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A Cladistic Approach to Biodiversity in the Ganodermataceae

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ABSTRACT: Morphological characters that are potentially phylogenetically informative for distinguishing evolutionary lineages in the Ganodermataceae are reviewed and used in cladistic analysis with ten taxa exhibiting diverse character combinations. Results indicate that there do exist taxonomic arrangements requiring less character-state changes during evolution, i.e., are more parsimonious, than taxonomic systems proposed to date. Among the 24 most parsimonious trees found in the morphological analysis there are trees in agreement with rDNA molecular phylogenies. Taken together, these results allow the delimitation of major evolutionary lineages in the Ganodermataceae. It is argued that these lineages are highly informative to evaluate genetic diversity in the Ganodermataceae. The number of potential species known in each lineage is discussed. Most taxa apparently are geographically restricted. Taxa used in folk medicine and pharmacological studies are not fully representative of the extent of genetic diversity in the family Ganodermataceae, although they do reflect diversity within the genus *Ganoderma,* the largest group in terms of number of species described.

1 INTRODUCTION

Addressing questions relative to biological diversity is a kind of systematic exercise. Phylogenetic classification provides information about evolutionary relationships and patterns of genetic variation, and can discern discrete pools of genetic diversity. Early systematic work in the Ganodermataceae was based exclusively on morphological characters and followed a phenetic approach to classification: organisms were grouped on the basis of morphological resemblance on the assumption that mor-

phologically similar taxa are also genetically similar. These concepts lead past authors (Steyaert 1972, Juhlich 1981, Furtado 1981) to propose different classification schemes in the Ganodermataceae. How these classifications developed is summarized below.

Ganoderma s. lato (Ganodermataceae Donk) is defined by the presence of a double-walled basidiospore. Because this character is unique among polypores and because basidiospore morphology has always been regarded by mycologists as a criterium of primary importance in distinguishing taxonomic units, the group is believed to be natural. Also, splitting the Ganodermataceae into major groups was nearly exclusively based on spore morphology. The typical 'ganodermatoid' basidiospore has the apex thickened (*Ganoderma* Karst.) and differs from the typical 'amaurodermatoid' basidiospore, which has the spore wall uniformly thickened (*Amauroderma* Murr.). Studies using light microscopy has shown reticulate 'ganodermatoid' basidiospores (*Humphreya* Stey.) and longitudinally crested 'amaurodermatoid' basidiospores (*Haddowia* Stey.). More recently, scanning electron microscopy has revealed longitudinally crested 'ganodermatoid' basidiospores in a few species (Hseu 1990, Buchanan and Wilkie 1995).

Pilear crust is also diverse in the Ganodermataceae and has been a source of taxonomic characters in the group. It can be thick, strongly laccate and composed of pilocystidia, as in the species of the *G. lucidum* group (*Ganoderma* subgen. *Ganoderma*); thin and shiny but not strongly laccate with pilocystidia present, as in *G. colossum* and *Humphreya eminii*; and dull and lack pilocystidia, as in species of the *G. applanatum - G. australe* group (*Ganoderma* subg. *Elfvingia*). In species having 'amaurodermatoid' basidiospores, the vast majority of taxa lack pilocystidia and the pileus is dull; however, a few laccate/pilocystidiate species have been described (e.g., *A. leptopus, A. renidens, Ha. aetii, Ha. longipes*). Some authors (Furtado 1965, Steyaert 1972) have attempted to distinguish between different types of dull pilei in both *Amauroderma* and *Ganoderma*, but their studies were inconclusive for delimiting natural groups. However, Imazeki (1939) created *Trachyderma* (an invalid name, see Ryvarden 1991) for *G. tsunodae*, for it has a coarse, asperulate pilear surface.

Macro-characteristics of the context tissue were used by Murrill (1905), who proposed the genus *Tomophagus* to accommodate *G. colossum*, for it bears an unusually large and soft context. However, most authors do not consider this character to be of sufficient taxonomic importance for use at the generic level, and in most taxonomic treatments of the Ganodermataceae *Tomophagus* is a synonym of *Ganoderma*. Phylogenetic analysis of molecular data indicates that *G. colossum* is basal to both *Ganoderma* and *Amauroderma* and supports generic rank for *Tomophagus*

