

ADVANCES IN MACROFUNGI

Diversity, Ecology and Biotechnology



Editors
Kandikere R. Sridhar
Sunil K. Deshmukh



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MACROFUNGI**
**Diversity, Ecology and
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ADVANCES IN MACROFUNGI

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Preface

Mycology is a potentially expanding area involving almost all facets of human health, nutrition and diseases. Diverse and ubiquitous distribution of fungi attained the status of '*Fifth Kingdom*' among the three major evolutionary lines along with plants and animals. Macrofungal diversity (macro- and macro-morphological) is enormous and dependent on a variety of substrates and geographic locations. A rough estimate reveals the macrofungi varieties to number 53,000 to 110,000 globally. They belong to a variety of basidiomycetes and ascomycetes known for their nutrition, medicinal value, novel metabolites, toxins and interaction with higher forms of life (plants and insects). Macrofungi are of special interest to explore their diversity, distribution, ecological functions and ecosystem services.

Interestingly, facts on edibility and medicinal novelty of many wild mushrooms are a product of ethnic knowledge of locals and tribals throughout the world. Mushrooms are a viable alternative non-conventional food source (other than plants and animals) owing to their nutritional, low-fat and low-calorie features (e.g., minerals, amino acids, vitamins and unsaturated fatty acids). However, few mushrooms are cultivated as a source of human nutrition and for therapeutic purposes. Wild and cultivated mushrooms are well known for their bioactive components (e.g., phenolics, tannins, vitamins, flavonoids, carotenoids, phytic acid, pigments and L-DOPA) and antioxidant activities (ferrous ion-chelation, DPPH radical-scavenging, reducing power, antioxidant activity, hydrogen peroxide scavenging, superoxide scavenging, lipid peroxidation, β -carotene-linoleic acid cooxidation and nitric oxide synthase activity). Many wild mushrooms are endowed with therapeutic potential, especially nutraceuticals, and are capable of preventing many lifestyle diseases (e.g., cardiovascular diseases, hypocholesterolaemic properties and anti-cancer agents).

Despite several hundred species of macrofungi having questionable edibility, they are the potential pool of valuable macromolecules and secondary metabolites of pharmacological and industrial interest. Bioactive polysaccharides, proteins, peptides, phenolic compounds and terpenes are known from various macrofungi. Macrofungi are a potential source of compounds responsible for the regulation of blood glucose and can demonstrate hepato-protective, antioxidant, cytotoxic, anti-inflammatory and antimicrobial potential. Some of the bioactive metabolites also serve as specific taxonomic markers. Many novel metabolites of macrofungi pave the way for the synthesis of new compounds. In addition, macrofungi are a valuable tool for green synthesis of nanoparticles, as opposed to the less ideal chemical and physical methods.

Another dimension of the macrofungi is their mutualistic association as ectomycorrhizae. Ectomycorrhizal fungi play an important role in the forestry/sylviculture/plantations resulting in uptake of water, absorption of minerals, protection against pathogens and below-ground nutrient transfer and prevention of erosion by binding the soil particles. Beyond mutualistic association, ectomycorrhizal fungal association is partly responsible for phytogeographical distribution in several habitats including extreme ecosystems. Besides involvement in biogeochemical cycles, macrofungi are known to degrade environmental pollutants, facilitating bioremediation.

Macrofungal research has become an important global commitment of the 21st century and there is an upsurge in understanding the roles of macrofungi in human, agricultural and environmental processes. In this contribution, we attempted to broadly balance the basic and applied aspects of diversity, ecology and biotechnology of macrofungi. To reflect the recent aspects, many colleagues contributed novel chapters based on their vast experience in consultation with voluminous literature. This book addresses: (1) the diversity and ecology of edible, toxic, medicinal and ectomycorrhizal macrofungi; (2) the impact of ectomycorrhizal fungi in terrestrial ecosystems, forests and plantations; (3) nutritional potential and cultivation of edible wild mushrooms; (4) novel metabolites of macrofungi useful in food, pharmaceutical and cosmeceutical industries; (5) eco-friendly synthesis of nanoparticles by mushrooms; (6) proteomics of edible and medicinal mushrooms. In addition, this book also encompasses experimental designs, methodological approaches, biogeochemical cycles, conceptual models, life history strategies and linking mycorrhizal diversity to plant performance.

This contribution hopes to initiate interest among the readers in order to expand their knowledge on macrofungi and to generate new ideas on basic and applied facets with future avenues. It is a valuable resource to graduates, post-graduates and researchers (in botany, microbiology, ecology, biotechnology, forestry, life sciences and environmental sciences) for understanding the diversity, ecology, therapeutic value, mutualistic associations and biotechnological potential of macrofungi. We are indebted to Prof. D.L. Hawksworth for an excellent overview, grateful to all contributors who delivered the chapters on time and for meticulous attention by the publisher to materialize production of this book.

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1

The Macrofungal Resource Extent, Current Utilization, Future Prospects, and Challenges

David L. Hawksworth

INTRODUCTION

As we progress towards the mid-21st century, concerns increase over the pressure on natural resources, how an exponentially burgeoning population can be fed, kept healthy, wastes disposed of safely, while simultaneously achieving environmental, ecosystem and wildlife protection. As macrofungi become better understood, it is becoming clear that they have the potential for addressing some of these key concerns.

In this overview, I explore aspects of the extent, current utilization, future prospects and challenges relating to the macrofungal resource.

Extent

Seventeen years ago, when 1.5 million was generally accepted as a conservative estimate of the number of species of fungi on Earth, I estimated that this could include around 140 000 mushroom species (Hawksworth, 2001). That figure was based on the number of known macrofungal species, then some 14 000, assuming that they were perhaps around 50% better known than other fungal morphologies, and taking note of the proportion of new species then being discovered in tropical regions, and adding an estimate for the extent of cryptic speciation.

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Since that time, molecular methods have enabled species concepts to be clarified in many genera and the sequencing of environmental samples has led to the discovery of a huge unexpected species diversity; as a result the 1.5 million figure (Hawksworth, 1991) has been revised upwards to between 2.2 and 3.8 million species (Hawksworth and Lücking, 2018). The fungi known only from environmental sequences have conveniently been dubbed “dark taxa” as they are not known from specimens or cultures and remain invisible to the eye (Ryberg and Nilsson, 2018). There are, however, possibilities for visualizing at least some of these new taxa by using sophisticated tailored fluorescent probes (Jones et al., 2011).

If the new estimates of species numbers are accepted, and the same assumptions as in 2001 are adopted as still being reasonable today, that would give an estimate of between 220 000 and 380 000 macrofungal species; that is, that we know perhaps just 3.7–6.4% rather than 10% of the estimated species as suggested in 2001. This is a daunting prospect for field mycologists and taxonomists, but simultaneously a most exciting one for those wishing to explore the ways in which novel mushrooms and other fungi may be exploited to benefit humankind and the environment.

At the regional level, the number of fungal species, growing on all substrates in an area, that can be detected in field surveys, can be expected to be around six times the number of vascular plant species (Hawksworth, 1991; Piepenbring and Yorou, 2017). In the case of India, as there are about 16,000 species of vascular plants recorded, that gives a figure of 96,000 species. In India, the number of known fungal species of all groups (including fungal analogues) currently stands at about 14,500, a figure that suggests there are at least 81,500 species awaiting recognition. Taking the estimate that 18.75% of the known fungi are mushrooms (Hawksworth, 2001), and then applying this percentage to the Indian estimated total fungal biota, there may be as many as 15,300 mushroom species remaining to be recognized in India. This total would include: (1) species new to science; and (2) species that had already been described and named from localities outside India but had not yet been found within India.

Current Utilization

The main current utilization of macrofungi today is for food. While most cultivated mushrooms come from just five genera, *Agaricus*, *Auricularia*, *Flammulina*, *Lentinula*, and *Pleurotus*, a relatively huge number are collected for food from the wild, both for local consumption and trade. A world list of 350 species used for human consumption has been prepared (Boa, 2004), but the actual number is much higher. For example, over 600 species are reported as edible just in Yunnan Province, China, and 60 of these are exploited commercially in that area (Yang, 2002). Clearly, there is a need to extend ethnomycological surveys in remote areas of many parts of the world, and it is pleasing to see that some progress in this direction is being made in India (e.g., Bhaben et al., 2011; Choudhary et al., 2015). A tried and tested model to emulate in carrying out ethnomycological surveys is that developed in Tanzania and Zambia (Härkönen et al., 2015).

In investigations into what local communities eat, edible species that are new to science are discovered quite frequently, as in the case of new *Cantharellus* species

in East Africa (Buyck, 1994) and new *Termitomyces* in China, the latter being first discovered on sale in local markets (Wei et al., 2004). While many of the fungi eaten are mycorrhizal, and so may be difficult to exploit on more than a local scale, newly discovered saprobic mushrooms that may be grown on agricultural wastes, may also be found; these will be more suitable for commercial exploitation. For example, native *Pleurotus* species grown on cylinders of paddy straw in Coimbatore, India (seen by me in 1991), and *Lentinus squarroides* cultivated on steam sterilized lignocellulosic substrates, also in India (Atri et al., Chapter 7). As many of these saprobic mushrooms have important ecological roles as decomposers (Dighton, Chapter 5), they have enormous potential to contribute to the sustainable use of resources.

