

Morels: the story so far

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Abstract

True morels, among the most glamorous and highly valued edible fungi, have been in the midst of taxonomical controversies for over a century. The use of molecular phylogenetic techniques and integrative taxonomical approaches have in recent years revolutionised our understanding of morels, resolving many of the old debates, but also giving rise to new ones. This review summarises the advances made and challenges met, with regards to this fascinating genus.

A genus locked in controversy

Worshipped by mycophagists, treasured by gourmet chefs and frantically hunted by mycophiles, *Morchella* Dill. ex Pers.: Fr., the true morels, are arguably the most striking and highly-prized of all epigaeous fungi. Yet, despite their supreme status as edible fungi, *Morchella* taxonomy has long been in flux. Typified by *Morchella esculenta* (L.) Pers.: Fr. (Persoon 1794), morels have in many ways epitomized the struggle between lumpers and splitters during much of the pre-DNA era, with some mycologists accepting as few as three taxa (Groves & Hoare 1953, Dennis 1978, Breitenbach & Kränzlin 1983) and others as many as thirty-four (Boudier 1897, Jacquetant 1984, Clowez 2012). As is becoming an increasingly familiar pattern nowadays, molecular phylogenetics has settled most of the old debates, but given rise to several new ones.

The first elaborate multigene analyses from Turkey (Taskin *et al.* 2010, 2012), North America (O'Donnell *et al.* 2011), and China (Du *et al.* 2012a, 2012b) confirmed that *Morchella* is indeed a species-rich genus, comprised of three distinct clades: the ancestral *M. rufobrunnea* clade (white morels), the *M. esculenta* clade (yellow morels), and the late-diverging *M. elata* clade (black morels) [see Table 1]. Using a 4-gene phylogeny, these studies recognized over sixty phylogenetically distinct lineages worldwide, most of them exhibiting high continental endemism and

provincialism. Linking the various phylospecies to old, widely used binomials, however, proved to be a far more challenging task: Boudier's herbarium had been burned, Jacquetant's herbarium had been lost, and most of the remaining types were simply too old to yield any informative molecular data.

The simultaneous description of several new taxa from Europe (Clowez 2012) and North America (Kuo *et al.* 2012), resulted in several synonymies further complicating matters, until a landmark study by Richard *et al.* (2015) resolved many of these problems. This study designated epitypes for several old, widely applied names and clarified many synonymies, linking 30 of the 66 genealogical lineages recognized until then to scientific binomials. The remaining 36 lineages segregated by molecular tools, were merely left with identifiers such as Mel-38, to designate, for example, the thirty-eighth phylospecies in the Elata clade. This paved the way for a systematic revision of the genus. Additional synonymies were clarified (Loizides *et al.* 2015) and more new species were described (Clowez *et al.* 2015, Voitk *et al.* 2015, Loizides *et al.* 2016, and Taskin *et al.* 2016).

In spite of these phylogenetic and taxonomical breakthroughs providing much needed nomenclatural stability to the genus, the morphological recognition of morel species remains nonetheless challenging. The old, widely applied notion of just a handful of species with a worldwide distribution has proven to be an entirely fallacious assumption, whilst morel ecology and morphoanatomy have been revealed as far more complex than previously assumed. At the same time, our knowledge of species distribution and biogeography is still fragmentary, rendering all monographic and systematic treatments predating the DNA-era pretty much obsolete. All this, understandably, can be disheartening for the non-expert, who is currently left with an array of synonymies, no keys to follow and very few updated species descriptions to go by. But hang on in there, there is light at the end of the tunnel.

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Major morel clades

	Rufobrunnea clade (Sect. <i>Rufobrunnea</i>) Ridges persistently silvery-white or buff, never dark, at least partially longitudinally arranged, sinus absent stipe with dark pruinescence, ascocarps usually acutely conical, often rufescent. Probably facultatively saprotrophic or endophytic.
	Esculenta clade (Sect. <i>Morchella</i>) Ridges buff or ochraceous, never dark at maturity, usually irregularly arranged, sinus absent or present, ascocarps usually ovoid, sometimes rufescent. Probably endophytic.
	Elasta clade (Sect. <i>Distantes</i>) Ridges at least at maturity dark brown or black, partially longitudinally arranged or ± parallel, sinus always present, ascocarps almost never rufescent, usually conical or cylindrical. Probably endophytic, some species facultatively or obligately pyrophilic.

