

## A review on the diversity, phylogeography and population genetics of *Amanita* mushrooms

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*Amanita* mushrooms are important for both human beings and ecosystems. Some members in this genus are valued edible species, whereas some others are extremely poisonous, and most species are ectomycorrhizal. Significant progress has been made in recent years in our understanding of the diversity, phylogeography and population genetics of *Amanita* mushrooms. A significant reason for the progress was due to the increasing application of molecular methods in the analyses. In this review, we summarize the researches in the diversity, phylogeography and population genetics of *Amanita* mushrooms, with the focus on advances over the past 20 years. We also discussed future research directions, including several unresolved topical issues.

**Keywords:** *Amanita*; ectomycorrhizal fungi; phylogeny; molecular markers

### Introduction

*Amanita* Pers. is one of the most specious and best-known fungal genera. The genus comprises about 500 described species and likely a similar number of undescribed species (Bas 2000; Yang 2000a; Tulloss 2005). Because it contains both deadly poisonous species, e.g. *Amanita phalloides* (Vaill. ex Fr.) Link and famous edible species, e.g. *Amanita caesarea* (Scop.) Pers., this genus has attracted the attention of mycologists since the very beginning of scientific mycology (Persoon 1801; Fries 1821). Moreover, a large majority of the species in this genus form ectomycorrhizal (EM) relationships with vascular plants and play important roles in ecosystems (Yang 1997). With the introduction of molecular methods at the end of last century in analysing the natural history of this genus (Weiß et al. 1998; Drehmel et al. 1999), our knowledge of genus *Amanita* has increased rapidly. The aim of this review is to summarize the progress about the diversity, phylogeography and population genetics of amanitas, emphasizing the results from the last 20 years.

### Diversity

*Amanita* mushrooms belong to Basidiomycota, Agaricomycetes, Agaricales and Amanitaceae. They are

characterized by having (usually) white, free to subfree gills with bilateral lamellar trama, white spore print, volval remnants as warts or patches on the pileal surface and the base of the stipe (Yang and Oberwinkler 1999). In addition, many have an annulus on the stem. This genus is divided into seven sections: *Amanita*, *Caesareae* Singer, *Vaginatae* (Fr.) Quél., *Amidella* (J.-E. Gilbert) Konrad & Maubl., *Lepidella* (J.-E. Gilbert) Veselý, *Phalloideae* (Fr.) Quél., and *Validae* (Fr.) Quél (Yang 1997). Most of the lethal species are included in section *Phalloideae*, whereas most of the edible species belong to the section *Caesareae* (Figure 1).

### New taxa

It has been estimated that there are 900–1000 species of *Amanita* worldwide (Tulloss 2005). Of these, about half have been described. Among these described species, about 100 are considered poisonous and about 50 are edible. For the remaining species, their edibility is largely unknown. Over the last two decades, about 220 new taxa (new species, new varieties and new forms) in *Amanita* have been reported from all over the world, especially in East Asia, Central and South America, South Africa and Australia. While many of these were due to the analyses of

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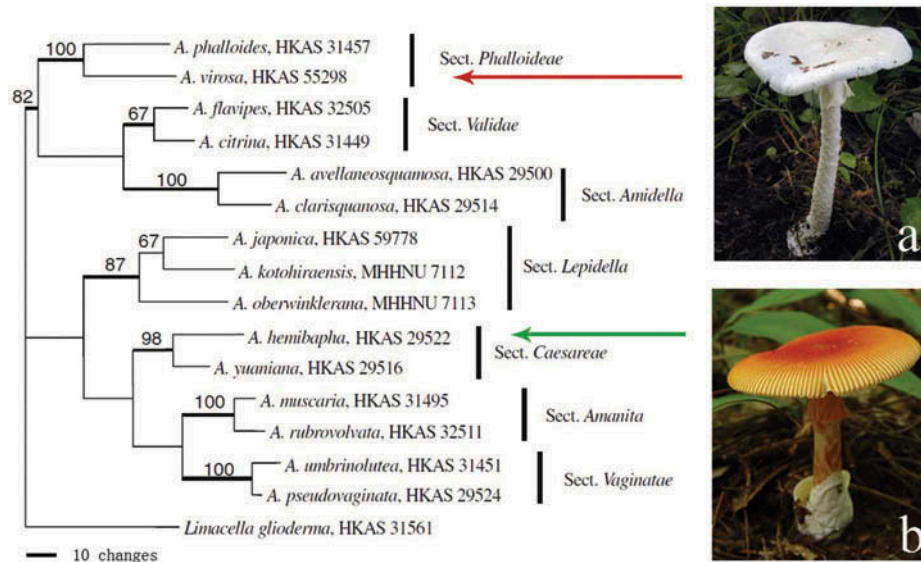


