



Mycosphere Essays 1: Taxonomic Confusion in the *Ganoderma lucidum* Species Complex

Hapuarachchi KK^{1,2,3}, Wen TC¹, Deng CY⁵, Kang JC¹ and Hyde KD^{2,3,4}

¹The Engineering and Research Center of Southwest Bio–Pharmaceutical Resource Ministry of Education, Guizhou University, Guiyang 550025, Guizhou Province, China

²Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, 132 Lanhei Road, Kunming 650201, China

³Center of Excellence in Fungal Research, and ⁴School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand

⁵Guizhou Academy of Sciences, Guiyang, 550009, Guizhou Province, China

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Abstract

The genus *Ganoderma* (Ganodermataceae) has been widely used as traditional medicines for centuries in Asia, especially in China, Korea and Japan. Its species are widely researched, because of their highly prized medicinal value, since they contain many chemical constituents with potential nutritional and therapeutic values. *Ganoderma lucidum* (Lingzhi) is one of the most sought after species within the genus, since it is believed to have considerable therapeutic properties. In the *G. lucidum* species complex, there is much taxonomic confusion concerning the status of species, whose identification and circumscriptions are unclear because of their wide spectrum of morphological variability. In this paper we provide a history of the development of the taxonomic status of the *G. lucidum* species complex. We present a phylogeny for the *G. lucidum* complex based on multigene analysis with combined 5.8S–ITS rDNA, RPB1, and EF-1 α sequence data for 17 taxa of the complex. The taxonomic standing of these species is briefly discussed. Further clarification is, however, required. Type specimens, epitypes, reference collections, fresh collections and vouchered multigene nucleotide sequence data of more informative DNA markers should be used to determine the taxonomy of species in the *G. lucidum* complex.

Key words – *Ganoderma lucidum* complex – Lingzhi – morphology – phylogenetic analyses – taxonomic status

Introduction

The genus *Ganoderma* was established by Karsten (1881) with *Ganoderma lucidum* (W. Curt, Fries.) as the only species. Donk (1948) introduced Ganodermataceae with the laccate and stipitate white rot fungus *Polyporus lucidus* W. Curtis as its type species (Moncalvo & Ryvarden 1997) and placed the family in Polyporales, Basidiomycotina (Schwarze & Ferner 2003). *Ganoderma* is a cosmopolitan genus (Cao & Yuan 2013). *Ganoderma* species have a worldwide distribution in green ecosystems both in tropical and temperate geographical regions. They are usually found in subtropical and tropical regions since they can survive under hot and humid

conditions (Pilotti et al. 2004). *Ganoderma* species grow as a facultative parasite that can live as saprobes on rotting stumps and roots (Pilotti et al. 2004). Basidiocarps, the sexual structures in *Ganoderma*, grow from a living, or more commonly, from a dead trunk or branch of a tree in the form of a bracket. One of the two types of basidiocarps is produced, depending on the species: a laccate fruiting body with a shiny upper surface, or a non – laccate fruiting body with a dull upper surface (Smith & Sivasithamparam 2000a, Pilotti et al. 2004).

Ganoderma species have important economic value due to their medicinal properties and pathogenicity (Dai et al. 2007a, Dai et al. 2009). *Ganoderma* species cause white rot of hard woods by decomposing lignin, cellulose and related polysaccharides (Hepting 1971, Adaskaveg et al. 1991). The root and stem rots caused by *Ganoderma* species, results in loss in forestry yields [e.g. *Elaeis guineensis* (oil palm), Glen et al. 2009] and other important trees [e.g. *Hevea brasiliensis* (rubber) worldwide (Monkai et al. 2014)]. *Ganoderma* is a mushroom used as a traditional medicine in Asia and is called “Ling Zhi”, Chi–zhi” or “Rui–zhi” in China, “Reishi”, “Munnertake” or “Sachitake” in Japan and “Youngzhi” in Korea (Wagner et al. 2003, Paterson 2006). Species of *Ganoderma* have been reported to contain chemical constituents such as polysaccharides, proteins, amino acids, fatty acids, terpenoids, steroids, alkaloids, and phenolic compounds, with potential nutritional and therapeutic values (Boh et al. 2007, Mizuno 1995, Paterson 2006, Singh et al. 2013). These bioactive constituents are reported to be responsible for anti–inflammatory, anti–tumor, anti–oxidant, immunomodulatory, anti–diabetic, anti–viral, anti–bacterial, and anti–fungal properties of the mushroom (Paterson 2006, Cao et al. 2013, De Silva et al. 2012a, b, De Silva et al. 2013). Hence, the fruiting bodies of *Ganoderma* species have gained wide popular use as dietary supplements in China, Japan, North America and the other regions of the world. *Ganoderma* has been used as a functional food to prevent and treat immunological diseases, such as hypertension, tumorigenesis, insomnia, diabetes, migraine, as well as arthritis, bronchitis, asthma, anorexia, gastritis, hemorrhoids, hypercholesterolemia, nephritis, dysmenorrhea, constipation, lupus erythematosus, hepatitis, and cardiovascular problems (Liu et al. 2002, Paterson 2006, Wang et al. 2012). *Ganoderma* products come in the form of coffee, powder, tea, dietary supplements, spore products, drinks, syrups, tooth pastes, soaps and lotions and have been commercialized as effective food and drug supplements (Figure 1) for health benefits (Chang & Buswell 1999, Lai et al. 2004, Singh et al. 2013).

There are 430 epithets listed in Index Fungorum (2015) for *Ganoderma*, while Kirk et al. (2008) estimates there are 80 species. The taxonomic situation within *Ganoderma* is unclear as the species and genus concepts are confused because similar fungi are found in *Fomes* (Fr.) Fr 1849, *Polyporus* P. Micheli 1729 and *Tomophagus* Murril 1905 (Paterson 2006). Richter et al. (2014) suggested using a combination of morphological, chemotaxonomic and molecular methods to develop a more stable taxonomy for the genus. For over a century, the highly prized medicinal fungus, known as “Lingzhi” in East Asia, has been assigned to *Ganoderma lucidum*, a species originally described from Europe (Cao et al. 2012). William Curtis described and illustrated this taxon as *Boletus lucidus* in (1781) and Karsten’s *Fungi Fenniae Exsiccati* (1865) contained a specimen under the name *P. lucidus* with rough basidiospores (Adaskaveg & Gilbertson 1986). *Ganoderma lucidum* was described by Curtis (1871) based on material from Peckham, London, UK and the epithet was sanctioned by Fries (1821).

