

North American Fungi



Volume 6, Number 4, Pages 1-12
Published March 25, 2011

A new species of *Daedalea* (Basidiomycota) and a synopsis of core species in *Daedalea sensu stricto*

Daniel L. Lindner¹, Leif Ryvarden² and Timothy J. Baroni³

¹US Forest Service, Northern Research Station, Center for Forest Mycology Research, One Gifford Pinchot Drive, Madison, Wisconsin 53726, USA

²Biological Institute, University of Oslo, P.O. Box 1066, Blindern, N-0316, Oslo, Norway

³Department of Biological Sciences, PO Box 2000, State University of New York, College at Cortland, Cortland, New York 13045, USA

Lindner, D. L., L. Ryvarden, and T. J. Baroni. 2011. A new species of *Daedalea* (Basidiomycota) and a synopsis of core species in *Daedalea sensu stricto*. *North American Fungi* 6(4): 1-12. doi: 10.2509/naf2011.006.004

Corresponding author: Daniel Lindner: dlindner@wisc.edu. Accepted for publication February 3, 2011.
<http://pnwfungi.org> Copyright © 2011 Pacific Northwest Fungi Project. All rights reserved.

Abstract: *Daedalea neotropica*, a species with striking violet stains on the pileus and pore surface, is described from material collected in the Maya Mountains of Belize. A synopsis of *Daedalea sensu stricto* is provided based on morphological and DNA sequence data. Analyses indicate that at least four species should be included in *Daedalea* s.s.: *D. dickinsii*, *D. neotropica*, *D. pseudodochmia*, and *D. quercina*. A key to the species of *Daedalea* s.s. is provided.

Key words: *Daedalea*, Fungi, Polyporaceae, polypore, wood-decay.

Introduction: In his validation of *Daedalea*, Fries (1821) copied and accepted Persoon's (1801) concept of the genus based on the sinuous, labyrinthine or daedaleoid hymenophore. Numerous species with similar hymenophores have been described or transferred to the genus since that time. As of November 2010, there are 271 legitimate names in the genus, according to the Aphyllophorales database of Centraalbureau voor Schimmelcultures (Utrecht, Netherlands). Index Fungorum (CABI Bioscience Databases, accessed 03 Nov. 2010) includes 390 names under *Daedalea*.

Based on recent DNA analyses, it is now widely accepted that hymenophore configuration is of restricted taxonomic value for delimiting evolutionary lineages of homobasidiomycetes (Hibbett & Donoghue 1995, Binder & Hibbett 2002, Hibbett & Binder 2002). Within the polyporoid clade, sinuous to daedaleoid hymenophores are found in at least two clades: the "core polyporoid clade" (e.g. *Daedaleopsis*) and the "Antrodia clade" (e.g. *Daedalea*) (Binder et al. 2005). Thus, many of the species traditionally placed in the genus *Daedalea* have been transferred or likely will be transferred to various other genera. Unfortunately there are still many species whose taxonomic position remains unresolved.

Currently, the genus *Daedalea* is restricted to species that produce brown rots and have basidiocarps with trimitic hyphal systems, clamped generative hyphae, cork-colored context, thick dissepiments, and distinct catahymenia of skeletal hyphae with widened apices (Gilbertson & Ryvarden 1986, Ryvarden 1991, Núñez & Ryvarden 2001). Unfortunately, no comprehensive DNA-based studies have examined the validity of defining the genus based on these morphological and physiological characters. Based on the small amount of sequence data available, *D. quercina* L.:Fr., the type species of the genus, falls in the Antrodia clade of true polypores near other brown rot

polypore genera such as *Fomitopsis* and *Piptoporus* (Binder et al. 2005). Apart from *D. quercina*, *D. dickinsii* Yasuda is currently the only other species in the genus for which sequence data have been deposited in GenBank (NCBI).

While conducting mycological inventories in Belize, the authors encountered a striking new *Daedalea* species (Fig. 1) associated with *Quercus*. In connection with the description of this new species, a synopsis of the genus *Daedalea sensu stricto* is provided. This work is based on morphological characters of basidiocarps, along with preliminary analyses of ITS regions of rDNA from the type species of the genus, *D. quercina*, and five additional species: *D. dickinsii* Yasuda, *D. microstricta* Cooke, *D. neotropica* D. L. Lindner, Ryvarden & T. J. Baroni, *D. pseudodochmia* (Corner) T. Hattori (= *D. incana* (Lév.) Ryvarden), and *D. stereoides* Fr. (= *Lenzites stereoides* (Fr.) Ryvarden). Future work with additional gene regions and greater taxon sampling is needed to better define the boundaries of *Daedalea* and to place these species in a broader phylogenetic context.

