REVIEW

A review on research advances, issues, and perspectives of morels

Xi-Hui Du*, Qi Zhao and Zhu L. Yang

Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650201, China

(Received 23 December 2014; accepted 2 February 2015)

Morels, a group of the world’s most prized edible and medicinal mushrooms, are of very important economic and scientific value. Here, we review recent research progress in the genus Morchella, and focus on its taxonomy, species diversity and distribution, ecological diversity, phylogeny and biogeography, artificial cultivation, and genome. We also discuss the potential issues remaining in the current research and suggest some future directions for study.

Keywords: Morchella; species diversity; species distribution; ecology; evolutionary history; cultivation; genome

Due to its high economic and scientific value, the genus Morchella Dill. ex Pers.: Fr. has become a hot research topic in China and abroad in recent years. Based on the recent research achievements, we present a review of its taxonomy, phylogeny, species and ecological diversity, geographical distribution and biogeography, artificial cultivation, and genome.

1. Economic importance of morels

True morels (Morchella spp.) belong to the Pezizales, Morchellaceae (Hibbett et al. 2007), with Morchella esculenta (L.) Pers. as the type species. They are mostly distributed in temperate regions of the northern hemisphere where they typically fruit for only a few weeks each spring. Due to their desirable flavor and short fruiting season, morels become the world’s most prized edible fungi. To meet the demand created by their growing popularity, wild morels, the main source of edible morels, are harvested commercially and exported extensively from China, India, Turkey, Mexico, and the United States (Pilz et al. 2007). In China, the annual export of dried morels increased fivefold from 181,000 kg to 900,000 kg over the past 5 years, averaging $160 US dollars per kilogram.

2. Species diversity in Morchella

2.1. Morphological taxonomy of Morchella

According to the latest information in the Index Fungorum (http://www.indexfungorum.org/names/names.asp), 315 names in Morchella have been reported (including species, subspecies, and varieties). Most of them were described from Europe, with only few described in Asia and USA. Due to insufficient microscopic characteristics and high levels of variability in form and color of asco-cars during different developmental stages (Du et al. 2014), affected by ecological and climate factors, the species number in Morchella varies from 3 to 50 or more, which has caused confusing use of homonyms and synonyms (Bresinsky et al. 1972; Gessner et al. 1987; Volk and Leonard 1989; Jung et al. 1993; Bunyard et al. 1994, 1995; Kanwal et al. 2011; Clowez 2012; Kuo et al. 2012; Mortimer et al. 2012; Richard et al. 2014).

Based on gross morphology, the species of Morchella were initially placed into three groups: black morels, yellow morels and semi-free capped morels. Later, Guzmán and Tapia (1998) presented a fourth group, namely, blushing morels, including M. rufobrunnea Guzmán & F. Tapia M. guatemalensis Guzmán et al. and M. rigidoides R. Heim, distributed in the tropics or subtropics.

2.2. Molecular phylogenetic species of Morchella

Recent rapid developments in DNA-sequencing techniques and phylogenetic analysis have enabled mycologists to overcome difficulties in fungal taxonomy and systematics and elucidate the morphological, ecological, and functional evolution of fungi (Koufopanou et al. 1997; Geiser et al. 1998; Yang 2011, 2013). Development of Genealogical Concordance Phylogenetic Species Recognition (GCPSR) (Taylor...
et al. 2000) provided a consensus criterion for resolving species relationships among fungi, including those of morels (Dettman et al. 2003; Revankar and Sutton 2010; Taşkı̈n et al. 2010, 2012; O’Donnell et al. 2011; Du et al. 2012a; Zeng et al. 2013; Elliott et al. 2014; Pildain et al. 2014; Voitk et al. 2014).

