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Progress report on the study of wood-decaying fungi in China

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This study addressed three important aims: (1) undermining the previously obtained raw data about wood-decaying fungi (WDF) distribution and continuously investigating permanent plots to address certain scientific questions in ecology, (2) resolving the higher-level phylogeny of WDF with the help of multiple loci, and (3) testing and estimating the medicinal values of species that are closely related to well-known medicinal species. More than 1200 species and 2469 strains of WDF in China were identified from 28908 specimens collected from a series of field investigations. Using these materials, studies in multiple disciplines, such as ecology, taxonomy and phylogeny, and medicine, have been performed. With respect to ecology, the diversity of wood-decaying polypores significantly differed among a boreal forest zone, a temperate and warm temperate forest zone, and a tropical and subtropical forest zone. For instance, from north to south, the number and proportion of brown-rot species and the proportion of species found on fallen trunks were both decreased. The ecological patterns of wood-decaying polypores on gymnosperm and angiosperm trees were also explored by a case study in Northeast China. Although the total species richness was similar between the two tree groups, several other characteristics were significantly different, such as community structure and richness in certain substrates. The taxonomy and phylogeny of wide samples were referred to and their phylogenetic positions were resolved or at least partially established. In particular, phylogenetic knowledge about four genera, *Fomitiporia*, *Ganoderma*, *Inonotus* and *Perenniporia*, which include medicinal species, was essential for further research to determine the medicinal values of these types of fungi. Among these medicinal species, we mainly focused on *Inonotus obliquus* for its medicinal purposes. Polyphenols, polysaccharides and lanostane-type triterpenoids, extracted from the sterile conk of this species, could dramatically decrease levels of free radicals, DPPH and hydroxyl radicals, respectively. The metabolic profiles (both production and composition) of cultured *I. obliquus* mycelia could be altered by co-culture with other medicinal species or by induction of S-nitrosylation and denitrosylation, which may enhance the antioxidant capacity of *I. obliquus*.

Mycota, ecology, taxonomy, phylogeny, medicinal metabolites

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Wood-decaying fungi (WDF) are a subset of macrofungi with various types of basidiocarps (Figure 1). They are not a natural taxonomic group, with members scattered across several orders of Agaricomycetes (Basidiomycota) [1]; however, they have developed similar habitats. WDF are able to inhabit all types of woods and soils with a layer of leaf litter [2]. During their life cycle, WDF decompose lignocellulose from plant cell walls for their growth and reproduction; meanwhile, they release nutrients, particularly carbon [2]. Therefore, they play an essential role in the function of global forest ecosystems. WDF also have important economic values as forest pathological [3–6], edible [7], medicinal [8,9], and biotechnological fungi [10].

In Europe and North America, studies on WDF have been performed for a long time, and many monographs on their taxonomy, which generally rely on morphology, have been published over the past decades [11–14]. After the molecular method was introduced, the phylogeny and taxonomy of WDF were dramatically amended [1], and many higher-level taxonomic ranks were proposed or confirmed [15–17]. Based on the comprehensive recognition of WDF, their ecological pattern [18], pathogenic potential [3] and industrial application [10] have attracted much attention.

