Systematics of *Ganoderma*

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Traditional Taxonomy of *Ganoderma*

Basidiospore shape and structure of the pilear surface have been used as primary taxonomic characters in mushroom systematics. The family *Ganodermataceae* was erected for polypore mushrooms having a double-walled basidiospore (Donk, 1964). The type species of the family is *Ganoderma lucidum* (W. Curt.: Fr.) P. Karsten, a laccate species described from England. The typical basidiospore of *Ganoderma* is ovoid, echinulate and enlarged or truncated at the apex (Fig. 2.1). Two kinds of basidiocarps producing this type of basidiospore have been distinguished: those with a shiny (laccate), yellowish or reddish-brown to black pilear surface, and those with a dull (non-laccate), grey–brown to black pilear surface. The genus *Elfvingia* was created to accommodate non-laccate *Ganoderma* taxa, with *Boletus applanatus* Pers. as the type species (Karsten, 1889). Modern authors (Corner, 1983; Ryvarden, 1991) consider *Elfvingia* a subgenus of *Ganoderma*. Murrill (1905a) proposed the genus *Amauroderma* to classify taxa with ganodermatoid basidiospores that differ from the typical form in having the spore wall uniformly thickened (Fig. 2.1). Additional genera, subgenera and sections were created on the basis of basidiospore shape, type of pilear crust or characteristics of the context tissue (Murrill, 1905b; Imazeki, 1952; Steyaert, 1972, 1980; Zhao, 1989). However, many of these groups remain controversial (Furtado, 1981; Corner, 1983; Ryvarden, 1991; Moncalvo *et al*., 1995a).

Table 2.1 shows a classification system for genera and subgenera in the *Ganodermataceae* that summarizes the works of earlier authors. 386 names were created to describe species in the *Ganodermataceae*. About 60 names

should be abandoned for various reasons (Moncalvo and Ryvarden, 1997). Most species were described in the genus *Ganoderma* (219 species), mainly from laccate collections (166 species). Many species are known only from a single collection or locality. Several names have been considered synonyms (reviewed in Moncalvo and Ryvarden, 1997), but I believe that more taxonomic synonyms still exist because a large number of species were

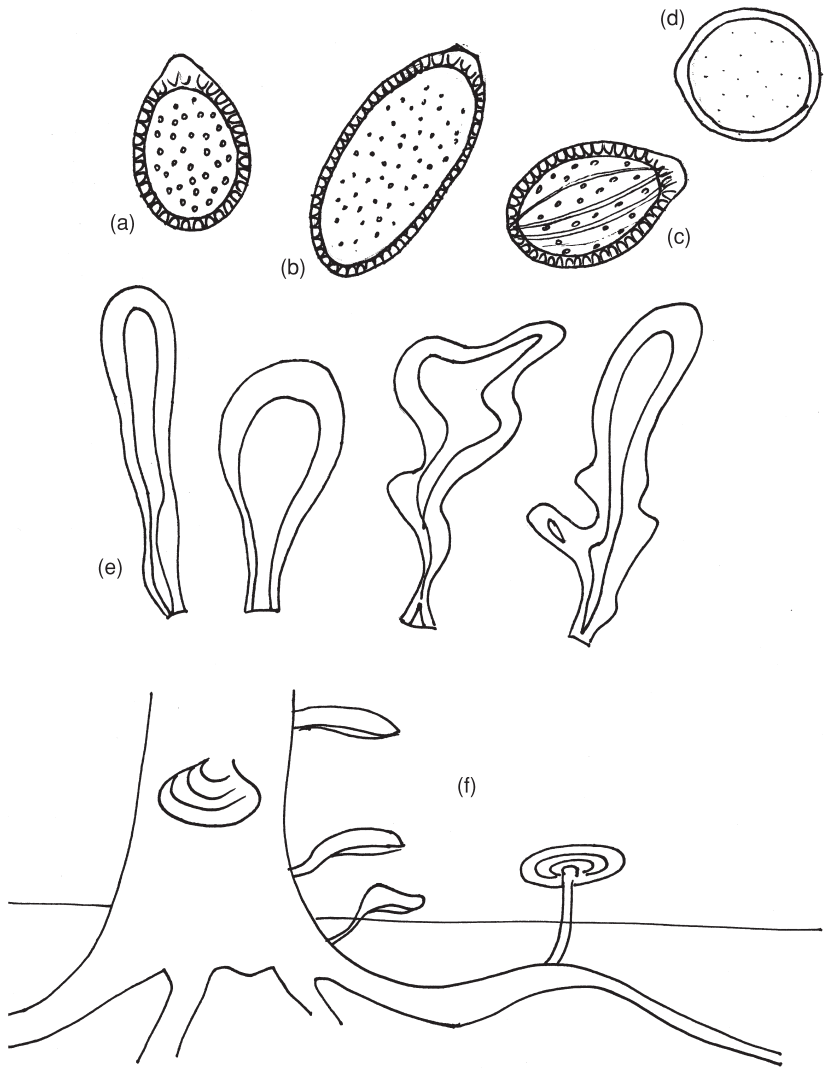

Fig. 2.1. Morphological characters traditionally used in *Ganoderma* systematics. (a) Typical basidiospore of *Ganoderma*. (b) Basidiospore of *G. boninense*. (c) Basidiospore of *G. formosanum* (longitudinal crests are barely seen in light microscopy). (d) Typical basidiospore of *Amauroderma*. (e) Various types of pilocystidia found in *Ganoderma*. (f) Stipitate versus dimidiate basidiocarps: relationships between stipe formation and location of basidiocarp development on wood.

Table 2.1. A summary of the traditional taxonomy in *Ganoderma*[a].