Figure 1. Phylogenetic position of a lethal species, *A. virosa* (a), and an edible species, *A. hemibapha* (b), in a most parsimonious tree of genus *Amanita* based on nuclear large subunit (nLSU) sequences (Zhang et al. 2010).

new samples from previously under-sampled geographic regions, the application of molecular markers helped reveal a significant number of new taxa (cryptic species) among existing collections, similar to those found in many other groups of basidiomycetes (Yang 2011).

Here, because of the large number of new taxa, we will not describe all the new species in detail. Instead, we will provide a representative summary of new species from diverse geographic regions. For example, Oda et al. (2001, 2002a, 2002b, 2002c) reported five species of *Amanita* from Japan. Interestingly, among these five species, *Amanita areolata* was later found to be a synonym of *Amanita zangii*, and *Amanita griseoturcosa* was later transferred from the section *Phalloideae* to the section *Lepidella* (Cai et al. 2014). Nagasawa and Mitani (2000) also reported a new species in the section *Lepidella*. Based on the intensive studies on amanitas from China and adjacent areas, Yang (2005) published Flora Fungorum Sinicorum Vol. Amanitaceae, and described 26 new species (Yang and Doi 1999; Yang et al. 1999, 2001, 2004; Yang 2000a, 2000b, 2002; Yang and Li 2001; Yang and Zhang 2002). However, despite the comprehensive update, additional species were continuously described from China. For example, Zhang et al. (2010) reported three lethal amanitas in East Asia. Deng et al. (2014) and Li and Cai (2014) each described a new *Amanita* species from South China. In other parts of Asia, many new species were also found. For example, five new taxa were found in India (Bhatt et al. 2003) and Pakistan (Tulloss et al. 2001).

Outside of Asia, Simmons et al. (2002) reported four new species of *Amanita* from Guyana. Tulloss et al. (1992) studied the amanitas from Andean Colombia,

and described 11 new species (or new varieties). Eicker et al. (1993) reported a new species named *Amanita reidii* from South Africa. However, because *A. reidii* was associated with *Eucalyptus*, he considered it an introduced species from Australia. Wood (1997) did extensive studies on genus *Amanita* in Australia and reported 34 new species. Even in Europe and North America, where *Amanita* had been intensively studied by fungal taxonomists, new *Amanita* taxa have also reported (Tulloss and Lindgren 1994; Tulloss et al. 1995; Neville and Poumarat 2004).

#### Intraspecific variations

Many *Amanita* species contain one or more varieties or forma (Tulloss et al. 1995; Yang 2005). How to define these infraspecies-level taxa remains a challenge. For some saprophytic basidiomycetes such as *Flammulina* and *Oudemansiella*, mating compatibility test is often used (Petersen and Halling 1993; Petersen et al. 1999). Unfortunately, most amanitas are EM and difficult to culture in the laboratory. Thus, mating test is unsuitable to identify their inter-fertility, so as to assign varieties and forma within *Amanita* species. Instead, the genealogical concordance phylogenetic analysis based on DNA nucleotide sequences has become popular in species and infraspecies recognition. According to the internal transcribed spacer (ITS) sequences analyses, Zhang et al. (2004) found four samples of *Amanita parvipantherina* from different geographical localities and with different colours and morphologies in their fruit bodies all belonged to the same species. Based

