nov. (*cf. *concentrica*) | JX658522 | MUCL 51268 | Present study | D.R. Congo |
| *Daldinia starbaeckii* | JX658489 | CBS 116727 | Bitzer *et al*. (2008) | Ecuador |
| | JX658487 | MUCL 44145 | Bitzer *et al*. (2008) | Cuba |
| | JX658488 | MUCL 45436 | Present study | French Guiana (**T**) |
| | JX658485 | MUCL 52886 | Present study | Martinique |
| *Daldinia steglichii* | JX658534 | MUCL 43512 | Van der Gucht (1994), Stadler *et al*. (2001c) | New Guinea (**PT**) |
| | JX658545 | MUCL 53886 | Present study | La Réunion |
| *Daldinia theissenii* | JX658468 | BCRC 34045, CBS 122875 | Ju *et al*. (1997) as *D. clavata* | Mexico |
| | AM749931 | CBS 113044 | Bitzer *et al*. (2008) | Argentina |
| *Daldinia vanderguchtiae* | JX658520 | CBS 113036 | Stadler *et al*. (2004c) | *Acer*, UK, Jersey (**T**) |
| *Daldinia vernicosa* | EF026146 | BCRC 34048 | Ju *et al*. (1999), Bitzer *et al*. (2008) | *Fagus*, Germany (**ET**) |
| | JX658501 | CBS 119314 | Bitzer *et al*. (2008) | *Carpinus*, Germany |
| | JX658448 | CBS 119315 | Bitzer *et al*. (2008) | *Corylus*, Germany |
| | AM749925 | CBS 119316 | Ju *et al*. (1999), Bitzer *et al*. (2008) | *Fagus*, Germany (same locality as **ET**) |
| | JX658470 | CBS 139.73 | Triebel *et al*. (2005) | Netherlands, originally dep. as *D. concentrica* |
| | JX658502 | CBS 157.32 | Child (1932) | USA, Missouri |
| | JX658519 | CBS 161.31 | Child (1932) | USA (**T** of *D. simulans*) |
| *Entonaema liquescens* | AY616686 | ATCC 46302 | Rogers (1982), Triebel *et al*. (2005) | USA, Florida |
| *Graphostroma platystoma* | JX658535 | CBS 270.87 | Pirozynski (1974) | *Crataegus*, France (**T**) |
| | JX658542 | MUCL 53890 | Present study | *Quercus*, France |
| *Hypoxylon anthochroum* | JX658532 | FU69799, STMA07040, MUCL 49881 | Bitzer *et al*. (2008) | Panama |
| *Hypoxylon fragiforme* | AY616690 | CBS 114745 | Triebel *et al*. (2005) | *Fagus*, Germany |
| *Hypoxylon fuscum* | AY616693 | CBS 113049 | Triebel *et al*. (2005) | *Corylus*, Germany |
| *Hypoxylon gibraicense* | JX658523 | MUCL 52698 | Fournier *et al*. (2010b) | Portugal (**T**) |
| *Hypoxylon haematostroma* | AM749924 | MUCL 47600 | Bitzer *et al*. (2008) | Panama |
| *Hypoxylon howeanum* | AM749928 | MUCL 47599 | Bitzer *et al*. (2008) | *Acer*, Germany |
| *Hypoxylon laschii* | JX658525 | MUCL 52796 | Present study | *Fraxinus*, France |
| *Hypoxylon monticulosum* | DQ223748 | SUT080 | Suwanassai *et al*. (2005) | Thailand |
| *Hypoxylon nicaraguense* | AM749922 | CBS 117739 | Bitzer *et al*. (2008) | Burkina Faso |
| *Hypoxylon petriniae* | AM749923 | CBS 114746 | Bitzer *et al*. (2008) | *Fraxinus*, France (**T**) |
| *Hypoxylon polyporus* | AM749941 | MUCL 49339 | Bitzer *et al*. (2008) | Ivory Coast |
| *Hypoxylon rubiginosum* | AM749936 | CBS 119309 | Bitzer *et al*. (2008) | *Fraxinus*, Germany |
| *Hypoxylon* sp. | JX658483 | CBS 222.61 | Martin (1969) as *D. eschscholtzii*; taxonomy revised here | Mexico |
| *Hypoxylon submonticolosum* | JX658449 | CBS 115280 | Present study | *Ulmus*, France |
| *Nodulisporium africanum* | JX658527 | MUCL 3531 | Bitzer *et al*. (2008) | D.R. Congo |
| *Nodulisporium gregarinum* | JX658528 | MUCL 3630 | Bitzer *et al*. (2008) | *Morus alba*, Pakistan |
| *Nodulisporium indicum* | JX658529 | CBS 124.83 | Bitzer *et al*. (2008) | India (**T**) |