Materials and Methods: Basidiocarps were examined microscopically and voucher specimens were deposited in the herbarium of the Center for Forest Mycology Research (CFMR), US Forest Service Northern Research Station, located in Madison, Wisconsin, or at the University of Oslo herbarium (O), Oslo, Norway. The specimens examined for this study are listed in Table I. The basidiocarp features of *Daedalea dickinsii*, *D. pseudodochmia*, and *D. quercina* are principally from East Asian Polypores, Volume 2 (Núñez & Ryvarden 2001). ITS regions of rDNA from basidiocarps were sequenced and analyzed following the methods of Lindner and Banik (2008), with the following exceptions: 1) a small piece of basidiocarp tissue, usually hymenial surface, was used for DNA extractions, and 2) only maximum parsimony was used to infer



FIGURE 1. Basidiocarps of *Daedalea neotropica* from the Maya Mountains of Belize. A. Young basidiocarps displaying characteristic violet staining (*DLC04-80*). B. Mature basidiocarps displaying the black cuticle that develops with age (*DLC04-74*, holotype). C. Detail of the hymenophore, which ranges from irregular poroid to daedaleoid (*DLC04-74*, holotype).

phylogenies. If an ITS sequence was successfully obtained from a specimen, the sequence was deposited in GenBank (Table I).

Results

DNA Sequencing

ITS sequences were obtained from 11 of 20 specimens (Table I). The parsimony analysis of ITS sequences (Fig. 2) indicates that *Daedalea dickinsii*, *D. neotropica*, *D. pseudodoehmia* and *D. quercina* form a clade (*Daedalea* s.s.) with

moderate statistical support (bootstrap value = 71). BLAST searches of GenBank indicated that *Fomitopsis* species showed high sequence similarity to *Daedalea* species, so two *Fomitopsis* species (*F. cajanderi* and *F. rosea*) were included in the analysis. Both *Fomitopsis* species were more closely related to *Daedalea* s.s. than *D. stereoides* or *D. microstricta*. *Daedalea stereoides* fell within the Antrodia clade, while *D. microstricta* fell within the core polyporoid clade. One “*D. quercina*” sequence from GenBank

Table I. Specimens examined for this study

Species	Collection Number*	Locality	Collector and Date	Host	GenBank Accession
<i>Daedalea dickinsii</i>	TAA-150237	Russia, Primorsk	E. Parmasto, Sept. 1987	<i>Quercus mongolica</i>	-
<i>D. microstricta</i>	TI-120 (10540)	Venezuela, Amazonas	T. Ilurriaga, Nov. 1984	unknown	-
<i>D. microstricta</i>	LR-43741 (18612)	Costa Rica, Alajuela	L. Ryvarden, July 2001	unknown	FJ403209
<i>D. microstricta</i>	23934 (17749)	Mexico, Quintana Roo	G. Guzman, Aug. 1983	unknown	-
<i>D. neotropica</i>	DLC04-74 (BZ-3670)	Belize, Maya Mountains	D. Lindner, Aug. 2004	<i>Quercus</i> sp.	FJ403216
<i>D. neotropica</i>	DLC04-80 (BZ-3676)	Belize, Maya Mountains	T. J. Baroni, Aug. 2004	<i>Quercus</i> sp.	FJ403217
<i>D. neotropica</i>	DLC04-100 (BZ-3696)	Belize, Maya Mountains	D. J. Lodge, Aug. 2004	<i>Quercus</i> sp.	FJ403218
<i>D. neotropica</i>	DLC04-174 (BZ-3770)	Belize, Maya Mountains	D. Lindner, Aug. 2004	<i>Quercus</i> sp.	FJ403219
<i>D. neotropica</i>	LR-42929	Costa Rica, Punta Arenas	L. Ryvarden, Mar. 2000	<i>Quercus</i> sp.	-
<i>D. pseudodochmia</i>	LR-21710/A (10533)	China, Jilin Prov.	L. Ryvarden, Sept. 1983	<i>Quercus dentata</i>	FJ403210
<i>D. quercina</i>	LR-19044 (17750)	Norway, Oslo	L. Ryvarden, Oct. 1981	<i>Quercus</i>	-
<i>D. quercina</i>	LR-47786	Norway, Telemark	L. Ryvarden, Oct. 2007	<i>Quercus</i> sp.	FJ403212
<i>D. quercina</i>	LR-47799	Norway, Vestfold	L. Ryvarden, Oct. 2007	<i>Quercus robur</i>	FJ403213
<i>D. quercina</i>	HHB-3803	USA, Maryland	H.H. Burdsall, Jr., Oct. 1969	<i>Quercus</i> sp.	-
<i>D. quercina</i>	HHB-8735	USA, Wisconsin	H.H. Burdsall, Jr., Oct. 1975	<i>Quercus</i> sp.	FJ403214
<i>D. quercina</i>	L-15889	USA	J. Lowe	unknown	-
<i>D. c.f. quercina</i> **	LR-45191 (BZ-2779)	Belize, Orange Walk District	L. Ryvarden, Oct. 2002	<i>Quercus</i> sp.	FJ403211
<i>D. stereoides</i>	10551	Ethiopia, Kaffa Prov.	Dawit Abate, Aug. 1996	unknown	FJ403215
<i>D. stereoides</i>	II-3854	India, Assam	B.K. Bakshi, Jan. 1950	<i>Shorea robusta</i>	-
<i>D. stereoides</i>	H-3908	India, Assam	B.K. Bakshi, Jan. 1945	<i>Shorea robusta</i>	-

* Alternate specimen numbers are listed in parentheses.