Genera	Subgenera	Distinctive features	Number of species		Number of names proposed as synonyms	Estimated number of known species
			Described	Known from a single locality		
Ganoderma		Spore wall enlarged at the apex				
	Ganoderma	Pilear surface laccate (presence of pilocystidia)	168	124	48	60–80
	Elfvingia	Pilear surface dull (absence of pilocystidia)	51	31	21	10–30
Amauroderma		Spore wall uniformly large	96	60	41	30–50
Haddowia[b]		Spore wall uniformly large and spore surface longitudinally crested	5	1	2	3
Humphreya[c]		Spore wall enlarged at the apex and spore surface reticulate	7	3	3	4

[a]Data from Moncalvo and Ryvarden (1997).
[b]Synonym of *Amauroderma* in Furtado (1981) and Corner (1983).
[c]Synonym of *Ganoderma* in Furtado (1981) and Corner (1983).

distinguished from characters that depend on growing conditions and developmental stage. For instance, careful observation *in vivo* shows that young, actively growing fruiting bodies generally have lighter and brighter surface colours than basidiocarps that are several weeks or months old: the latter have been exposed to repeated periods of rain and dryness, covered with dust, attacked by insects, or even colonized by algae. Presence, absence, size and insertion of the stipe have also been used to circumscribe species (e.g. *G. gibbosum*, *G. dorsale*, etc.), but it has been shown that stipe development can be controlled *in vitro* by the duration and intensity of exposure to light and by carbon dioxide concentration (Hseu, 1990). *In vivo*, stipe development also depends on the location in the host: a basidiocarp that develops from a buried root is more likely to develop a stipe than a basidiocarp that develops higher in the trunk (Fig. 2.1). Ryvarden (1995) examined the variability of 53 Norwegian specimens of *G. lucidum*, and concluded that macromorphological characters are of very limited value for the identification of *Ganoderma* species.

Reliable morphological characters for *Ganoderma* systematics appear to be spore shape and size, context colour and consistency, and microanatomy of the pilear crust. However, the typical spore of *G. lucidum* is similar for dozens of different species. Scanning electron microscopy (SEM) has been useful in distinguishing between spores that appear similar under light microscopy (Pegler and Young, 1973; Gottlieb and Wright, 1999), and has revealed the existence of distinctive, slightly longitudinally crested basidiospores in the *G. australe* and *G. sinense* species complexes (Hseu, 1990; Buchanan and Wilkie, 1995; Tham, 1998). Context colour and consistency may change slightly with the age of the fruit body or upon drying, and are also somewhat subjective characters, but it is still possible to distinguish at least three very distinctive types: (i) light coloured and/or duplex context in *G. lucidum* and its allies; (ii) uniformly brown to dark brown context as in the *G. sinense* and *G. australe* complexes; and (iii) very soft, cream to pale ochraceous context in *G. colossum*. Relationships between the microstructure of the pilear crust, the age of the basidiocarp, and the exposure to environment are not well known, but different types of pilocystidia and hyphal arrangement can be distinguished among both laccate and non-laccate taxa (Steyaert, 1980; Fig. 2.1). The laccate appearance of *Ganoderma* basidiocarps is associated with the presence of thick-walled pilocystidia (Fig. 2.1) that are embedded in an extracellular melanin matrix. The exact origin and chemical composition of this matrix remain to be elucidated.

High phenotypic plasticity at the macroscopic level, uniformity of microscopic characters, and subjective interpretation of various features such as colour or consistency have resulted in the creation of numerous unnecessary names (synonyms), and a lack of handy identification keys. The absence of a world monograph has also contributed to problems with species circumscriptions and identifications in *Ganoderma*.

Culture and enzymatic studies have produced additional and useful taxonomic characters in *Ganoderma* systematics (Adaskaveg and Gilbertson, 1986, 1989; Hseu, 1990; Wang and Hua, 1991; Gottlieb *et al.*, 1995; Gottlieb

and Wright, 1999). It appears that chlamydospore production and shape, and to a lesser extent the range and optima of growth temperatures, are extremely useful culture characters for distinguishing between morphologically similar species. Mating studies have also been conducted to circumscribe biological species within species complexes (Adaskaveg and Gilbertson, 1986; Hseu, 1990; Yeh, 1990; Buchanan and Wilkie, 1995). However, all these studies were restricted in scope, and the techniques employed, although useful at the species level, have limitations for addressing phylogenetic relationships between taxa and the development of a natural classification system.

Molecular Systematics of *Ganoderma*

With recent advances in both sequencing techniques to produce taxonomic characters and cladistic methods to infer natural relationships between organisms, molecular systematics has become a paradigm in biology. To date, the most widely used molecules in fungal molecular systematics have been the ribosomal genes (rDNA). Hibbett and co-workers (Hibbett and Donoghue, 1995; Hibbett *et al.*, 1997) produced molecular phylogenies for hymenomycetous fungi using sequence data from the nuclear small subunit (18S, or nSSU) and mitochondrial small subunit (12S, or mtSSU) rDNA, and showed that *Ganoderma* belongs to a larger group of white-rot fungi that also includes the genera *Trametes*, *Fomes*, *Polyporus*, *Lentinus*, *Datronia*, *Pycnoporus*, *Cryptoporus*, *Daedalopsis*, *Lenzites* and *Dentocorticium*. Additional phylogenetic studies using sequence data from the nuclear large ribosomal subunit (25–28S, or nLSU) rDNA showed that genera *Amauroderma*, *Irpex*, *Loweporus* and *Perenniporia* also belong to this group (Moncalvo *et al.*, 2000; Thorn *et al.*, 2000; Moncalvo, unpublished). Combined evidence of nLSU and mtSSU-rDNA data support the placement of *Amauroderma* as a sister genus to *Ganoderma* (Moncalvo and Hibbett, unpublished). However, nucleotide sequence data from nuclear and mitochondrial rDNA encoding sequences do not offer enough variation to infer phylogenetic relationships between *Ganoderma* species.

Appropriate nucleotide sequence variation for systematics of *Ganoderma* was found in the internal transcribed spacers (ITS) of the nuclear rDNA gene (Moncalvo *et al.*, 1995a, b, c). The ITS phylogenies produced in these studies indicated that many names were commonly misapplied (e.g. *G. lucidum* and *G. tsugae*), and that the proposed subgenera and sections in Steyaert (1972, 1980) and Zhao (1989) were not monophyletic and should be abandoned.