**Table 13.** (Continued).

| Species | Acc. No. (GenBank) | Specimen/ Strain No. | References | Host/Country |
|---|---|---|---|---|
| *Phylacia poculiformis* | FN428830 | CBS 123581 | Stadler *et al.* (2010a) | Panama |
| *Phylacia sagrana* | AM749919 | CBS 119992 | Bitzer *et al.* (2008) | Panama |
| *Pyrenomyxa morganii* | AM749920 | CBS 116990 | Stadler *et al.* (2005), Bitzer *et al.* (2008) | Far Eastern Russia (**T**) |
| *Rhopalostroma angolense* | FN821965 | CBS 126414 | Stadler *et al.* (2010c) | Burkina Faso |
| *Ruwenzoria pseudoannulata* | GU053568 | MUCL 51394 | Stadler *et al.* (2010b) | D.R. Congo (**T**) |
| *Thamnomyces camerunensis* | FN428828 | MUCL 51396 | Stadler *et al.* (2010a) | Cameroon |
| *Thuemenella cubispora* | JX658531 | CBS 119807 | Present study | USA |

**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*.

| Taxon Ju *et al*. (1997, 1999) | Taxon (present study) |
|---|---|
| **Unchanged** | *D. bakeri* , *D. bambusicola, D. brachysperma, D. caldariorum, D. cuprea, D. graminis, D. loculata, D. lloydii, D. loculata, D. macrospora, D. mexicana, D. petriniae, D. sacchari, D. singularis* |
| **Not included** | *D. albofibrosa*, *D. barkalovii, D. concentrica*, D. dennisii*, D. govorovae, D. macaronesica*, D. martinii*, D. nemorosa, D. palmensis*, D. raimundi*, D. steglichii* |
| *D. clavata* | *D. albozonata* + *D. clavata* + *D. theissenii* |
| *D. grandis* | *D. andina* + *D. grandis* + *D. novae-zelandiae* + *D. loculatoides* (+ *D. hausknechtii*?) |
| *D. cudonia* | *D. asphalatum* |
| *D. concentrica* | *D. childiae* (+ *D. australis* + *D. pyrenaica*?) |
| *D.* sp. from Russian Far East | *D. carpinicola* |
| *D.* sp. from Denmark | *D. decipiens* |
| *D. eschscholtzii* | *D. eschscholtzii* + *D. rehmii* + *D. starbaeckii,*(+ *D. vanderguchtiae*?) |
| *D. fissa* | *D. vernicosa* (+ *D. gelatinoides*) |
| *D. gelatinosa* | *D. gelatinosa* (+ *D.* sp. nov. ined., cf. *D. bakeri*, represented by WSP 54679/WSP 54729 from Idaho) |
| *Hypoxylon placentiforme* | *D. placentiformis* |
| *Versiomyces cahucuchosus* | *D. cahucuchosa* |

group of nodulisporium-like endophytes with apparently pantropical distribution were finally linked to a sexual stage, which turned out to be a hitherto undiscribed taxon. It cannot be excluded that the yet widely unknown putative new taxa in *Daldinia* of which we provided only preliminary descriptions based on teleomorphic characters will also eventually turn out to have a similar interesting life cycle and chemical ecology.

Recently, Ng *et al.* (2012) have announced a "draft genome sequence" of *D. eschscholtzii*, which is to our knowledge the first fully sequenced genome sequence of a member of the *Xylariales*. The sequenced strain was supposedly obtained from a "blood culture", according to the title of the paper, while the abstract suggested that the strain was an endophyte. The respective brief publication did not contain any further detailed information and is 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 unambiguisly 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.