Since 1916, the year the first mycological report was

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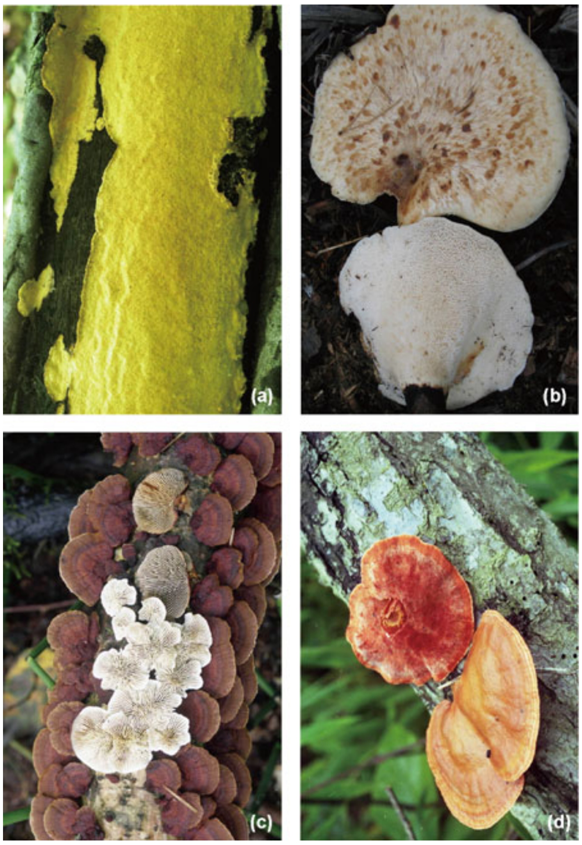

Figure 1 Basidiocarps of four WDF species. (a) *Perenniporia maackiae* (Bondartsev & Ljub.) Parmasto (Dai 8258, IFP 006467 from Changbaishan, Jilin Province); (b) *Polyporus squamosus* (Huds.) Fr. (Dai 8082, IFP 005041 from Shenyang, Liaoning Province); (c) *Daedaleopsis tricolor* (Bull.) Bondartsev & Singer (Dai 7073, IFP 001391 from Changbaishan, Jilin Province); (d) *Pycnoporus sanguineus* (L.) Murrill (Dai 7484, IFP 011910 from Huidong, Guangdong Province).

published by a Chinese [19], China has had several mycologists. As pioneering founders of the field, Profs. TAI FungLai (1893–1973) and TENG ShuChun (1902–1970) initiated study of the Mycology discipline in China. Later, Prof. ZHAO JiDing (1916–1995) made an internationally known work in taxonomy of the genus *Ganoderma* and also other polypores, while Prof. ZANG Mu (1930–2011) mainly focused on the taxonomy of the fungi in southwestern China. Over the past two decades, investigation and application of WDF as a resource have prospered. More than 1200 species have been recorded in China [20–22], of which 160 are newly described [23–49], 152 are forest pathogens [6] and 158 have medicinal functions [8]. Therefore, it is fair to say that the study of WDF in China, especially that on taxonomy, has been top-notch worldwide.

In this review, we comprehensively detail current advances in the knowledge of WDF in China, especially those made by our research group. This progress is presented with respect to three areas: mycota, taxonomy and phylogeny, and medicinal values. The ongoing and future directions of our research group are also provided.

1 National survey and biodiversity

China has various landscape patterns, including a very large forest area, and thus maintains a high diversity of WDF. A total of 184 localities situated in almost all of the forest types in China have been investigated by our research group (Figure 2). In field trips, the forests are randomly wandered with a bias in favor of humid regions. During the collection of basidiocarps of WDF, *in situ* photos are often taken and their ecological niches are also recorded in detail. When backing to the laboratory, strains are isolated from fresh basidiocarps and stored at a lower temperature; the basidiocarps are then dried using a mushroom dryer and identified with the aid of a microscope. After a series of thorough investigations, a total of 28908 specimens and 2469 strains have been deposited at the herbaria of the Institute of Applied Ecology, Chinese Academy of Sciences (IFP) and the Institute of Microbiology, Beijing Forestry University (BJFC) for further study. Using these materials, the species lists of WDF for each provincial level district and certain famous mountains and hot-spot regions of China have been published [50–57], besides those in the whole country [20–22].