Adaskaveg & Gilbertson (1986) suggested Karsten (1881) has mistakenly attributed the epithet *lucidum* to Von Leysser, and this error has been established in numerous publications throughout history. *Ganoderma lucidum sensu lato* has been reported from East Asia (China, Japan and South Korea), East Africa (Ghana, Kenya and Tanzania) as well as Europe (almost all the European countries), North America (Canada and U.S.A.), Oceania (Australia), South America (Argentina, Brazil and Uruguay), South and Southeast Asia (India, Indonesia, Philippines, Thailand and Vietnam). However, the collections named as *G. lucidum* from different parts of the world are scattered in several separated lineages in phylogenetic analyses of the genus (Wang et al. 2012).

As early as 800 years ago in the Yuan Dynasty (A.D. 1280 – 1368), *Ganoderma lucidum* has been represented in paintings, carvings, furniture, carpet design, jewelry, perfumes and many more

creative artworks (Wasser & Weis 1999a). Anon (1955) stated, that the *G. lucidum* species complex have been used as Traditional Chinese Medicine for over two millennia (Zhou et al. 2014). This species viewed as ‘herb of spiritual potency’ or ‘mushroom of immortality’, and symbolizes sanctity, success, goodness and longevity (Gao & Zhou 2003, Wasser 2005, Lin 2009, De Silva et al. 2012). *Ganoderma lucidum* has been widely used for naming the commercialized “Lingzhi” products in the world market of the mushroom industry, since it has health benefits (Lai et al. 2004). The annual sale of products derived from *G. lucidum* is estimated to be more than US\$ 2.5 billion in Asian countries, including China, Japan, and South Korea (Li et al. 2013).

In the mid–nineties of the 20th century, molecular phylogenetic analyses indicated that collections named as *G. lucidum* in East Asia were in most cases not conspecific with *G. lucidum* from Europe (Yang & Feng 2013). The taxonomy of the *G. lucidum* complex has long been subject to debate and even after many years of discussions, the taxonomy of the *G. lucidum* complex remains still problematic. The main purpose of this paper is to identify the taxonomic problems in the *G. lucidum* species complex. In this study, the phylogeny of the *G. lucidum* complex was examined by analysis of 5.8S–ITS rDNA, RPB1, and EF-1 α sequence data representing species from Asia, Europe and North America to clarify the phylogenetic relationships within this complex.



Fig. 1 – *Ganoderma* products use as drug supplements and food. a. *Ganoderma* fruit body. b. *Ganoderma* spore powder. c. *Ganoderma* spore powder capsules. d. *Ganoderma* compound capsules. e. Broken *Ganoderma lucidum* spore powder capsules. f. *Ganoderma* spore essence capsules. g. *Ganoderma* spore oil. h. *Ganoderma lucidum* tea, i. Se enriched *Ganoderma* nutrition complements.

History of *Ganoderma* taxonomy

Traditional Chinese books classified *Ganoderma* into six species with reference to the colour of the fruit body: *Sekishi* is red, *Shishi* violet – like, *Kokushi* black, *Oushi* yellow, *Hakushi* white and *Seishi* blue and assigned based on different triterpenoid patterns (Szedlay 2002). Ganodermataceae contains five genera: *Ganoderma* P. Karst 1881, *Amauroderma* Murril 1905, *Haddowia* Steyaert 1972, *Humphreya* Steyaert 1972 and *Polyporopsis* Audet 2010 (Richter et al. 2014). Patouillard (1889) listed 48 species of *Ganoderma* worldwide (Adaskaveg & Gilbertson 1986). *Ganoderma* includes the subgenus *Ganoderma* that includes Sect. *Ganoderma* and Sect. *Phaenema*, subgenus *Eflvingia* and subgenus *Trachyderma* (Zhao & Zhang, 2000). *Trachyderma* Imazeki 1952 is illegitimate because there is a lichenised genus called *Trachyderma* Norman 1853 which is considered as a synonym of *Ganoderma* (Richter et al. 2014). The traditional taxonomy of *Ganoderma* is based on its morphological traits and this genus was divided into two distinct groups, the laccate (*G. lucidum* complex) and the non-laccate (*G. applanatum* complex) species, which refer to the subgenera *Ganoderma* and *Eflvingia* respectively (Zheng et al. 2007).

Unique morphological features of *Ganoderma*

The double walled basidiospores with interwall pillars are a key diagnostic feature for the genus (Smith & Sivasithamparam 2000a). *Ganoderma* species have the following characteristics: Basidiomes annual or perennial, stipitate to sessile, pileus surface with a thick, dull cuticle or shiny and laccate with a thin cuticle or cuticle of clavate end cells, context cream coloured to dark purplish brown, soft and spongy to firm–fibrous, pore surface cream coloured, bruising brown, the pores regular, 4–7 per mm, tube layers single or stratified, pale to purplish brown, stipe when present central or lateral, hyphal system dimitic, generative hyphae with clamps, skeletal hyphae hyaline to brown, non-septate, often with long, tapering branches, basidia broadly ellipsoid, tapering abruptly at the base, cystidia absent, basidiospores broadly to narrowly ellipsoid with a truncate apex and apical germ pore, wall two-layered, the endosporium brown and separated from the hyaline exosporium by inter-wall pillars, negative in Melzer's reagent, 7–30 µm long (Ryvarden 2004).

Why *Ganoderma* has a confused nomenclature?

Ganoderma species identification and circumscriptions have often been unclear and taxonomic segregation of the genus has been controversial (Moncalvo et al. 1995). A number of *Ganoderma* collections and species have been misnamed. This is because the presence of heterogenic forms, taxonomic obstacles and inconsistencies in the way the genus has been subdivided (Mueller et al. 2007). Since *Ganoderma* species are genetically heterogeneous, a wide range of genetic variation has been reported and caused by out crossing over generations and different geographical origins (Miller et al. 1999, Pilotti et al. 2003). This has led to variation in their listed morphological characteristics, even within same species (Hong et al. 2001). Environmental factors, variability, inter hybridization and individual morphological bias, mean identification of *Ganoderma* species is difficult (Zheng et al. 2007). Naming a species within this genus is confused and traditional taxonomic methods based on morphology are inconclusive for establishing a stable classification system for *Ganoderma* species (Hseu et al. 1996, Hong et al. 2002). Hence an uncertain nomenclature has resulted. This confusing situation is mainly the result of different authors using various criteria during identification. Some authors strictly only focus on host–specificity, geographical distribution and macro morphology of basidiomes, while other authors only focus on spore characters as the primarily taxonomic characters (Sun et al. 2006, Ekanjjo 2012).