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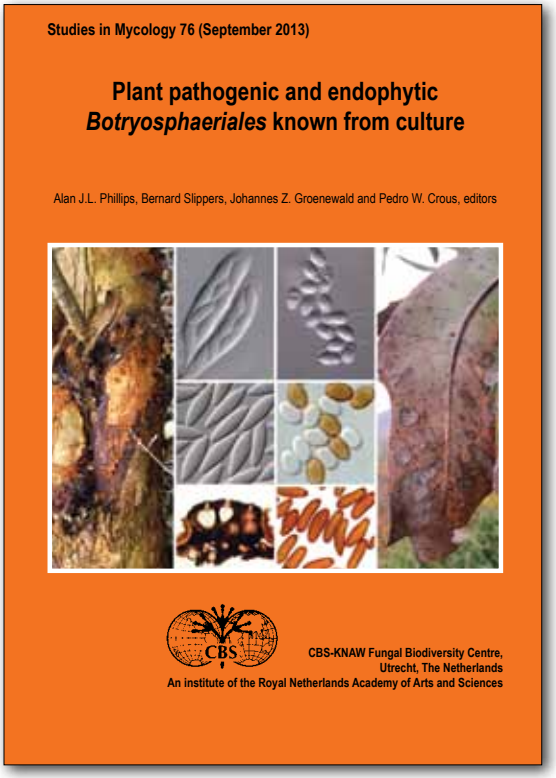



## Studies in Mycology 76: Plant pathogenic and endophytic *Botryosphaeriales* known from culture

A.J.L. Phillips, B. Slippers, J.Z. Groenewald, P.W. Crous (eds)

This volume of Studies in Mycology is dedicated to Robert (Bob) A. Shoemaker, who monographed several important genera of *Dothideomycetes*, and also published fundamental papers revising species and genera in the *Botryosphaeria* complex. The issue contains three contributions dealing with a revision of the *Botryosphaeriales*, an order containing plant pathogenic fungi of quarantine and economic importance. In the first paper the *Phyllostictaceae* is resurrected for *Phyllosticta*, the generic name chosen over *Guignardia* for this genus of fungi. By employing a multi-gene phylogenetic analysis on 129 isolates, 12 new species are introduced, while epitype and neotype specimens are designated for a further seven species. One species of interest is *P. citrimaxima* associated with tan spot of *Citrus maxima* fruit in Thailand, which adds a fifth species to the citrus black spot complex. Other than the *Phyllostictaceae*, a further five families are recognised in the second paper, including the newly introduced *Aplosporellaceae* (*Aplosporella* and *Bagnisiella*), *Melanopsaceae* (*Melanops*), and *Saccharataceae* (*Saccharata*). Furthermore, molecular clock dating on radiations within the *Botryosphaeriales*, based on estimated mutation rates of the rDNA SSU locus, suggests that the order originated in the Cretaceous period around 103 (45–188) mya, with most of the diversification in the Tertiary period. In the third paper an account is given of all genera and species in the *Botryosphaeriaceae* known from culture. Included is a historical overview of the family, the morphological features that define the genera and species and detailed descriptions of the 17 genera and 110 species. Keys to the genera and species are also provided, along with definitive DNA barcodes for the species in each genus.

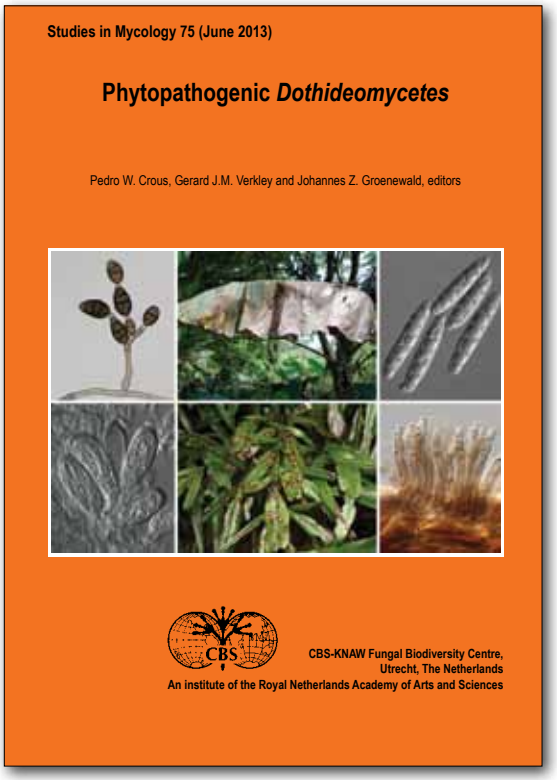
**176 pp., fully illustrated with colour pictures (A4 format), paperback, 2013. € 65**