Edible mushrooms form a substantial proportion of the diet in some societies, and there have been many studies of their nutritional value (e.g., Ghate and Sridhar, Chapter 6). They can be of particular value to vegetarians as they contain essential amino acids and a wide range of vitamins, some generally available only through animal products. They also have applications in weight-loss programmes as they are low in carbohydrates and rich in fibre (indigestible chitin), and are commended as dietary supplements or nutraceuticals (Badalyan and Zambonelli, Chapter 9).

Some macrofungal genera have species that are valued for medicinal applications (Ocañas et al., Chapter 8), for example, in enhancing immunological functions, or with anti-tumor properties, as is the case in *Ganoderma* (Paterson, 2015; Papp, Chapter 2), *Phellinus* (Deshmukh et al., Chapter 12), and *Ophiocordyceps* (Baral et al., 2015). Huge numbers of bioactive compounds are formed (Agyare and Agana, Chapter 10), and now their biosynthesis is being investigated by proteonomics (Fung and Razif, Chapter 16). Some are also extremely important toxicologically as poisons or recreational hallucinogens (Benjamin, 1995; Guzmán et al., 2000). In addition, some of the huge array of bioactive compounds may have value as antifeedants against insect pests (Clericuzio and Vizzini, Chapter 11). Particularly exciting has been the discovery of strobilurin fungicides from *Strobilurus tenacellus* that inhibit plant pathogenic fungi, primarily by disrupting their mitochondria (Bartlett et al., 2002).

Ectomycorrhizal macrofungi have a major role in maintaining tree health and so are of vital importance in commercial forestry (Rutz and Luna, Chapter 4), which now extends to the inoculation of containerized trees with spore suspensions prior to planting out (Hall et al., Chapter 13).

Future Prospects

In addition to the established areas utilizing macrofungi and macrofungal products, there are also prospects for novel applications. A particularly exciting new use of mushrooms has been developed during the last decade. Ecovative, a company based in New York State, has started developing a diverse range of materials using mushroom mycelium and a wide range of waste plant materials and gypsum. They have taken out numerous US Patents, including use as an alternative to styrofoam for producing packaging materials, boards, and even insulating brick blocks. This material evidently has the potential largely to replace many uses of plastics globally (Gunther, 2013). The prospects for this new application are phenomenal

as it simultaneously addresses the environmental plastics crisis, and recycles waste materials.

The production of the meat substitute mycoprotein Quorn™ from the filamentous fungus *Fusarium venetatum*, cultured in a continuous liquid culture system, has been a remarkable success, and its products provide some 500 000 meals each day in the UK alone. Development of this system started in the mid-1960s, and involved the assessment of around 3000 isolates, strain selection, and complex calculations of fungal growth rate. This strain of *Fusarium* has a doubling time of 3.5–4.1 h so that 300–350 kg biomass is produced each hour (Wiebe, 2004; Finnigan, 2011). If the investment were available, it is conceivable that a similar system could be developed, using mycelium from edible mushrooms which are already familiar to the public. This would avoid the image problem Quorn has experienced with public perception; last year it was ruled in the US that the fungus used should be referred to as a “mould”, not a relative of the mushroom. If this vision of using known edible fungi in continuous culture systems could be realized, the contribution to global food security could be enormous—and would also have the environmental advantage of reducing land necessary for animal husbandry, and for disposing of animal waste.

Fungi are an extraordinary source of novel natural products (Cole et al., 2003; Bills and Gloer, 2018), but most of these have been discovered in ascomycetes, and other microfungi rather than macrofungi. In the macrofungi, the focus has been on toxic and neurotropic compounds, and these have been accorded less attention by drug discovery companies because they do not grow as readily in liquid culture systems. The compounds produced can be expected to confer some aspect of fitness to the fungi, or else the biosynthetic pathways that produce them would surely have been lost in the course of evolution. It is likely that most are bioactive, acting against bacteria and fungi that infect basidiomes and cause them to decay more quickly. They might also act as effective poisons or antifeedents against insects, and other invertebrates, that would otherwise feed and lay eggs on them. More intensive screening of mushrooms, in particular those already used for medicinal purposes by local peoples, could lead to the discovery of novel pesticides (as was the case with the strobilurins; see above), or anti-bacterial or anti-fungal antibiotics. The search for new antibiotics is of urgent global concern as pathogenic bacteria and medically important fungi are both developing resistance to the drugs now on the market. On 15 February 2018, the World Health Organization (WHO; <http://www.who.int/en/news-room/fact-sheets/detail/antimicrobial-resistance>) stressed that antimicrobial resistance was an increasingly serious threat to global public health and that this required action across all government sectors and society. The potential of macrofungi, merits renewed attention in this regard (Suryanarayanan and Hawksworth 2018), though sadly, drug discovery from living organisms has become frustrated by two sets of regulations that have effectively stopped natural product drug discovery operations in many companies: these include the Nagoya Protocol to the Convention on Biological Diversity that came into effect in 2014 (Verkeley, 2015), and misguided national plant health regulations (Hawksworth and Dentinger, 2013). On the positive side, when the genes responsible for the production of compounds of interest have been located in the fungal genome, possibilities for transferring them into other,

faster growing, filamentous fungi or yeasts for expression are now conceivable (Keller et al., 2005).

Another emerging promising area for the future is the use of mushrooms in the biosynthesis of nanoparticles of precious metals, discussed here by Tarmizi et al. (Chapter 15).

As increases in greenhouse gasses lead to climate change, and latitudinal movement of vegetation, there may be a major issue with respect to the maintenance of mutualistic ectomycorrhizal relationships. In particular, will tree movements be limited by the absence of appropriate ectomycorrhizal partners in areas being colonized? There is much uncertainty and speculation over the impact upon, and responses of, mycorrhizal associations (Mohan et al., 2014), and this issue is sure to become a major research area in the foreseeable future.

Challenges

As the focus of this book is work by Indian scientists on macrofungi, it is appropriate to draw attention to five challenges which currently constrain realizing their potential in India.

- (1) *Cataloguing*: There is a long tradition of cataloguing the fungi recorded from India, of which the first major effort was that of Butler and Bisby (1931). Unfortunately, they omitted the lichen-forming fungi, which was usual at that time, but there have been several supplements and updates published over the years, and the lichen-forming fungi have now been ably dealt with by Awasthi (1991, 2000, 2007). In the 21st century, however, free online databases are needed and, indeed, this is the only way a system can operate in real time and have a chance of catching the vast amount of new data expected to emerge as more and more species are discovered. A start to this end, the “Fungi from India” online database project has now been launched and already holds records on some 6 000 species (Ranadive et al., 2017).
- (2) *Barcoding*: DNA barcoding will increasingly facilitate identification (Dutta and Acharya, Chapter 14), but remains limited in that so many already known fungi have never been sequenced; only some 35 000 of the known 120 000 fungal species have sequences deposited in GenBank (Hawksworth and Lücking, 2017). There is a major need to obtain ITS barcode sequences for as many known species as possible and, fortunately, in the case of macromycetes, DNA can often be recovered from dried reference material deposited in fungaria (Brock et al., 2009). This work needs to be expedited, with an emphasis on sequencing type material or designating modern sequenced collections as epitypes where no DNA is recoverable from the original material (Ariyawansa et al., 2014).
- (3) *Collections*: Collections of dried reference specimens of fungi (fungaria) and, where possible, permanently preserved living cultures (biological resource collections) underpin all mycological research. These are essential to fix the application of names, facilitate identifications by direct comparisons with reliably named material, and preserve voucher material for the fungi used in all kinds of inventory and experimental investigations. The maintenance of

reference collections is costly and requires considerable space and curatorial staff as collections grow but, regrettably, their scientific value is often not fully appreciated by the institutions where they are housed. In India, collections are currently dispersed through various university and government institutions; in itself, that is not a bad arrangement as it spreads risk, as well as making material accessible in different regions. Now that data on collections can be held in databases (e.g., Ranadive et al., 2017), accessibility is less of an issue than for previous generations. Just how mycology might be better organized in India was an issue close to the heart of the late C.V. Subramanian (1924–2016) who looked forward to a national centre concentrating on tropical mycology (Subramanian 1982, 1986). This issue has been highlighted more recently with respect to genetic resource collections by Suryanarayanan et al. (2015) who stress the importance of fungi to the bioeconomy, but action by pertinent authorities is awaited.