By undermining these cumulative data, certain scientific questions about the ecological patterns of WDF have been addressed. A case study has been performed to compare the preferences of wood-decaying polypores among a boreal forest zone, a temperate and warm temperate forest zone, and a tropical and subtropical forest zone in China [58]. Among these three geographic zones, polypore diversity was highest in the tropical and subtropical forest zone, which harbored the highest tree species diversity. The temperate and warm temperate forest zone had a polypore community structure that was more similar to the boreal forest zone than to the tropical and subtropical forest zone, although the geographic distance between the temperate and

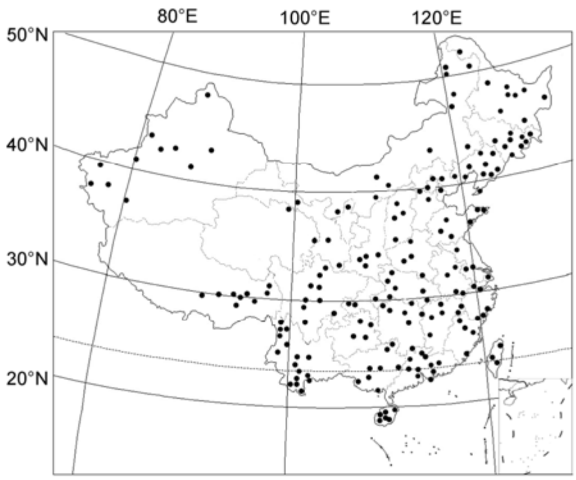

Figure 2 The locations of investigated areas in China by our research group (black dots).

warm temperate forest and the boreal forest zones is greater than that between the temperate and warm temperate forest and the tropical and subtropical forest zones. The number and proportion of brown-rot polypore species were lower in the boreal forest than in the tropical and subtropical forest zones. The proportion of polypore species on fallen trunks was also lower in the boreal forest than in the tropical and subtropical forest zones, although fallen trunks were the most attractive substrate in all three forest zones.

Zhou and Dai [59] recognized that species richness between the wood-decaying polypores associated with gymnosperm and angiosperm trees was not significantly different in the case of Fenglin and Changbaishan Nature Reserves in Northeast China. However, in several other areas, the ecological patterns of polypores between the two tree groups were significantly different. For instance, the polypore community structure among gymnosperm trees was more similar than the structure among angiosperm trees. In addition, compared to angiosperm trees, gymnosperm trees displayed lower polypore species richness both on fallen trunks and in unprotected forests, fewer common polypores but more occasional species, and a lower proportion of white rot polypores but a higher proportion of brown rot species. Although this study is specific for a local region, it might be a valuable reference for further worldwide studies.

With respect to certain hot-spot regions of biodiversity, such as the Changbaishan Nature Reserve, a long-term ecological investigation has been ongoing for several years. In the Changbaishan plot (the CBS plot), the most northern plot of the China Network, the community structure and distribution of WDF on a certain tree genus, *Acer*, were analyzed [60]. The results showed that among 690 recorded individuals representing 79 species (45 genera, 14 families), *Hyphodontia flavipora* (Berk. & M.A. Curtis ex Cooke) Sheng H. Wu, *Irpex lacteus* (Fr.) Fr., *Oxyporus populinus* (Schumach.) Donk, *Stereum subtomentosum* Pouzar and *Trametes versicolor* (L.) Lloyd were the dominant species, comprising more than 45% of all individuals, and more than 55% of the species inhabiting early decaying stage wood were pioneers in the degradation of lignocelluloses of plant cell walls.