**Although similar to *D. quercina*, this specimen has a very thin context and the ITS analysis suggests this is an undescribed species.

(DQ491425) fell well outside of *Daedalea* s.s., but within the Antrodia clade (Fig. 2).

Within the *Daedalea* s.s. clade, *Daedalea neotropica* sequences formed a well-supported clade (bootstrap value = 100) distinct from all other *Daedalea* species. *Daedalea quercina* sequences also formed a distinct clade (bootstrap value = 77), although one specimen from Belize ("*D. quercina*" LR-45191) fell close to *D. neotropica*. *Daedalea dickinsii* and *D. pseudodochmia* fell closely together in a well-supported clade (bootstrap value = 95) (Fig. 2).

Synopsis of *Daedalea* s.s. with key to species

In addition to the DNA analysis, basidiocarps were examined macroscopically and microscopically (see Table I for a list of specimens examined). Our brief synopsis of core species in *Daedalea* s.s., which follows, summarizes these results. A key to species in *Daedalea* s.s. is provided.

DAEDALEA Pers.: Fr.

Syst. Mycol. 1:331, 1821. - *Daedalea* Pers. Syn.

Meth. Fung. p. 499, 1801.

Basidiocarps perennial, pileate, broadly sessile; pileus surface smooth to velutinate, often concentrically sulcate; hymenophore irregular, partly poroid, partly split into sinuous pores, labyrinthine/daedaleoid, or strictly lamellate, ochraceous; context light to deep brown; hyphal system trimitic; generative hyphae thin-walled, hyaline, with clamps; binding hyphae tortuous with short, stout branches, hyaline to light yellowish brown; skeletal hyphae thick-walled to completely occluded, light ochraceous brown, bending from the trama into the hymenium and developing a catayahmenium; basidiospores oblong-ellipsoid to cylindrical, thin-walled, hyaline, negative in Melzer's reagent; chlamydospores present in some tropical species; on hardwoods producing a brown rot.

Type species: *Daedalea quercina* L.:Fr.

Remarks. Defining characters are the trimitic hyphal system; clamped generative hyphae; a catayahmenium formed by skeletal hyphae; a