Gene trees and species trees

A gene tree is not necessarily equivalent to a species tree, and phylogenetic trees inferred from the sequences of different genes can be contradictory for several reasons, including differences in their power or level of phylogenetic

resolution, incorrect recovery of evolutionary relationships by phylogenetic reconstruction methods (e.g. 'long branch attraction', Felsenstein, 1978), discordance in rates and modes of sequence evolution (Bull *et al.*, 1993), different phylogenetic histories due to lineage sorting or difference in coalescence time (Doyle, 1992, 1997; Maddison, 1997), or horizontal gene transfer. Incongruences between gene trees are more likely to occur at lower taxonomic levels (species, populations). In fact, it is expected that gene trees are incongruent among interbreeding individuals because these individuals are connected by gene flow and recombination: their relationships are therefore tokogenetic (reticulate) rather than phylogenetic (divergent) (Hennig, 1966; Doyle, 1997). Overall, a phylogenetic hypothesis is more likely to be correct if it is supported from multiple, independent data sets rather than from a single gene tree.

ITS phylogeny versus manganese-superoxide dismutase (Mn-SOD) phylogeny

Thirty-three *Ganoderma* taxa were used to conduct separate phylogenetic analyses of sequence data from ITS and Mn-SOD genes. The incongruence length difference (ILD) test of Farris *et al.* (1994), also known as the partition-homogeneity test, indicated absence of statistically significant conflict ($P = 0.08$) in phylogenetic signals between the two data sets. Results of the analyses are shown in Fig. 2.2. Tree topologies are fully congruent for all nodes having bootstrap statistical support (BS) greater than 50%, with two exceptions:

1. the type specimen of *G. microsporum* clusters with *G. weberianum* CBS219.36 in the ITS analysis (88% BS), but clusters with a strain labelled *G.* cf. *capense* ACCC5.71 in the Mn-SOD analysis (98% BS); and
2. the cultivar *G.* cf. *curtisii* RSH.J2 nests with strain RSH-BLC in the ITS analysis (58% BS) but with RSH-J1 (83% BS) in the Mn-SOD analysis.

The latter three collections are known to be intercompatible (i.e. belong to the same biological species; Hseu, 1990), therefore conflicting gene phylogenies for these strains are not surprising. Strains labelled *G. microsporum*, *G. weberianum* and *G.* cf. *capense* are probably also conspecific: the synonymy of the first two names was already suggested by Peng (1990).

Both data sets strongly support similar terminal clades, and do not fully resolve basal relationships among *Ganoderma* taxa. The ITS data set offers slightly more resolution for deeper branches (Fig. 2.2), whereas higher sequence divergence between closely related taxa was found in the Mn-SOD gene (in particular in two introns that were excluded from the analyses because nucleotide sequences could not be unambiguously aligned across all the taxa sampled). Ongoing sequencing and analyses of β-tubulin genes also

support similar terminal clades to those from ITS and Mn-SOD data (Moncalvo and Szedlay, unpublished).

Therefore, preliminary data suggest that phylogenies derived from ITS sequences are congruent with those from other genes, and that ITS phylogenies may accurately reflect natural relationships between *Ganoderma* species.

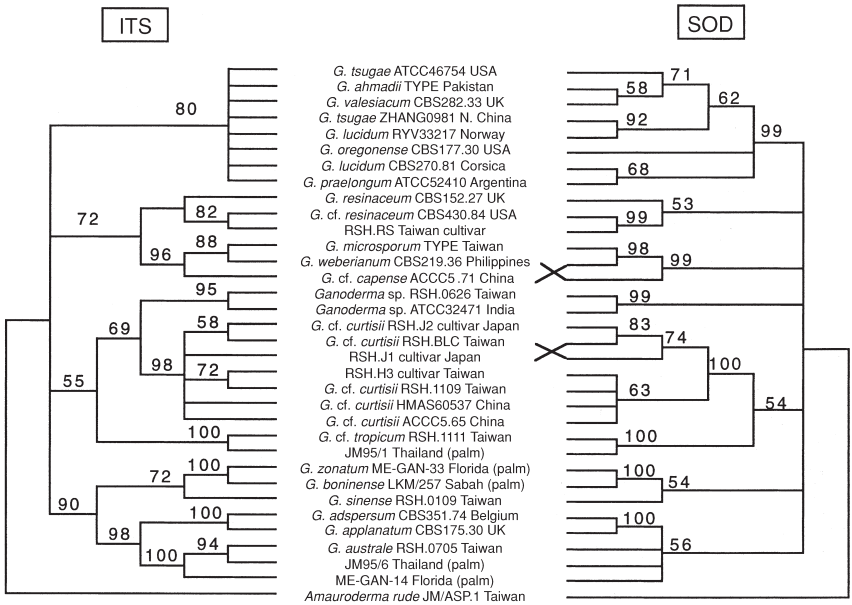

Fig. 2.2. Comparison between internal transcribed spacer (ITS) and manganese-superoxide dismutase (Mn-SOD) nucleotide sequence phylogenies for 33 *Ganoderma* taxa. Sequences from one species of genus *Amauroderma* were used to root the trees. Trees depicted are strict consensus trees produced from maximum parsimony searches. Bootstrap statistical supports greater than 50% are shown above branches. Mn-SOD data were from Wang (1996; GenBank accession numbers U56106-U56137), and Moncalvo and Szedlay (unpublished). Analyses were conducted in PAUP* (Swofford, 1998) and employed maximum parsimony with heuristic searches using 50 replicates of random addition sequences with TBR branch swapping. Bootstrap statistical supports were evaluated with 100 bootstrap replicates of random addition sequence with TBR branch swapping. Regions with ambiguous alignment were removed from the alignment, and unambiguously aligned gaps were scored as 'fifth character state'. The ITS data set used 81 parsimony-informative characters and produced 24 equally parsimonious trees of length 232, with a consistency index of 0.703. The SOD data set used 105 parsimony-informative characters and produced 58 equally parsimonious trees of length 329, with a consistency index of 0.623.