## Studies in Mycology 75: Phytopathogenic *Dothideomycetes*

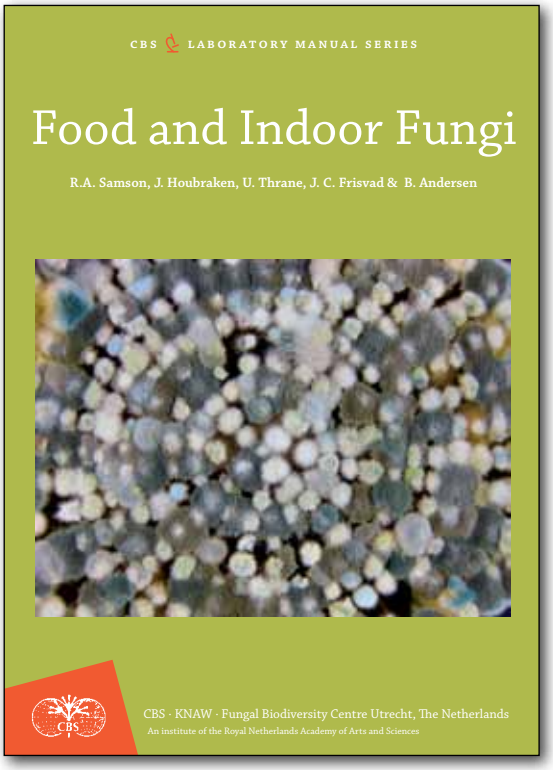
P.W. Crous, G.J.M. Verkley and J.Z. Groenewald (eds)

This volume of Studies in Mycology is dedicated to the plant health officers of the world, who are constantly confronted by a range of plant pathogenic fungi that cause devastating diseases of agricultural and forestry crops. Five main groups of fungi are dealt with, namely *Alternaria*, *Cercospora*, *Phoma*, *Pseudocercospora* and *Septoria*. In the first paper *Phoma* sections *Plenodomus*, *Heterospora* and *Pilosa* were reinvestigated, resulting in the introduction of several novel genera and species. The second paper deals with the paraphyletic genus *Pseudocercospora*; host specificity was considered for 146 species of *Pseudocercospora* occurring on 115 host genera from 33 countries. From these results we concluded that the application of European and American names to Asian taxa, and vice versa, was often not warranted. The third paper deals with the genus *Cercospora*, which contains more than 5 000 different species. Isolates used in the molecular phylogeny were obtained from 161 host species, 49 host families and 39 countries. Although some species were found to host-specific, others were isolated from a wide host range. The fourth paper deals with phylogenetic lineages within the genus *Alternaria*, which was revealed to represent a well-supported node containing 24 internal clades and six monotypic lineages. Several genera were placed in synonymy with *Alternaria*, for which 16 new sections were proposed. Two papers deal with the genus *Septoria*, which was shown to be poly- and paraphyletic, leading to the introduction of 15 new genera, and more than 40 new species. Although some species were shown to be highly specific, other taxa were revealed to occur on hosts in more than six different plant families. For all taxa investigated multi-gene DNA data were deposited in GenBank and other databases to expedite future identification of these plant pathogenic fungi. No single locus was found to be the ideal DNA barcode gene for these taxa, and species identification will have to be based on a combination of gene loci and morphological characters.