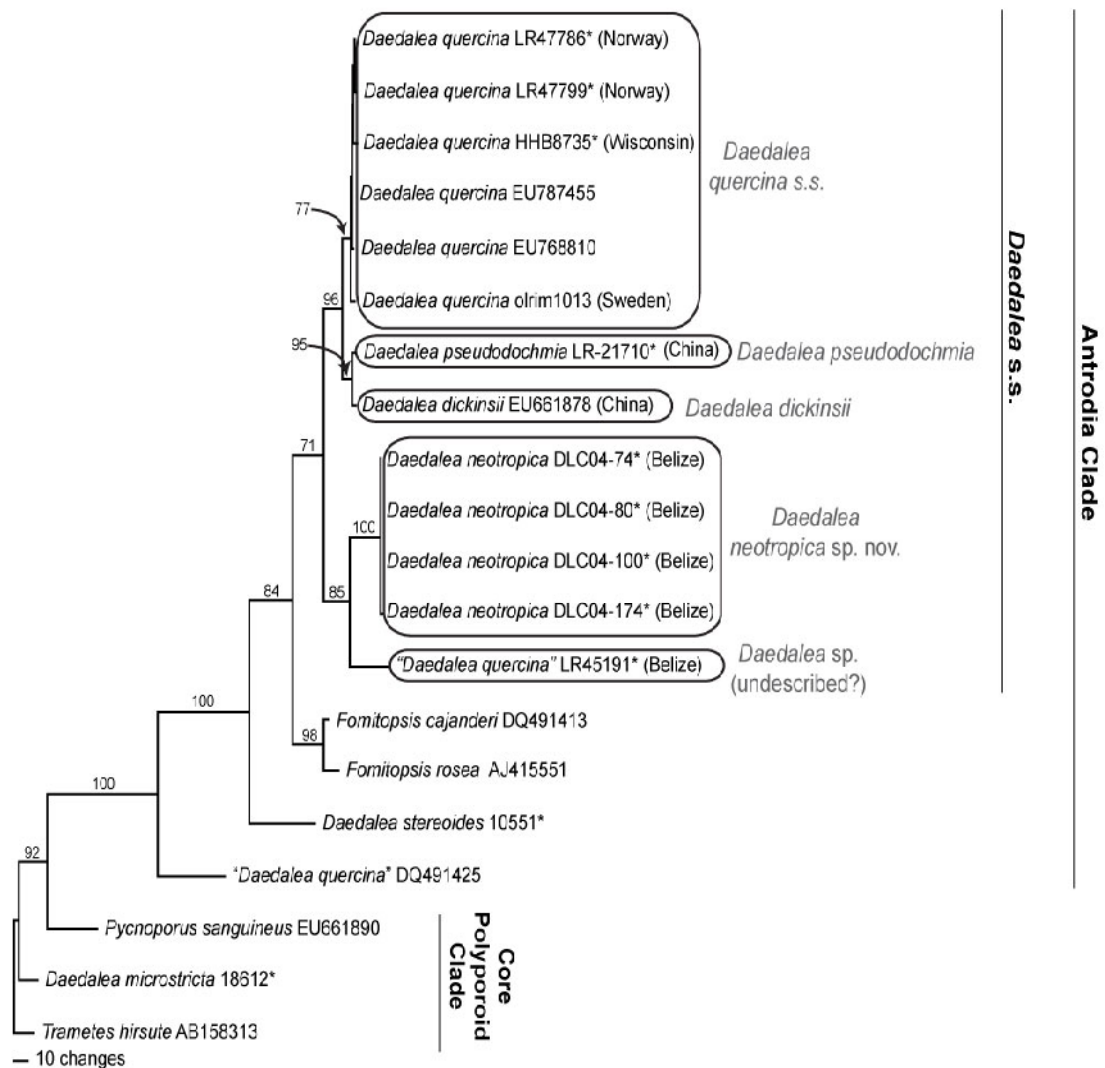


Figure 2. Results of maximum parsimony analysis based on ITS sequences. The tree shown is one of 12 equally parsimonious trees (length = 547, CI = 0.773, RI = 0.838). Bootstrap support is indicated above branches and is based on 1000 bootstrap replicates. Specimens sequenced for this study are marked with an asterisk and are labeled with collection numbers. All other sequences were obtained from GenBank (NCBI) and are labeled with GenBank accession numbers, with the exception of *D. quercina* olrim1013, which was provided by Rimvydas Vasaitis (Swedish University of Agricultural Sciences, Uppsala, Sweden). Quotation marks around species names indicate specimens that may have been misidentified.

cork-colored context; small, hyaline, subcylindrical spores and production of a brown rot.

Key to species in *Daedalea* s.s.

1. Hymenophore primarily poroid; rarely daedaleoid.....2
1. Hymenophore primarily daedaleoid; pores or lamellae 1-4 mm wide..... ***D. quercina***
2. Neotropical species; pileus with violet spots or zones.....***D. neotropica***
2. Asian species; pileus without violet spots or zones3
3. Tropical to subtropical species; with a black cuticle when old***D. pseudodochmia***
3. Temperate species; without a black cuticle when old***D. dickinsii***

Daedalea dickinsii Yasuda

Bot. Mag. Tokyo 36:127, 1922.

Basidiocarps annual to perennial, sessile, dimidiate, applanate to triquetrous, up to 20 cm long, 10 cm wide, and 5 cm thick, margin usually dull; pilear surface pale ochraceous with a pinkish buff tint, glabrous, with lighter outgrowths from the base of the pileus, broadly concentrically sulcate; pore surface concolorous with the pileus, pores circular to angular, some elongated, 1-2 per mm, dissepiments thick and entire, tubes up to 1.5 cm deep; context tough corky, pinkish buff, up to 2 cm thick.

Hyphal system trimitic; generative hyphae with clamps, hyaline, thin-walled, 1.5-3 μm wide; skeletal hyphae hyaline to pale brown, thick-walled to almost solid, unbranched, 2.4-4.5 μm wide; binding hyphae moderately branched, up to 2.5 μm wide.

Cystidia absent; skeletal hyphae with widened apices protruding in the hymenium, 23-48 x 1.5-4 μm .

Basidia subclavate, 18-25 x 4.5-6 μm , with four sterigmata.

Basidiospores cylindrical, 4-5.5 x 1.8-2.5 μm .

Substrata. On hardwoods, mostly on *Fagus* and *Quercus*.

Distribution. Temperate Asia, from India to Japan, and at high elevations in Taiwan.

Remarks. Roy and Pal (1994) reported Indian specimens of *D. dickinsii* to be compatible with *D. quercina*. However, our DNA analysis suggests that *D. dickinsii* is distinct from *D. quercina*, and is in fact more closely related to *D. pseudodochmia*.

Daedalea neotropica D. L. Lindner, Ryvardeen & T. J. Baroni *sp. nov.* [Figs. 1 & 3] (MycoBank Accession MB 519174)

Ad Daedalea pseudodochmia (Corner) T. Hattori *sed pileus violaceus et cuticula niger*.

Holotype: **BELIZE**. Toledo District: Maya Mountains, Cockscomb Ridge, Doyle's Delight, South Trail, 16° 30' N, 89° 3' W (UTM coordinates 1,824,500 N 281,600 E), 1000-1124 m asl, 12 Aug 2004, *D. L. Lindner DLC04-74 (BZ-3670)*, holotype in CFMR, isotypes deposited in the herbarium of the University of Oslo (O), the Forestry Department herbarium in Belize (BRH), and the US National Fungus Collections (BPI).