O’Donnell et al. (2011) first used the GCPSR method for conducting phylogenetic and biogeographic studies of the genus Morchella based on the LSU-efl-a-rpb1-rpb2 combined-gene dataset. This study presented the genus Morchella consisting of the Esculenta Clade (yellow morels), the Elata Clade (black morels) and the Rufobrunnea Clade (blushing morels), respectively, consisting of 16, 32, and 1 species. More importantly, their results indicated that semifeatured morels were deeply nested within the Elata clade (black morels), contradicting an earlier opinion that semifeatured morels were the separate genus Mitrophora (Breitenbach and Kränzlin 1984). Because morphological plasticity of morels complicates the application of Latin binomials with confidence to all these species, O’Donnell et al. proposed identifying species by clade (Mel for Elata, Mes for Esculenta) followed by a unique Arabic number for each species within the two clades. But in this study, samples from eastern Asia, especially from China, were underrepresented.

Based on a broad sampling of morels in China, Du et al. (2012a) further evaluated species diversity of Morchella and conducted a molecular phylogeny and biogeography study. Their analyses identified 61 species in the genus, including 27 species in the Esculenta Clade (Mes-1–Mes-27), 33 species in the Elata Clade (Mel-1–Mel-34, please note Mel-13 and Mel-26 have been combined into one species based on the analysis in this study), and one in the Rufobrunnea Clade. Their results also suggested that East Asia or China (ca. 30 species) is the center of diversity and distribution of the modern species of the genus (Du et al. 2012a).

Taşkı̈n et al. (2012) reported M. anatolica described in Işıloğlu et al. (2010) also belonged to Rufobrunnea Clade which was represented by two extant species, M. rufo-brunnea and M. anatolica.

Recently, three new species in the Elata Clade have been separately identified using ITS-efl-a-rpb1-rpb2 combined-gene sequences, namely, Mel-35 (M. australiana T.F. Elliott, Bougher, O’Donnell & Trappe) from Australia (Elliott et al. 2014), Mel-36 from Canada (Voitk et al. 2014), and Mel-37 from Argentina (Pildain et al. 2014).

Thus far, 65 phylogenetically distinct species have been recognized in Morchella.

2.3. Relationship between phylogenetic and morphological species of Morchella

According to recent studies, 29 phylogenetic species in Morchella could be given Latin binomials (O’Donnell et al. 2011; Kuo et al. 2012; Elliott et al. 2014; Richard et al. 2014). Mes-1, Mel-1, Mel-3, Mel-4, Mel-15, Mel-36, M. anatolica, and M. rufo-brunnea, respectively, correspond to M. steppicola Zerova (Zepona 1941), M. tomentosa M. Kuo (Stefani et al. 2010), M. semilibera DC. (Fries 1822), M. punctipes Peck (Peck 1903), M. angusticeps Peck (Peck 1879), M. australiana (Elliott et al. 2014), M. anatolica (Işıloğlu et al. 2010), and M. rufo-brunnea (Guzmán and Tapia 1998). Another 21 species have been described, respectively, in Kuo et al. (2012), Clowez (2012) and Richard et al. (2015, Figure 1). The remaining undescribed species need further intensive study on their morphological characters.

Note: Six species names described by Kuo et al. (2012) and Clowez (2012) have been discovered to be synonyms. Because the epithets proposed by Clowez (2012) have priority over those applied to conspecifics in Kuo et al. (2012), Richard et al. (2014) assess what taxon in the latter study represent nomenclatural synonyms of taxa validly published by Clowez (2012).

2.4. Dedicated web for rapid identification of Morchella phylogenetic species – Morchella MLST

Du et al. (2012b) observed that the ITS-efl-a-rpb1-rpb2 combined-gene data could successfully identify all the phyllospecies in Morchella, with the ITS gene alone identifying 77.4% of them. Unfortunately, at least two-thirds of ITS sequences of Morchella in GenBank were found to be misidentified, a problem noted for other groups of fungi (Vilgalys 2003; Ryberg et al. 2008).

To minimize potential problems created by poorly annotated sequences in GenBank, and accurately identify known and novel species, the Morchella MLST database (multilocus sequence typing, http://www.cbs.knaw.nl/Morchella/) was constructed (Du et al. 2012b). Sequences generated in recent studies (Taşkı̈n et al. 2010, 2012; O’Donnell et al. 2011; Du et al. 2012a, 2012b) have been recorded in this site. The scientific community not only can freely download these sequences and access information for voucher specimens and/or cultures from this website, but also can contribute their validated sequences and information to the site.