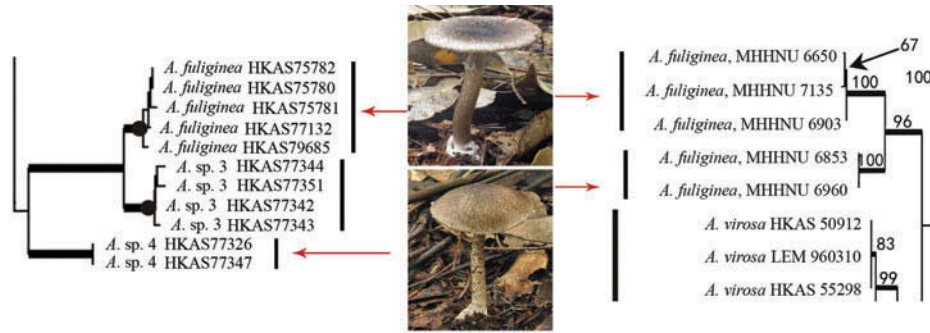


Figure 2. Two sub-clades of *A. fuliginea* in two phylogenetic trees (parcel) of *Amanita* based on ITS sequences (left: Cai et al. 2014; right: Zhang et al. 2010). *Amanita* sp. 4 in left tree is corresponding to *A. fuliginea* MHHNU 6853 and 6960 in right tree.

on multilocus DNA sequence data, Geml et al. (2008) confirmed the existence of several distinct phylogenetic species within *Amanita muscaria*. Zhang et al. (2010) found two sub-clades within *Amanita fuliginea* and suggested that they should be named different forma or even different species. Indeed, recently, Cai et al. (2014) confirmed that these two sub-clades represented two different species (Figure 2).

Albefaction is a common phenomenon in *Amanita* species. Here, albefaction refers to white varieties, forma or morphotypes in some coloured *Amanita* species. Indeed, ‘var. alba’ or ‘f. alba’ has been reported in many species of this genus (Tulloss et al. 1995; Yang 2005). A putative reason for albefaction is mutation in genes related to pigment synthesis, though the specific mechanisms and process are not clear. For some species, e.g. *Amanita subjunquillea*, albefaction is accompanied by other genetic changes. However, for other species, e.g. *Amanita pallidorosea*, the white morphotypes showed no obvious change except fruiting body colour, with natural fruiting bodies forming a continuous redistribution of colours and morphotypes (Zhang et al. 2010) (Figure 3).

### Gasteromycetation

Gasteromycetation has happened independently several times in different groups of fungi (Hibbett 2007). Secotioid and gasteroid forms also occur in genus *Amanita* as well as in some other groups of Basidiomyceta (Yang 2011). A secotioid genus *Torrendia* and a gasteroid genus *Amarrendia* Bougher & T. Lebel were postulated as close relatives of agaricoid amanitas over 60 years ago (Malencon 1955; Bas 1975). These hypotheses were later confirmed by molecular sequence information (Moncalvo et al. 2002). In 2010, Justo et al. (2010) formally transferred members of *Torrendia* and *Amarrendia* to genus *Amanita*. In addition, they suggested that the Mediterranean climate was responsible for the convergent evolution of these sequestrate fungi (Figure 4).

### Phylogeography

#### Distribution patterns

Studies on geographic distribution patterns are fundamental for understanding the phylogeographic history of all organisms. We note that due to recent taxonomic revisions



Figure 3. A ‘normal’ form (left) and an alba form (right) of *A. pallidorosea*.