Ganoderma lucidum species complex

Ganoderma lucidum sensu lato is a species complex. The taxonomy of this complex has long been the subject of debate, and different opinions have been raised regarding the validity of its members. The *G. lucidum* species complex includes 12 taxa (Table 2). These species are accepted as members of the *G. lucidum* species complex. In East Africa, Ryvarden and Johansen (1980)

parsimoniously treated all names of the *G. lucidum* complex as the ‘*G. lucidum* group’, because of the lack of a morphological solution to name species in this complex.

***Ganoderma lucidum* in China**

Patouillard (1907) reported *G. lucidum* from China and later on Teng (1934) accounted more collections of *G. lucidum* from different regions (Wang et al. 2012). Liu (1974) compiled a monograph of Traditional Chinese Medicinal fungi, and he assigned *G. lucidum* to “Lingzhi” in his book. Since then, *G. lucidum* was accepted as the scientific binomial of “Lingzhi” in many reports on Chinese edible and medicinal mushrooms (Ying et al. 1987, Mao 1998, Dai et al. 2009, Cao 2012). Several species morphologically similar to *G. lucidum* have also been described from all over the world, including *G. multipileum* D. Hou (Hou 1950), *G. sichuanense* J.D. Zhao and X.Q. Zhang (Zhao et al. 1983) and *G. lingzhi* (Cao et al. 2012) from China, *G. resinaceum* Boud (Patouillard 1889) from Europe, and *Ganoderma* Murrill, *G. sessile* Murrill, *G. tsugae* Murrill and *G. zonatum* Murrill (Murrill 1902, 1908) from USA (Cao et al. 2012, Zhou et al. 2014).

Studies of Moncalvo et al. (1995) highlighted that *G. lucidum sensu stricto* was distributed in northern and southern Europe, and probably extended to China. Further he found, the species named *G. lucidum* from both Europe and mainland China was not conspecific based on analyses of ITS and 25S ribosomal DNA sequences (Moncalvo et al. 1995a). Later, some authors (Moncalvo et al. 1995a, Pegler & Yao 1996, Hong & Jung 2004) have confirmed this idea, but misapplication of this name yet to be correct. Later, it was found that *G. lucidum*, distributed in tropical Asia is *G. multipileum* Ding Hou, which is not conspecific with the *G. lucidum sensu stricto* distributed in Europe, even not conspecific with the real “Lingzhi” distributed in East Asia (Wang et al. 2009b). Wang et al. (2012) further stated that the misapplication of *G. lucidum* to the Chinese species has a very short history, although it has become dominant in the last few decades because the successful cultivation and medicinal value of the species. Meanwhile, the distribution of genuine *G. lucidum* in China was also confirmed by Cao et al. (2012) and Yang & Feng (2013). Wang et al. (2012) proposed the name ‘*G. lucidum*’ as used for the Chinese species is erroneous and should be corrected and used as *G. sichuanense*. However, *G. lucidum* is incorrectly recorded in China, and around the world (Wang et al. 2012).

Mystification of “lingzhi” in China

The Chinese “lingzhi” has continuously been referred to the name *G. lucidum* in monographic works on Ganodermataceae in China. At first, Moncalvo et al. (1995) suggested the widely used medicinal species *G. lucidum* is a different species. Hawksworth (2005) proposed to conserve the name *G. lucidum* to an Asian type and introduce a new name for the European species (Yang & Feng 2013). Later, Cao et al. (2012) named the medicinal species *G. lucidum* as *G. lingzhi*. Among the Chinese *Ganoderma* species, *G. flexipes* Pat, *G. multipileum* D. Hou, *G. sichuanense* J.D. Zhao and X.Q. Zhang, *G. tropicum* (Jungh.) Bres. and *G. tsugae* Murrill are the most similar species to *G. lingzhi* (Cao et al. 2012).

***Ganoderma lucidum* in North America**

Overholts (1953) identified four North American species in the *G. lucidum* group and placed them in the Friesian genus *Polyporus* instead of *Ganoderma* and further he recognized *Polyporus lucidus* and *P. tsugae* as a distinct species in North America. Overholts (1953) taxonomy was based on geographical distribution, host-specificity, macroscopic morphology and spore characteristics (Adaskaveg & Gilbertson 1986). Both Overholts (1953) and Steyaert (1972) considered *Ganoderma sessile*, *G. polychromum*, *G. zonatum* and *G. sulcatum* as synonyms or varieties of *P. lucidus* (Moncalvo & Ryvarden 1997). Moncalvo et al. (1995) proposed that *G. boninense* might be the correct name of the American specimens labeled as *G. lucidum*. Later Zhou et al. (2014) has clearly distinguished *G. boninense*, from *G. sessile* and *G. tsugae*, both which have been wrongly considered by several authors (Haddow 1931, Overholts 1953, Steyaert 1978) to be the American

G. lucidum. The species originally described from the USA critically need to researched, because most of these species are old and were never subjected to phylogenetic analysis (Zhou et al. 2014).

Unique morphological characteristics of *Ganoderma lucidum*

The species *Ganoderma lucidum* itself is believed to grow only on hardwoods (Szedlay 1996). The basidiocarp is stipitate, with a pileus more or less imbricate. The surface of the pileus is covered with a dark red laccate layer, in the case of young fruit bodies with a non-laccate yellow to white margin. Basidiospores are ovate with a truncate apex. The basidiospores have numerous, narrow inter-wall pillars and "smooth" walls. The pilocystidia are medium long, clavate, amyloid, thick-walled, with abruptly tapering shafts (occasionally branched) intermixed with branching non-swollen hyphae in the mature pilear surface tissue (Szedlay 1996). The hyphal system is trimitic. Different authors describe different spore sizes. The Chinese *G. lucidum* has deeper coloured context (cream to buff, even darker near tube layer), a shorter cutis elements ($20 - 40 \times 7 - 15 \mu\text{m}$) (Wang et al. 2012). The European *G. lucidum* has slightly smaller basidiospores $7 - 12 \times 6 - 8 \mu\text{m}$ (Paterson 2006). The African specimens of *G. lucidum* were considered to match the description of *G. lucidum* strains from Europe, also with smaller basidiospores $7 - 12 \times 6 - 8 \mu\text{m}$ (Ryvarden & Johansen 1980). Different articles have therefore used the same name for different taxa.