3. Species distribution and ecological diversity of Morchella

In this section, the results reported in Taşkı̈n et al. (2010, 2012), O’Donnell et al. (2011), Du et al. (2012a, 2012b), Voitk et al. (2014), Elliott et al. (2014), Pildain et al. (2014), Beug and O’Donnell (2014) and Richard et al. (2014) have been integrated to provide a comprehensive picture of the species distribution and ecological diversity of Morchella.
3.1. Global distribution pattern of Morchella

Of the 65 phylospecies identified in Morchella, more than half are represented in East Asia or China (34 species) including 20 endemic species, most of them representing lineages that originated in the middle Miocene. Less species diversity was found in Europe than in East Asia. Of the 27 species present in Europe, 12 are endemic. Twenty-one species have been found in North America, but most of them were basal species, including 14 endemic species. Based on the latest published data, East Asia or China still served as the modern species diversity center of Morchella.

Among the 25% species with disjunct distributions in Morchella, M. eximia M. Kuo (Mel-7) is the most widely distributed species, found in western North America, Europe, Asia, Australia, and South America. The detailed
distribution information of each species is shown in Figure 1.

Interestingly, high continental endemism and provincialism have been identified in species of the Esculentia Clade, nearly 60% of which were endemic in East Asia and only 11% of which had disjunct distribution. In contrast, broad distributions were detected in nearly 31% of the species of the Elata Clade, and a higher species diversity was found in Europe than in East Asia for this clade.

3.2. Distribution pattern of Morchella in China
Following Wu and Wu’s (1996) geographic divisions of Chinese seed plants, Du et al. (2014) divided the distribution of moresls in China into seven regions. Of 30 species detected in China, 20 were distributed in the Sino-Japanese Forest Subkingdom, 17 in the Sino-Himalayan Forest Subkingdom, four in the Qinghai-Xizang Plateau Subkingdom, four in the Eurasia Forest Subkingdom and one in the Malesian Subkingdom. No representative was discovered based on the present survey in the Eurasia Steppe Subkingdom and the Central Asiatic Desert Subkingdom.

The Sino-Himalayan Forest Subkingdom and the Sino-Japanese Forest Subkingdom, as the two main morel-producing regions in China, harbor roughly equivalent numbers of species, but given that the area of the latter is three times that of the former, the Sino-Himalayan Forest Subkingdom was considered by Du et al. (2014) to have the highest species richness of morels and serve as the center of species diversity of this genus in China. We attributed this to its diverse habitats and environmental heterogeneity. But, we also found species of Esculentia Clade and species of Elata Clade, respectively, were mainly distributed in the Sino-Japanese Forest Subkingdom and in the Sino-Himalayan Forest Subkingdom.

3.3. Ecological diversity of Morchella
The trophic status of morels has for long been a source of scientific interest and debate. Buscot and Kottke (1990, 1993) and Dahlstrom et al. (2000) reported moresls could form ectomycorrhizae with Pinaceae plants. Stark et al. (2009) speculated morels were associated with orchids, based on evidence obtained through PCR-amplification directly from root-extracted DNA and cloning of the PCR products. Hobbie et al. (2001) and Li et al. (2013) assessed the trophic status of morels by examining the relative abundance of stable isotopes. Hobbie et al. (2001) suggested that morels were largely saprophytic, but Li et al. (2013) suggested that morels with black pilei were saprophytic and those with yellow pilei were mycorrhizal. Baynes et al. (2012) detected Morchella as an endophyte in the aboveground stem tissue of cheatgrass and reported that M. sextelata M. Kuo and M. snyderi M. Kuo & Methven could infect cheatgrass roots. So far, the trophic strategies of Morchella have not been settled, but the available data seems to indicate that Morchella probably includes not only saprophytic species and mycorrhizal species, but also facultative mycorrhizal species.

Based on long-term field observations, the following ecological characteristics of Morchella have been noted.