Basidiocarps perennial, single or with a several pilei fused laterally, broadly sessile to dimidiate, semicircular, up to 15 cm wide, 12 cm broad and 3 cm thick, strongly attached to the substrate, corky to woody and hard; upper surface of pileus flat to slightly convex, often with a slightly raised base, glabrous and finely tuberculate, inner parts black with a thin cuticle spreading from the base, further towards the margin light to deep violaceous becoming paler and finally ochraceous at the margin which produces narrow sulcate zones, the violaceous color fades over years in the herbarium, but is often retained close to the black basal zones or outgrowths; pore surface flat to oblique, especially close to the substrate, ochraceous, hymenophore of some basidiocarps mostly poroid, in parts irregular and daedaleoid, but usually including not more than 3 to 5 pores,

in regular parts about 3 pores per mm, other basidiocarps daedaleoid with some pores, pore surface violaceous from the base fading towards the margin to ochraceous or cork-coloured shades, tubes up to 2 cm deep, with distinct zones, concolorous with pore surface, context up to 1.5 cm thick, ochraceous to tobacco brown, with indistinct annual zones; but with narrow black lines towards the top due to embedding of previous areas with black cuticle.

Hyphal system trimitic; generative hyphae thin-walled, hyaline, with clamps, 2-4 μm wide; binding hyphae tortuous with short branches, thick-walled to solid, light golden yellowish brown; skeletal hyphae dominating, thick-walled to solid, light brown, 3-6 μm wide.

Cystidia none, but skeletal hyphae bend into the hymenium and in places form a catahymenium with cystidia-like, rounded and thick-walled apices, often with a fine granular incrustation.

Basidia few observed.

Basidiospores cylindrical, hyaline, thin-walled, smooth, negative in Melzer's reagent, 5-5.5 x 2-3 μm . Few basidiospores were observed, suggesting the period of sporulation is short, as in other species of *Daedalea*.

Type of rot. Associated with a brown rot.

Substrata. Only recorded on *Quercus* spp. (*Q. cortesii*, *Q. humboldtii*, *Q. insignis* or *Q. skinneri*), stump and dead fallen logs.

Additional specimens examined. BELIZE.

Toledo District: Maya Mountains, Cockscomb Ridge, Doyle's Delight, East Trail, 16° 30' N, 89° 3' W (UTM coordinates 1,824,500 N 281,600 E), 1000-1124 m asl, 12 Aug 2004, *T. J. Baroni* DLCo4-80 (BZ-3676), deposited CFMR, BRH; South Trail, 13 Aug 2004, *D. J. Lodge* DLCo4-100 (BZ-3696), deposited CFMR, BRH; west-north-west trail from helipad, 17 Aug 2004, *D. L. Lindner* DLCo4-174 (BZ-3770), deposited CFMR, BRH.

COSTA RICA. Punta Arenas: Coto Brus, Sabalito, sendero Hiyveron, 1200 m asl, 29 March 2000, *L. Ryvar* 42929, deposited O.

Distribution. Probably widespread in Central America wherever oak is growing.

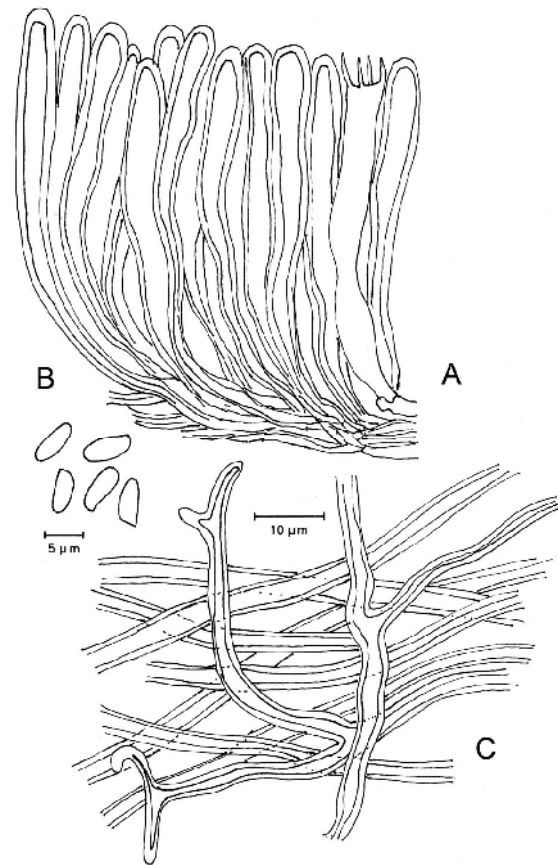


FIGURE 3. Microscopic features of *Daedalea neotropica* (LR-42929). A. Catahymenium with a single basidium. B. Basidiospores. C. Contextual skeletal hyphae.

Remarks. *Daedalea neotropica* is easy to recognize by the violaceous coloration that occurs in irregular patches on the pileus and pore surfaces, a rather exceptional color among polypores. For comments concerning *D. violacea* Lév. see the discussion below.