- (4) *Conservation*: The penultimate challenge I will highlight is the conservation of fungi of all kinds. Despite the key roles of fungi in ecological processes, and the dependence of plants on them through mycorrhizal associations, it is only in the last 25 years that fungal conservation has started to be taken seriously, especially after the stimulus provided by Moore et al. (2001). Fungi do not, of course, occur in isolation but need to be integrated into conservation programmes (Heilmann-Clausen et al., 2014). Criteria for producing Red Lists of fungi, which assess conservation status species by species at the national or international level, are now available (Dahlberg and Mueller, 2014). Progress has been slow, with just 56 fungi evaluated globally to date by IUCN (International Union for the Conservation of Nature). To make assessments of all the 14 500 species of fungi known from India is a daunting task, yet one that could be overcome with sufficient determination and resources. For example, a Red List assessment of the macrofungi of China, which dealt with almost 10 000 species and involved around 140 mycologists, has just been completed; 97 species were classified as nationally threatened (Fang et al., 2018). National Assessments should be carried out in all countries that are signatories to the Convention on Biological Diversity (United Nations Environment Programme, 1992), of which India is one. Article 4 (b) of the Convention requires nations to monitor the components of biodiversity, paying particular attention to those requiring conservation measures. Assessments of the conservation status of species are a pre-requisite for recognizing those that are of conservation concern. One country that has made enormous progress in this respect in recent years is Chile, which now has fungi embedded in its conservation legislation, and around 30 government mycologists are involved in fungal conservation. This is the result of a project largely driven by one charismatic individual, Giuliana Furci (Anon, 2015).
- (5) *Status and training*: The issue of training the next generation of whole organism mycologists is a major problem in many countries, and not one confined to “developing” nations. In many countries, including most European ones, the USA, as well as India, there has been a pattern of distinguished mycologists rising to become heads of botany departments and morphing those into centres

of excellence for mycology. They run post-graduate courses, award PhDs, secure research grants with post-doctoral positions, and generate pertinent research papers and key reference works. A particularly fine example in India was the work of C.V. Subramanian in Chennai (see above) who developed what became the Centre for Advanced Study in Botany of the then University of Madras. He trained or influenced many of the mycologists in senior positions in the country today. When such influential people retire from “Botany” departments and institutions, however, they are rarely replaced by mycologists, so centres of excellence for training new mycologists are lost. Mycologists remain, what I have termed, “orphans” in botany (Hawksworth, 1997). Sadly, perceptions are difficult to change, even if it is pointed out that fungi would, in any case, be better placed in departments of zoology as, genetically, they are closer to animals than plants. Mycologists need to become more active in promoting mycology as an independent discipline. Suggestions as to how that can be done individually, and collectively, have been made (Hawksworth, 2003; Minter, 2011), but these need to be actioned.

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Global Diversity of the Genus *Ganoderma* Taxonomic Uncertainties and Challenges

Viktor Papp

INTRODUCTION

The cosmopolitan polypore genus *Ganoderma* (Polyporales, Basidiomycota) comprises white-rot species, some of them being important pathogens of horticultural plants, such as *G. philippii* of cacao, coffee and tea, or *G. boninense* of oil palm. Greater attention is paid to those *Ganoderma* species which are used for their medicinal properties. The health benefits of the various *Ganoderma* species (e.g., *G. applanatum*, *G. cupreolaccatum*, *G. lingzhi*, *G. lucidum*, *G. resinaceum*, *G. sinense* and *G. tsugae*), and their compounds responsible for beneficial effects are intensely studied worldwide (e.g., Paterson, 2006; Baby et al., 2015; Hapuarachchi et al., 2017). Despite the fact that the genus has an enormous economic value, from the taxonomic point of view, *Ganoderma* is one of the most complex and misunderstood genera among the polypores. The taxonomical and nomenclatural confusion have arisen due to the high morphological variability of *Ganoderma* fruiting bodies. As a result, taxonomists have created many synonyms, or in the other case used wide species concept and merged different species. The difficulties of identification and the different species concepts have resulted in ambiguous species delimitation and identification systems. Names of *Ganoderma* are often misused because of the uncertain identification, making it hard to interpret the results of applied mycological studies; thus it would be important to carry out these studies

on a suitable and scientifically correct taxonomical basis. Owing to these disparities, this Chapter discusses: (i) the systematic state of *Ganoderma* genus and of its relative genera; (ii) the possibilities of species separation; (iii) the current taxonomical state and biogeography of the most important *Ganoderma* taxa in the light of most recent research results.

Classification and Nomenclature of *Ganoderma sensu lato*

Ganodermatoid fungi (*Ganoderma sensu lato*) are generally characterized by the unique doublewalled basidiospores with a coloured endosporium ornamented with columns or crests, and a hyaline smooth exosporium. These species were first separated systematically from the other conks-producing polypores in the beginning of the 19th century, when the spore morphology became an important taxonomic character. Within Agaricomycetes, the systematic state of species producing typical ganodermatoid spores was unclear due to the various systematic concepts. What follows is a review of the systematic state of ganodermatoid species. The different generic concepts affecting nomenclatural questions will also be discussed.

Systematics of Ganoderma sensu lato in Subgeneric Level

The first step towards circumscribing the ganodermatoid species in subgeneric level was taken by Donk (1933), who proposed the subfamily Ganodermatoideae in the Polyporaceae; and subsequently raised this morphological group to family level (Donk, 1948). Later, Jülich (1981) segregated the family Haddowiaceae from Ganodermataceae sensu Donk and proposed the order Ganodermatales with the two families. However, the results of preliminary phylogenetic studies are not supported by the distinction of Ganodermatales and suggested that *Ganoderma s. lato* does not form a well separated clade in the Polyporales (Moncalvo, 2000). Based on a multi-gene phylogenetic and genomic analysis in the Polyporales, Binder et al. (2013) found that *Ganoderma* and *Amauroderma* species are grouped together with several other poroid taxa in the Core polyporoid clade: for example, *Corioloopsis* spp., *Cryptoporus volvatus* (Peck) Shear, *Dichomitus squalens* (P. Karst.) D.A. Reid, *Donkioporia expansa* (Desm.) Kotl. & Pouzar, *Pachykytospora tuberculosa* (Fr.) Kotl. & Pouzar, and *Perenniporia medulla-panis* (Jacq.) Donk. In the revised phylogenetic overview of the Polyporales, Justo et al. (2017) recommended wide family concept of Polyporaceae and discussed Ganodermataceae as a synonym of the latter. Therefore, the recent phylogenetic studies suggest that despite the unique spore characteristics, ganodermatoid taxa do not form a separated lineage on the family level. The formerly proposed ganodermatoid genera (Table 1) are not consistently accepted in the literature and dividing each group on generic level arises many questions.

What is *Ganoderma sensu stricto*? Generic Concepts and Classification

The generic classification of ganodermatoid species dates back to the second half of the 19th century, when Karsten (1881) established the genus *Ganoderma* based on one single species, *Boletus lucidus* Leyss. (syn. *B. lucidus* Curtis). Some years later,

Table 1. Overview of the described ganodermatoid genera with the number of the proposed names in species rank.

Genus	Year	Type species	Names	Notes
<i>Ganoderma</i> P. Karst.	1881	<i>Boletus lucidus</i> Leyss.	345	
<i>Elfvigia</i> P. Karst.	1889	<i>Boletus applanatus</i> Pers.	16	Widely accepted as a synonym of <i>Ganoderma</i> P. Karst. (see Moncalvo and Buchanan, 2008)
<i>Amauroderma</i> Murrill	1905	<i>Fomes regulicolor</i> Berk. ex Cooke	121	Phylogenetically polyphyletic (see Costa-Rezende et al., 2017)
<i>Dendrophagus</i> Murrill	1905	<i>Polyporus colossus</i> Fr.	1	Illegitimate under Art. 53.1 (non- <i>Dendrophagus</i> Toumey 1900); Synonym of <i>Tomophagus</i> Murrill
<i>Tomophagus</i> Murrill	1905	<i>Polyporus colossus</i> Fr.	2	
<i>Friesia</i> Lázaro Ibiza	1916	<i>Boletus applanatus</i> Pers.	5	Illegitimate under Art. 53.1 (non- <i>Friesia</i> Spreng. 1818); synonym of <i>Ganoderma</i> P. Karst.
<i>Trachyderma</i> (Imazeki) Imazeki	1952	<i>Polyporus tsumodae</i> Yasuda ex Lloyd	2	Illegitimate under Art. 53.1 (non <i>Trachyderma</i> Norman 1853)
<i>Haddowia</i> Steyaert	1972	<i>Polyporus longipes</i> Lév.	3	
<i>Humphreya</i> Steyaert	1972	<i>Ganoderma lloydii</i> Pat. & Har.	4	
<i>Magoderma</i> Steyaert	1972	<i>Fomes subresinosus</i> Murrill	3	
<i>Archeterobasidium</i> Koeniguer & Locq.	1979	<i>A. syrtae</i> Koeniguer & Locq.	1	Fossil genera; type has ganodermatoid spore (see Koeniguer and Locquin, 1979)
<i>Thermophymatospora</i> Udagawa et al.	1986	<i>Th. fibuligera</i> Udagawa et al.	1	Anamorphic synonym of <i>Tomophagus</i> Murrill (see Adaskaveg and Gilbertson, 1989)
<i>Ganodermites</i> A. Fleischm et al.	2007	<i>G. libycus</i> A. Fleischm. et al.	1	Fossil genera; the type morphologically closely related to the <i>Elfvigia</i> group (see Fleischmann et al., 2007)
<i>Foraminispora</i> Robledo et al.	2017	<i>Porothelium rugosum</i> Berk.	1	
<i>Furtadoa</i> Costa-Rezende et al.	2017	<i>F. biseptata</i> Costa-Rezende et al.	3	Illegitimate under Art. 53.1 (non- <i>Furtadoa</i> M. Hotta 1981)