Table 1 Different spore sizes of *Ganoderma lucidum*

| Author | Year | Basidiospore size (μm) |
|------------------------|------|---------------------------------------------------------|
| Pegler & Yong | 1973 | $9 - 13 \times 6 - 8$ |
| Adaskaveg & Gilbertson | 1986 | $10.6 - (11.5) - 11.8 \times 6.8 - (7.4) - 7.8$ |
| Wang & Hua | 1991 | $7 - 12 \times 6 - 8$ |
| Wang et al | 2012 | $9 - 11.5 \times 6 - 8$ and $6.5 - 8.56 \times 5 - 6.5$ |

Smith & Sivasithamparam (2003) proposed a new species, *G. steyaertanum* B.J. Smith & K. Sivasithamparam, to replace the mistakenly named *G. lucidum* in Australia and Indonesia which was named as *G. lucidum* by Cooke (1883, 1884, 1892), McAlpine (1895), Blackford (1944), and Smith & Sivasithamparam (2003). It has a larger basidiospores ($7.3 - 12.7 \times 5 - 9.5 \mu\text{m}$) than *G. lucidum sensu stricto*, pale yellow to grayish orange pores and small cutis cells ($20 - 27 \times 4.5 - 9.9 \mu\text{m}$, (Smith & Sivasithamparam 2003).

Table 2 Taxa belong to *G. lucidum* complex.

| Taxa | References |
|------------------------------------------------------|-----------------------------|
| <i>Ganoderma tsugae</i> Murr. | Murril 1902 |
| <i>Ganoderma valesiacum</i> Boud. | Murril 1908 |
| <i>Ganoderma oregonense</i> Murr. | Murril 1908 |
| <i>Ganoderma resinaceum</i> Boud. | Patouillard 1889 |
| <i>Ganoderma pfeifferi</i> Bres. | Bazzalo & Wright 1982 |
| <i>Ganoderma oerstedii</i> (Fr.) Torr. | Adaskaveg & Gilbertson 1986 |
| <i>Ganoderma ahmadii</i> Stey. | Steyaert 1972 |
| <i>Ganoderma multipileum</i> D. Hou. | Hou 1950 |
| <i>Ganoderma sichuanense</i> J.D. Zhao & X.Q. Zhang. | Zhao et al. 1983 |
| <i>Ganoderma lingzhi</i> Wu et al. | Cao et al. 2012 |
| <i>Ganoderma sessile</i> Murrill. | Murril 1902 |
| <i>Ganoderma zonatum</i> Murrill. | Murril 1902 |

Phylogenetic Analysis

In this phylogeny nucleotide sequence data of 17 species together with 49 strains or taxa of *G. lucidum* species complex from Asia, America and Europe were obtained from GenBank. Molecular

data comprised 5.8S–ITS rDNA, 20 EF–1 α , 20 RPB1 sequence data from 49 strains (Table 3). The initial alignment was done in *MEGA* 5.05 (Tamura et al. 2011) and then manually using BioEdit v. 7.2 (Hall 1999) and ClustalX (Kohli and Bachhawat 2003). *Trametes versicolor* (L.) Lloyd. 1921 (EU273523) was selected as the out group taxon. Maximum Parsimony analysis was performed with PAUP version 4.0b10 (Swofford 2001) using a Heuristic search and TBR (tree bisection–reconnection) swapping for 1000 random replicates. Gaps were set as “missing” data and the characters were specified as unordered and equally weighted for bootstrap analysis (Hillis & Bull 1993) performed with 1000 replications with simple addition sequences to obtain estimates of reliability for nodes. The concatenated dataset resulted in an alignment comprising 2477 characters, of which 1774 are constant, 352 parsimony–uninformative and 351 parsimony–informative. Topology, along with BS values by MP analyses above 50% is shown above the branches.

Table 3 Sequences used in the phylogenetic analysis.

| Species | Voucher / strain ^{1,2} | Origin | 5.8 ITS | RPB1 | EF–1 α | Reference |
|----------------------------|---------------------------------|---------------------------|----------|----------|---------------|---------------------------------|
| <i>Ganoderma ahmadii</i> | FWP 14329 (type) | Pakistan | Z37047 | – | – | Smith & Sivasithamparam (2000a) |
| <i>Ganoderma boninense</i> | WD2085 (FFPRI) | Japan | KJ143906 | KJ143945 | KJ143925 | Zhou et al. 2014 |
| <i>Ganoderma boninense</i> | WD2028 (FFPRI) | Japan | KJ143905 | KJ143944 | KJ143924 | Zhou et al. 2014 |
| <i>Ganoderma carnosum</i> | K(M) 109415 | UK | AY884175 | – | – | Genbank unpublished |
| <i>Ganoderma carnosum</i> | MQN001 (NARC) | Phulchoki Mountain, Nepal | AB763348 | – | – | Genbank unpublished |
| <i>Ganoderma flexipes</i> | Wei5200 (IFP) | | JN383978 | – | – | Cao & Yuan 2013 |
| <i>Ganoderma flexipes</i> | Wei5494 (IFP) | Hainan, China | JN383979 | – | – | Cao & Yuan, 2013 |
| <i>Ganoderma lingzhi</i> | HKAS76642 (type) | (Iso)Yunnan, China | KC222318 | – | – | Yang & Feng 2013 |
| <i>Ganoderma lingzhi</i> | Dai12574 (IFP) | Liaoning, China | KJ143908 | JX029985 | JX029977 | Cao et al 2012 |
| <i>Ganoderma lingzhi</i> | Cui9166 (BJFC) | Shandong, China | KJ143907 | JX029982 | JX029974 | Cao et al 2012 |
| <i>Ganoderma lingzhi</i> | HSD06B | Taihang mountains, China | KC511557 | – | – | Genbank unpublished |
| <i>Ganoderma lucidum</i> | RYV (Lectotype) | 33217Norway | Z37096 | – | – | Smith & Sivasithamparam (2000a) |
| <i>Ganoderma lucidum</i> | Dai11593 (IFP) | Finland | JQ781852 | – | – | Cao et al 2012 |
| <i>Ganoderma lucidum</i> | K175217 | UK | KJ143911 | KJ143950 | KJ143929 | Zhou et al. 2014 |
| <i>Ganoderma lucidum</i> | MT2610 (BRNM) | Czech Republic | KJ143912 | KJ143951 | KJ143930 | Zhou et al. 2014 |
| <i>Ganoderma lucidum</i> | BR 4195 (Rivoire) | France | KJ143909 | KJ143948 | – | Zhou et al. 2014 |
| <i>Ganoderma lucidum</i> | Cui 9207 (BJFC) | Yunnan, China | KJ143910 | KJ143949 | KJ143928 | Zhou et al. 2014 |
| <i>Ganoderma lucidum</i> | Dai2272 (IFP) | Sweden | JQ781851 | – | – | Cao et al. 2012 |
| <i>Ganoderma lucidum</i> | KCTC 6531 | Korea | AF248341 | – | – | Yang & Feng 2013 |
| <i>Ganoderma lucidum</i> | HKAS76455 | Yunnan, China(Cultivated) | KC222320 | – | – | Yang & Feng 2013 |
| <i>Ganoderma lucidum</i> | HKAS48969 | Yunnan, China | KC222323 | – | – | Yang & Feng 2013 |
| <i>Ganoderma lucidum</i> | HKAS71088 | Yunnan, China | KC222321 | – | – | Yang & Feng,2013 |
| <i>Ganoderma lucidum</i> | OE–234 | India | AY636059 | – | – | Genbank unpublished |
| <i>Ganoderma lucidum</i> | GICN04 | Italy | AM906058 | – | – | Cao & Yuan, 2012 |