(Moncalvo *et al.* 1995c). Corner (1983) emphasized the importance of hyphal construction in understanding the systematics of Ganodermataceae, although he did not propose a taxonomic system on that basis. Hyphal construction in the context of *T. colossus* differs from typical *Ganoderma* in lacking numerous skeletal binding hyphae or arboriform skeletal hyphae. In fact, the context of *T. colossus* tends more to be dimitic than trimitic. Dimitic or nearly dimitic context is also found in *G. hildebrandii*, *G. leucocreas* (Moncalvo and Ryvarden 1995), *Humphreya eminii*, and other species. The hyphal system in *Amauroderma* has generally been reported as trimitic (Furtado 1980, Ryvarden and Johansen 1980, Zhao 1989) but the binding hyphae and the thin branches of the arboriform skeletal hyphae are rather brittle, unlike those in *Ganoderma* (Ryvarden and Johansen 1982). Corner (1983) described variations in hyphal construction within the Ganodermataceae and stressed differences between typical *Ganoderma* species, in which arboriform skeletal cells are generally terminal, and typical *Amauroderma* species, in which they are both terminal and intercalary. However, both Steyaert (1972) and Corner (1983) stressed that, as in the pilear crust, there is no clear-cut distinction between the different hyphal types of the context.

Other morphological characters that have been used for systematics in the Ganodermataceae (colors, spore size, shape and size of pores, characteristics of the stipe) are of little help in distinguishing among major evolutionary lineages. For instance, it has been shown in some *Ganoderma* species growing *in vivo* (see Corner 1983) or *in vitro* (Hseu 1990) that stipe formation depends on external constraints.

Species of the Ganodermataceae all cause white-rot but are otherwise ecologically diverse. They grow on living or dead wood, on dicotyledons (angiosperms as well as gymnosperms) or monocotyledons (palms, bamboo). Host-specificity is poorly known. However, *Amauroderma* species are generally found on the ground (and attached on dead wood or roots underneath) or on the expanding roots of tropical trees or stumps, whereas most *Ganoderma* species grow at the base of trunks or higher. In nature, the transition between ground-growing taxa and trunk-growing taxa probably has occurred more than once, but this characteristic may nevertheless have evolutionary significance.

I have drawn in Figs 1-3 phylogenetic relationships based on classification schemes proposed by past authors on the basis of the morphological characters summarized above. All authors distinguish *Amauroderma* and *Ganoderma* on the basis of spore-wall thickness. Within *Ganoderma,* all authors distinguish laccate species (subg. *Ganoderma*) from non-laccate species (subgen. *Elfvingia*). Juhlich (1981) excluded from the Ganodermataceae taxa with ornamented basidiospores

and created the Haddowiaceae for *Haddowia* and *Humphreya* (Fig. 1). In a Furtado-based (1981) system, *Haddowia* is classified within *Amauroderma* whereas *Humphreya* and *Tomophagus* are nested within *Ganoderma* (Fig. 2). In a Steyaert-based (1972) system (Fig. 3), *Ganoderma, Amauroderma, Tomophagus, Haddowia* and *Humphreya* represent five distinct lineages with unresolved basal relationships.