**406 pp., fully illustrated with colour pictures (A4 format), paperback, 2013. € 70**



# CBS Laboratory Manual Series




## CBS Laboratory Manual Series 2: Food and Indoor Fungi

R.A. Samson, J. Houbraken, U. Thrane, J.C. Frisvad and B. Andersen

This book is the second in the new CBS Laboratory Manual Series and is based on the seventh edition of INTRODUCTION TO FOOD AND AIRBORNE FUNGI. This new version, FOOD AND INDOOR FUNGI, has been transformed into a practical user's manual to the most common micro-fungi found in our immediate environment – on our food and in our houses. The layout of the book starts at the beginning with the detection and isolation of food borne fungi and indoor fungi in chapters 1 and 2, describing the different sampling techniques required in the different habitats. Chapter 3 deals with the three different approaches to identification: morphology, genetics and chemistry. It lists cultivation media used for the different genera and describes step by step how to make microscope slides and tape preparations for morphological identification. The chapter also describes how to do molecular and chemical identification from scratch, how to evaluate the results and warns about pitfalls. Chapter 4 gives all the identification keys, first for the major phyla (*Ascomycetes*, *Basidiomycetes* and *Zygomycetes*) common on food and indoors, then to the different genera in the *Zygomycetes* and the *Ascomycetes*, with a large section on the anamorphic fungi and a section for yeasts. The section on anamorphic fungi contains two keys to the different genera: a dichotomous key and a synoptic key. For each genus a key to the species treated is provided, followed by entries on the different species. For each species colour plates are accompanied by macro- and a micro-morphological descriptions, information on molecular and chemical identification markers, production of mycotoxins, habitats and physiological and ecological characteristics. The book is concluded with an extensive reference list and appendices on the associated mycobiota on different food types and indoor environments, mycotoxins and other secondary metabolites, a glossary on the mycological terms used in the book and lastly a detailed appendix on the media used for detection and identification.

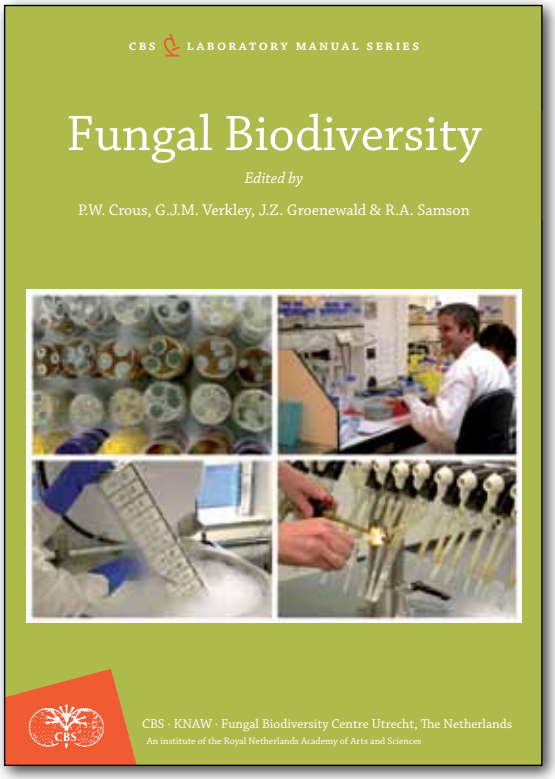
**390 pp., fully illustrated with colour pictures (A4 format). Hardbound, 2010. € 70**

## CBS Laboratory Manual Series 1: Fungal Biodiversity

P.W. Crous, G.J.M. Verkley, J.Z. Groenewald and R.A. Samson (eds)

This book is the first in the new "CBS Laboratory Manual Series", and focuses on techniques for isolation, cultivation, molecular and morphological study of fungi and yeasts. It has been developed as a general text, which is based on the annual mycology course given at the CBS-KNAW Fungal Biodiversity Centre (Centraalbureau voor Schimmelcultures). It provides an introductory text to systematic mycology, starting with a concise treatise of *Hyphochytridiomycota* and *Oomycota*, which have long been subject of study by mycologists, but are now classified in the Kingdom *Chromista*. These are followed by sections on the groups of "true fungi": *Chytridiomycota*, *Zygomycota*, *Ascomycota* and *Basidiomycota*. This descriptive part is illustrated by figures of life-cycles and schematic line-drawings as well as photoplates depicting most of the structures essential for the study and identification of these fungi. Special attention is given to basic principles of working with axenic cultures, good morphological analysis, and complicated issues for beginners such as conidiogenesis and the understanding of life-cycles. Exemplar taxa for each of these fungal groups, in total 37 mostly common species in various economically important genera, are described and illustrated in detail. In a chapter on general methods a number of basic techniques such as the preparation and choice of media, microscopic examination, the use of stains and preparation of permanent slides, and herbarium techniques are explained. Further chapters deal with commonly used molecular and phylogenetic methods and related identification tools such as BLAST and DNA Barcoding, fungal nomenclature, ecological groups of fungi such as soil-borne and root-inhabiting fungi, water moulds, and fungi on plants and of quarantine importance. Some topics of applied mycology are also treated, including fungi in the air- and indoor environment and fungi of medical importance. Common mycological terminology is explained in a glossary, with reference to illustrations in the book. A chapter providing more than 60 mycological media for fungal cultivation, and a comprehensive list of cited references are also provided. The book is concluded with an index, and dendrograms reflecting our current understanding of the evolutionary relationships within the *Fungi*.