Daedalea pseudodoehmia (Corner) T. Hatt. Mycoscience 46:303, 2005 – *Trametes pseudodoehmia* Corner, Beih. Nova Hedwigia 97:138, 1989

Basidiocarps perennial, applanate, semicircular and dimidiate, up to 10 cm wide and long, up to 2 cm thick at the base, coriaceous to woody hard when dry; pilear surface dull, pale cinnamon to ochraceous, when young with a pinkish tint, becoming darker, glabrous, narrowly sulcate in concentric bands, often covered with lighter and velvety outgrowths that spread irregularly towards the margin, when old developing a black cuticle that becomes irregularly rimose; pore surface ochraceous to pale cinnamon, pores angular to elongate, 1 - 2 (3) per mm, tubes concolorous with the pore surface except the inner parts that are stuffed with white mycelium, distinctly stratified, up to 1.5 cm deep; context ochraceous in different shades, in some specimens with distinct thin black lines separating various layers of outgrowths on the pileus, the upper zones paler than the lower ones, total context up to 6 mm thick.

Hyphal system trimitic; generative hyphae with clamps, 2-3.5 μm wide; skeletal hyphae completely occluded to thick-walled, golden brown, 2.5-6 μm wide, tortuous, clavate hyphal ends protruding towards the tube lumen; binding hyphae solid and moderately branched, golden brown, often tortuous, 2-5 μm wide, emerging in the hymenium (catahymenium) with apices up to 5 μm wide.

Basidia not seen.

Basidiospores broadly ellipsoid, 5.5-6 x 3-3.5 μm .

Substrata. On hardwoods.

Distribution. Asia, known from India, Nepal, Sri Lanka, China (Changbai, Jiangxi), Japan, and the Philippines.

Remarks. The large pores and the rimose, black cuticle that develops with age are distinct characteristics. The pore surface is reminiscent of *Daedalea dickinsii*, but that species does not develop a black cuticle when old. The DNA analysis suggests that *D. dickinsii* and *D. pseudodochmia* are closely related. As noted by Hattori (2005), *Daedalea pseudodochmia* also has been known as *Daedalea incana* (Lév.)

Ryvarden, Mycotaxon 20:148, 1984, an illegitimate homonym of *Daedalea incana* (P. Karsten) Saccardo & D. Saccardo, Syll. Fung. 17: 139, 1905.

***Daedalea quercina* L.:Fr.**

Syst. Mycol. 1:333, 1821. - *Agaricus quercinus* L. Spec. Plant. p. 1176, 1753.

Basidiocarps perennial, single or with a few pilei fused laterally, broadly sessile to dimidiate, semicircular, up to 20 cm wide, 15 cm broad and 8 cm thick, strongly attached to the substrate, corky to woody and hard; upper surface of pileus flat to slightly convex, often with a slightly raised base, smooth to finely velutinate, in some specimens with tufts of raised hyphae or scattered nodulae or warts, the base rougher or more scrupose than the margin, which is usually smooth; margin ochraceous, inner parts deeper brownish to grayish in old specimens, sometimes with pads or smaller areas with fresh outgrowth of light ochraceous mycelium, acute; pore surface flat to oblique, especially close to the substrate, ochraceous, hymenophore irregular, along the margin elongated-poroid, in the inner parts with sinuous pores or daedaleoid or almost lamellate, on oblique parts the pores are deeply split in front, mostly 1-4 mm wide measured tangentially, walls 1-3 mm thick; context up to 1 cm thick, ochraceous to tobacco brown, with indistinct annual zones; tubes up to 4 cm deep, light ochraceous on the inner tube walls while the trama is distinctly darker.

Hyphal system trimitic; generative hyphae thin-walled, hyaline, with clamps, 1.5-4 μm wide; binding hyphae tortuous with short branches, thick-walled to completely occluded, light golden yellowish brown; skeletal hyphae dominating, thick-walled to solid, light brown, 3-6 μm wide.

Cystidia none, but skeletal hyphae bend into the hymenium as a dense catahymenium with cystidia-like, rounded and thick-walled apices, often with a fine granular exudate; some skeletal hyphae slightly swollen and pointed at the apex, strikingly similar to true hymenial cystidia unless

followed into the vertical trama where they originate.

Basidia very difficult to find even if fresh specimens are examined, occurring singly between the projecting skeletal hyphae, clavate, 20-27 x 6-7.5 μm , 4-sterigmate, with a basal clamp.

Basidiospores cylindrical, hyaline, thin-walled, smooth, negative in Melzer's reagent, 5.5-6 x 2.5-3.5 μm , difficult to find in most specimens as the periods of sporulation seem to be short and the basidia collapse rapidly on drying.

Type of rot. Causes a brown rot in the heartwood of living trees and eventually results in large hollows in the host; also continues decay in stumps.

Substrata. In North Europe growing exclusively on *Quercus*, often occurring on very hard wood. In Central and Southern Europe also noted on other hosts such as *Acer*, *Castanea*, *Corylus*, *Eucalyptus*, *Fagus*, *Fraxinus*, *Juglans*, *Populus*, *Prunus*, *Sorbus*, *Tilia* and *Ulmus*. In North America most common on *Quercus*, but also recorded from *Castanea*, *Fagus*, *Fraxinus*, *Juglans*, *Populus*, *Prunus* and *Ulmus*.