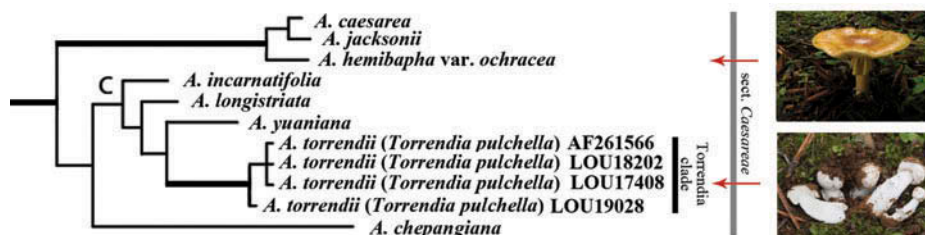


Figure 4. *Torrendia* and *Amanita* in a phylogenetic tree based on nLSU sequences (Justo et al. 2010).

early literature on the distribution of some *Amanita* species may be outdated. One example is *Amanita gemmata*, a species originally described from Europe (Fries 1838) and later reported from North America (Coker 1917; Jenkins 1986) and eastern Asia (Nagasawa and Hongo 1985). Later molecular phylogenetic analysis (Zhang et al. 2004) showed that the so-called *A. gemmata* in North America and eastern Asia actually belong to species distinctly different from *A. gemmata* in Europe. These and other analyses suggest that *Amanita* species are more endemic than previously thought. For example, *Amanita exitialis* is restricted to South China and southwestern China, *A. fuliginea* in tropical and subtropical East Asia, and *Amanita virosa* in Europe and northeast Asia (Cai et al. 2014). However, there are several widely distributed species. *A. muscaria*, the type species of genus *Amanita*, is found in Europe (Moser 1983), North America (Jenkins 1986) and temperate eastern Asia (Imazeki and Hongo 1987). Oda et al. (2004) analysed the biogeography of *A. muscaria* based on ITS and  $\beta$ -tubulin sequences, separating it into at least three groups (Eurasian, Eurasian sub-alpine and North American). Geml et al. (2006, 2008) drew a similar conclusion about the phylogeographic structure and suggested that *A. muscaria* likely originated from the Siberian-Beringian region. *Amanita pantherina* is another widespread species found in Europe (Gilbert 1941), Asia (Imazeki and Hongo 1987), Africa (Reid and Eicker 1991), and North and Central America (Tulloss et al. 1995). This species is divided into at least two groups, the North American group and the Eurasian group. The relationships among samples from within both Eurasia and North America were closer to each other than the relationships among samples from between the two continents (Oda et al. 2004).

### Dispersal

Due to the lack of fossil records, the place and time for the origination of the genus *Amanita* are still uncertain. Current evidence suggests that members of this genus were present before the break-up of Gondwana and hence geographical populations have likely been isolated since then through continental drift (Cai et al. 2014). If

this were the case, we should find endemic amanitas from the southern hemisphere. The results of investigation in South America (Bas 1978; Garrido and Bresinsky 1985; Bas and de Meijer 1993) were consistent with this hypothesis. However, long-distance migration is also possible. A study based on phylogenetic analysis and ancestral area reconstructions suggested that lethal amanitas (Section *Palloideae*) probably originated in the palaeotropical zone in the Palaeocene, migrated from the Eurasian continent to North America through the Beringian Land Bridge, and then extended to Central America during Oligocene to Miocene (Cai et al. 2014). Similarly, a recent study on edible amanitas (Section *Caesareae*) indicated that this group probably originated between the Palaeocene and Eocene in a Palaeotropical setting, most likely in Africa, subsequently dispersed into other temperate and tropical areas during the Miocene and Pliocene (Sánchez-Ramírez et al. 2015). The results of these studies are in agreement with the Eurasia-North America disjunct distribution pattern or the Eurasia-North/Central America distribution pattern for some species or sister species in this genus.