| Species | Voucher / strain ^{1,2} | Origin | 5.8 ITS | RPB1 | EF-1 α | Reference |
|-------------------------------------|---------------------------------|-------------------------|----------|----------|---------------|-------------------------------------|
| <i>Ganoderma lucidum</i> | G1T099 | Italy | AM269773 | – | – | Cao & Yuan 2012 |
| <i>Ganoderma multipileum</i> | CWN 04670(TNM) | Taiwan, China | KJ143913 | KJ143952 | KJ143931 | Zhou et al. 2014 |
| <i>Ganoderma multipileum</i> | HMAS242384 | Sichuan Province, China | JF915409 | – | – | Wang et al. 2012 |
| <i>Ganoderma multipileum</i> | Dai 9447(IFP) | Hainan, China | KJ143914 | KJ143953 | KJ143932 | Zhou et al. 2014 |
| <i>Ganoderma multipileum</i> | DYU | Taiwan, China | KJ868083 | – | – | Genbank, unpublished |
| <i>Ganoderma oerstedii</i> | GO138 | Argentina | DQ425011 | – | – | Genbank Unpublished |
| <i>Ganoderma oregonense</i> | ATCC 46750 | Canada | Z37061 | – | – | Genbank Unpublished |
| <i>Ganoderma pfeifferi</i> | CBS 747.84 | Netherlands | JQ520198 | – | – | Park et al. 2012 |
| <i>Ganoderma pfeifferi</i> | K(M)120818 | UK | AY884185 | – | – | Park et al. 2012 |
| <i>Ganoderma pfeifferi</i> | 874 (CAS–IM) | Czech Republic | AM906059 | – | – | Guglielmo 2008 |
| <i>Ganoderma resinaceum</i> | BR 4150(Rivoire) | France | KJ143915 | KJ143957 | – | Zhou et al. 2014 |
| <i>Ganoderma resinaceum</i> | Gre4 | Italy(Modena) | KJ509598 | – | – | Genbank Unpublished |
| <i>Ganoderma sessile</i> | NY 00985711 | USA(NJ) | KJ143918 | – | – | Zhou et al. 2014 |
| <i>Ganoderma sessile</i> | LDW 20121017(IFP) | USA(CT) | KJ143917 | – | KJ143935 | Zhou et al. 2014 |
| <i>Ganoderma sichuanense</i> | CGMCC5.2175 (epitype) | Sichuan, China | KC662402 | – | – | Yao et al. 2013 |
| <i>Ganoderma sichuanense</i> | HMAS 42798(Holotype) | Sichuan China | JQ781877 | – | – | Zhou et al. 2014 |
| <i>Ganoderma tropicum</i> | BCRC37122 (TNM) | Taiwan, China | EU021457 | – | – | Wang & Wu 2007 |
| <i>Ganoderma tropicum</i> | Yuan 3490 (IFP) | Yunnan, China | JQ781880 | – | KJ143938 | Cao et al 2012 and Zhou et al. 2014 |
| <i>Ganoderma tsugae</i> | Dai3937 (IFP) | China | JQ781853 | – | – | Cao et al. 2012 |
| <i>Ganoderma tsugae</i> | Dai 12760 (IFP) | USA(CT) | KJ143920 | KJ143961 | KJ143940 | Zhou et al. 2014 |
| <i>Ganoderma valesiacum</i> | CBS 428.84 | USA | JQ520218 | – | – | Park et al. 2012 |
| <i>Ganoderma valesiacum</i> | CBS 282.33 | UK | Z37056 | – | – | Moncalvo et al 1994 |
| <i>Ganoderma zonatum</i> | FL02 (TNM) | USA(FL) | KJ143921 | KJ143962 | KJ143941 | Zhou et al. 2014 |
| <i>Ganoderma zonatum</i> | FL03 (TNM) | USA(FL) | KJ143922 | – | KJ143942 | Zhou et al. 2014 |
| <i>Trametes versicolor</i> | XSD–4 | EU273523 | | | | Genbank unpublished |

* ATCC, American Type Culture Collection, Maryland, USA, BJFC, Beijing Forestry University, BRNM, Moravian Museum in Brno, CAS–IM, Academy of Sciences of Czech Republic Institute of Microbiology Department of Experimental Mycology, Videnska, Czech Republic, CBS, Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands, CGMC China General Microbiological Culture Collection Center, Chinese Academy of Sciences, Di. Va.P.R.A, Department of Exploitation and Protection of the Agricultural and Forestry resources, University of Torino, Grugliasco (Italy),FFPRI ,the Forest Products Research Institute, FWP, Fungi of West Pakistan, Jardin Botanique de Belgique, Belgium, HMAS, Mycological Herbarium of the Institute of Microbiology, Chinese Academy of Sciences, HKAS, Kunming Institute of Botany, Chinese Academy of hidden flowers herbarium, IFP, Institute of Applied Ecology, Chinese Academy of Sciences, JV, The private herbarium of Josef Vlasak, KEW, the Royal Botanical Garden, Kew, Surrey, UK,KTCC, Korean Type Culture Collection, NARC, Nepal Agricultural Research Center, NY, the New York Botanical Garden, Rivoire, the private collection of Bernard Rivoire, RYV, Herbarium of Leif Ryvar den, Oslo, Norway, TNM, the Herbarium of the National Museum of Natural Science.