Distribution. Follows the distribution of *Quercus* species everywhere in the temperate zone, occurring circum-globally throughout Asia, North Africa, Europe and North America. In North America most common east of the Mississippi, very rare west of the Mississippi.

Remarks. *Daedalea quercina* is easy to recognize because of the even pale color, the very hard basidiocarps, and the irregular daedaleoid hymenophore. The DNA analysis confirmed that *D. quercina* from northern Europe and northern North America are conspecific. However, one specimen from Belize (LR-45191) originally identified as *D. quercina* was found to be more closely related to *D. neotropica* in the DNA analysis. This particular specimen had a significantly thinner context (2-4 mm) than other *D. quercina* specimens. Further work is needed to determine whether cryptic species exist within *D. quercina* s.l.

Discussion: Based on our morphological and DNA-based investigations of *Daedalea* s.l., *D. dickinsii*, *D. neotropica* and *D. pseudodochmia* were found to be closely related to *D. quercina*, the type of the genus. We consider these four species to comprise the core of the genus *Daedalea* s.s., although future investigations will surely find more species that fall within *Daedalea* in this restricted sense. In particular, four *Daedalea* species (*D. aurora*, *D. dochmia*, *D. fulvirubida*, and *D. lusor*) reported by Hattori (2005) from lowland peninsula Malaysia were not considered in the current work, although morphological characteristics suggest these species may fall within *Daedalea* s.s.

Another species that appears to fall in *Daedalea* s.s. is an apparently un-described species from Belize, based on a single collection with a thin pileus context (Fig. 2, "*D. quercina*" LR-45191). Although the basidiocarp of this specimen superficially resembles *D. quercina*, possessing a strongly daedaleoid hymenophore, the thin context and divergent ITS sequence suggest this collection represents a distinct species within *Daedalea* s.s. DNA data indicate this taxon is closely related to *D. neotropica*, despite the morphological similarity to *D. quercina* s.s. Unfortunately, we were able to examine only one collection exhibiting these characteristics, so examination of additional material from the same biogeographic region is needed.

One *Daedalea quercina* ITS sequence deposited at GenBank under *D. quercina*, and based on a voucher collection originating from Germany (Kim et al. 2007) (Fig. 2, *D. quercina* DQ491425), fell well outside the *Daedalea* s.s. clade. This collection requires further examination to determine if the specimen was misidentified. While the core group of isolates comprising *D. quercina* s.s. did exhibit some variation ($\approx 1\%$), the divergence exhibited by DQ491425 ($\approx 20\%$, relative to other *D. quercina* isolates) is well outside the range expected within a species.

The DNA analysis confirmed that *Daedalea neotropica* is well separated from other *Daedalea* species for which DNA data are available. During the course of our investigations, the possibility was considered that our *D. neotropica* specimens could be referred to *D. violacea* Lév., a species described from Cuba in 1846 (Léveillé 1846). However, the description of *D. violacea* and Léveillé's accompanying comments, including a comparison of the violet coloration of *D. violacea* to that of *Polyporus auferianus* (= *Rigidoporus microporus*), suggest that *D. violacea* and *D. neotropica* are not conspecific. Unfortunately the type material of *D. violacea* apparently has been lost. In a study of Léveillé's type collections, Ryvarden (1981) was unable to locate type material, which is consistent with the findings of Murrill (1908), who listed *D. violacea* as a "Doubtful Species" and stated that authentic specimens could not be located. Our inquiries to two herbaria (PC and BPI) turned up no authentic material of *D. violacea*. It has been suggested that *D. violacea* may in fact represent *Trichaptum sprucei* (= *Daedalea sprucei*), a species with violet coloration and a somewhat daedaleoid hymenophore that is known to occur on *Quercus* in Cuba (C. Decock, pers. comm.).

The large difference in ITS regions between *D. neotropica* and *D. quercina* ($\approx 10\%$) was somewhat surprising given their similar morphologies and shared host preference for *Quercus* species. Although ITS sequences from multiple collections exist for both *D. quercina* and *D. neotropica*, more sequence data are needed for *D. dickinsii* and *D. pseudodochmia*. Based on the single ITS sequence available for both *D. dickinsii* and *D. pseudodochmia*, these species appear to be closely related, which is consistent with their similar morphologies.

Two well-supported clades were found within *Daedalea* s.s., indicating that further work is needed to determine whether this genus requires further subdividing. One clade (bootstrap value = 96) contained *D. dickinsii*, *D. pseudodochmia*,

and *D. quercina*, while the other clade (bootstrap value = 85) contained *D. neotropica* and the unusual "*D. quercina*" (LR-45191) specimen from Belize. Future work with additional gene regions, such as the large subunit region of rDNA, is needed to determine whether these two groups represent distinct subgenera or even genera. Given the morphological and ecological similarities exhibited by species in both clades, we prefer to keep these species in one genus for the time being.