ITS phylogeny

The current ITS sequence database for *Ganoderma* and *Amauroderma* species includes about 300 taxa. Numerous small nucleotide insertions and deletions make sequence alignment problematic in several regions, but at least 380 characters can be aligned unambiguously across the entire data set, yielding about 200 parsimony-informative characters. Phylogenetic analysis of large molecular data sets is still a controversial field (Lecointre *et al.*, 1993; Hillis, 1996; Graybeal, 1998; Poe, 1998). One commonly encountered problem with large data sets concerns the applicability and/or accuracy of standard descriptors commonly used to assess branch robustness. For instance, the use of branch decay indices (Bremer, 1994) is not practical for large data sets because of the large number of trees that cannot be sampled; and consistency indices (Sanderson and Donhogue, 1989), bootstrap (Felsenstein, 1985) and jackknife (Farris *et al.*, 1996) statistical supports are sensitive to sample size. However, evidence from various studies (Hillis, 1996, 1998; Moncalvo *et al.*, 2000) suggests that increasing taxon sampling generally increases phylogenetic accuracy, and that bootstrapping or jackknifing methods are still useful tools to determine the robustness of clades.

Parsimony analyses of ITS data for 248 *Ganoderma* taxa reveal about 50 clades with bootstrap statistical support greater than 50% (Fig. 2.3 and Table 2.2), that are also consistent with morphological and/or geographical data. Terminal clades in this phylogeny represent either a population, a species, a species complex, or a group of closely related species. In Table 2.2, tentative names for the most well-supported clades are proposed, although 16 clades have not been named (the original data set included 36 species names and many unnamed taxa). Basal relationships are either poorly supported or unresolved, but phylogenetic analyses of various data sets using maximum parsimony and maximum likelihood consistently reveal three larger groups: these are labelled Groups 1–3 in Fig. 2.3 and Table 2.2.

ITS phylogeny suggests that the laccate habit has been derived more than once (or lost several times), making the laccate *Ganoderma* taxa polyphyletic. This conflicts with traditional systems of classification that accommodate laccate and non-laccate *Ganoderma* taxa in subgenera *Ganoderma* (laccate) and *Elfvingia* (non-laccate), respectively (see Table 2.1). However, within the *Ganodermataceae*, there is already evidence for non-monophyly of laccate taxa because at least three laccate species have been traditionally classified in genus *Amauroderma* (Furtado, 1981). A revised classification for subgenera and sections in *Ganoderma* seems therefore necessary, and will be formally proposed elsewhere. For now discussion is limited to some taxonomic groupings revealed by ITS sequence data, as summarized in Table 2.2.

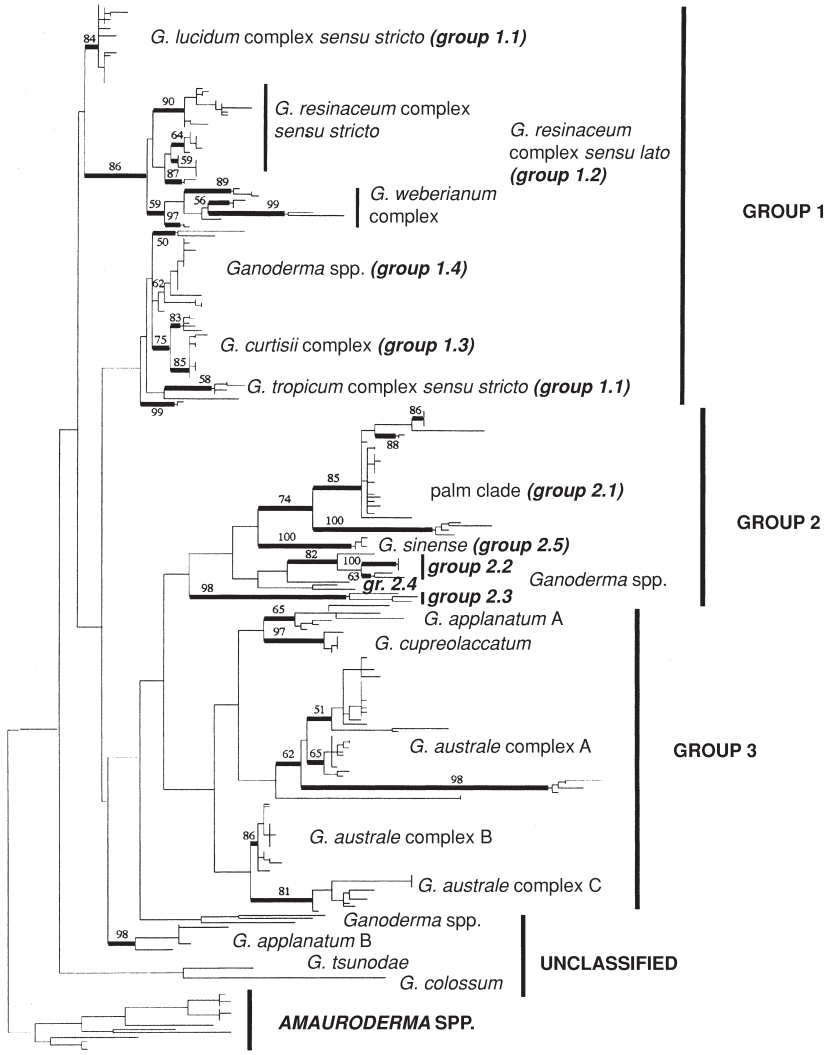

Fig. 2.3. Internal transcribed spacer (ITS) phylogeny for 248 taxa of *Ganodermataceae* (sequences from several *Amauroderma* species were used to root the tree). The tree depicted is one of 100 equally parsimonious trees produced using maximum parsimony in PAUP* (Swofford, 1998) with heuristic searches, random addition sequences (100 replicates), TBR branch swapping, and MAXTREES set to 100. Statistical supports for branch robustness were evaluated in PAUP* with 100 bootstrap replicates, random addition sequence, TBR branch swapping, and MAXTREES set to 10. Bootstrap values are only given for branches in bold that refer to groups or clades that are presented in Table 2.2. Groups 1 and 1.4 are not monophyletic in the figure they were retained as such to facilitate the discussion. Details about Groups 1–3 and unclassified taxa are given in the text and Table 2.2.