Karsten (1889) proposed the initially monotypic genus *Elfvigia*, typified on *Boletus applanatus* Pers. This morphological group generally comprises of species with perennial basidiocarps and dull pileal surface. Many mycologists doubted that the genus *Elfvigia* should be segregated from *Ganoderma*, and they discussed it under the latter (e.g., Imazeki, 1939; Steyaert, 1980). Although based on morphological traits, it also belongs to this group, a structurally preserved (permineralized) fruiting body fossil from Lower Miocene (Libia, North Africa) was named *G. libycus* A. Fleischm et al. and classified into a new monotypic genus (*Ganodermites* A. Fleischm et al.) (Fleischmann et al., 2007). In contrast to the former opinion of the authors, the spore morphology of another monotypic genus (*Archeterobasidium* Koeniguer & Locq.), described from its fossilized fruiting body (also from Libia), does not suggest relationship with the *Heterobasidion* Bref. genus (Koeniguer and Locquin, 1979) but shows ganodermatoid characteristics. We have very little data regarding ganodermatoid fossils, but in addition to the above mentioned ones, findings are known which are thought to be *G. adpersum*, *G. applanatum* and *G. lucidum* (Fleischmann et al., 2007; Taylor et al., 2015). The taxonomical state of these findings, the possibility that the *Archeterobasidium* and *Ganodermites* genera are identical to each other, and the validity of their segregation from the *Ganoderma* genus should further be investigated.

The genus *Tomophagus*, established by Murrill (1905b), was based on one single species, *Polyporus colossus* Fr. *Tomophagus colossus* (Fr.). Murrill macroscopically differs from other *Ganoderma* s. str. species, by having a soft and light basidiocarp, with thick and pale context (Furtado, 1965). However, based on its spore and microstructural characteristics, several authors have not supported the generic segregation of this species (e.g., Torrend, 1920; Furtado, 1965; Steyaert, 1972, 1980; Corner, 1983; Ryvardeen, 1991; Wasser et al., 2006a; Torres-Torres et al., 2015). In contrast, certain phylogenetic studies showed that *Tomophagus* represents an independent lineage (Hong and Jung, 2004; Costa-Rezende et al., 2017) composed of two species: *T. colossus* (Fr.) Murrill and *T. cattienensis* Le Xuan Tham & J.M. Moncalvo (Le et al., 2011). It is considered that *Thermophymatospora fibuligera* Udagawa, Awao & Abdullah was described as a thermotolerant hyphomycete from Iraq (Udagawa et al., 1986) and it is identical to the chlamydospore of *Tomophagus colossus* (Adaskaveg and Gilbertson, 1989). In this case, the monotypic genus *Thermophymatospora* Udagawa, Awao & Abdullah is an anamorphic synonym of *Tomophagus*. Imazeki (1939) segregated a new subgenus in *Ganoderma* based on *G. tsunodae* Yasuda, and later it was discussed on a generic level (Imazeki, 1952). Based on the morphological characteristics of the type specimen (lectotype) of *G. tsunodae*, Hattori and Ryvardeen (1994) noted that this species resembles *Tomophagus colossus* and the two species are probably congeneric. The close relationship between these species were also suggested by a recent phylogenetic study (Costa-Rezende et al., 2017), but it is still unclear whether these two species belong to the same genus. From the nomenclatural point of view, the generic name *Trachyderma* (Imazeki) Imazeki is illegitimate as it is a homonym of the formerly described lichen genus *Trachyderma* Norm.; therefore, the systematic position and as well as the correct nomenclature of *Ganoderma tsunodae* is unclear. Besides this species, only *Fomes subresinosus* Murrill has been proposed by Imazeki to be placed

in *Trachyderma*. This species later was selected by Steyaert (1972) as a type for the new genus *Magoderma* Steyaert. Besides, *M. subresinosum*, two other species were placed to the new genus by Steyaert: *M. infundibuliforme* (Wakef.) Steyaert and *M. vansteenisii* Steyaert. The separation of these species in generic level was questioned by certain authors (e.g., Corner, 1983; Teixeira, 1992; Ryvar den, 1991; Moncalvo and Ryvar den, 1997), although the sequences of *M. subresinosum* (as *Amauroderma subresinosum*) forms a distinct lineage from other ganodermatoid genera (e.g., Gomes-Silva et al., 2015; Costa-Rezende et al., 2017). Based on the ornamentation of the basidiospores, Steyaert (1972) proposed two further stipitate ganodermatoid genera: *Haddowia* and *Humphreya*. The genus *Haddowia* Steyaert was typified on *Polyporus longipes* Lév. and characterized by its unique longitudinally costate spores. Besides the type, one more species was discussed in the genus by Steyaert (1972) described as new from Indonesia: *H. aetii* Steyaert. Later, Teixeira (1992) combined *Ganoderma neurosporum* J.S. Furtado into *Haddowia*, which has been reported throughout tropical America (Moncalvo and Ryvar den, 1997). The species of the genus have not yet been analyzed by molecular methods, so the phylogenetic state of the genus can only be clarified with further investigations. The genus *Humphreya* Steyaert comprises species bearing basidiospores with reticulate, honey-comb or cristulate endosporium (Steyaert, 1972; Costa-Rezende et al., 2017). Formerly four species were accommodated in the genus from Indonesia, South and Central America and tropical Africa: *H. endertii* Steyaert, *H. coffeata* (Berk.) Steyaert, *H. eminii* (Henn.) Ryvar den and *H. lloydii* (Pat. & Har.) Steyaert (Steyaert, 1972; Ryvar den and Johansen, 1980; Decock and Figueroa, 2007). Amongst of these species only *H. coffeata* was studied by phylogenetic perspective, and the systematic position of *Humphreya* at genus level is still uncertain (Costa-Rezende et al., 2017).

Based on the morphological characteristics of the basidiospores, Patouillard (1889) in his monographic study divided *Ganoderma* species into two sections: *Ganoderma* sect. *Ganoderma* and *G.* sect. *Amauroderma*. Torrend (1920) transferred the section *Amauroderma* to generic level, with *Polyporus auriscalpium* Pers. as the type. However, the proposal of Torrend is illegitimate, because Murrill (1905a) used this name earlier and it has priority. Murrill introduced a different taxonomic circumscription of the genus when he selected *Fomes regulicolor* Berk. ex Cooke (syn. *Amauroderma schomburgkii* (Mont. & Berk.) Torrend) as the type species, which was not included in the section established by Patouillard. The tropical (or subtropical) genus *Amauroderma* Murrill traditionally circumscribed mainly by the globose to ellipsoid basidiospores, without a truncate apex (Ryvar den, 2004). However, the recent studies using molecular phylogenetic methods have shown that the genus is polyphyletic and will need to be revised (Gomes-Silva et al., 2015; Song et al., 2016; Costa-Rezende et al., 2017). The genus *Polyporopsis* Audet was discussed by Richter et al. (2015) in Ganodermataceae. This genus was described based on one single species, *Albatrellus mexicanus* Laferr. & Gilb. (Laferrière and Gilbertson, 1990). However, in contrast to the original description, the subsequent studies on the holotype revealed that the spores of *A. mexicanus* are not glabrous and have a double wall separated by interwall pillars (Zheng and Liu, 2006), which suggests similarity with the ganodermatoid *Amauroderma* genus (Audet, 2010). Although the phylogenetic state of *Polyporopsis mexicanus* is not clarified,

it is possibly related to the albatrelloid lineage, since certain species have similar basidiospores in the *Polyporoletus* clade, which is close to the Albatrellaceae family (Russulales): for instance *Leucophleps spinispora* Fogel, *Mycolevis siccigleba* A.H. Sm., *Polyporoletus sublividus* Snell (Albee-Scott, 2007). In a recent study, Costa-Rezende et al. (2017) segregated two new genera from *Amauroderma* based on morphological observations and molecular evidence. The genus *Foraminispora* Robledo, Costa-Rezende & Drechsler-Santos typified on *Porothelium rugosum* Berk. is morphologically characterised by the unique endosporic ornamentation of basidiospores. The other proposed genus, *Furtadoa* Costa-Rezende, Robledo & Drechsler-Santos is accommodate species with monomitic context and glabrous pilear surface: *F. biseptata* Costa-Rezende, Drechsler-Santos & Reck, *F. brasiliensis* (Singer) Costa-Rezende, Robledo & Drechsler-Santos and *F. corneri* (Gulaid & Ryvardeen) Robledo & Costa-Rezende.