3.3.1. Phylogenetic niche conservation (PNC)
Both the Esculentia Clade and the Elata Clade have preferential habitats. In the Esculentia Clade, approximately 70% of the species are found within temperate deciduous forests, while a few species are found on sandy beach grassland or in proximity to bamboos or reeds. In the Elata Clade, approximately 70% of the species are found in coniferous forest, while a few species are found within temperate deciduous forests (Figure 1). When the two Clades began to diversify in the late Cretaceous (Du et al. 2012a), both temperate deciduous biome and coniferous biome were well established in the northern hemisphere (Axelrod 1960), so these niches have probably been conserved for the past 100 million years. Phylogenetic niche conservation (PNC, Donoghue 2008) in Morchella has been speculated to persist throughout its evolutionary history (Du et al. 2012a).

3.3.2. Cold tolerance
The Elata Clade is preferentially distributed at higher altitudes (above 2000 m) whereas the Esculentia Clade is mainly distributed on lower mountains (below 1200 m) and plains (yet Mes-14 fruiting at high altitude in Venezuela). In addition, the preferred niches of the two clades were dark coniferous forests and temperate deciduous forests, respectively. Based on these habitat preferences, we suggest that species in the Elata Clade might have stronger cold tolerance than those in the Esculentia Clade. Svenning (2003) considered cold tolerant plants to be much more capable of thriving and becoming widespread during the severe Plio-Pleistocene extinctions in Europe. Likewise, the stronger cold tolerance of the Elata Clade might have contributed to its survival during the Quaternary Ice Age, which probably explains why there are more widespread species in the Elata Clade.

3.3.3. Post-fire adapted ability
Several species within Morchella can fruit in post-fire habitats. These fire-adapted species proliferate mainly in coniferous forests following a wildfire during spring or summer, usually for 1 or 2 years, after which the yield rapidly declines and disappears. To date, four
obligate fire-adapted species (M. tomentosa, M. sextelata, M. eximia, and Mel-8) collected on burned sites and two facultative fire-adapted species (M. exuberans M. Kuo & M.C. Carter and M. importuna M. Kuo, O’Donnell & T.J. Volk) collected on both burned and nonburned sites, were found in the Elata Clade (marked by red asterisks in Figure 1), while none in the Esculenta Clade. O’Donnell et al. (2011) and Du et al. (2012a) suggested these adaptive shifts evolved convergently and ecological speciation have likely played an important role during the evolutionary history of morels.

3.3.4. Diverse fruiting seasons

Spring is the main fruiting season of Morchella, but a few species fruit in summer or fall. For example, in Yunnan, SW China, where spring-fruiting, summer-fruiting and fall-fruiting species are distributed, most species fruit in spring (from March to May), but three fire-adapted species in the Elata Clade fruit in summer (July, indicated by red arrows in Figure 1), and one species in the Esculenta Clade fruits in fall (October, indicated by a green arrow in Figure 1). Neven et al. (2014) suggested the variation in fruiting behavior (spring vs. autumn) in M. esculenta s. lat. might depend on differences in life cycle elements/phases, which could represent two different adaptive life strategies (ecotypes or species). Further in-depth studies are needed to elucidate the cause and mechanism of fruiting season diversity.

4. Evolutionary history of Morchella

The historical biogeography of Morchella was first studied by O’Donnell et al. (2011) whose work set a foundation for subsequent investigations. Further study by Du et al. (2012a) contributed to a comprehensive understanding of the evolutionary history of the genus, especially in identifying East Asia or China as the modern species diversity and distribution center. Additionally, Elliott et al. (2014) and Pildain et al. (2014) broadened the previous understanding of species diversity and distribution of morels in South America and Australia. These studies need to be integrated with other studies to systematically extend the biogeographic analysis. Here, we discuss the evolutionary history of Morchella mostly based on the work of O’Donnell et al. (2011) and Du et al. (2012a).