Table 2.2. Groupings of *Ganoderma* taxa based on a phylogenetic analysis of ITS nucleotide sequence data (Fig. 2.3), with geographic origin and host relationships of the strains examined.

	Geographic categories													Hosts		
	S. Africa	Europe	India, Pakistan	China, Korea	Japan	Taiwan	S.E. Asia	Indo, PNG	Australia	New Zealand	S. America	Neotropics	Florida	N. America	Woody dicots	Conifers	Palms
Group 1																	
1.1 *G. lucidum* complex *sensu stricto* (84% BS)																	
G. lucidum		●													●	●	
G. valesiacum		●														●	
G. carnosum		●														●	
G. ahmadii			●												●		
G. tsugae				●										●		●	
G. oregonense														●		●	
G. praelongum, G. oerstedii											●				●		
1.2 *G. resinaceum* complex *sensu lato* (86% BS)																	
G. resinaceum complex *sensu stricto*:																	
G. resinaceum (*'G. pfeifferi'*) (90% BS)	●	●													●		
G. cf. *resinaceum* (*'G. lucidum'*) (64% BS)													●	●	●		
G. cf. *resinaceum* (*G. sessile, G. platense*) (59% BS)											●				●		
G. weberianum complex (59% BS):																	
G. weberianum (= *G. microsporum*) (89% BS)						●	●		●						●		
G. cf. *capense* (56% BS)				●			●								●		
Ganoderma sp. (99% BS)							●								●		
Ganoderma sp. (*'G. subamboinense'*) (97% BS)											●	●			●		
G. trengganuense (87% BS)							●								●		

Table 2.2. *Continued.*

	Geographic categories														Hosts		
	S. Africa	Europe	India, Pakistan	China, Korea	Japan	Taiwan	S.E. Asia	Indo, PNG	Australia	New Zealand	S. America	Neotropics	Florida	N. America	Woody dicots	Conifers	Palms
1.3 *G. curtisii* complex (75% BS):																	
G. curtisii (= *G. meredithae*) (83% BS)												●	●	●	●	●	
G. cf. *curtisii* (*G. fulvellum*, '*G. tsugae*') (85% BS)				●	●	●	●								●		
1.4 *G. tropicum* complex *sensu lato*:																	
Ganoderma spp. 'clade A' (50% BS)							●					●			●		
Ganoderma sp. 'clade B' ('*G. lucidum*') (62% BS)			●			●	●								●		
Ganoderma sp. 'clade C' (99% BS)								●	●						●		
Ganoderma sp.		●													●		
Ganoderma sp.												●			●		
G. tropicum complex *s. stricto* (*G. fornicatum*) (58% BS)						●	●								●		●
Group 2																	
2.1 'palm clade' (74% BS):																	
G. zonatum-boninense group (85% BS):																	
G. zonatum (86% BS)													●				●
Ganoderma sp. (88% BS)		●		●													●
G. boninense					●		●	●	●								●
Ganoderma sp. (100% BS)							●		●						●		●
2.2 *Ganoderma* species (82% BS):																	
Ganoderma sp.		●													●		
Ganoderma sp. (100% BS)												●			●		
Ganoderma sp. ('*G.* cf. *tornatum*') (63% BS)							●								●		

Continued

Table 2.2. *Continued.*

	Geographic categories														Hosts		
	S. Africa	Europe	India, Pakistan	China, Korea	Japan	Taiwan	S.E. Asia	Indo, PNG	Australia	New Zealand	S. America	Neotropics	Florida	N. America	Woody dicots	Conifers	Palms
2.3 *G.* cf. *balabacense* (98% BS)	●						●								●		
2.4 *Ganoderma* sp.							●								●		
2.5 *G. sinense* (100% BS) (= *G. formosanum*, = ?*G. neojaponicum*)				●		●									●		
Group 3																	
G. australe-applanatum complex *sensu lato*:																	
G. applanatum A (*G. lobatum, G. adspersum*) (65% BS):		●			●									●	●		
G. cupreolaccatum (= *G. pfeifferi*) (97% BS)		●													●		
G. australe complex *sensu stricto*:																	
G. australe complex A (62% BS):																	
'Clade A.1' (51% BS)				●		●	●	●							●		●
'Clade A.3' (65% BS)												●	●		●		●
'Clade A.2' (98% BS)							●								●		●
G. australe complex B (86% BS)	●								●	●	●				●		
G. australe complex C (81% BS)			●	●		●	●			●	●				●		

Table 2.2. *Continued.*

	Geographic categories													Hosts		
	S. Africa	Europe	India, Pakistan	China, Korea	Japan	Taiwan	S.E. Asia	Indo, PNG	Australia	New Zealand	S. America	Neotropics	Florida	N. America	Woody dicots	Conifers	Palms
Unclassified																	
G. applanatum B (98% BS)			●											●	●		
Ganoderma sp. (100% BS)		●					●								●		
Ganoderma sp. (85% BS)												●			●		
G. tsunodae (*Trachyderma*)					●										●		
G. colossum (*Tomophagus*)		●					●					●	●		●		

Names in parentheses are commonly misapplied names (in 'quotes'), synonyms (=) or possible alternative names. Frequency values (% BS) following taxa names are bootstrap statistical support for that clade (only supports higher than 50% are given). Geographic categories and samplings are as follows: 'S. Africa' includes collections from South Africa and Zimbabwe; 'Europe' includes collections from UK, Norway, France, The Netherlands, Belgium, Austria, and Germany; 'China' includes collections from mainland China with exclusion of subtropical and tropical collections from Yunnan; 'S.E. Asia' includes subtropical and tropical collections form Yunnan, Thailand, Vietnam, Philippines, Peninsular Malaysia, Sabah, and Singapore; 'Indo, PNG' includes collections from Bali, Malukku, and Papua New Guinea; 'S. America' includes collections from Argentina and Chile; 'Neotropics' includes collections from Costa Rica, Puerto Rico, Equador, and French Guyana.