**270 pp., fully illustrated with colour pictures (A4 format). Hardbound, 2009. € 50**

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# CBS Biodiversity Series


## No. 13: Cultivation and Diseases of *Proteaceae*: *Leucadendron*, *Leucospermum* and *Protea*

Pedro W. Crous, Sandra Denman, Joanne E. Taylor, Lizeth Swart, Carolien M. Bezuidenhout, Lynn Hoffman, Mary E. Palm and Johannes Z. Groenewald

*Proteaceae* represent a prominent family of flowering plants in the Southern Hemisphere. Because of their beauty, unique appearance, and relatively long shelf life, *Proteaceae* cut-flowers have become a highly desirable crop for the export market. The cultivation of *Proteaceae* is a thriving industry that provides employment in countries where these flowers are grown, often in areas that are otherwise unproductive agriculturally. Diseases cause a loss in yield, and also limit the export of these flowers due to strict phytosanitary regulations. In this publication the fungi that cause leaf, stem and root diseases on *Leucadendron*, *Leucospermum* and *Protea* are treated. Data are provided pertaining to the taxonomy, identification, host range, distribution, pathogenicity, molecular characteristics and control of these pathogens. Taxonomic descriptions and illustrations are provided and keys are included to distinguish species in genera where a number of species affect *Proteaceae*. Disease symptoms are described and colour photographs are included. Where known, factors that affect disease epidemiology are discussed. Disease management strategies are also presented that will assist growers and advisors in making appropriate choices for reducing disease in specific areas. Information is also provided relating to crop improvement, cultivation techniques, harvesting and export considerations. Further development and expansion of this industry depends on producing and obtaining disease-free germplasm from countries where these plants are indigenous. For that reason it is important to document the fungi that occur on *Proteaceae*, and to establish the distribution of these fungi. These data are essential for plant quarantine services for use in risk assessments.

**360 pp., fully illustrated (A4 format). Hardbound, 2013. € 75**

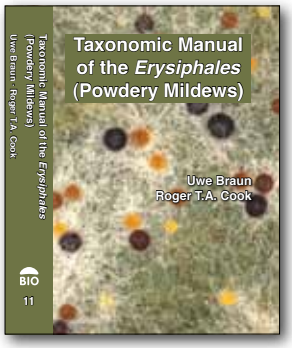

## No. 12: Ophiostomatoid Fungi: Expanding Frontiers

Keith A. Seifert, Z. Wilhelm de Beer and Michael J. Wingfield (eds)

The 1992 Convention on Biological Diversity created a new awareness of the economic impact of living organisms. Regulators and quarantine specialists in governments all over the world now scrutinise dots on maps, as real-time online disease mapping and prediction models allow us to track (and try to prevent) the spread of diseases across borders. Woodlands are more managed, include less genetic diversity, and seem to be more susceptible to rapidly spreading disease. Different jurisdictions use different terminology, Biosecurity, Alien Invasive Species, Quarantine, but it is now commonplace to see large signs in airports, along highways, and on public hiking trails, warning citizens not to accidentally or deliberately facilitate the spread of unwanted pests or microbes. With the ophiostomatoid fungi, scientists have to cope with the overlapping behaviour of a triumvirate of kingdoms, the fungi, the animals (bark beetles, mites or nematodes), and how all of these impact trees in our forests and cities.