It is speculated that Morchella originated in western North America (Figure 2) during the late Jurassic and diverged into the basal lineage M. rufobrunnea. In the early Cretaceous, the ancestors of the Esculenta and Elata Clades originated in western North America, and then spread to eastern North America. Due to the emergence of the Mid-Continental Seaway in the mid Cretaceous and the subsequent uplift of the Rocky Mountains during the late Cretaceous (Sanmartín et al. 2001), significant obstacles to gene flow among the morels formed between western and eastern North America, leading to the divergence of the ancestors of the Esculenta and Elata Clades diverging into the Elata Clade and the Esculenta Clade in western and eastern North America, respectively, during the late Cretaceous. New species evolved in eastern and western North
America independently, with little exchange between the two regions (such as *M. americana* M. Kuo, Dewsbury, Moncalvo & S.L. Stephenson). Some basal species spread to Europe via the Thulean North Atlantic Land Bridge. Most species crossed the Beringian Land Bridge and dispersed to Asia. In the late Oligocene, and continuing in the Miocene, new folding of the Rocky Mountains and uplift of the Sierra Madre Oriental Range caused cooler and drier climates in central North America (Sanmartín et al. 2001; Donoghue and Smith 2004), which probably resulted in the widespread extinction of *Morchella* in that region.

During the middle Miocene to the Pleistocene, about 84% (51/61) of *Morchella* species rapidly evolved, including the radiational differentiation of 85% of the species of the Esculenta Clade in East Asia and 64% of the species of the Elata Clade in Europe. This differentiation might have been induced by the gradually cooling climate at mid- to high-latitudes of the North Hemisphere and the climate changes and environmental heterogeneity in East Asia caused by the rise of the Qinghai-Tibetan Plateau.

During the Quaternary glaciation, the abrupt cooling of the climate and the frequent fluctuations between the glacial and interglacial phases highly impacted the biological diversity and distribution. Refugia created by microclimatic variations provided some protection, and habitat fragmentation caused new speciation and diversification (Hewitt 2000; Harrison et al. 2001; Yang 2005). As indicated by the current published data, distribution areas of morels in North America and Europe are concentrated on the west and east coasts and the Mediterranean coast, which have been recognized as probable refugia in several studies (Hewitt 2000; Soltis et al. 2006). The Quaternary glaciation was not as severe and destructive in China as in Europe and some parts of North America, and complicated topography and more-or-less longitudinal arrangement of mountain ranges in China perhaps offered useful refugia for many ancient species (Yang 2005; Qiu et al. 2011), possibly explaining East Asia or China’s position as the center of species diversity and distribution of the modern *Morchella*.

5. **Cultivation of morels**

Morels are difficult to grow commercially. Five reports of their cultivation in the USA, Israel and China have been published (Ower 1982; Kuo 2008; Zhu 2008; Zhao et al. 2009; Masaphy 2010). The commercial cultivation of only *M. rufobrunnea* (Kuo 2008) and *M. importuna* (Zhao et al. 2009) has been successfully achieved separately in the USA and China. Whether other species of *Morchella* could be cultivated is unknown and deserves further research.

6. **Genomics of Morchella**

The worldwide demand for these delicious and highly prized edible mushrooms has stimulated intense efforts to cultivate morels. Sequencing the morel genome will provide unprecedented insights into its trophic status, sex, and fruiting at the molecular level. The identification of processes that condition and trigger fruit body formation will be uncovered by a thorough analysis of genomic traits, potentially leading to efficient commercial production. To date, the genome of only one species in the Elata Clade has been completed and reported in the 1000 Fungal Genomes project supported by the DOE Joint Genome Institute (http://genome.jgi.doe.gov/).

7. **Issues and perspectives**

Gratifying progress in the study of morels has been made in recent years, but there are still some problems which urgently need to be resolved. Currently, species delimitations of *Morchella* are defined using the criteria of GCP-SR, while the morphological characteristics of many phylogenetic species without Latin binomials need deep and thorough investigation. We lack understanding of the speciation mechanisms in *Morchella* and the significance of ecological diversity. The key factors which permit the successful cultivation of *M. rufobrunnea* and *M. importuna* need to be identified as well as whether other species in this genus could be cultivated.