Phylogenetic Relationships and Biogeography in *Ganoderma*

Phylogenetic relationships

Group 1: the *G. lucidum* complex *sensu lato*

Group 1 is either monophyletic or paraphyletic, and includes *G. lucidum sensu stricto* and many other similar laccate *Ganoderma* taxa, of which several collections were incorrectly identified as *G. lucidum*. In this group, basidiospore shape and size is very uniform, and taxa generally have a reddish to dark-brown pileus and light-coloured context. On the basis of ITS phylogeny, Group 1 can be divided into at least four clades, which are discussed below.

GROUP 1.1: THE *G. LUCIDUM* COMPLEX *SENSU STRICTO.* The *G. lucidum* complex *sensu stricto* includes only collections from temperate regions of both the northern and southern hemispheres. Members of this group do not produce chlamydospores in culture. ITS sequence variation among taxa of this clade is very low and does not allow for subdivision into smaller entities. European taxa of this clade (*G. lucidum*, *G. valesiacum* and *G. carnosum*) might be conspecific (Ryvarden and Gilbertson, 1993): *G. valesiacum* was primarily distinguished from *G. lucidum* based on host specificity (conifers versus hardwood, respectively; Ryvarden and Gilbertson, 1993), but a recent study by Ryvarden (1995) suggests that *G. lucidum* in Norway grows on both hardwood and conifers; *G. carnosum* (= *G. atkinsonii*) has been reported only on conifers, and is distinguished from both *G. lucidum* and *G. valesiacum* by having rougher spores (Kotlaba and Pouzar, 1993; Ryvarden and Gilbertson, 1993). The type specimen of *G. ahmadii* from Pakistan (Steyaert, 1972) belongs to this clade: several collections of this species in Steyaert's herbarium have been examined, and all can be distinguished from typical *G. lucidum* in having a less shiny pileus and a darker context, which is entirely brown and duplex. The two North American taxa of this clade (*G. tsugae* and *G. oregonense*) are believed to be restricted to conifers and might be conspecific (Gilbertson and Ryvarden, 1986). Basidiocarps of *G. lucidum* from Europe and *G. tsugae* from the USA are practically impossible to distinguish. The Argentine collections of this clade (*G. praelongum*) were not examined for this study, but Gottlieb and Wright (1999) distinguished the taxon from *G. lucidum*.

GROUP 1.2: THE *G. RESINACEUM* COMPLEX *SENSU LATO.* The production of chlamydospores in culture unites the members of this clade. *G. resinaceum*, a species described from Europe, is differentiated from *G. lucidum* by having smoother spores (Steyaert, 1972; Pegler and Young, 1973). European *G. resinaceum* has been shown to be intercompatible with collections generally assigned to '*G. lucidum*' in North America (Adaskaveg and Gilbertson, 1986), suggesting conspecificity of these isolates. However, ITS data distinguish between populations of *G. resinaceum* from Old World (Europe and Africa), North America,

and South America; these populations might therefore be completely disjunct and genetically isolated from each other, and may warrant recognition at the species level. However, additional sampling and more extensive mating studies are needed before a firm taxonomic conclusion can be reached.

The counterpart of the *G. resinaceum* complex in tropical Asia is the *G. weberianum* complex (Steyaert, 1972), which includes *G. weberianum*, *G. microsporum*, *G.* cf. *capense*, *G. lauterbachii*, *G. rivulosum*, etc.). It is distinguished from *G. resinaceum* by having smaller spores (6–9 × 4–7 μm).

Based on ITS data, *G. trengganuense* also belongs to this clade. This species is known from Malaysia and Vietnam and is well characterized in having subreticulate spores (Corner, 1983), but is similar to *G. resinaceum* in the other characters.

GROUP 1.3: THE *G. CURTISII* COMPLEX. Members of this clade do not produce chlamydospores in culture. This well-supported clade (75% BS) can be divided in two groups which correspond to the geographic origin of the collections. One group is composed of collections from eastern North America and Costa Rica. These collections can be identified as *G. curtisii* (a species described from eastern America) based on descriptions in Lloyd (1912, 1917) and Steyaert (1972, 1980), and *G. meredithae* (Adaskaveg and Gilbertson, 1988) can be considered a taxonomic synonym. The sister group of these taxa is represented by collections from eastern Asia (Korea, China, Taiwan, Japan and Vietnam), and includes many cultivars from this region mistakenly identified as '*G. tsugae*' or '*G. lucidum*'.

GROUP 1.4: THE *G. TROPICUM* COMPLEX *SENSU LATO*. This group is heterogeneous and may not be monophyletic, but is retained here for convenience. Members of this group have been collected throughout tropical and subtropical regions. Only a few taxa have been examined in culture, and they all produced chlamydospores. In this group, several distinct, well-supported clades revealed by ITS data are also supported by differences in basidiocarp or culture characteristics. For instance, Group 1.4 includes:

- three species from Taiwan distinguished by Hseu (1990) on the basis of enzymatic, culture, and mating studies ('*G. lucidum*', *G. tropicum*, and *G. fornicatum*);
- a very distinctive taxon from Australia with a light, thick and soft context, a thin and yellowish crust, and a bright, dark-red laccate stipe (maybe *G. septatum*, described from Africa by Steyaert, 1962);
- undescribed collections from Costa Rica with purple–orange basidiocarps;
- a specimen from Argentina, first identified as *G. oerstedii* by Bazzalo and Wright (1982) and then assigned to '*G. resinaceum*' by Wright (personal communication).

Many taxa in this group are still represented by a single or only a few collections, and the correct naming of species remains problematic.

Group 2

Group 2 includes laccate taxa easily distinguished from *G. lucidum sensu lato* by a difference in spore shape (e.g. elongated spores in *G. zonatum* and *G. boninense*), and/or by a darker pileus and/or context colour (e.g. black pileus and uniformly brown context in *G. sinense*). This group also includes non-laccate (or 'sublaccate'?) taxa. Group 2 is mostly composed of tropical and subtropical collections, but also includes collections from temperate Japan, Korea and China. Strains placed in group 2 that have been examined in culture did not produce chlamydospores.