This book includes 21 papers divided among five themes, plus an appendix. It is a sequel to *Ceratocystis* and *Ophiostoma*: Taxonomy, Ecology, and Pathogenicity, published by the APS Press in 1993, and like that book is derived from an international symposium, this one held on North Stradbroke Island, Australia prior to the 9th International Mycological Congress. A year before this volume was completed, mycological taxonomy formally abandoned the historical two name system, known as dual nomenclature, and we are now adopting a single name binomial system. The appendix to this book provides a preliminary view of the nomenclature of the ophiostomatoid fungi using the new single name system. In an attempt at consistency, this naming system is used in all chapters.

**337 pp., fully illustrated (A4 format). Hardbound, 2013. € 75**




## No. 11: Taxonomic Manual of the *Erysiphales* (Powdery Mildews)

Uwe Braun and Roger T.A. Cook

The "Taxonomic Manual of the *Erysiphales* (Powdery Mildews)" is a fully revised, expanded new version of U. Braun's former monograph from 1987, which is out of print. The present book covers the taxonomy of all powdery mildew fungi. New chapters have been prepared for phylogenetic relationships, conidial germination, conidia as viewed by Scanning Electron Microscopy, fossil powdery mildews, and holomorph classification. The treatment of the *Erysiphales*, its tribes and genera are based on recent molecular phylogenetic classifications. A key to the genera (and sections), based on teleomorph and anamorph characters is provided, supplemented by a key solely using anamorph features. Keys to the species are to be found under the particular genera. A special tabular key to species based on host families and genera completes the tools for identification of powdery mildew taxa. In total, 873 powdery mildew species are described and illustrated in 853 figures (plates). The following data are given for the particular species and subspecific taxa: bibliographic data, synonyms, references to descriptions and illustrations in literature, full descriptions, type details, host range, distribution and notes. A further 236 taxonomic novelties are introduced, comprising the new genus *Takamatsuella*, 55 new species, four new varieties, six new names and 170 new combinations. A list of excluded and doubtful taxa with notes and their current status is attached, followed by a list of references and a glossary. This manual deals with the taxonomy of the *Erysiphales* worldwide, and provides an up-todate basis for the identification of taxa, as well as comprehensive supplementary information on their biology, morphology, distribution and host range. This monograph is aimed at biologists, mycologists and phytopathologists that encounter or study powdery mildew diseases.

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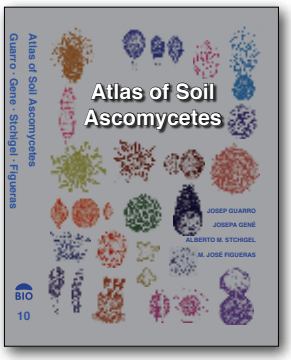


## No. 10: Atlas of Soil Ascomycetes

Josep Guarro, Josepa Gené, Alberto M. Stchigel and M. José Figueras

This compendium includes almost all presently known species of ascomycetes that have been reported in soil and which sporulate in culture. They constitute a very broad spectrum of genera belonging to very diverse orders, but mainly to the *Onygenales*, *Sordariales*, *Eurotiales*, *Thelebolales*, *Pezizales*, *Melanosporales*, *Pleosporales*, *Xylariales*, *Coniochaetales* and *Microascales*. The goal of this book is to provide sufficient data for users to recognise and identify these species. It includes the description of 146 genera and 698 species. For each genus a dichotomous key to facilitate species identification is provided and for each genus and species the salient morphological features are described. These descriptions are accompanied by line drawings illustrating the most representative structures. Light micrographs, supplemented by scanning electron micrographs and Nomarski interference contrast micrographs of most of the species treated in the book are also included. In addition, numerous species not found in soil but related to those included in this book are referenced or described. This book will be of value not only to soil microbiologists and plant pathologists concerned with the soilborne fungi and diseases, but also to anyone interested in identifying fungi in general, because many of the genera included here are not confined to soil. Since most of the fungi of biotechnological or clinical interest (dermatophytes, dimorphic fungi and opportunists) are soil-borne ascomycetes, the content of this book is of interest for a wide range of scientists.