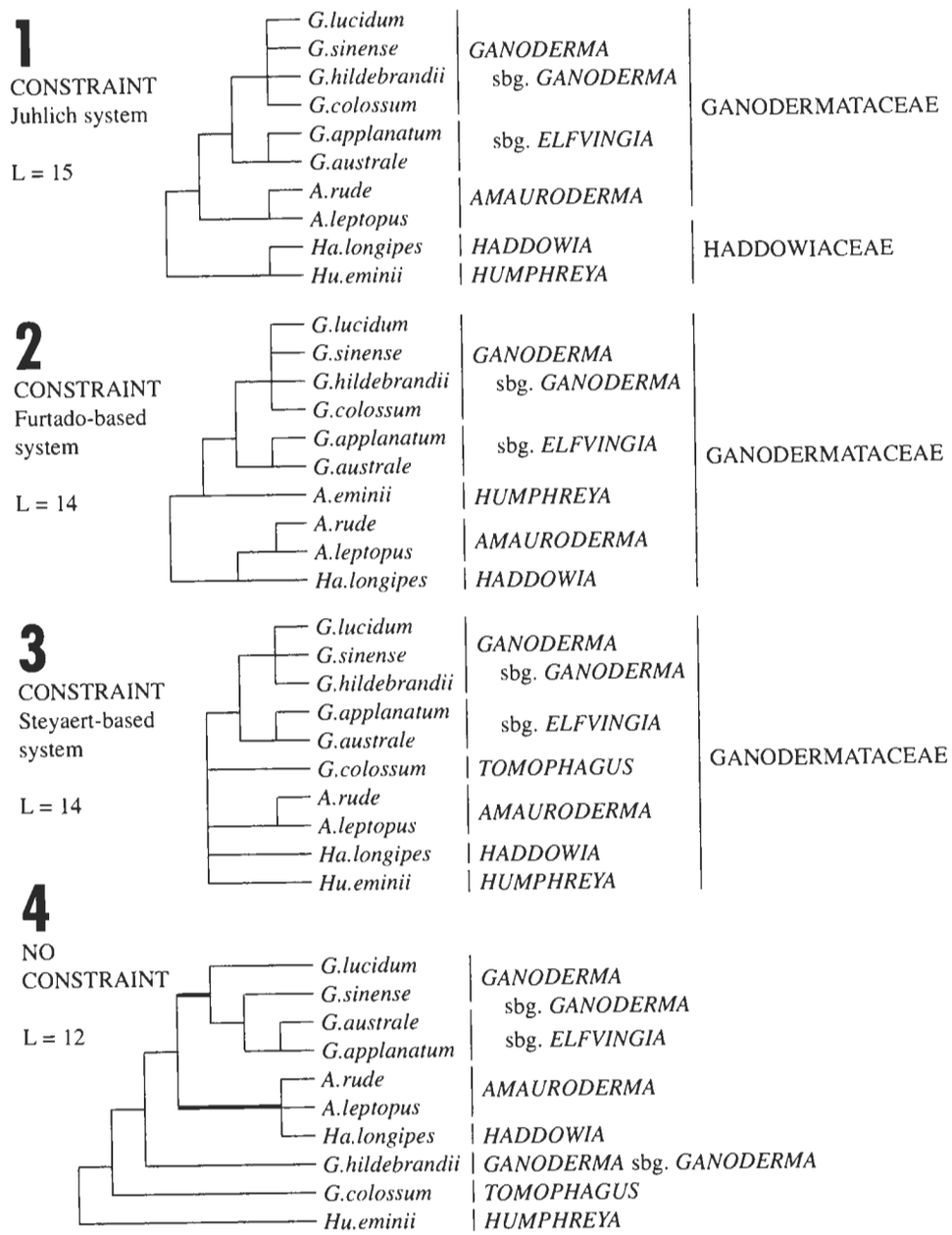
From Figs. 1-3 and above, it is clear that morphological and ecological traits of Ganodermataceae are diverse and interpretation of this diversity has lead different authors to propose different taxonomic systems. It is also shown that, as in the majority of fungi, there are only a limited number of morphological characters for studying group relationships. Fortunately, additional phylogenetic characters are now being gathered through molecular data. Most taxonomists now follow Hennig (1966) and use a cladistic approach to classification instead of a phenetic approach. In the polypore phylogeny of Hibbett and Donoghue (1995a) based on mitochondrial ribosomal DNA sequences (mt rDNA), *Ganoderma* nests in a clade that includes *Polyporus* s.stricto, *Trametes, Daedalopsis* and *Lentinus*. Molecular studies based on the 25s rDNA and the ITS region of the rDNA have been conducted in the Ganodermataceae by the present author (Moncalvo et al. 1995a,b,c). Molecular studies suggest that *Ganoderma* is of recent origin, and suggest that the double-walled basidiospore may have been derived from smooth spore. Hibbett and Donhogue (1995) indicated that the Ganodermataceae could eventually be reduced to sub-family rank in the Polyporaceae to better reflect its evolutionary history within the polyspores.

In this presentation, I will use cladistic analyses of morphological and molecular data to delimit major evolutionary lineages in the Ganodermataceae. These lineages can serve as a basis to evaluate biological diversity in the group. I will also estimate the number of taxa that have been distinguished to date within each lineage, and assess the reported geographic distribution of these taxa. In conclusion, I will determine what part of the biological diversity of the Ganodermataceae has been sampled for medicinal use.