GROUP 2.1: THE PALM CLADE. A well-supported clade (74% BS), composed only of collections from palms, which can be divided into three smaller groups corresponding to the geographic origin of the strains: (i) *G. zonatum* from Florida; (ii) *G. boninense* from South-East Asia, the Australo-Pacific region and Japan; and (iii) unidentified collections from Zimbabwe and India. *G. zonatum* and *G. boninense* have elongated basidiospores and an uniformly brown-coloured context, but in *G. zonatum* the basidiospores are slightly longer (11–14 × 5–7 versus 9–13 × 5–7 μm), the pileus has a lighter colour, and the pilear crust is thinner. Additional sampling and mating studies will be necessary to determine the robustness of the geographic structure, delimit species boundaries, and to evaluate specificity on palms.

A sister group to the *G. zonatum-boninense* clade comprises collections from Vietnam, Malaysia, Thailand and Australia, from both palm and woody dicots. These collections differ from *G. zonatum* and *G. boninense* in having a black pileus and ovoid spores. SEM revealed that basidiospores of the Vietnam collection are longitudinally striate (Tham, personal communication). These collections somewhat resemble those in the *G. sinense* clade (Group 2.5).

GROUP 2.2. Group 2.2 includes three clades, and encompasses macromorphologically distinct taxa from three different continents. These taxa remain to be named. All have a uniformly brown context. Basidiocarps collected in Costa Rica and Puerto Rico have a shiny black pileus, and a white pore surface that turns dark brown upon ageing. Basidiocarps from Vietnam (originally identified as '*G. tornatum*', a non-laccate taxon) and Yunnan are dull, greyish to black. Finally, an immature specimen from Zimbabwe has a dull, brownish-red surface.

GROUP 2.3. Two collections cluster together strongly (98% BS): one collection from Vietnam with a shiny, yellow–brown to dark-brown pileus and a brown context, identified as *G.* cf. *balabacense* by its collector (Dr Le Xuan Tham), and one collection from Zimbabwe for which the basidiocarp is lacking.

GROUP 2.4. A non-laccate collection from Malaysia growing on an ornamental tree, received from Dr Faridah Abdullah as *Ganoderma* sp., stands within Group 2, apart from all the other taxa.

GROUP 2.5: THE *G. SINENSE* COMPLEX. Th1is clade includes collections from China, Taiwan and Korea. Chinese collections correspond to *G. sinense*, a species described from China. It has a distinctive, shiny black pileus and a brown to dark-brown context (Zhao, 1989). The Taiwan collection included in this study (labelled *G. formosanum*, but considered a synonym of *G. sinense*) has basidiospores longitudinally slightly striated, as shown in SEM by Hseu (1990). SEM examination of spores has not been conducted for the other collections of this clade. The Korean collection was received from Dr Dong-Suk Park as *G. neojaponicum*. Both *G. sinense* and *G. neojaponicum* are black and laccate taxa with a brown context, but whether or not the two names are synonyms remains to be investigated.

Group 3: the *G. australe-applanatum* complex

Group 3 comprises the bulk of non-laccate taxa of the *G. australe-applanatum* complex (subgenus *Elfvingia* in Table 2.1), but also includes a laccate species from Europe: *G. cupreolaccatum* (= *G. pfeifferi*). All members of this group lack chlamydospores in culture.

The placement of *G. cupreolaccatum* in the *G. australe-applanatum* complex is surprising, but this species differs from other laccate species (especially from those in Group 1) in having a dark-brown context, very similar in colour and consistency to that in *G. australe* and *G. applanatum*. It is also interesting to note that the culture strain CBS250.61 identified as '*G. applanatum*' by K. Lohwag classifies in *G. cupreolaccatum* based on ITS sequence data. Careful examination of *G. cupreolaccatum* collections shows that in older basidiocarps the pileus surface turns greyish-black and is not very shiny; various encrustations and erosion of the melanin wax of the crust may alter the laccate appearance of the basidiocarps, which then would more closely resemble those of *G. applanatum* or *G. australe*.

Although most collections belonging to this group were originally identified *G. australe* or *G. applanatum*, some collections were also assigned to *G. tornatum*, *G. adspersum*, *G. lobatum*, *G. philippii*, *G. pseudoferreum*, or *G. gibbosum*. These names are scattered inconsistently (if not randomly) in the ITS phylogeny, demonstrating the limitations of morphological taxonomy in this species complex. A large amount of ITS sequence divergence was found in this group (see branch length in Fig. 2.3), and several smaller clades can be distinguished.

A well-supported clade (65% BS) consists entirely of collections from temperate areas of the northern hemisphere (Europe, Japan and North America), and is provisionally assigned the name '*G. applanatum* A' (*G. applanatum* was first described from Europe, and *G. australe* from a Pacific island). The remaining clades do not include European collections, and are provisionally grouped under the name '*G. australe* complex *sensu stricto*'. On the basis of ITS sequence data, this complex can be subdivided further into at least three well-supported clades, showing remarkable and complex geographic patterns (Table 2.2): Clade A is pantropical, but also includes collections from Korea and China, and

in that clade neotropical collections are distinct from Old World collections; Clade B is composed only of collections from the southern hemisphere; and Clade C includes collections from Asia and the southern hemisphere. Mating data produced by Yeh (1990) and Buchanan and Wilkie (1995) indicate at least two intersterile groups of '*G. australe*' in Taiwan and New Zealand, respectively. Mating data and ITS phylogeographic patterns suggest several genetically isolated groups (species) in the *G. australe* complex.

Unclassified taxa

'*G. APPLANATUM* B'. A strongly supported clade (98% BS) composed of non-laccate collections from Europe and eastern North America remains unclassified: it clusters at the base of Groups 2 and 3 in Fig. 2.3, but also nests at the base of Group 1 in some analyses. Because this clade includes non-laccate taxa from Europe, it is provisionally named as '*G. applanatum* B'.