The systematics of the ganodermatoid species on genus level is based upon spore morphology, which is fundamentally accepted by the most recent systematic studies dealing with multigene phylogenetic analyses (e.g., Costa-Rezende et al., 2017). However, the phylogenetic reconstructions built from the currently known sequences do not always confirm the suitability of spore morphology for lineage distinction. The classification of the ganodermatoid species on genus level has many questionable points, and currently there is no consensus in the topic. If we follow the narrow genus concept, it will be necessary to separate further genera, although the low level of nucleotide difference in the known barcoding regions and the seemingly monophyletic lineage of the ganodermatoid taxa suggests the possibility that a wide genus concept might be viable. Hereinafter, however, we follow the narrow genus concept, dealing only with the *Ganoderma* s. str. genus.

Species Delimitation in *Ganoderma*

Historically, the species description in the genus *Ganoderma* was mostly based on macro- and micromorphological characteristics of the basidiocarp. Based on a detailed morphological study on laccate *Ganoderma* species, Torres-Torres and Guzmán-Dávalos (2012) considered that the color of the context, resinous deposits, structure of the basidiospores and protuberances of the pileipellis cells are among the most important features for characterization of the species. In addition to morphological examination of the basidiocarp, several authors studied cultural and mating characteristics in *Ganoderma* in order to provide new tools for species-level systematics (e.g., Adaskaveg and Gilbertson, 1986, 1989). The first molecular genetic studies dealing with ribosomal DNA sequence analyses in the *Ganoderma* genus began in the middle of the 90s (e.g., Moncalvo et al., 1995a,b), but until the end of the last decade the new species were still described on the basis of morphological traits (e.g., Wu and Zhang, 1996; Ryvardeen, 2000, 2004; Ipuleit and Ryvardeen, 2005; Torres-Torres et al., 2008). It is a kind of exception, that Smith and Sivasithamparam (2003) described *G. steyaertanum* B.J. Smith & Sivasith., citing one of their previous studies dealing with phylogenetic analyses in which this species is yet discussed under the name “*G. sp. Grp 6.3*” (Smith and Sivasithamparam, 2000), the ITS1 and ITS2 sequences of the type of *G. steyaertanum* only became accessible in the

GeneBank database many years later. In 2009, however, with the description of *G. carocalcareum* Douanla-Meli, barcoding sequences were also published besides the morphological characterisation (Douanla-Meli and Langer, 2009). Following this, further 21 new *Ganoderma* species were described mostly with the addition of ITS sequences, and in some cases, with the addition of further barcoding regions (Table 2). In the molecular era, several markers (e.g., protein-coding genes, rDNA loci, mtSSU rDNA sequence and multilocus marker systems) were used by different authors in order to clarify taxonomic difficulties in the genus *Ganoderma* (e.g., Hong and Jung, 2004; Sun et al., 2006; Zheng et al., 2009; Wang et al., 2012; Thakur et al., 2015; Zhou et al., 2015; Xing et al., 2018), from which, the ITS region became the most popular. In the public databases (GeneBank, UNITE) the ITS sequence of nearly 70 different *Ganoderma* binoms are deposited. Nevertheless, due to the unclear taxonomic interpretation of these *Ganoderma* species and the exclusively morphological based identification, the majority of the *Ganoderma* sequences accessible in the GeneBank are labeled as misidentified or ambiguously (e.g., Jargalmaa et al., 2017; Papp et al., 2017). Therefore, it would be essential to sequence the types of those *Ganoderma* species which were used in the modern scientific literature and previously described based on morphological features. This was carried out only in some cases: for example, *G. microsporium* R.S. Hseu, *G. ahmadii* Steyaert, *G. sichuanense* J.D. Zhao & X.Q. Zhang (Moncalvo et al., 1995a; Cao et al., 2012). Although morphological study combined with DNA sequencing has been the most relevant approach for identification of *Ganoderma* species, an integrative taxonomy combined morphological and phylogenetic methods with secondary metabolite-based chemotaxonomy has presumably attained a more stable taxonomy in the genus (Richter et al., 2015; Welti et al., 2015).

***Ganoderma* Species Around the World: Taxonomy and Biogeography**

The *Ganoderma* genus has a cosmopolitan distribution, but in many cases, due to the taxonomical uncertainties, little is known about the area of the species. Because of the different taxonomical concepts, some of the species were reported from all around the world (e.g., *G. applanatum*, *G. australe* and *G. lucidum*), while many others are only known from type locality (Moncalvo and Ryvardeen, 1997). In some recent studies, the biogeography of the *Ganoderma* taxa was investigated through phylogenetic analyses (e.g., Moncalvo and Buchanan, 2008; Zhou et al., 2015). The distribution of the species can also be reevaluated based on the accessible barcoding sequences. In contrast to the earlier theory that certain species have wide distributions and largely unstructured populations, recent genetic and biogeographic studies have indicated that most of the studied *Ganoderma* taxa are geographically restricted. In the majority of cases, we do not have sufficient information about the taxonomical state and so the distribution of most of the described *Ganoderma* species, therefore it has not been possible to comprehensively review the biogeography of the genus yet. Thus, what follows is an attempt to review the most recent results of the taxonomical state and biogeography of the most widely investigated *Ganoderma* species (e.g.,

Table 2. New *Ganoderma* species described in the last twenty years (1998–2017). The formerly described *Ganoderma* species were listed in Moncalvo and Ryvarden (1997). The table includes the proposed name of the new species and the data of the holotype specimens. Herbarium codes: BJFC – Beijing Forestry University (China); DAR – Orange Agricultural Institute (Australia); ENCB – Instituto Politécnico Nacional (Mexico); GACP – Guizhou Agricultural College (China); GDGM – Guangdong Institute of Microbiology, Guangdong Academy of Sciences (China); HKAS – Herbarium of Cryptogams, Kunning Institute of Botany, Chinese Academy of Sciences, IFP – Institute of Applied Ecology, Academia Sinica (China); LIP – Université de Lille (France); MIN – University of Minnesota (USA); MUCL – Université Catholique de Louvain (Belgium); O – Botanical Museum, University of Oslo (Norway); PERTH – Western Australian Herbarium; PREM – National Collection of Fungi in South Africa (South Africa); QCA/QCAM – Pontificia Universidad Católica del Ecuador (Ecuador); TNM – National Museum of Natural Science (Taiwan); VEN – Universidad Central de Venezuela (Venezuela); (*) isotype; (**) ex-culture.

Species	Year	Geographic origin	Voucher no.	Herbarium code	Published sequence (GenBank no.)	Reference of the original description
<i>G. concinnum</i>	2000	Colombia	Ryvarden 16840	O (NY*)	-	Ryvarden (2000)
<i>G. longistipitatum</i>	2000	Venezuela	Ryvarden 40558	VEN (O*) (NY*)	-	Ryvarden (2000)
<i>G. multicornum</i>	2000	Venezuela	G. J. Samuels	NY (O*)	-	Ryvarden (2000)
<i>G. steyaertianum</i>	2003	Indonesia	DAR3780 PERTH 05509114	DAR** PERTH	EU239395/EU239396 (ITS)	Smith and Sivasithamparam (2003)
<i>G. citriporum</i>	2004	Venezuela	Ryvarden 40466	VEN (O*)	-	Ryvarden (2004)
<i>G. elegantum</i>	2004	Ecuador	Ryvarden 44573	O (QCA*)	-	Ryvarden (2004)
<i>G. guianense</i>	2004	French Guiana	MUCL 43922	MUCL	-	Ryvarden (2004)
<i>G. turbinatum</i>	2005	Uganda	Ipulet 477	O	-	Ipulet and Ryvarden (2005)
<i>G. vivianimercedianum</i>	2008	Mexico	E. Bastidas-Varela	ENCB	-	Torres-Torres et al. (2008)
<i>G. carocalcareum</i>	2009	Cameroon	DMC 322	HUYI (O*)	EU089969 (ITS) EU089968 (mtSSU)	Douanla-Meli & Langer (2009)
<i>G. martinicense</i>	2010	Martinique	SW 55	LIP	KF963256 (ITS)	Welti and Courtecuisse (2010)
<i>G. neogibbosum</i>	2010	Martinique	SW 37	LIP	Not published	Welti and Courtecuisse (2010)
<i>G. parvigibbosum</i>	2010	Martinique	SW 22	LIP	Not published	Welti and Courtecuisse (2010)
<i>G. ryvardenii</i>	2010	Cameroon	HKAS 58053	HKAS	HMI138671 (ITS)	Kinge and Mith (2011)

Table 2 contd. ...

... Table 2 contd.