2 MATERIAL AND METHODS

2.1 *Morphological analysis*

Ten taxa of Ganodermataceae showing extreme morphological differences were selected for morphological analysis. Table 1 briefly describes these taxa with emphasis on characters believed to be relevant for taxonomic



Figs. 1-4. Cladistic analysis of 5 morphological characters for 10 taxa of Ganodermataceae. The data matrix used in maximum parsimony analysis was constructed from Table 1. Tree topologies were constrained following Juhlich (Fig. 1), Furtado-based (Fig. 2) or Steyaert-based (Fig. 3) systems (see text), or were not constrained (Fig. 4). Resulting tree lengths (L) are indicated in the figures. The unconstrained analysis found 24 equally most parsimonious trees (consistency index = 0.6667, retention index = 0.7333), of which one is given in Fig. 4: bold lines indicate branches found in all 24 trees. Trees were rooted by the mid-point method.

segregation at higher levels. Table 1 also shows how these characters segregate in members of allied genera, and how they were coded in cladistic analyses. Only five characters were retained, of which two refer to basidiospore morphology, in agreement with earlier studies that emphasize spore shape in the taxonomy of the Ganodermataceae. Macro-characteristics of the pilear crust (laccate, shiny, or dull) were lumped with micro-characteristics (presence/absence of pilocystidia, derm-type in absence of pilocystidia) because 1) the two sets of data provide redundant information, as laccate/shiny pilei have pilocystidia whereas dull pilei have no pilocystidia, and 2) the different types of derm described when pilocystidia are lacking (anamixoderm, plecoderm, trichoderm, inoderm) are not readily distinguishable. For simplification, the hyphal system in the context tissue was categorized as being 'dimitic' when binding or

Table 1. Taxonomic groups representative of morphological variation in *Ganoderma* and related genera, and character coding for cladistic analysis (see text).

	basidiospore									
taxa	wall	*	surface	*	pilear crust	*	context hyphae	*	occurrence	*
G. lucidum group	double-walled, appex thickened	2	echinulate	1	laccate, pilocystidia	0	trimitic	2	wood	1
G sinense	double-walled, appex thickened	2	echinulate, crested	3	laccate, pilocystidia	0	trimitic	2	wood	1
G. (Tomophagus) colossus	double-walled apex thickened	2	echinulate	1	shiny, thin, pilocystidia	1	dimitic	0	wood	1
G. hildebrandii, G. leucocreas	double-walled, apex thickened	2	echinulate	1	laccate, pilocystidia	0	dimitic	0	ground	0
G. (Elfvingia) applanatum group	double-walled, apex thickened	2	echinulate	1	dull	2	trimitic	2	wood	1
G. (Elfvingia) australe group	double-walled apex thickened	2	echinulate, crested	3	dull	2	trimitic	2	wood	1
Humphreya eminii	double-walled, apex thickened	2	echinulate, reticulate	2	shiny, thin, pilocystidia	1	dimitic	0	ground	0
Amauroderma gr. (typical spp.)	double-walled uniformly thick	1	echinulate	1	dull	2	intermediate	1	ground	0
A. leptopus and *A. renidens*	double-walled, uniformly thick	1	echinulate	1	laccate pilocystidia	0	intermediate	1	ground	0
Haddowia aetii and *Ha. longipes*	double-walled uniformly thick	1	echinulate, crested	3	laccate pilocystidia	0	intermediate	1	ground	0
coll. JM-T93.1 cf *Fomitopsis?*	single-walled	0	smooth	0	dull	2	trimitic	2	wood	1
Trametes versicolor	single-walled	0	smooth	0	dull	2	trimitic	2	wood	1
Polyporus arcularius	single-walled	0	smooth	0	dull	2	dimitic	0	wood	1

*indicate character coding for cladistic analysis

skeletal arboriform hyphae are either lacking or rare, 'trimitic' when that kind of hyphae are abundant and solid as in the majority of *Ganoderma* species, and 'intermediate' when these hyphae are numerous but brittle, as in the majority of *Amauroderma* species.

Cladistic analysis used a data matrix constructed from Table 1 and was performed using PAUP version 3.1.1 (Swofford 1993) and a tester version of PAUP* (Swofford, in prep.). I used maximum parsimony with equal character weighting and unordered characters.Trees were searched with an exact algorithm (branch and bound). Tree lengths of Juhlich, Furtado-based and Steyaert-based taxonomic systems were calculated by constraining searches in PAUP with trees that were based on these systems (Figs. 1-3).