Facing the challenges mentioned above, we could advance in the following directions: (1) more in-depth morphological studies need to be conducted to apply proper Latin binomials on unnamed phylogenetic species and popularize those names for effective scientific and commercial communication; (2) considering the diverse ecological habitats that support morels, it would be useful to select some species with unique habitats to do a trophic status study, moving morel research into an ecosystems perspective; (3) more genome studies should be on the agenda, comparing genetic mechanisms among species, especially with regard to mating type genes and reproductive modes, which will provide an effective theoretical and technical framework for the cultivation, protection and utilization of morels.

**Acknowledgments**

The authors are very grateful to Kerry O’Donnell, Bacterial Foodborne Pathogens, and Mycology Research Unit, National Center for Agricultural Utilization for the help during our research on the phylogeny and biogeography studies of *Morchella*.

**Disclosure statement**

No potential conflict of interest was reported by the authors.
Funding
This study was supported by the National Natural Science Foundation of China [No. 31300022], and by West Light Foundation of The Chinese Academy of Sciences.

ORCID
Xi-Hai Du  http://orcid.org/0000-0003-2650-7523

References
Axelrod DJ. 1960. The evolution of flowering plants. In: Tax D, editor. Evolution after Darwin. Vol. 1. Chicago (IL): University of Chicago Press; p. 227–305.
Baynes M, Newcombe G, Dixon L, Castlebury L, O’Donnell K. 2012. A novel plant-fungal mutualism associated with fire. Fungal Biol. 116(1):133–144.
Beug M, O’Donnell K. 2014. Morel species Mel-19-preliminary report. Omphalina. 5:13–14.
Breitenbach J, Kränzlin F. 1984. Fungi of Switzerland. Ascomycetes. Vol. 1. Luzern: Mykologia.
Bresinsky A, Glaser W, Stangl J. 1972. Untersuchungen zur Sippenstruktur der Morchellaceae. Ber Bayer Bot Ges. 43:127–143.
Bushan SP, Yu G, Takahara H, Prentice IC. 2001. Palaeovegetation (communications arising): diversity of temperate plants in East Asia. Nature. 413:129–130.
Hewitt GM. 2000. The genetic legacy of the quaternary ice ages. Nature. 405:907–913.
Hibbett D, Binder M, Bischoff JF, Blackwell M, Cannon PF, Eriksson OE, Huhndorf S, James T, Kirk PM, Lucking R, et al. 2007. A higher-level phylogenetic classification of the Fungi. Mycol Res. 111:509–547.
Hobbie EA, Weber NS, Trappe JM. 2001. Mycorrhizal vs saprotrophic status of fungi: the isotopic evidence. New Phyto. 150:601–610.
Işığloğlu M, Alii H, Spooner BM, Solak MH. 2010. Morchella anatotica (Ascomycota), a new species from southwestern Anatolia, Turkey. Mycologia. 102:455–458.
Jung SW, Gessner RV, Kendall KC, Romano MA. 1993. Systematics of Morchella esculenta complex using enzyme-linked immunosorbent assay. Mycologia. 85:677–684.
Kamal HK, Acharya K, Ramesh G, Reddy MS. 2011. Molecular characterization of Morchella species from the western Himalayan region of India. Curr Biol. 62:1245–1252.
Koulopanou V, Burt A, Taylor JW. 1997. Concordance of gene genealogies reveals reproductive isolation in the pathogenic fungus Coccidioides immitis. Proc Natl Acad Sci USA. 94:5478–5482.
Kuo M. 2008. Morchella tomentosa, a new species from western north America, and notes on M. rufobrunnea. Mycologia. 100:441–446.
Kuo M, Dewsbury DR, O’Donnell K, Carter MC, Rehner SA, Moore JD, Moncalvo JM, Canfield SA, Stephenson SL, Methven AS, et al. 2012. A taxonomic revision of true morels (Morchella) in Canada and the United States. Mycologia. 104:1159–1177.
Li QL, Ding C, Fan L. 2013. Trophic manner of morels analyzed by using stable carbon isotopes. Mycosystema. 32:213–223.
Masaphy S. 2010. Biotechnology of morel mushrooms: successful fruiting body formation and development in a soilless system. Biotechnol Lett. 32:1523–1527.
Matoečić N, Kušan I, Mrvoš D, Raguzin E. 2014. The autumnal occurrence of the vernal genus Morchella(Ascomycota, Fungi). Nat Croat. 23:163–178.
Mortimer PE, Karunarathna SC, Li QH, Gui H, Yang XQ, Yang XF, He J, Ye L, Guo YJ, Li HL, et al. 2012. Prized edible Asian mushrooms: ecology, conservation and sustainability. Fungal Divers. 56:31–47.
O’Donnell K, Rooney AP, Mills GL, Kuo M, Weber NS, Rehner SA. 2011. Phylogeny and historical biogeography of true morels (Morchella) reveals an early Cretaceous origin and