* Type specimens are in bold.

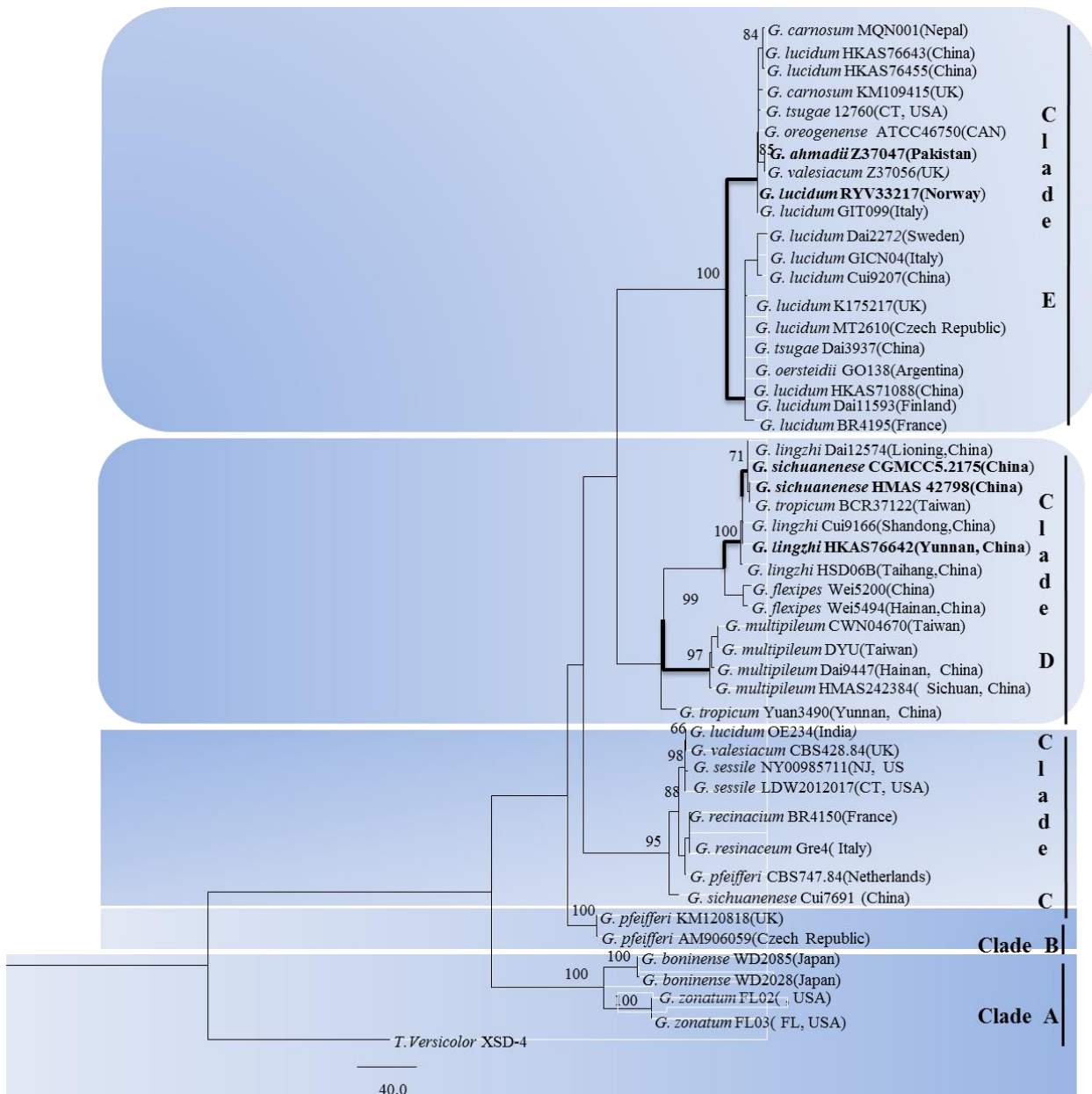


Fig. 2 – Phylogeny of the *Ganoderma lucidum* species complex based on the data from a combination 5.8S–ITS rDNA, EF–1 α and RPB1 genes. Topology and bootstrap values were obtained from maximum parsimony above 50 %. The tree is rooted to *Trametes versicolor* (XSD–4). All ex–type strains are in bold.

Results and Discussion

In the current phylogeny, the 49 specimens and strains from the *G. lucidum* species complex representing 17 species with high support values. These 17 species are *G. ahmadii* (85), *G. boninense* (100), *G. carnosum* (84), *G. flexipes*, *G. lingzhi* (100), *G. lucidum* (100), *G. multipileum* (97), *G. oerstedii*, *G. oregonense*, *G. pfeifferi* (100), *G. resinaceum*, *G. sessile* (98) *G. sichuanense* (71), *G. tropicum*, *G. tsugae*, *G. valesiacum* and *G. zonationum* (100). In the presented phylogeny 17 species from the *Ganoderma lucidum* species complex clustered into five clades (Clade A, B, C, D and E in Figure 2) even though some of them are from similar environments. Hence, the evolutionary histories for these species are unclear and the morphology data and the geographical distributions themselves are not sufficient to place them in a correct order. More data is needed from other laccate species as well non laccate species to clarify the taxonomic position of species in the *Ganoderma lucidum* complex.

Table 4 Recommended taxa for *Ganoderma lucidum* species complex.

| Taxa | References |
|--------------------------------------------------------|-----------------------------|
| <i>Ganoderma ahmadii</i> Stey. | Steyaert 1972 |
| * <i>Ganoderma lingzhi</i> Wu et al. | Cao et al. 2012 |
| * <i>Ganoderma lucidum</i> (Curtis) P. Karst | Karsten 1881 |
| * <i>Ganoderma multipileum</i> D. Hou. | Hou 1950 |
| <i>Ganoderma oerstedii</i> (Fr.) Torr. | Adaskaveg & Gilbertson 1986 |
| <i>Ganoderma oregonense</i> Murr. | Murril 1908 |
| <i>Ganoderma pfeifferi</i> Bres. | Bazzalo & Wright. 1982 |
| <i>Ganoderma resinaceum</i> Boud. | Patouillard 1889 |
| <i>Ganoderma sessile</i> Murrill. | Murril 1902 |
| * <i>Ganoderma sichuanense</i> J.D. Zhao & X.Q. Zhang. | Zhao et al. 1983 |
| <i>Ganoderma tsugae</i> Murr. | Murril 1902 |
| <i>Ganoderma valesiacum</i> Boud. | Murril 1908 |
| <i>Ganoderma zonatum</i> Murrill. | Murril 1902 |

*Suggested species that need further work on taxonomy.