2.2 *Molecular analysis*

Molecular data used in this work is from divergent domain D2 of the large ribosomal subunit gene (LSU-D2) and from the internal transcribed spacers (ITS) of nuclear ribosomal DNA. The source of data is Moncalvo *et al.* (1995a,b,c), except for *Polyporus arcularius* and *Trametes versicolor* (Hibbett and Vilgalys 1993) which served as outgroup in the analyses. Choice of outgroup taxa is based on Hibbett and Donoghue (1995). Sequences of the following taxa are new in this study: *Humphreya eminii* RYV 33928 (Zimbabwe, coll. L. Ryvarden), *Ganoderma* cf *capense* (China, ACCC 5.71) and *Ganoderma* 'VZ' (Taiwan, coll. R. S. Hseu as *G. neojaponicum*). Cladistic analysis of molecular data was performed using PAUP version 3.1.1 (Swofford 1993) and a tester version of PAUP* (Swofford, in prep.). I used maximum parsimony with equal character weighting, unordered characters, and gaps were treated as fifth base. Only cladistically informative characters were used in the analyses.

2.3 *Number of taxa described and their biogeographic distribution*

The source of information about number of taxa described and their reported biogeographic distribution are taken from Moncalvo and Ryvarden (in prep.).

3 RESULTS

3.1 *Morphological analysis*

Fig. 4 shows one of the 24 most equiparsimious trees (tree length L = 12) generated with morphological characters, and indicates clades found in all equally most parsimonious trees. Topologies of trees constrained either by

a Furtado-based or Steyaert-based system require two more steps (L=14) than the shortest trees. Tree topology constrained by Juhlich's system requires the highest number of character changes at the nodes of the tree (L=15).

3.2 *Molecular analysis*

Nucleotide sequences of the LSU-D2 region align unambiguously among all taxa of this study. After removal of all positions with missing or ambiguous data, 20 phylogenetically informative characters were retained. Several strains of *Ganoderma* have identical nucleotide sequence. In contrast, the ITS sequences of *Polyporus arcularius, Trametes versicolor* and *Humphreya eminii* do not align with those of the other taxa of this study. We therefore performed two separated analyses, a first using only data of the LSU-D2 region and a second using only data of the ITS region.

In the first analysis, in order to avoid a sampling bias toward *Ganoderma* we removed taxa having redundant sequences and retained only eight *Ganoderma* sequences along with those of *Amauroderma, Tomophagus, Humphreya, Trametes* and *Polyporus*. The latter two taxa were used to root the trees. We performed an analysis using molecular data only and an analysis that included the five morphological characters shown in Table 1, and obtained similar results (Fig. 5). The tree in Fig. 5 shows that the three taxa in which ITS sequences were unalignable with those of *Ganoderma* taxa (*Polypous, Trametes* and *Humphreya*) also form a separate group in the LSU-D2 sequence analysis. The limited number of characters used in the analysis may explain the low bootstrap supports found along branches. However, the topology of the tree is in agreement with ITS data (Fig. 6). The tree shown in Fig. 5 supports the monophyly of the Ganodermataceae if *Humphreya eminii* is excluded from the family.

Results of the ITS analysis are shown in Fig. 6. The tree depicted is very similar to a tree published elsewhere using a similar data set (Moncalvo *et al.* 1995c). However, the tree shown in Fig. 6 is somewhat more resolved than the tree previously published probably because removal of taxa having redundant sequences and introduction of new taxa having different sequences may have decreased a sampling bias effect in the analysis. An interesting feature in this tree that did not appear in earlier studies (see Moncalvo *et al.* 1995a, however) is the presence of a clade that groups two black, laccate species having longitudinally crested basidiospore (*G. sinense* and *Ganoderma* 'VZ') and the non-laccate taxa of the *Elfvingia* group of which one (*G. australe*) also has longitudinally crested 'ganodermatoid' basidiospores.

4 DISCUSSION

The morphological analysis performed in this study was limited by the very few characters that remained after exclusion of adaptive and intra-taxon variable traits. Additional morphological characters should be available from detailed observation of basidiopores using electron microscopy techniques, and by examination of hyphal construction during basidiome ontology. However, although the morphological analysis did not provide any strong taxonomic resolution, results showed that the classifications based on Juhlich (1981), Furtado (1981) or Steyaert (1972) require more character-state changes (i.e., require more evolutionary steps on the premise that evolution proceeds in accordance with parsimony) than the most parsimonious arrangements of the taxa bearing these characters. The analysis produced 24 equally most parsimonious trees, and the strict consensus of the 24 trees resolved two clades (Fig. 4): the first clade includes trimitic species having 'ganodermatoid' basidiospore (i.e., the core group