2 Taxonomy and phylogeny

Since the era of Linnaeus, the taxonomy of many different species has attracted the attention of natural historians worldwide. With the application of molecular sequencing for fungi in the early 1990s [61], the taxonomy and phylogeny of WDF boomed. The high diversity of WDF in China provides an abundant resource for this kind of analysis. Recently, based mainly on Chinese specimens and strains and on type and authentic specimens outside China, the phylogenies of genera belonging to four orders (Hymenochaetales, Polyporales, Russulales and Thelephorales) of Agaricomycetes were resolved or preliminarily characterized, such as *Antrodia* P. Karst. [62], *Bondarzewia* Singer [63], *Daedalea* Pers. [64], *Fomitiporia* Murrill [65], *Fomitopsis* P. Karst. [66], *Ganoderma* P. Karst. [67], *Grammothele* Berk. & M.A. Curtis [68], *Hymenochaete* Lév. [69], *Inonotus* P. Karst. [70], *Lenzitopsis* Malençon & Bertault [71], *Lignosus* Lloyd ex Torrend [72], *Perenniporia* Murrill [73], *Phellinus* Quél. [74], *Phylloporia* Murrill [75], *Pseudochaete* T. Wagner & M. Fisch. [76], *Theleporus* Fr. [68], *Tinctoporellus* Ryvarden [77], *Veluticeps* (Cooke) Pat. [78] and so on. Among these genera, *Fomitiporia*, *Ganoderma*, *Inonotus* and *Perenniporia* include many famous medicinal species, and thus knowledge of their phylogeny could reveal more species with potentially similar medicinal values. Moreover, the exact identification of this kind of natural resource could facilitate its application and the continuation of studies by different research groups.

2.1 Fomitiporia

Fomitiporia belongs to the family Hymenochaetaceae (Hymenochaetales) and is characterized by its hyaline, subglobose to globose and thick-walled basidiospores with strongly cyanophilous and dextrinoid reactions [79]. This genus was split from *Phellinus* s.l. with *Fomitiporia langloisii* Murrill as the generic type and was determined to be monophyletic based on molecular data [65,80,81]. *Fomitiporia hartigii* (Allesch. & Schnabl) Fiasson & Niemelä, *F. punctata* (Pilát) Murrill and *F. robusta* (P. Karst.) Fiasson & Niemelä were documented as medicinal species [82]. Until now, a total of six validated species had been originally described from China [65,79], including *Fomitiporia ellipsoidea* B.K. Cui & Y.C. Dai (Figure 3), which produced the largest fungal basidiocarp in the world [83]. This news attracted worldwide attention and was reported by the British Broadcasting Corporation (BBC; http://www.bbc.co.uk/nature/14294283). However, the phylogeny of this genus worldwide has not yet been thoroughly characterized. As such, our research group, together with Belgian mycologist DECOCK Cony, is now working on this issue, specifically using four gene loci. Based on preliminary analysis, at least six undescribed species (clades) were identified, and more importantly, the global phylogeny of *Fomitiporia* could be addressed, which could provide essential clues to explore the evolution and origin of *Fomitiporia*, and thus could facilitate recognition of potential medicinal species of this genus.

2.2 Ganoderma

Ganoderma is the type genus of the family Ganodermataceae (Polyporales). Some species of this genus were thought of as a type of sovereign remedy in Traditional Chinese Medicine (i.e., Ling Zhi), and thus, they have been

Figure 3 A basidiocarp of *Fomitiporia ellipsoidea*, showing a part of the largest fruitbody in the world (Dai 12145, BJFC010399 from Jianfengling, Hainan Province).

issued for artificial cultivation and marketing [8]. The taxonomic study of *Ganoderma* in China can be dated back to more than 100 years ago [84]. However, many studies over the last century were of low value and led to taxonomic chaos [85], because their results relied on unstable macro-morphological characters, which are easily affected by unessential events in evolution [86]. Subsequently, according to more reliable (micro) morphological and molecular evidence, some species that were originally described by such studies were amended to be synonyms of earlier described species [87–89]. Nevertheless, it still should go a long way towards the natural classification of *Ganoderma*. Recently, Cao et al. [67] performed a phylogenetic analysis of *Ganoderma* subgen. *Ganoderma* P. Karst. based on ITS sequences from 51 isolates representing 11 species of *Ganoderma*. This study indicated that the legendary medicinal species (Ling Zhi) in Chinese folklore was not *Ganoderma lucidum* (Curtis) P. Karst. (generic type), which was originally described from the UK; this species was newly described as *Ganoderma lingzhi* Sheng H. Wu, Y. Cao & Y.C. Dai (Figure 4) with basidiocarp images and microscopic illustration [67]. The distribution of the real *G. lucidum* was updated as from Europe to Northeast China [67]. The phylogeny of the other subgenus, *Ganoderma* subgen. *Elfvingia* (P. Karst.) Imazeki, is also currently being studied. Many types and authentic Chinese specimens should be checked to clarify their real taxonomic and phylogenetic positions. These studies could provide a general framework for further in-depth phylogenetic analyses, perhaps inferred from multiple loci.