Species in clade A

Two species from Japan and USA, *Ganoderma zonatum* and *G. boninense* clustered in clade A (Figure 2). They are subtropical species and thus *G. boninense* is the correct name for *G. lucidum* species in America. Gottlieb et al. (2000) found, *G. sessile* and *G. zonatum* are conspecific based on ITS phylogeny, whereas Zhou et al. (2014) showed that they are two independent species with the help of molecular and morphological data by observing specimens from the type localities. Zhou et al. (2014) clearly distinguished *G. boninense*, from *G. sessile* and *G. tsugae*.

Species in clade B

Two strains of *G. pfeifferi*, a wood rooting taxon from the UK and Czech Republic, clustered in clade B (Figure 2). Another strain of *G. pfeifferi* clustered in clade C. *Ganoderma pfeifferi* seems restricted to Eurasia with a few records in Eastern regions (Corner et al. 1983). *Ganoderma pfeifferi* species fit in the *G. lucidum* complex (Hseu et al. 1996, Wang et al. 1996), but Cao & Yuan (2012) stated in their phylogenetic study, that *G. pfeifferi* does not cluster with *G. lucidum*, but mostly resembles *G. resinaceum*, a species, that has mistakenly been placed in the *G. lucidum* group. In our study, *G. pfeifferi* does not belong to the *G. lucidum* species complex since *G. pfeifferi* specimens had clustered separately, as clade B (Figure 2). However *G. pfeifferi* specimen from Netherland clustered with *G. resinaceum* in clade B. This led us to believe that there are differences even within the European specimens based on type locality and questioning the reliability of the nucleotide sequences used.

Species in clade C

Five species clustered in clade C: *Ganoderma sichuanense* from China, a collection of *G. pfeifferi* (described in clade B) from Netherlands, *G. resinaceum* from France and Italy, *G. sessile* from USA, *G. valesiacum* from UK and *G. lucidum* from India. The *G. lucidum* strain from India is distinct from all other *G. lucidum* species from Europe and China (Figure 2).

This indicates that the South Indian *G. lucidum* species mostly resembles the European *G. resinaceum* and American *G. sessile*. Wang et al. (2009) showed the Indian strain of *G. lucidum* to be consistent with *G. multipileum*. The nucleotide sequences and the nomenclature of the Indian specimen are doubtful since it forms a distinct lineage in the phylogenetic tree. This specimen is phylogenetically more close to *G. lingzhi* and *G. multipileum* from China (Figure 2).

One *G. valesiacum* strain clustered in Clade C (Figure 2). Hseu et al. (1996) stated that this species belongs to the *G. lucidum* species complex, however one of the strains had clustered with *G. lucidum* (Clade E) and one strain has delineated and clustered with *G. sessile* group in clade C (Figure 2). Both taxa were from the UK. *Ganoderma lucidum* and *G. valesiacum* are synonyms

according to morphological observations of Steyaert (1972). Moncalvo (1996) reported that *G. valesiacum* and *G. lucidum* were different species, even *G. valesiacum* clustered with *G. lucidum* based on his molecular data. *Ganoderma sessile* was described from New York, USA by Murrill 1902 (Zhou et al. 2014) and was treated as a synonym of *G. resinaceum* by Haddow (1931), while Overholts (1953) considered that *G. lucidum* should be the correct name for specimens classified as *G. sessile*. Nobles (1965) pointed out that the specimens classified as *G. lucidum* in the USA actually represented *G. sessile*. She therefore changed the names of her species previously listed as *G. lucidum* to *G. sessile*. Furthermore, Steyaert (1972) considered *G. sessile* a synonym of *G. resinaceum* (Adaskaveg & Gilbertson 1986). Gottlieb et al. (2000) provided evidence that *G. sessile* is conspecific with *G. zonatum* based on ITS phylogeny and considered their differences in morphology to be a result of divergent evolution. Zhou et al. (2014) clearly showed that *G. sessile* is a distinct species from *G. zonatum* based on his phylogenetic analysis.

Staplers (1978) believed that *Ganoderma resinaceum* is the correct name for the fungus described as *G. lucidum*. Steyaert (1980) and Ryvarden (1985) considered numerous names as synonyms of *Ganoderma resinaceum*. Moncalvo et al. (1995) strongly suggested that *G. resinaceum* was different from *G. lucidum* and probably belongs to *G. pfeifferi*. Cultural characteristics and morphological observations of the basidiocarp and basidiospores supported this observation (Wang & Hua 1991, Ryvarden & Gilbertson 1993). Moncalvo et al. (1995) strongly believed that, based on molecular data, that *G. resinaceum* is a species complex. Hong & Jung (2004) found that *G. resinaceum* could not be distinguished phylogenetically from *G. lucidum* (Mohanty et al. 2011). *Ganoderma resinaceum* was shown to be distinct from *G. lucidum* by Mohanty et al. (2011). Furthermore it was suggested that European species of *G. resinaceum* differed from *G. lucidum* species from Europe and China (Cao et al. 2012, Zhou et al. 2014). In our phylogeny the European species of *G. resinacium* clustered with *G. pfeifferi* (Figure. 2).

Species in clade D

Ganoderma flexipes. *G. lingzhi*, *G. multipileum*, *G. sichuanense* and *G. tropicum* clustered in clade D (Figure 2). The validity of *G. lingzhi* and *G. sichuanense* has been recently debated. Wang & Yao (2009) proposed that *G. sichuanense* can represent '*G. lucidum*' in China. With the aid of molecular phylogeny, Wang et al. (2009) divided Asian specimens classified as *G. lucidum* into two clades; both clades were separated from the European *G. lucidum*. One clade, composed of tropical collections, represented *G. multipileum*, while the other clade is unnamed. As *G. sichuanense* had previously been described, Wang et al. (2009) proposed this name for *G. lucidum* in China. In parallel, Cao et al. (2012) found that the holotype of *G. sichuanense* was not conspecific with the unnamed clade, and proposed it as a new species called *Ganoderma lingzhi*, which was considered to be the most widely cultivated species in China. Yao et al. (2013) proposed *G. sichuanense* and *G. lingzhi* as synonymous based on morphological data from an epitype of *G. sichuanense*. However Zhou et al. (2014) again challenged this opinion, with *G. lingzhi* and *G. sichuanense* being an independent and taxonomically valid species by stressing that species types depends on geographical distributions. In our phylogeny some strains (*G. sichuanense* Cui 7691) clustered with *G. resinaceum*, *G. pfeifferi* and *G. sessile*, while others were clustered with *G. lingzhi* (Figure 2).