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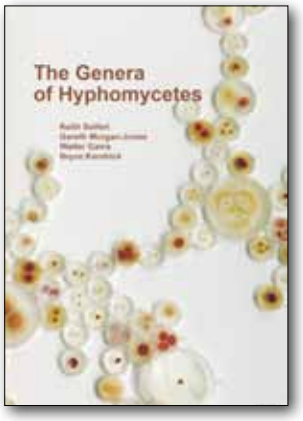
# CBS Biodiversity Series

### No. 9: The Genera of Hyphomycetes




Keith Seifert, Gareth Morgan-Jones, Walter Gams and Bryce Kendrick

The Genera of Hyphomycetes is the essential reference for the identification of moulds to all those who work with these fungi, including plant pathologists, industrial microbiologists, mycologists and indoor environment specialists, whether they be professionals or students. The book compiles information on about 1480 accepted genera of hyphomycetes, and about 1420 genera that are synonyms or names of uncertain identity. Each accepted genus is described using a standardized set of key words, connections with sexual stages (teleomorphs) and synanamorphs are listed, along with known substrates or hosts, and continental distribution. When available, accession numbers for representative DNA barcodes are listed for each genus. A complete bibliography is provided for each genus, giving the reader access to the literature necessary to identify species. Most accepted genera are illustrated by newly prepared line drawings, including many genera that have never been comprehensively illustrated before, arranged as a visual synoptic key. More than 200 colour photographs supplement the line drawings. Diagnostic keys are provided for some taxonomic and ecological groups. Appendices include an integrated classification of hyphomycete genera in the phylogenetic fungal system, a list of teleomorph-anamorph connections, and a glossary of technical terms. With its combination of information on classical morphological taxonomy, molecular phylogeny and DNA diagnostics, this book is an effective modern resource for researchers working on microfungi.

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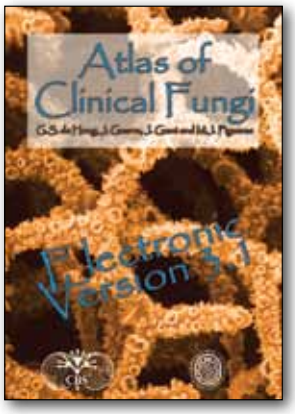


### Atlas of Clinical Fungi CD-ROM version 3.1

G.S. de Hoog, J. Guarro, J. Gené and M.J. Figueras (eds)

A new electronic version of the 3rd edition is available since November 2011. It will allows fast and very comfortable search through the entire Atlas text the engine is fully equiped for simple as well as advanced search. Items are strongly linked enabling direct use of the electronic version as a benchtool for identification and comparison. Text boxes with concise definitions appear explaining all terminology while reading. Illustrations are of highest quality and viewers are provided for detailed observation. The Atlas is interactive in allowing personal annotation which will be maintained when later versions will be downloaded.

The electronic version has been developed by T. Weniger. The third edition will contain about 530 clinically relevant species, following all major developments in fungal diagnostics. Regular electronic updates of the Atlas are planned, which should include numerous references to case reports, as well as full data on antifungals. Future features will include links to extended databases with verified molecular information. Note: The Atlas runs on Windows only! Not compatible with Mac

**Atlas of Clinical Fungi version 3.1, interactive CD-ROM, 2011. € 105**

### Identification of Common *Aspergillus* Species


Maren A. Klich

Descriptions and identification keys to 45 common *Aspergillus* species with their teleomorphs (*Emericella*, *Eurotium*, *Neosartorya* and *Sclerocleista*). Each species is illustrated with a one page plate and three plates showing the most common colony colours.

**116 pp., 45 black & white and 3 colour plates (Letter format), paperback, 2002. € 45**


### A revision of the species described in *Phyllosticta*

Huub A. van der Aa and Simon Vanev

2936 taxa are enumerated, based on the original literature and on examination of numerous herbarium (mostly type) specimens and isolates. 203 names belong to the genus *Phyllosticta s.str.*, and are classified in 143 accepted species. For seven of them new combinations are made and for six new names are proposed. The great majority, 2733 taxa, were redisposed to a number of other genera. A complete list of these novelties, as included in the book's abstract, can also be consulted on the web-site of CBS.

**510 pp. (17 x 25 cm), paperback, 2002. € 55**

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