2.3 Inonotus

Inonotus was formerly one of the largest genera in the Hymenochaetaceae. Recent molecular phylogeny work has transferred some species of this genus to *Inocutis* Fiasson & Niemelä, *Inonotopsis* Parmasto, *Mensularia* Lázaro Ibiza and *Onnia* P. Karst., while several species that used to belong to *Phellinus* were combined into *Inonotus* [15,79]. At the moment, the reduced size genus includes several well-known medicinal species, such as *I. baumii* (Pilát) T. Wagner & M. Fisch., *I. lonicericola* (Parmasto) Y.C. Dai, *I. sanghuang* Sheng H. Wu, T. Hatt. & Y.C. Dai (Figure 5) and *I. vaninii* (Ljub.) T. Wagner & M. Fisch. [82,90], which have been used in China since ancient times, according to traditional folklore. These medicinal species differ from other species of *Inonotus* mainly in their perennial hard woody basidiocarps and in their dimitic hyphal system in trama, from a morphological perspective [79]. With respect to phylogeny inferred from nLSU or ITS combined mt-SSU sequences, these species form a strongly supported clade and have been tentatively named as a medicinal group [70] that is isolated from other species [15,91]. A combination of the morphological and phylogenetic evidence indicated that the current concept of *Inonotus* is still polyphyletic, and its characteristics should be further delimited. To result in a comprehensive understanding, a multi-locus phylogenetic analysis for the worldwide species of *Inonotus* should be performed. We expect that new taxonomic units at the above-species level will likely be erected.

2.4 Perenniporia

Perenniporia (Polyporales) is a large and cosmopolitan genus, comprising approximately 90 wide-sense species worldwide [50,53,92–100]. This genus is heterogeneous in

Figure 4 Basidiocarps of *Ganoderma lingzhi* (Cui 9164, BJFC008102 from Taian, Shandong Province).

Figure 5 A basidiocarp of *Inonotus sanghuang* (Dai 12723, BJFC012876 from Guangyuan, Sichuan Province).

morphology; for example, its species can have a dimitic or trimitic hyphal system and dextrinoid or indextrinoid basidiospores and vegetative hyphae [101]. Phylogenetically, *Perenniporia* has also been repeatedly indicated to be polyphyletic [93,102,103]. The latest phylogenetic study, inferred from ITS combined nLSU sequences, showed that 31 species of *Perenniporia* formed seven strongly supported clades, viz., clades *Perenniporia* s.s., *Truncospora* Pilát, *Perenniporiella* Decock & Ryvarden, *Abundisporus* Ryvarden, *Vanderbylia* D.A. Reid, *Perenniporia subacida* (Peck) Donk and *Hornodermoporus* Teixeira [73]. Obviously, sequences of the other two thirds of the species of this genus are needed to construct a comprehensive phylogeny of *Perenniporia.* In addition, phylogenetic data inferred from multiple loci could provide more reliable evidence for erecting new genera, according to the currently known or newly emerged clades. *Perenniporia robiniophila* (Murrill) Ryvarden (Figure 6), which belongs to the clade *Vanderbylia*, is an attractive medicinal species. A series of studies on its medicinal functions and metabolites have been performed [104]. However, whether the other two species, which are also confirmed members of the clade *Vanderbylia*, *Perenniporia fraxinea* (Bull.) Ryvarden and *P. vicina* (Lloyd) Decock & Ryvarden, have similar medicinal values has not been considered. This might be a future direction for the exploration of new medicinal species. Furthermore, the identification of more species belonging to this clade would provide more candidates for medicinal exploitation.