Species	Year	Geographic origin	Voucher no.	Herbarium code	Published sequence (GenBank no.)	Reference of the original description
<i>G. lingzhi</i>	2012	China, Hubei	Wu 1006-38	TNM (BJFC*) (IFP*)	JQ781858 (ITS) JX029989 (mtSSU) JX029984 (RPB1) JX029980 (RPB2) JX029976 (TEF1- <i>a</i>)	Cao et al. (2012)
<i>G. mutabile</i>	2012	China, Yunnan	Yuan 2289	IFP	JN383977 (ITS)	Cao and Yuan (2012)
<i>G. austroafricanum</i>	2014	South Africa	PREM 61074	PREM	KM507324 (ITS) KM507325 (LSU)	Crous et al. (2014)
<i>G. destructans</i>	2015	South Africa	PREM 61265	PREM	KR183856 (ITS) KR183860 (LSU)	Coetzee et al. (2015)
<i>G. enigmaticum</i>	2015	South Africa	PREM 61264	PREM	KR183855 (ITS) KR183859 (LSU)	Coetzee et al. (2015)
<i>G. leucocontextum</i>	2015	China, Tibet	GDGM 40200	GDGM	KF011548 (ITS)	Li et al. (2015)
<i>G. wiroense</i>	2015	Ghana	MIN 938704	MIN	KT952363 (ITS) KT952364 (LSU)	Crous et al. (2015)
<i>G. aridicola</i>	2016	South Africa	Dai12588	BJFC (IFP*)	KU572491 (ITS) KU572502 (TEF1- <i>a</i>)	Xing et al. (2016)
<i>G. ecuadoriense</i>	2016	Ecuador	QCAM3430	QCAM	KU128524 (ITS) KX228350 (LSU)	Crous et al. (2016)
<i>G. mbrekobenum</i>	2016	Ghana	MIN 850481	MIN	KX000896 (ITS) KX000897 (LSU)	Crous et al. (2016)
<i>G. wuzhishanensis</i>	2016	China, Hainan	GACP14081689	GACP	KU994772 (ITS)	Li et al. (2016)
<i>G. mizoramense</i>	2017	India, Mizoram	MIN 948145	MIN	KY643750 (ITS) KY747490 (LSU)	Crous et al. (2017a)

<i>G. podocarpense</i>	2017	Ecuador	QCAM6422	QCAM	MF796661 (ITS) MF796660 (LSU)	Crous et al. (2017b)
<i>G. angustisporum</i>	2018	China, Fujian	Cui 13817	BJFC	MG279170 (ITS) MG367563 (<i>TEFI-α</i>) MG367507 (<i>RPB2</i>)	Xing et al. (2018)
<i>G. casuarinicola</i>	2018	China, Guangdong	Dai 16336	BJFC	MG279173 (ITS) MG367565 (<i>TEFI-α</i>) MG367508 (<i>RPB2</i>)	Xing et al. (2018)
<i>G. ellipsoideum</i>	2018	China, Hainan	GACP14080966	GACP	MH106867 (ITS)	Hapuarachchi et al. (2018)
<i>G. dunense</i>	2018	South Africa	CMW42157	PREM	MG020255 (ITS), MG020150 (β -tubulin), MG020227 (<i>TEFI-α</i>)	Tchotet Tchoumi et al. (2018)

G. applanatum, *G. boninense*, *G. lingzi*, *G. lucidum* and *G. sinense*) and morpho-groups in the applied research.

The *Ganoderma lucidum* Aggregate

In the second half of the 18th century, the species scientifically named *G. lucidum* (Curtis) P. Karst. (Fig. 2d,e) was described many times under several names. Among the 14 different binomials given to this species by pre-Friesian European mycologists, the epithet *lucidus* proposed by Curtis (1781) and accepted by Fries (1821) proved to be the most popular name, thereafter spreading worldwide. Currently *G. lucidum* seems to be the most often incorrectly used name within the genus and taxonomically represents a difficult complex with uncertain species boundaries (Papp et al., 2017). The type of *G. lucidum* was described from Europe, where currently three morphologically similar species have been accepted (Ryvarden and Melo, 2014). Among these, *G. carnosum* Pat., was described from France (Patouillard, 1889) and considered to be identical to *G. atkinsonii* H. Jahn, Kotl. & Pouzar which is typified on a specimen collected in the Czech Republic (Jahn et al., 1980, 1986). In the subsequent literature, *G. carnosum* had often been misidentified as *G. valesiacum* Boud., which was described by Boudier (1895) from a collection found on *Larix decidua* in Switzerland. The microscopic structures of *G. valesiacum* were similar to those of *G. carnosum* and *G. lucidum* and only macroscopical features separate the species in this complex (Wasser et al., 2006a). Preliminary molecular genetic studies indicated that *G. carnosum* and *G. valesiacum* are not separated from *G. lucidum* on species level, however without type studies and detailed phylogenetic analysis, the species delimitation of the European *G. lucidum* complex is not fully understood.

In the early 20th century, four *Ganoderma* species were described from various coniferous trees in North America by Murrill (1902, 1908), which are considered as *G. tsugae* complex. The type specimen of *Ganoderma tsugae* Murrill was found on *Tsuga canadensis* and in the description it is characterized as a species that is closely related to *G. lucidum* (as *G. pseudoboletus*) (Murrill, 1902). The close relationship between *G. tsugae* and the European *G. lucidum* aggregate was confirmed by morphological examinations (Steyaert, 1977; Wasser et al., 2006a), cultural studies (Stalpers, 1978; Adaskaveg and Gilbertson, 1986) and phylogenetic analysis based on ribosomal DNA markers (Moncalvo et al., 1995a,b; Hong and Jung, 2004). The most recent molecular study based on multilocus phylogenetic analysis confirmed that *G. tsugae* is an independent species, and grouped together with *G. oregonense* Murrill and *G. lucidum* s. str. (Zhou et al., 2015). Murrill (1908) differentiated *G. oregonense* from *G. tsugae* mainly by its host species preference (found on *Picea sitchensis*) and geographic distribution. The two species morphologically are rather similar, but the large size of the basidiocarp, the generally duplex context, the larger spores and the long-shafted pileocystidia without apical projections seem to be the main morphological features that distinguish *G. oregonense* from *G. tsugae* (Adaskaveg and Gilbertson, 1988; Torres-Torres et al., 2015). The other two conifer-inhabiting species (*G. nevadense* Murrill and *G. sequoiae* Murrill) described by Murrill (1908) are characterized by sessile basidiocarps and separated based on host



Fig. 1. Basidiocarps of *Ganoderma* species in natural habitat: a–b, *G. cupreolaccatum*; c, *G. applanatum*; d–e, *G. lucidum* (Photocredit: V. Papp).

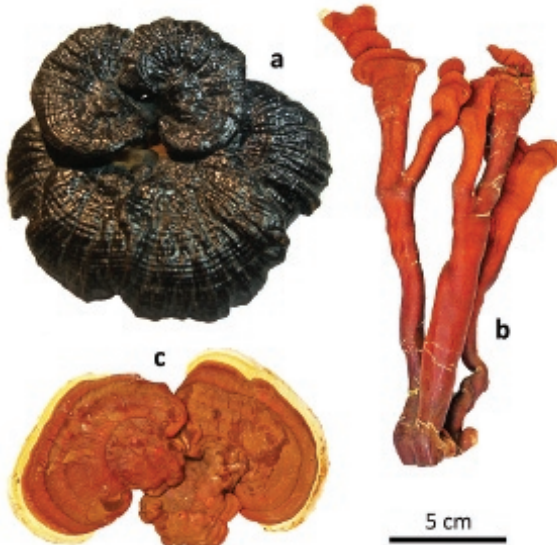


Fig. 2. Cultivated *Ganoderma* species in East Asia: a, basidiocarp of *G. sinense*; b–c, basidiocarps of *G. lingzhi* (Photo credit: V. Papp).

preference and the rimose or unbroken crust of the pileus. However, the taxonomic concept described by Murrill, which was based on geographic distribution and host specificity, was not supported in further studies, and based on morphological characteristics *G. nevadense* and *G. sequoiae* were considered to be synonyms for *G. oregonense* (Steyaert, 1980; Ryvardeen, 1985).

Besides North America, *G. tsugae* was also reported from Asia (e.g., Zhao, 1989), and according to morphological observations, a new variety of this species (var. *jannieae* S. Wasser et al.) was isolated based on a collection found in Northeast China (Wasser et al., 2006b). From temperate Asia three further *Ganoderma* species have been described, which are closely related to *G. lucidum*. Based on a specimen originating from Pakistan, Steyaert (1972) described *G. ahmadii* Steyaert, which was also reported from India and China (Steyaert, 1972; Zhao, 1989). The ITS and LSU-D2 regions of type specimen were sequenced by Moncalvo et al. (1995a) and in his phylogeny *G. ahmadii* is nested together with the European and North American coniferously related species, although it was collected on a legume hardwood species *Dalbergia sissoo*. The other species, *G. mongolicum* Pilát described from Hebei Province in China (Zhao, 1989), is synonymised with *G. tsugae* by Steyaert (1980) based on uniform basidiospore morphology. By contrast, other mycologists accepted *G. mongolicum* as a separate species (Zhao, 1989; Wu and Dai, 2005); however, *G. mongolicum* is only known from the type locality (Moncalvo and Ryvardeen, 1997) and no DNA sequence data has been published to date for this species. The morphological features and phylogenetic position based on ITS analysis of the recently described *G. leucocontextum* T.H. Li et al., placed this species in the *G. lucidum* complex. This new taxa known from the Tibet Autonomous Region and Sichuan Province of China is characterised by its white context and slightly smaller spores (Li et al., 2015).