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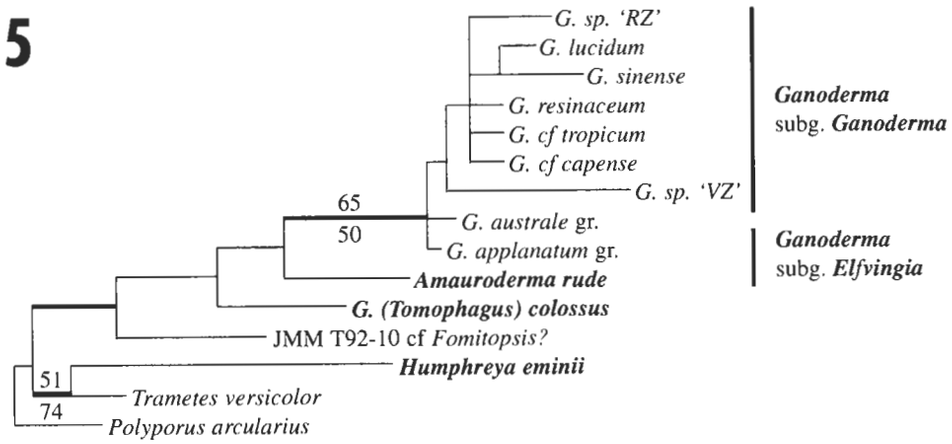

Fig. 5. Phylogenetic relationships of *Ganoderma* and allied genera based on nucleotide sequences of the D2 region of the 25s rRNA (20 phylogenetically informative positions), with and without inclusion of the five morphological characters in Table 1. The tree is the 50% majority-rule consensus of 31 equally most parsimonious trees found by a branch and bound search in PAUP using molecular and morphological data. Tree length = 63 steps, consistency index = 0.5873, retention index = 0.5938). An identical topology is found using only molecular data. Branches in bold are present in the strict and the semi-strict consensus trees in both analyses. Bootstrap supports greater than 50% are shown above branches for the analysis with morphological and molecular data and below branches for the analysis with molecular data alone. Branch lengths are proportional to character differences and were determined using ACCTRAN in PAUP. The tree was rooted with *P. arcularius* and *T. versicolor*.

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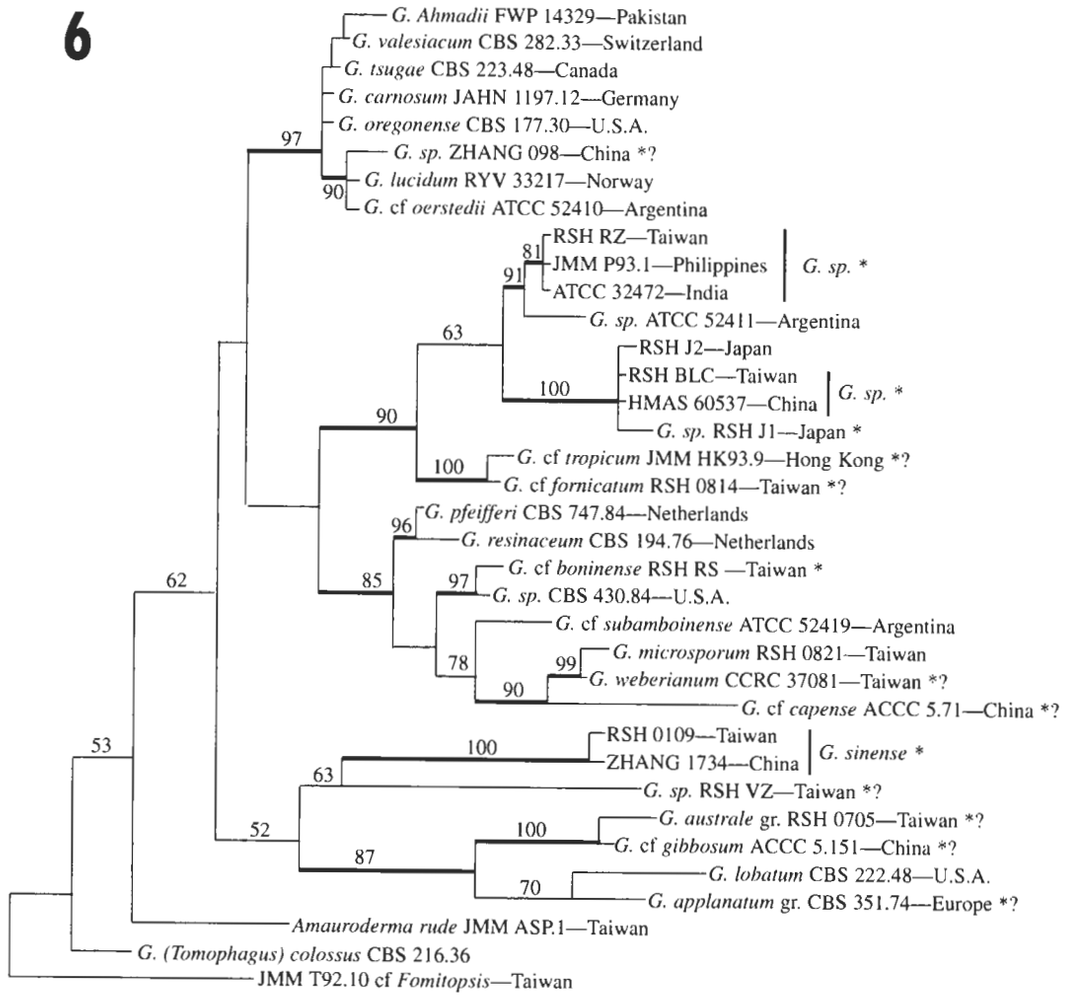