While oceans are important barriers restricting the dispersal of *Amanita* species, other factors such as deserts and mountains may also play a role similar to that of ocean in terms of vicariance. Tulloss (2005) found that Arizona in southwestern US shared few *Amanita* species with New Jersey and Long Island regions in northeastern US. However, southwestern US shared many species with Central and South America as far as Colombia. Since most *Amanita* species are EM fungi, their dispersals were likely accompanied by the dispersals of host plants. For example, the border of the Andean Colombian region appears to be the 'end of the line' for amanitas associated with *Quercus* and members of the Pinaceae (Tulloss 2005). This region is also the 'end of the line' for trees in the *Quercus* genus and several Pinaceae genera (Manos and Stanford 2001; Lin et al. 2010). Many amanitas from the south or east of this region are symbionts of leguminous or polygonaceous plants (Bas 1978). Whether these amanitas were associated with their current host plants from the initial stage or switched from other plants remains uncertain. As in many groups of Basidiomycetes, basidiospores

likely play important roles in the dispersal of *Amanita* species. Theoretically, basidiospores may disperse by air flow for thousands of kilometres. However, a recent study found that most basidiospores of *Amanita* could only disperse for very limited distance. Li (2005) studied the release and dispersal of basidiospores from *A. muscaria* var. *alba*, and found that fewer than 2% of basidiospores dispersed to areas beyond 5.2 m from the basidiomata. Although long-distance dispersal events are rare, migration via spores is more likely to explain the Eurasia-North America disjunct distribution pattern in some species (Geml et al. 2006, 2008).

### Effects of human activities

With the rapid developments of human societies and modern technologies, intercontinental travel and exchanges of goods have become more and more frequent. Some EM fungi including *Amanita* species have likely dispersed among continents with their host plants due to human activities. For example, *A. phalloides*, a notoriously poisonous mushroom originally described from Europe (Fries 1821) and repeatedly recorded in North America from the nineteenth century (Schweinitz 1834; Harknes and Moore 1880; Taylor 1897), was considered an introduced fungus in North America (Pringle and Vellinga 2006). A subsequent phylogeographical analysis based on six loci supported this hypothesis (Pringle et al. 2009), which was further confirmed by Wolfe et al. (2010). In addition, *A. phalloides* is known to have been artificially introduced to Australia, New Zealand and South Africa together with its host plants (Dunstan et al. 1998). *A. muscaria* is another EM fungus known to be introduced to Australia (Sawyer et al. 2001). Thus, human activity is a major factor that needs to be considered in the phylogeographical researches of *Amanita* mushrooms.

### Population genetics

One of the fundamental properties of fungal populations in nature is genet size. A genet refers to a group of sporocarps that have identical genetic backgrounds and resulted from the same mating event (Zhou et al. 2000, 2001). Genet size differs among EM fungal species, ranging from a few metres to 100 m in diameter (Dahlberg 2001; Sawyer et al. 2001). Molecular methods provide more sensitive and effective markers in the identification of genet of EM fungi and are now being widely applied in population genetic studies of *Amanita*, as well as in other group of fungi (e.g. Timonen et al. 1997; Bonello et al. 1998; Junghans et al. 1998; Sawyer et al. 1999). Polymerase chain reaction-restriction fragment length polymorphism, random amplified polymorphic DNA, amplified fragment length polymorphism (AFLP), inter-simple sequence repeat (ISSR) and single

nucleotide polymorphisms (SNPs) are popular polymorphic markers applied in population genetics of EM fungi. Among them, AFLP and ISSR markers are the most widely used in population genetics of *Amanita* species. High-throughput SNP is another recent type of molecular marker. It has the advantages of high stability, low mutation rate, co-dominance and ease of scoring. However, SNPs have not been used in population genetic studies of *Amanita* mushrooms.