According to the literature, *G. lucidum* has been reported to have a worldwide distribution, nevertheless, phylogenetic studies have shown that the examined strains labeled as “*G. lucidum*” were polyphyletic according to geographic origin. Moncalvo et al. (1995) explained that the *G. lucidum* aggregate (incl. *G. tsugae* complex) might be too young to have spread worldwide, so this taxa is restricted to the temperate region. The results of recent phylogenetic studies also indicate that *G. lucidum* s. str. (excluding the other members of the *G. lucidum* complex) is a Eurasian species, with widespread distribution in Europe toward temperate Eurasia (Europe, northwestern and northeastern China) to Sichuan and Yunnan Provinces (southwestern China) (e.g., Yang and Feng, 2013; Zhou et al., 2015; Papp et al., 2017). According to Zhou et al. (2015), the representatives of the *G. lucidum* aggregate in North America are *G. tsugae* and *G. oregonense*. Besides of these two species, surprisingly, the occurrences of *G. lucidum* sensu stricto was also confirmed by Loyd et al. (2018) in the United States. However, they noted that *G. lucidum* s. str. was found only in disturbed habitats in geographically restricted areas, which suggests that this species is not native in North America and the collections possibly derived from mushroom growers producing *G. lucidum* outdoors. Further studies should be carried out in order to prove the European and Asian distribution of these species, since the taxonomy of the group is unclear.

Formerly, Adaskaveg and Gilbertson (1986) have found that the North American taxon identified as “*G. lucidum*” are interfertile with *G. resinaceum* Boud. Basidiocarps of *G. resinaceum* is somewhat similar to *G. lucidum* s. str., but it differs in terms of the color of the context and the characteristics of the basidiospores (Steyaert, 1980). Molecular phylogenetic studies showed that the European specimens of *G. resinaceum* grouped in a well separated lineage from the *G. lucidum* aggregate (incl. *G. ahmadii*, *G. carnosum*, *G. leucocontextum*, *G. lucidum* s. str., *G. oregonense*, *G. tsugae* and *G. valesiacum*) (e.g., Zhou et al., 2015; Papp et al., 2017). However, the literature discusses at least 13 *Ganoderma* species described from North America (California, Florida, New York, Ohio), Middle America (Honduras, Mexico), the Caribbean region (Cuba, Jamaica, Grenada), South America (Argentina, Venezuela) and Australia, which are considered to be the synonyms of *G. resinaceum* based on previous morphological studies (e.g., Steyaert, 1972; Bazzalo and Wright, 1982; Ryvar den, 1985; Buchanan and Ryvar den, 1993). The taxonomical status of this group was discussed by Steyaert (1980), who reported specimens under *G. resinaceum* from several countries in Europe, temperate and tropical Asia, Northern and Southern America (incl. South America and the Caribbean region) and Africa. Amongst the synonymised *Ganoderma* species, *G. sessile* Murrill specimens from the type locality and other USA states were studied by phylogenetic perspective and were found to be different from the European *G. resinaceum* (Zhou et al., 2015). The majority of the other species are only known from their type locality, and further investigations are needed to clarify the taxonomical state of the *G. resinaceum* complex and the distribution of *G. resinaceum* s. str.

The Prized East Asian Medicinal Mushroom

The correct taxonomical status of the highly prized medicinal *Ganoderma* species distributed in East Asia and that it has been described in traditional Asian medicine under several popular names (such as “Ling-zhi” in China, “Mannentake” or “Reishi” in Japan, and “Yeongji” in Korea) are intensively studied in the molecular era. Based on similarities in morphology, in therapeutic practice and in the literature, the scientific binomial “*G. lucidum*” has widely been accepted for the commercially cultivated East Asian medicinal mushroom. However, early molecular studies in *Ganoderma*, based on analyses of ITS1, ITS2, and the D2 domain of LSU (Moncalvo et al., 1995a), and mtSSU rDNA sequences (Hong and Jung, 2004) have indicated that the European collections of *G. lucidum* are clearly different from the East Asian ones. However, in these works the Asian “*G. lucidum*” samples were not identified on species level, and without a proposed scientific name, the “Ling-zhi” medicinal mushroom has continuously been referred to as *G. lucidum* in the scientific literature. Based on comprehensive morphological observations and multilocus phylogenetic analyses, Wang et al. (2012) concluded that the species representing “Ling-zhi” is identical to *G. sichuanense* J.D. Zhao & X.Q. Zhang, originally described from the Sichuan Province in Southwest China. By contrast, in a similar study published at almost the same time, Cao et al. (2012) found that the ITS sequence from the holotype of *G. sichuanense* did not belong to the lingzhi clade and grouped together

with specimens identified as *G. weberianum* (Bres. & Henn. ex Sacc.) Steyaert. The authors claimed that lingzhi was hitherto an undescribed species, therefore the binomial *G. lingzhi* Sheng H. Wu et al. (Fig. 2b,c) was proposed, reflecting the traditional Chinese name. Yao et al. (2013) queried the published ITS sequence of the *G. sichuanense* holotype and supposed that DNA from the holotype and paratype of *G. sichuanense* was degraded irreparably and, thus, impossible to sequence. In favor of fixing the application of the name *G. sichuanense*, they designated an epitype and its ITS sequence; however, this is identical to the holotype of *G. lingzhi*. By contrast, Paterson and Lima (2015) emphasized that Yao et al. did not provide supporting data, that the DNAs of the type and authentic materials of *G. sichuanense* were damaged, thereby undermining their interpretations. Zhou et al. (2015) rejected the epitypification of *G. sichuanense*, and suggested that both species are independent and taxonomically valid. This statement was also confirmed by Dai et al. (2017) in a recent study, in which the taxonomy and nomenclature of the “Lingzhi” mushroom has been thoroughly discussed. They noted, that the first possible name applied to “Lingzhi” in East Asia was *Boletus dimidiatus* Thunb., which was described by Thunberg (1784) based on specimens collected from Japan. *Ganoderma dimidiatum* (Thunb.) V. Papp is definitely the first validly published laccate *Ganoderma* species from East Asia and the valid name of *G. japonicum* (Fr.) Sawada as pointed out by Papp (2016). However, the correct taxonomic status of this species remains unclear, due to the fact that the lectotype of *G. dimidiatum* was not available for loan. Therefore, Dai et al. (2017) concluded that the rejection of the name *Boletus dimidiatus* is better in order to stabilize the scientific binomial for “Lingzhi”.

The type specimen of *G. lingzhi* was designated from Hubei Province located in central China, and it was also reported from other Chinese Provinces, viz. Anhui, Henan, Hunan, Jiangsu, Liaoning, Shandong, Sichuan, Tianjin, Yunnan and Zhejiang (Cao et al., 2012; Wang et al., 2012). Outside China, *G. lingzhi* was reported from Bangladesh, Japan and Korea (Cao et al., 2012; Wang et al., 2012; Kwon et al., 2016) and recently it is published under the name *G. sichuanense* from Thailand (Thawthong et al., 2017). Moreover, the ITS sequences of 4 specimens collected from legume trees (*Cassia* spp., *Delonixregia*) in southern India differ only in 2 nucleotide positions from the holotype of *G. lingzhi*. These are probably the westernmost known localities of *G. lingzhi* so far (Papp et al., 2017). The natural range of *G. lingzhi* seems to be restricted to East and Southeast Asia (i.e., central to eastern China, Japan, Korea and Thailand), and it also occurs in Bangladesh and South India.

The *Phaeonema* Group: Medicinal Mushrooms, and Plant Pathogens

The section *Phaeonema* Zhao et al. was typified on *Ganoderma sinense* J.D. Zhao et al. (Fig. 2a) and morphologically characterised by laccate pilear surface, and uniformly brown to deep red context (Zhao et al., 1979). *Ganoderma sinense* was recorded as one of the “Ling-zhi” sources in Chinese pharmacopoeia (besides *G. lingzhi*), and long has been used in traditional Chinese medicine (TCM). This species was described from Hainan (South China) and characterised by annual and stipitate basidiocarp with purplish-black to black laccate pileus and mostly uniform

brown context. *Ganoderma sinense* is frequently referred in the scientific literature to *G. japonicum* Fr. The nomenclatural status of this familiar name was discussed by Papp (2016), who concluded that *G. japonicum* is a superfluous name of the formerly described species from Japan, named *G. dimidiatum* (Thunb.) V. Papp. Chang and Chen (1984) described *G. formosanum* T.T. Chang & T. Chen as a new species from Taiwan based on a specimen growing on formosan sweetgum (*Liquidambar formosana*). This species morphologically is similar to *G. sinense*, but it is formerly accepted by certain authors as a separate species based on its duplex context and ovoid basidiospores with persistent apex (Zhao and Zhang, 2000; Wu and Dai, 2005). The type specimens of both species was studied by Wang et al. (2005), who concluded that the discrimination between these two species resulted from variable characters and incomplete description, thus, they stated that *G. formosanum* is a later synonym of *G. sinense*. This proposal confirmed by preliminary molecular results, but it should be noted that only one material was sequenced, which was labeled “*G. fornicatum*” by Moncalvo et al. (1995b). Without type sequencing, the taxonomical position of the popular medicinal mushroom which was generally identified as *G. sinense* remains unclear. To clarify the taxonomy and nomenclature of numerous East-Asian stipitate *Ganoderma* species, particularly of those which have blackish and laccate pileus (e.g., *G. atrum* J.D. Zhao et al., *G. austrofujianense* J.D. Zhao et al., *G. formosanum* T.T. Chang & T. Chen, *G. neojaponicum* Imazeki and *G. sinense*), further morphological and more serious molecular studies and the inclusion of more specimens and type materials is required.