Fig. 6. Phylogenetic relationships of *Ganoderma* based on nucleotide sequences of the internal transcribed spacers (ITS) of nuclear ribosomal DNA. The tree is the strict consensus of 18 equally most parsimonious trees produced by a heuristic search in PAUP using 30 random addition sequence replicates and 143 phylogenetically informative characters. Tree length = 466 steps, consistency index = 0.543, retention index = 0.745. Bootstrap support is shown above each branch. The tree was rooted with the isolate tentatively identified as *Fomitopsis*. Branch lengths are proportional to nucleotide differences and were determined using ACCTRAN in PAUP. Asterisks (*) show taxa use for medicinal purpose or likely to have been used (*?).

of *Ganoderma* species), and the second clade includes the species having 'amaurodermoid' basidiospores (*Amauroderma* and *Haddowia*). Among these trees was one tree (Fig. 4) that has a topology in agreement with molecular data (Figs. 5-6) in that it placed *Humphreya eminii* basal to the other taxa, *Tomophagus* basal to both *Amauroderma* and *Ganoderma*, and *G. sinense* as sister taxon to *Elfvingia*. Overall comparison among trees based on morphological characters (Fig. 4) and molecular data of the LSU-D2 region (Fig. 5) and the ITS region (Fig. 6) shows no conflict.

It is not my purpose here to extensively discuss the different analyses nor to propose a formal systematic revision of the Ganodermataceae (which would requires more data and inclusion of many additional taxa). Instead, I will use the results depicted in Figs. 4-6 to delimit major evolutionary lineages in the Ganodermataceae.

I have listed below clades representing potentially distinctive evolutionary units, their importance in term of number of known taxa, and their reported biogeographic characteristics. Several factors preclude adequate evaluation of species distribution. First of all, there is presently insufficient knowledge in *Ganoderma* biology to circumscribe species in the group, whatever the species concept we wish to use (see Moncalvo 1995 or Hibbett and Donoghue 1995b for a discussion about choice of species concept and implications for biodiversity studies or conservation strategies). Nothing is known about gene flow among populations. About one third of the species described are from a single locality or a single collection. Therefore, only a very rough evaluation of species distribution is possible.

1) The *Ganoderma* clade includes trimitic species with 'ganodermatoid' basidiospore. Species grow on wood. This clade includes about 280 described species. More than 70% of the described species are from the tropics, about 42% are from Asia, 23% from Africa and 21% from tropical America. Recent studies (Moncalvo *et al.* 1995b) have shown that species believed to have a large distribution (e.g., *G. lucidum, G. tsugae, G. resinaceum*) are apparently geographically narrowly restricted, although long distance dispersal has occurred even within recently diverged taxa, as also shown in Fig. 7, e.g., between *G. lucidum* (Europe) and its sister taxon *G.* cf *oerstedii* (Argentina). Three lineages can be distinguished:
   - The *Ganoderma* group (*Ganoderma* subgen. *Ganoderma*). This group is by far the largest in terms of number of species described. It includes *G. lucidum* and allied species: I have recorded about 220 described species, including ca 30 invalid names, untraceable specimens or taxa excluded from *Ganoderma*, 75 species known only from the type locality, and

50 names proposed as synonyms. The actual number of species in this group should be between 40 and 100 depending on the species concept used. The group occurs worldwide with an estimated 20-25 species in temperate areas, probably more in the tropics.