The two additional *Daedalea* species investigated for this study, *D. microstricta* and *D. stereoides*, fell outside of the genus *Daedalea* s.s. *Daedalea stereoides* fell in the Antrodia clade, along with other polypores causing brown rots, while *D. microstricta* fell in the core polyporoid clade. The core polyporoid clade is made up primarily of white rot species, so more work is needed to confirm the type of rot produced by *D. microstricta*. Fidalgo and Fidalgo (1967) report the type of rot produced by *D. microstricta* as "unknown."

Only a fraction of the species that have been placed in the genus *Daedalea* were investigated for this study. Much additional work is needed to determine how other species in *Daedalea* are related to the core group of species established in this work, and a large effort will be needed to resolve the many nomenclatural issues that remain. We hope this preliminary work facilitates future investigations of this large but little-studied group of brown-rot species.

Acknowledgements: Fieldwork in Belize was made possible by a grant from the National Science Foundation, Biodiversity Surveys and Inventories Program to the State University of New York, College at Cortland (DEB-0103621) in collaboration with Dr. D. J. Lodge and the Center for Forest Mycology Research, Northern Research Station, US Forest Service. We are particularly grateful to D. J. Lodge, who helped

coordinate logistical support and who provided useful commentary on previous versions of the manuscript. This work would not have been possible without the airlift support of the British Forces of Belize, who provided transportation to the peak Doyle's Delight in the Maya Mountains, where most *Daedalea neotropica* collections were made. Alan Whitelaw, the commanding officer of the Belize Forces, and Sharon Matola, Director of the Belize Zoo, were responsible for making the expeditions possible. Several other individuals with government and non-governmental agencies in Belize are kindly acknowledged for their help and guidance: Hector Mai, John Pinelo, and Natalie Rosado of The Conservation Division, Belize Forestry Department, Belmopan; and Celso Poot, Station Manager of the Tropical Education Center in Belize.

Literature cited

- Binder, M. and D. S. Hibbett. 2002. Higher-level phylogenetic relationships of Homobasidiomycetes (mushroom-forming fungi) inferred from four rDNA regions. *Molecular Phylogenetics and Evolution* 22:76-90. <http://dx.doi.org/10.1006/mpev.2001.1043>
- Binder, M., D. S. Hibbett, K-H. Larsson, E. Larsson, E. Langer and G. Langer. 2005. The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). *Systematics and Biodiversity* 3:113-157. <http://dx.doi.org/10.1017/S1477200005001623>
- Fidalgo, O. and M. E. P. K. Fidalgo. 1967. Polyporaceae from Trinidad and Tobago. II. *Mycologia* 59:833-869. <http://dx.doi.org/10.2307/3757195>
- Fries, E. M. 1821. *Systema Mycologicum*. Vol 1, Lund, 520 pp.
- Gilbertson, R. L. and L. Ryvarden. 1986. *North American Polypores*. Vol 1. Oslo, Norway: Fungiflora. 433 p.
- Hattori, T. 2005. Type studies of the polypores described by E.J.H. Corner from Asia and West Pacific Areas. VII. Species described in *Trametes* (1). *Mycoscience* 46:303-312. <http://dx.doi.org/10.1007/s10267-005-0250-z>
- Hibbett, D. S. and M. Binder. 2002. Evolution of complex fruiting-body morphologies in homobasidiomycetes. *Proc R Soc Lond B* 269:1963-1969. <http://dx.doi.org/10.1098/rspb.2002.2123>
- Hibbett, D. S. and M. Donoghue. 1995. Progress toward a phylogenetic classification of the Polyporaceae through parsimony analysis of mitochondrial ribosomal DNA sequences. *Can J Bot* 73:S853-S861. <http://dx.doi.org/10.1139/b95-331>
- Léveillé, J. H. 1846. Description des champignons de l'herbier du Muséum de Paris. *Ann Sci Nat*, Series 3 (Botany) 5:111-167.
- Lindner, D. L. and M. T. Banik. 2008. Molecular phylogeny of *Laetiporus* and other brown-rot polypore genera in North America. *Mycologia* 100:417-430. <http://dx.doi.org/10.3852/07-124R2>
- Murrill, W. A. 1908. *North American Flora (Agaricales), Polyporaceae-Agaricaceae*. Vol. 9, Part 2:73-132. New York Botanical Garden.
- Núñez, M. and L. Ryvarden. 2001. *East Asian Polypores*. Vol. 2. *Polyporaceae s. lato*. Synopsis Fungorum 14. Oslo, Norway: Fungiflora. p 170-522.
- Persoon, C. H. 1801. *Synopsis Methodica Fungorum*. Gottingae, 708 p.

Roy, A. and S. Pal. 1994. Study of *Trametes dickinsii* Berk. sensu aucts., a synonym of *D. quercina*. *Mycotaxon* 51:81-89.

Ryvarden, L. 1981. Type studies in the Polyporaceae 13. Species described by J. H. L  veill  . *Mycotaxon* 13:175-186.

Ryvarden, L. 1991. *Genera of Polypores: Nomenclature and Taxonomy*. Synopsis Fungorum 5. Oslo, Norway: Fungiflora. 363