The morphological group, *Phaeonema* sensu Zhao, comprises several important *Ganoderma* species besides *G. sinense*, such as *G. boninense* Pat., *G. capense* (Lloyd) Teng, *G. cupreolaccatum* (Kalchbr.) Z. Igmándy, *G. tropicum* (Jungh.) Bres. or *G. zonatum* Murrill. Among these, the species named as “*G. boninense*” has an enormous economic value, because it is the causal agent of basal stem rot, one of the most devastating diseases of the oil palm (Mercière et al., 2015). *Ganoderma boninense* was described by Patouillard (1889), based on a collection from Bonin Island. The correct taxonomical state of this species is rather complicated; as a result, several similar, but taxonomically poorly known species were described by taxonomists. Moncalvo and Ryvardeen (1997) discussed *G. boninense* in the “*G. chalconeum*–*boninense* complex”, in which 27 different *Ganoderma* species were listed. The synonymy of *G. boninense* with the formerly described *G. chalconeum* (Cooke) Steyaert was suggested by Corner (1983) in agreement with Ryvardeen (1983). Later, Ryvardeen (2000) synonymized *G. boninense* with *G. orbiforme* (Fr.) Ryvardeen, a species described from Guinea (West Africa). The taxonomical state of *G. orbiforme* and allies was recently discussed by Wang et al. (2014) based on morphological observations and phylogenetic evidence. They concluded, that *G. boninense* is presumably not identical with *G. orbiforme*, although five other *Ganoderma* species, namely *G. cupreum* (Cooke) Bres., *G. densizonatum* J.D. Zhao & X.Q. Zhang, *G. limushanense* J.D. Zhao & X.Q. Zhang, *G. mastoporium* (Lév.) Pat. and *G. subtornatum* Murrill are synonyms of the latter. They emphasized that the recently described *G. ryvardeenii* Tonjock & Mih (as *G. ryvardense*), which is a pathogenic species of oil palm in Cameroon (Central Africa) shows a close

relationship to *G. boninense* and *G. orbiforme*, thus the relationships among these species require further clarification.

The peculiar *Ganoderma* species with perennial basidiocarp covered by laccate surface and usually named as *G. pfeifferi* Bres. is most likely identical to the formerly described *G. cupreolaccatum* (Fig. 1a,b), which is based on a specimen collected from Austria (Central Europe) (Steyaert, 1980; Papp and Szabó, 2012). This perspective medicinal species (Lindequist et al., 2015) is mostly reported from natural beech forests and its distribution is presumably restricted to Europe (Ryvarden and Melo, 2014). However, Corner (1983) described *G. pfeifferi* var. *bornense* from Mt Kinabalu (Borneo), what should be confirmed, or taxonomically revised. A specimen found on *Quercus* sp. in Belgium and described as *G. soniense* Steyaert is later considered to be identical to *G. cupreolaccatum* (Steyaert, 1967). An other species described from Italy under the name *G. puglisii* Steyaert has similar cutis to *G. cupreolaccatum*, but according to Steyaert (1972) the basidiospores are larger. *Ganoderma puglisii* is known only from the type locality and the taxonomical state of this species is still unclear. Phylogenetically, the sequenced specimens of *G. cupreolaccatum* (as *G. pfeifferi*) are not grouped with other *Phaeonema* (e.g., *G. sinense* and *G. boninense*) and are closely related to *G. mutabile* Y. Cao & H.S. Yuan and other species belonging to the *Elfvigia* group (Papp et al., 2017).

The *Elfvigia* Group: *Ganoderma applanatum* and Related Species

The morphological group traditionally labeled as *Elfvigia* is mostly comprised of the species with sessile or substipitate perennial basidiocarps with dull pileal surface. Moncalvo and Ryvarden (1997) listed 51 species in the *Elfvigia* group, of which they considered 21 to be synonyms. The taxonomical uncertainty is increased by the fact that the majority of the listed species are represented by one or few collections, all restricted to the type locality and adjacent regions: For example, *G. chilense* (Fr.) Pat. (from Chile), *G. dubiocochlear* (Lloyd) Sacc. & Trotter (from Madagascar), *G. wuhuense* X.F. Ren (from Anhui province, Eastern China), *G. luteicinctum* Corner (from Singapore), *G. dejongii* Steyaert and *G. hoehnelianum* Bres. (from Java, Indonesia). Within the *Elfvigia* group, Steyaert (1980) separated three sub-genera based on the microscopic structure of the pileipellis: (i) *Ganoderma* subgen. *Elfvigia* (*G. applanatum*), (ii) subgen. *Anamixoderma* (*G. adpersum*), and (iii) subgen. *Plecoderma* (*G. philippii*). Wasser et al. (2006a) proposed to discuss *Anamixoderma* and *Plecoderma* as sections beneath the *Elfvigia* subgenus. They noted, that besides the differences in the pileipellis structure all of these species are rather uniform in their basic fomitoid structure and basidiospores with smooth type of the surface. Because the phylogenetic state of the elfvingioid *Ganoderma* species is not yet sufficiently clear, in the majority of cases it is discussed under the name “*Elfvigia* group” or “*Ganoderma applanatum-australe* species complex” in the literature (Moncalvo and Buchanan, 2008).

The central species of the *Elfvigia* group is *G. applanatum* (Pers.) Pat. (Fig. 1c), which is considered to be identical to *G. lipsiense* (Batsch) G.F. Atk. Although the latter name was previously described, eventually the Nomenclature Committee for

Fungi sanctioned the basionym *Boletus applanatus* Pers. against *B. lipsiensis* Batsch (Redhead et al., 2006; Demoulin, 2010; Norvell, 2011). The neotype of *B. applanatus* s. str. selected by Redhead et al. (2006) was examined by Niemelä and Miettinen (2008). They proved that it conforms morphologically with the current European concept of *G. applanatum* and is distinct from the superficially similar species, *G. adspersum* (Schulzer) Donk. It is also suggested by the phylogenetic studies that only two non-laccate, and perennial *Ganoderma* species are known from Europe, therefore the other species with similar fruiting body described from the continent might be the synonym of *G. adspersum* or *G. applanatum*: *G. europaeum* Steyaert, *G. gelsicola* (Berl.) Sacc., *G. kosteri* Steyaert, *G. linhartii* (Kalchbr.) Z. Igmándy, *G. lipsiense* and *G. vegetum* (Fr.) Bres. Species considered to be synonyms of *G. applanatum* even originated from other continents than Europe. The type specimen of *G. incrassatum* (Berk.) Bres., a species originally described from Australia was studied by Ryvar den (1984), who concluded that it is identical to *G. applanatum*. Three other species described from the United States, namely *G. brownii* (Murrill) Gilb., *G. leucophaeum* (Mont.) Pat. and *G. megaloma* (Lév.) Bres. are also considered as a synonyms of *G. applanatum* in the literature (Gottlieb and Wright, 1999; Lowe and Gilbertson, 1961; Ryvar den, 1982). However, amongst these, the correct taxonomical state of *G. brownii* is the most controversial (see Moncalvo and Ryvar den, 1997); and certain authors accepted it as a distinct species apparently restricted to California (e.g., Gilbertson and Ryvar den, 1986; Zhou et al., 2016). In the literature, *G. applanatum* is reported as a cosmopolitan species, although Seo and Kirk (2000) emphasised that “*G. applanatum*” (besides *G. lucidum*) is probably the most frequently misapplied name in the genus. Therefore, to circumscribe the real distribution of *G. applanatum* s. str., the taxonomic revision of morphologically similar species and specimens identified as *G. applanatum* from different geographical regions (especially from the tropics) would be necessary.

Future Challenges

The following statement of Moncalvo (2005) should continue to be emphasized: “incorrect taxonomic identification of *Ganoderma* strains hampers comprehensive strategies for drug discovery as well as for monitoring and managing diseases caused by *Ganoderma* in woody crops and forest ecosystems”. However, a lot of new taxonomical information on *Ganoderma* was published recently, due to the rapid spread of molecular genetic methods; the extremely diverse nomenclature, caused by the difficulties in the identification and by the different taxonomical concepts, makes it very hard to understand the new results of the applied mycological research carried out on *Ganoderma* species. In the upcoming scientific papers, it would be important to report barcoding sequences (i.e., ITS or *Tef1- α*) from the examined *Ganoderma* samples as many times as it is possible, because it could help greatly to understand the published results correctly. Besides describing new species from those *Ganoderma* samples which can not be identified by unambiguous morphological characteristics nor by molecular genetic analyses, greater efforts should be made to analyse the types of the previously described species. In order to clarify the nomenclatural and

taxonomical problems, first the valid *Ganoderma* names should be typified, and these representative collections should be sequenced and studied using molecular genetic methods.

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