Elliott TF, Bougher NL, O’Donnell K, Trappe JM. 2014. Morchella australiana sp. nov., an apparent Australian endemic from New South Wales and Victoria. Mycologia. 106:113–118.
Fries EM. 1822. Systema mycologicum. 2:10. Reprint. Italy: Confederatio Europaea Mycologiae Mediterraneensis, 1994.
Geiser DM, Pitt JI, Taylor JW. 1998. Cryptic speciation and recombination in the aflatoxin producing fungus Aspergillus flavus. Proc Natl Acad Sci USA. 95:388–393.
Gessner RV, Romano MA, Schultz RW. 1987. Allelic variation and segregation in Morchella deliciosa and Morchella esculenta. Mycologia. 79:683–687.
Guzmán G, Tatia F. 1998. The known morels in Mexico, a description of a new blushing species, Morchella rufobrunnea, and new data on M. guatemalensis. Mycologia. 90:705–714.

Du XH, Zhao Q, Yang ZL, Hansen K, Taşkin H, Büyükalaca S, Dewsbury D, Moncalvo JM, Douhan GW, Robert Vincent ARG, et al. 2012b. Morchella ITS rDNA phylogenetics - how well do ITS rDNA sequences differentiate species of true morels (Morchella)? Mycologia. 104:1351–1368.
high continental endemism and provincialism in the Holarctic. Fungal Genet Biol. 48:252–265.
Ower R. 1982. Notes on the development of the morel ascomycarp - *Morchella esculenta*. Mycologia. 74:142–144.
Peck CH. 1879. Report of the botanist. Annual report. New York: New York State Museum Natural History. 32:17–72.
Peck CH. 1903. New species of fungi. Bull Torrey Bot Club. 30:95–101.
Pildain MB, Visnovsky SB, Barroetave C. Forthcoming 2014. Phylogenetic diversity of true morels (*Morchella*), the main edible non-timber product from native Patagonian forests of Argentina. Fungal Biol. 118:755–763.
Pilz D, McLain R, Alexander S, Villarreal R, Berch S, Wurtz TL, Parks CG, McFarlane E, Baker B, Molina R, et al., 2007. Ecology and management of morels harvested from the forests of western north America. General Technical Report PNW-GTR-710. Portland (OR): US Department of Agriculture, Forest Service, Pacific Northwest Research Station; 161 p.
Qiu YX, Fu CX, Comes HP. 2011. Plant molecular phylogeography in China and adjacent regions: tracing the genetic imprints of quaternary climate and environmental change in the world’s most diverse temperate flora. Mol Phylogenet Evol. 59:225–244.
Revankar SG, Sutton DA. 2010. Melanized fungi in human disease. Clin Microbiol Rev. 884–928.
Richard F, Sauve M, Bellanger JM, Clowez P, Hansen K, O’Donnell K, Urban A, Courtecuisse R, Moreau PA. 2014. True morels (*Morchella*, Pezizales) of Europe and North America: evolutionary relationships inferred from multilocus data and a unified taxonomy. Mycologia. doi:10.3852/14-160.
Ryberg M, Nilsson RH, Kristiannsson E, Töpel M, Jacobsson S, Larsson E. 2008. Mining metadata from unidentified ITS sequences in GenBank: a case study in *Inocybe* (Basidiomycota). BMC Evol Biol. 8:50.
Sannmann I, Enghoff H, Ronquist F. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biol J Linn Soc. 73:345–390.