ITS data support the view that at least two non-laccate species exist in Europe (Pegler and Young, 1973; Ryvarden and Gilbertson, 1993). Either '*G. applanatum* A' or '*G. applanatum* B' represents the true *G. applanatum*. The two clades can not be distinguished from basidiocarp characteristics. Also, since these ITS-based clades are so far composed only of northern temperate collections (Table 2.2), it is possible that *G. applanatum sensu stricto* only occurs in the temperate regions of the northern hemisphere.

G. TSUNODAE, G. COLOSSUM AND OTHER TAXA. *G. tsunodae*, known only from Japan (Imazeki, 1952) and China (Zhao, 1989), and *G. colossum*, a pantropical species (Ryvarden and Johansen, 1980), remain unclassified. They are on long branches in ITS phylogenies, generally at the base of the trees, and both might warrant segregation into separate genera as proposed by Imazeki (1939) and Murrill (1905b). Several unidentified taxa also remain unclassified: for instance, a non-laccate species collected in French Guyana and Puerto Rico, that is easily recognizable from the cinnamon colour of its context, and laccate collections from Zimbabwe and Vietnam, with a reddish-brown to blackish pileus and dark-brown context.

Biogeography

The number of known *Ganoderma* species can be estimated at about 60–80 laccate and 10–30 non-laccate species (Table 2.1), and it is likely that new taxa are yet to be discovered in poorly studied tropical regions. These numbers are based on a literature survey, examination of type specimens, numerous field collections in various regions of the world, molecular phylogenetic data and, in some cases, mating data. On a similar basis, it can be estimated that the current sampling of ITS sequences encompasses at least 80% of all known taxa from temperate regions, about half of the taxa from South-East and eastern

Asia (it would seem that the number of species described from China by Zhao and his collaborators (Zhao, 1989) has been overestimated), and 20–40% of neotropical taxa. Molecular data from African material is almost entirely lacking.

Based on these sampling estimates and the ITS phylogeny summarized in Fig. 2.3 and Table 2.2, it appears that *Ganoderma* taxa repeatedly show similar patterns of geographic distribution, between and/or within clades: e.g. disjunction between temperate and tropical taxa, disjunction between Old (Europe, Asia, Africa) and New (the Americas) Worlds, a link between southern hemisphere taxa (South Africa, Argentine, Chile, New Zealand, Papua New Guinea and Australia), and connection between the more tropical regions of the southern hemisphere (northern Australia and Papua New Guinea) and South-East Asia.

Current ITS data indicate the existence of 5–7 species in Europe and 7–8 in North America; these estimates are in agreement with the more recent traditional floras for these regions (Gilberston and Ryvarden, 1986; Ryvarden and Gilbertson, 1993), although there is still some disagreement between ITS and morphological data in circumscribing and naming taxa. ITS phylogeny identifies at least 12 taxa in temperate and subtropical Asia (China, Korea, Japan and Taiwan), but more species probably exist in this area. Within undersampled and species-rich regions, Table 2.2 indicates the presence of at least 18 ITS-based taxa in tropical Asia, and eight in the Neotropics.

Taxa from Africa remain poorly sampled in molecular studies. The unidentified taxa from South Africa and Zimbabwe that were included in this work are diverse, and either nest in isolated positions or cluster with European or Asian strains. A high level of taxonomic diversity (and perhaps also endemism) is expected in Africa, because several well-characterized species have not been reported outside that continent, e.g. *G. alluaudii* (Ryvarden, 1983), *G. chonoides* (Steyaert, 1962), *G. sculpturatum* (Ryvarden and Johansen, 1980), *G. hildebrandii* (Moncalvo and Ryvarden, 1995), etc.

Host relationships

Host specificity has been used to circumscribe *Ganoderma* taxa. In the northern temperate regions *G. valesiacum*, *G. carnosum*, *G. tsugae* and *G. oregonense* have been distinguished from *G. lucidum*, mainly because they are all believed to be restricted to conifers, as discussed above. All these taxa belong to clade 1.1 (the *G. lucidum* complex *sensu stricto*, Table 2.2). However, before a conclusion can be reached about host specificity on conifers, there is still need for a better understanding of species boundaries in clade 1.1; collections from conifers at higher altitudes in tropical or subtropical regions should also be examined.

Steyaert (1967) was the first to extensively study collections from palms. He reported five laccate and one non-laccate species:

- *G. zonatum*, in America and Africa, mostly on palms but also found on *Eucalyptus*;
- *G. miniatotinctum*, in South-East Asia and Solomon Islands, found only on palms;
- *G. boninense*, from Sri Lanka to the Pacific islands and Japan to Australia, mostly on palms but also found on *Casuarina*;
- *G. cupreum*, paleotropical, on both palms and woody dicots;
- *G. xylonoides*, restricted to Africa, on both palms and woody dicots; and
- *G. tornatum*, in Asia and some Pacific islands, only on palms.

The ITS phylogeny also distinguishes at least five laccate taxa on palms (Table 2.2), but these differ slightly from those described in Steyaert (1967) with respect to their geographic distribution and host specificity. Table 2.2 also indicates the presence of 1–3 non-laccate species growing on palms, but again these results differ slightly from Steyaert's (1967) concerning the geographic distribution and host specificity. The ITS phylogeny also strongly suggests a single origin (monophyly) for four out of the five laccate taxa growing on palms (Table 2.2).

Conclusions

The data presented here show that ITS-based clades are generally consistent with morphology or geography. Species boundaries within ITS clades still need to be addressed with mating studies, multigene phylogenies, or both. Type specimens must be studied where available before naming ITS clades in the Linnean system of classification. However, given the difficulties of taxonomic identification of *Ganoderma* collections using traditional methods, the ease and reducing costs of PCR amplification and direct sequencing techniques, and the rapid expansion of molecular databases for a broad array of fungi, molecular methods might become the easiest way to identify *Ganoderma* and other problematic fungal strains. This is particularly appealing for the preventive care of woody plant crops, because vegetative mycelia extracted from wood could be identified quickly using molecular techniques. Sequence data used in this study will be made available in both GenBank and the Internet address http://www.botany.duke.edu/fungi/

Construction of a web site on *Ganoderma* systematics is also in progress, and will be found at the same address.

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