Our knowledge of population genetics of genus *Amanita* is currently limited to only a few taxa. Redecker et al. (2001) determined the size of genets of three EM fungi in field sites in coastal northern California using AFLPs fingerprinting. The results showed *Amanita franchetii* formed small genets with the biggest at 4.7 m across. Sawyer et al. (2003) studied the distribution and persistence of *A. muscaria* genotypes in three *Pinus radiata* plantations in New South Wales, Australia. The presence of common genotypes at the three sites indicated that they were introduced as vegetative inocula when seedlings were planted and have persisted for up to 36 years. Population structure and spreading strategy of a species in natural forests is different from that in plantation forests. Genotypes of five Australian *Amanita* species, *Amanita alboverrucosa*, *Amanita ochrophylla*, *Amanita pyramidifera*, *Amanita conicoverrucosa* and *Amanita punctata*, were investigated using ISSR fingerprinting (Sawyer et al. 2003). Genotypes of *A. ochrophylla*, *A. conicoverrucosa* and *A. punctata* were spread over areas with the largest dimensions ranging from 10 to 60 m, suggesting evidence of vegetative spread via large below-ground mycelial genets. In contrast, genotypes of *A. alboverrucosa* were more spatially restricted, suggesting recent establishment via basidiospores and more limited below-ground vegetative spread. Interestingly, two groups of *A. pyramidifera* basidiomes with the same genotype were separated by 600 m, suggesting the vegetative tissue might have been moved by vehicular activity. The population genetic structure of *Amanita manginiana* in a natural forest in southwest China was examined over two years using ISSR markers (Liang et al. 2005). In contrast to the relatively large genets, the results indicated that each sporocarp represented a single genet, and no identical genets were found between 2001 and 2002. Although the genetic variances were mainly found among individuals of the same year, the variance between years was statistically significant.

### Prospects

Extensive collection, precise identification and comprehensive evaluations and comparisons are fundamental issues of taxonomic studies. Further, taxonomy is the foundation for phylogeographic investigations. In some areas such as Europe and North America, fungal

taxonomy studies have been carried out for about two centuries. In contrast, surveys of fungal flora are still in their preliminary stages in tropical Africa and South America. It is anticipated that new taxa of *Amanita* will be discovered in these regions in the future, and these taxa will contribute to a better understanding of the origin and evolution history of this genus. Molecular-data-based systematics and taxonomies have evolved very rapidly and revealed a large number of cryptic species. Documentation and integration of these cryptic species into the established framework are urgent tasks in the near future. Interestingly, even in geographic areas that have been intensively studied by taxonomists, new taxa continue to emerge. Recent studies have shown that many morphological species such as *Amanita pseudoporphyria*, *Amanita vaginata* and *Amanita hemibapha* are actually species complexes with each containing multiple divergent lineages. More extensive molecular phylogenetic studies using sequences at multiple loci should help reveal the cryptic species within each of these species complexes (Yang 2005).

Recently, molecular phylogenetic analyses of a few selected groups of *Amanita* have helped reveal their origins and evolution (Oda et al. 1999, 2004; Geml et al. 2006, 2008; Cai et al. 2014). It is hoped that future phylogeographic studies will provide a more comprehensive picture of the origin and evolution at the genus level.

Population genetic studies of *Amanita* are still at an early stage. Up to now, only in a few species have been analysed (Redecker et al. 2001; Sawyer et al. 2003; Liang et al. 2005). Both spatial and temporal factors need to be considered when analysing natural populations. Spatially, a diversity of scales, from fine local scale to regional-, national- and global-level investigations, is needed. To examine how fungal populations change over time, long-term monitoring is also needed. Since *Amanita* mushrooms include both lethal and gourmet species, studies on population genetics of these species will reveal the differences between poisonous and edible mushrooms on strategies of reproduction, dispersal and succession. The advent of molecular biology, decreasing cost of sequencing and increasing availability of sequenced genomes made it easier to exploit new markers (e.g. SNP markers) for fungal population genetic analyses. Population genetics will not only help us to understand these species better, but also benefit to forest management and conservation of some valued edible species (e.g. *A. hemibapha*, *A. caesarea*).

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