Stark C, Babik W, Dutka W. 2009. Fungi from the roots of the common terrestrial orchid *Gymnadenia conopsea*. Mycol Res. 113:952–959.
Solís DE, Morris AB, McLachlan JS, Manos PS, Solís PS. 2006. Comparative phylogeography of unglaciated eastern North America. Mol Ecol. 15:4261–4293.
Stefani F, Sokolski S, Wurtz TL, Piché Y, Hamelin RC, Fortin JA, Bérubé JA. 2010. *Morchella tomentosa*: a unique below-ground structure and a new clade of morels. Mycologia. 102:1082–1088.
Svenning JC. 2003. Deterministic Plio-Pleistocene extinctions in the European cool temperate tree flora. Ecol Lett. 6:646–653.
Taşkı́n H, Büyükalaca S, Dogan HH, Rehner SA, O’Donnell K. 2010. A multigene molecular phylogenetic assessment of true morels (*Morchella*) in Turkey. Fungal Genet Biol. 47:672–682.
Taşkı́n H, Büyükalaca S, Hansen K, O’Donnell K. 2012. Multilocus phylogenetic analysis of true morels (*Morchella*) reveals high levels of endemics in Turkey relative to other regions of Europe. Mycologia. 104:446–461.
Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC. 2000. Phylogenetic species recognition and species concepts in fungi. Fungal Genet Biol. 31:21–32.
Vilgalys R. 2003. Taxonomic misidentification in public DNA databases. New Phyt. 160:4–5.
Voitik A, Burzynski M, O’Donnell K, Voitik M, Marceau A. 2014. Mel-36—preliminary description of a new morel species. Omphalina. 5:13–14.
Volk TJ, Leonard TJ. 1989. Experimental studies on the morel. I. Heterokaryon formation between monoascosporous strains of *Morchella*. Mycologia. 81:523–531.
Wu ZY, Wu SG. 1996. A proposal for a new floristic kingdom (realm) - the E. Asiatic kingdom, its delimitation and characteristics. In: Zhang AL, Wu SG, editors. Proceedings of the first international symposium on floristic characteristics and diversity of East Asian plants. Beijing: China Higher Education Press, Springer-Verlag; p. 3–42.
Yang ZL. 2005. Diversity and biogeography of higher fungi in China. In: Xu JP, editor. Evolutionary genetics of Fungi. Norfolk: Horizon Bioscience; p. 35–62.
Yang ZL. 2011. Molecular techniques revolutionize knowledge of basidiomycete evolution. Fungal Divers. 50:47–58.
Yang ZL. 2013. Fungal taxonomy in the genomics era: opportuni ties and challenges. Mycosystema. 32:931–946. Chinese.
Zeng NK, Tang LP, Li YC, Tolgor B, Zhu XT, Zhao Q, Yang ZL. 2011. Molecular techniques revolutionize knowledge of basidiomycete evolution. Fungal Divers. 50:47–58.
Zeng NK, Tang LP, Li YC, Tolgor B, Zhu XT, Zhao Q, Yang ZL. 2013. The genus *Phylloporus* (*Boletaceae, Boletales*) from China: morphological and multilocus DNA sequence analyses. Fungal Divers. 58:73–101.
Зерова МЯ. 1941. Новий зморшок із цілинного степу (*Morchella steppicola* Zerova sp. nov.). *Bo. Tan. Журн*. АН УРСР. 2:155–159.
Zhou Q, Xu ZZ, Cheng YH, Qi SW, Hou ZJ. 2009. Bionic cultivation of *Morchella conica*. Southwest China J Agr Sci. 22:1690–1693. Chinese.
Zhu DX. 2008. Research advances on artificial cultivation of morels. Edible Fungi China. 27:3–5. Chinese.