Ganoderma sichuanense is distantly related to *G. lingzhi*, but it is phylogenically close to *G. resinaceum*, although they are morphologically distinct (Cao et al. 2012). Our studies phylogenically verified the idea that *G. sichuanense* was closely related to *G. resinaceum*; hence the Chinese strain from Guangdong Province, clustered with *G. resinaceum* in clade C (Figure.2). In addition, we suggest that *G. sichuanense* is phylogenetically closely related to *G. lingzhi*, since the strain from Sichuan, China, had clustered with *G. lingzhi* in clade D. According to previous studies, we suppose that *G. lucidum*, *G. sichuanense* and *G. lingzhi* are three independent species in China, however further critical clarification is needed using morphological data with type species supported by molecular data.

Phylogenetic evidence indicates that *G. tropicum* is a distinct species (Cao et al. 2012, Wang et al. 2012, Yang & Feng 2013, Li et al. 2013, Zhou et al. 2014) and this species can be widely found across subtropical and tropical Asia (Moncalvo & Ryvarden 1997). Some researchers have shown in their phylogenies that *G. tropicum* is phylogenetically more similar to *G. multipileum* (Wang et al. 2012, Cao et al. 2012). *Ganoderma tropicum* resembles *G. multipileum* in morphology and habitat even though they are distinct species (Wang et al. 2009). In the present phylogeny one of the strains of *G. tropicum* from Taiwan clustered with *G. sichuanense*, while the other from Yunnan Province, China, clustered with *G. multipileum* (Figure 2). Hence, the *G. tropicum* strain from Taiwan is phylogenetically more similar to *G. sichuanense*, whereas the other strains from Yunnan Province are phylogenetically more similar to *G. multipileum*.

Ganoderma atrum J.D. Zhao et al. *G. calidophilum* J.D. Zhao et al. *G. hainanense* J.D. Zhao et al. and *G. parviungulatum* J.D. Zhao & X.Q. Zhang, are described from Hainan Province, China by J.D. Zhao and his colleagues, but they are synonyms of *G. flexipes* (Cao et al. 2012). Cao & Yuan (2012) showed that *G. flexipes* from China nested with *G. philippii* from Malaysia and *G. fornicatum*. Li et al. (2013) found *G. flexipes* from China nested with Chinese *G. lingzhi*, *G. multipileum*, *G. tropicum* and *G. curtsii*. With the aid of molecular evidence many researchers reported *G. flexipes* species in China are more similar to *G. lingzhi*, *G. multipileum* and *G. tropicum* species found in China. (Cao et al. 2012, Yang & Feng 2013, Zhou et al. 2014). Our studies confirmed the same opinion. *G. multipileum* can be found in tropical China and other tropical Asian countries, such as India and Philippines (Cao et al. 2012). *Ganoderma multipileum* species had previously been misidentified as *G. lucidum* (Zhou et al. 2014). As stated above, Wang (2009a) found that the Chinese *G. lucidum* species is actually *G. multipileum*.

Species in clade E

Ganoderma lucidum, the generic type, *G. tsugae*, *G. oerstidii*, *G. carnosum*, *G. oregonense*, *G. ahmadii* and *G. valesiacum* cluster in clade E (Figure 2). Moncalvo et al. (1995) used molecular data to conclude that *G. oregonense* belongs to the *G. valesiacum* species complex and clearly identified the American specimen labeled as *G. lucidum* as *G. oregonense*. This was subsequently followed by various researchers (Cao et al. 2012, Zhou et al. 2014), who considered *G. lucidum* and *G. oregonense* as to be distinct species. In our phylogeny, (Figure 2), *G. oregonense* clustered with *G. lucidum* and hence it is more close to Chinese *G. lucidum sensu lato* phylogenically, than the European *G. lucidum*. Moncalvo et al. (1995) found *G. carnosum* was a species in the *G. valesiacum* species complex since it was phylogenetically similar to *G. valesiacum* based on molecular data; however these two species were morphologically very different from each other.

Ganoderma ahmadii was reported only from Pakistan, India and South China (Steyaert 1972, Zhao 1989). Moncalvo et al. (1995) found *G. ahmadii* was a morphologically and phylogenetically distinct species. After that many of the researches followed Moncalvo's data (Hseu et al. 1996, Smith & Sivasithamparam 2000, Li et al. 2013) for their studies, but this species has not been discussed broadly. Our phylogenetic tree showed *G. ahmadii* clustered with European *G. valesiacum*; hence this species is phylogenetically more close to European *G. valesiacum* (Figure 2).

Ganoderma tsugae might be conspecific with *G. valesiacum* as these taxa have morphological, ecological and cultural similarities (Stalpers 1978). This was followed by Adaskaveg & Gilbertson (1986), Gilbertson & Ryvarden (1986); however, Moncalvo (1995) found *G. tsugae* was a distinct species in the *G. valesiacum* group, based on morphological and molecular observations. Many researchers have confirmed with molecular data that *G. tsugae* is a distinct species from *G. lucidum* (Wang & Yao 2005, Smith & Sivasithamparam 2000, Li et al. 2013, Yang & Feng 2013, Zhou et al. 2014). In our phylogeny (Figure 2), the *G. tsugae* specimen from the USA is phylogenetically closely related to the Asian *G. lucidum*, but less close to the European *G. lucidum*. The Chinese strain of *G. tsugae* is very close to the European *G. lucidum* phylogenically.

Ganoderma oerstidii was described from Argentina and it is a distinct species which differs from *G. lucidum* both morphologically and phylogenetically (Moncalvo et al. 1995, Figure 1). Earlier this species has been misidentified as *G. lucidum*.

Drawbacks

Lack of multigene nucleotide sequence data and lack of careful morphological study of species of *Ganoderma lucidum* are the main challenges. Hence classification of the species is a difficult task.

Future studies

To resolve the relationships and taxonomic issues among *G. lingzhi*, *G. sichuanense*, *G. lucidum* and other species in the complex, an epitype for *G. sichuanense* and for *G. lingzhi* should be selected from their type locality, and nucleotide sequences of more informative DNA markers should be used to delimit the species in the complex.

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