3 Medicinal exploitation

As a type of medicinal resource, WDF have been used for medicinal evaluation mainly in China, and in South Korea [105,106], Japan [107], USA [108], Canada [109], Mexico [110], Europe [111] and others. Some species of WDF, such as those from *Inonotus* and *Ganoderma*, have been cultivated and commercialized (Figure 7). It is well known that certain species of WDF have antioxidant, antitumor and immunity-boosting functions [82]. Natural metabolites of WDF are fundamental to these medicinal functions. Therefore,

Figure 6 Basidiocarps of *Perenniporia robiniophila* (Dai 11740, BJFC008853 from Dali, Yunnan Province).

Figure 7 Cultivated basidiocarps of *Ganoderma lingzhi*.

characterization and extraction of metabolites are the initial essential step in studying and utilizing WDF for medicine discovery.

Over the past 10 years, extensive attention has been paid to *Inonotus obliquus* (Ach. ex Pers.) Pilát. From the sterile conk of this species (Figure 8), which is known as Chaga in the Far East, phenolic compounds, polysaccharides, lanostane-type triterpenoids and melanins have been extracted (reviewed in [112]). Among these active metabolites, polyphenols dramatically decrease levels of free radicals, while polysaccharides and a few lanostane-type triterpenoids can partially scavenge DPPH and hydroxyl radicals, respectively [113]. With respect to melanins, the most unique products of *I. obliquus*, their antioxidant qualities are still poorly understood [112].

Basidiocarps of *Inonotus obliquus* have become increasingly difficult to find in nature. This might result from the reduction of natural habitats for *I. obliquus* growth. Additionally, relatively long growth periods are required to produce basidiocarps after basidiospore germination. To obtain more metabolites, cultivated fungal hyphae are a good alternative. However, compared to natural basidiocarps, mycelial cultures have poorer yields. As such, efforts to increase accumulation of bioactive metabolites have been

Figure 8 The sterile conk of *Inonotus obliquus* (Dai 11102, IFP 008580 from Genhe, Inner Mongolia Autonomous Region).

undertaken. It has been reported that co-culture of *I. obliquus* with *Phellinus punctatus* Pilát (=*Fomitiporia punctata*), another medicinal species, could increase the production of metabolites [114]. The alternative metabolites also have a higher antioxidant potential [114]. This provides a candidate for promoting production of metabolites. More co-culture combinations of *I. obliquus* and other medicinal species should be tested and evaluated in future studies. It was also showed that the involvement of S-nitrosylation and denitrosylation could regulate the metabolic pathway of polyphenols and could thus alter metabolic profiles, enhancing production of metabolites [115].

4 Future prospects

Through the effort of generations, studies of WDF in China have produced much knowledge. To continue making progress, the following directions must be pursued.

As the investigation of WDF across China continues, the raw data could be a good resource for addressing the ecological issues of WDF, such as their distribution along elevational gradients within a region. Meanwhile, plot-targeted field studies over a long period are needed to explore certain scientific questions. For instance, identification of the ecology theory that dictates the distribution of WDF and how the distribution of WDF changes over a (long or short) time scale is an interesting area to explore.

DNA sequence analysis has not only allowed for higher resolution in the delimitation of species complex of WDF, but has also provided a relatively uniform standard for higher-level taxonomy. This method gives researchers an opportunity to amend the current taxonomic frame and could result in a more natural relationship in the family and order ranks. As mentioned above, multiple loci and even whole genome sequences in the near future are needed to deal with these kinds of issues. In light of the fact that the number of sequences in public databases is rapidly increasing, this research should be performed by Chinese researchers as soon as possible.

According to phylogenetic results, some previously known and newly described species have been implicated as closely related to medicinal WDF. While the medicinal values of these species should be further tested by physiological experiments, they are undoubtedly likely candidates for screening metabolites with higher efficacy and more functions.

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