- The 'VZ' group: basidiospores are longitudinally crested, and the two species known so far (*Ganoderma* 'VZ' and *G. sinense*) are black and strongly laccate.
- The *Elfvingia* group (*Ganoderma* subgen. *Elfvingia*): species are dull, basidiospores are longitudinally crested (*G. australe* group) or not (*G. applanatum* group). About 57 species described, including 26 names proposed as synonyms and 14 taxa known only from the type locality. My estimation is that the actual number of known species in this group should not exceed 20, with ca five in temperate areas.

The latter two lineages may be sister groups as indicated by molecules (Figs. 6-7) and the occurrence of longitudinally crested basidiospores in both groups.

2) The *Amauroderma* clade includes species with 'amaurodermatoid' basidiospores. Species are generally stipitate and found on the ground or on roots. The *Amauroderma* clade is exclusively tropical. Among the 54 accepted species that we were able to trace, 22 (41%) are known only from Asia, 12 (22%) only from America, 10 (19%) only from Africa, one only from the Pacific, 5 from both Africa and Asia, 2 from both America and Asia, and 2 are pantropical. As in *Ganoderma*, the data suggests that most species have a limited pattern of distribution, although long-distance dispersal has occurred in few cases. There are three potential lineages:

- The dull species: this comprises the majority of *Amauroderma* species. There are ca 50 species presently recognized (ca 92 species described of which ca 42 were proposed as synonyms).
- The laccate species with typical 'amaurodermatoid' spores. Two species are known: *A. leptopus* in West Africa and Indonesia, and *A. renidens* in Brasil.
- The *Haddowia* group includes the laccate species with longitudinally crested 'amaurodermatoid' basidiopores. Two species are known: *Ha. aetii*, known only from Borneo and *Ha. longipes* (pantropical).

The *Amauroderma* clade may be the sister group of the *Ganoderma* clade (Figs. 4-6)

3) The *G. hildebrandii* group: species are stipitate, terrestrial, dimitic and have 'ganodermatoid' spores. About five species are known, all are tropical. Whether or not this group forms an independent evolutionary lineage is yet unknown, but I speculate that the group may be basal to *Amauroderma* and *Ganoderma* and may include dimitic species with 'amaurodermoid' basidiospores.

4) *Tomophagus*, with a single species known to date: *T. colossus*, characterized by a context macroscopically soft that tends to be dimitic, and a shiny but never strongly laccate pileus. The basal position of *T. colossus* in Figs. 5-6 and its pantropical distribution suggest that it may be a relict species.

5) The *Humphreya eminii* group, basal to all the other clades and showing important molecular divergence with all other Ganodermataceae used in this study. 4 species (all tropical) if the 3 other *Humphreya* species described to date are monophyletic with *Hu. eminii*. These species are *Hu. lloydii* (tropical Africa), *Hu. coffeatum* (tropical America and south China?) and *Hu. endertii* (tropical Asia). Other species may belong to this group, e.g., *G. trengganuense* described by Corner (1983) from Malaysia.

The position of *Humphreya eminii* and a putative *Fomitopsis* species in Fig. 6 leads to the question of whether or not the Ganodermataceae are monophyletic. This question will be addressed elsewhere. Questions also remain concerning the placement of *G. ('Trachyderma') tsunodae* and other peculiar species not mentioned here.

Within the major clades presented in this work, it appears that only members of the *Ganoderma* clade have been used in folk medicine or in pharmaceutical and clinical studies (Fig. 6). rDNA nucleotide sequence divergence within this group is relatively low (see Fig. 5 and Moncalvo *et al.* 1995a) and may indicate that all the species in the group are genetically rather similar. However, species traditionally used for their medicinal properties belong to the three different lineages delimited in that clade. Interestingly, the group labeled 'VZ' includes *G. sinense*, a species well known as 'zhi-zhi' in China (Zhao 1989) and greatly appreciated in folk medicine for its black and shiny appearance which has been intuitively indicative as a complementary drug to 'ling-tze', the orange-red laccate species. Whether or not the four other clades represent an untapped source of potentially bioactive compounds is in need of evaluation, especially in light of the phylogenetic position of *Trametes (Coriolus) versicolor* in Fig. 5, another well-known fungus in pharmacology.

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