Table 1: Major *Morchella* clades and their diagnostic traits.

Traditional vs contemporary *Morchella* taxonomy

Traditional (monothetic)

Biogeography

Everything is everywhere

Ecology

Broad, generally no tree associations

Macromorphology

Colour, orientation of ridges, presence or absence of a sinus

Micromorphology

Spore size, ascus size, paraphyses, presence or absence of heteroparaphyses

Contemporary (polythetic)



Biogeography

High levels of endemism & provincialism



Ecology

Narrow, often highly specific tree associations



Macromorphology

Colour, size, orientation of primary & secondary ridges, sinus depth & attachment, stipe length & surface, rufescence, smell, developmental stages



Micromorphology

Spore size, shape & surface, ascus size and spore arrangement, paraphyses & orientation of the septa, acroparaphyses & presence or absence of capitate elements, shape and size of stipe hairs (ectal excipulum)

Table 2: Traditional vs contemporary *Morchella* taxonomy.

Okay, there are many species, but can we really tell them apart?

The answer is a definite...usually. Whilst a revised, comprehensive monograph on the genus might still be some time away, significant progress in systematics and species recognition has been achieved in recent years. As with most other fungi, morel taxonomy traditionally followed a monothetic model (based on a single characteristic, or a series of single characteristics), largely ignoring ecological niches and relying on a small set of characters to delineate between species, dismissing intermediate forms. This rigid method of classification was unable to cope with the high morphological plasticity seen in *Morchella* and inevitably failed to recognize most species in the genus (see Table 2). Contemporary *Morchella* taxonomy has shifted towards a polythetic system, where a larger set of traits are carefully evaluated and compared, none them essential or in themselves sufficient for identification. Hence taxonomic placement is usually decided on a 'best match' basis, rather than on consistently occurring dichotomous differences (Loizides *et al.* 2015, 2016).

Morels can hardly be identified from exsiccata, therefore careful observation of their macromorphological aspect and developmental stages in the field are paramount. Ascocarps belonging to the same species can often look remarkably different between their immature and mature stages, but each species' process of maturation is usually very distinct (see Fig. 2). The colour, size, shape and orientation of the primary and secondary ridges are critical and usually allow for the placement of the species in the appropriate clade (see Fig. 1 & Table 1). In Distantes, the maturation process of the sterile ridges has further diagnostic significance, as some species tend to develop purplish or vinaceous tinges before darkening, while others do not (*Morchella tridentina* is the only Distantes species with non-darkening ridges, see Fig. 5). The shape, and particularly the depth of the sinus (or 'vallécule'), the attachment of the pileus to the stipe, is somewhat comparable to the gill attachment in basidiomycetes and very important in identification. The surface of the stipe, as well as its length proportionate to the pileus, provide further clues, as does any rufescence (reddening) of the ascocarps.



Figure 1: Composite image of morphologically diverse *Morchella* species. From left: *M. dunensis*, *M. disparilis*, *M. semilibera*, *M. arbuthiphila* and *M. steppicola*. Images © M. Loizides, B. Assyov & M. Slavova.



Figure 2: Young (top) and old (bottom) ascocarps of the Mediterranean species *Morchella dunalii*, showing distinct darkening of the sterile ridges at maturity, a feature seen in all *Distantes* species except *M. tridentina*. Images © M. Loizides.

Microscopically, chronically neglected features such as the apices and septal arrangement of the paraphyses, the shape and apices of the acroparaphyses (the terminal elements on the sterile ridges, distinctly different from the paraphyses), the terminal elements (or “hairs”) of the stipe hyphae, as well as the average spore length, have all been revealed to be highly valuable in identification and occasionally diagnostic (Loizides *et al.* 2015, 2016). In contrast, structures like the heteroparaphyses, first discussed by Jaquetant

(1984), are likely random malformations of normal paraphyses and acroparaphyses, and probably not diagnostically significant. Spore surface, for a long time assumed to be uniformly smooth in *Morchella* (e.g. Dennis 1978), is usually striate or creased when viewed in the appropriate medium or under SEM, as demonstrated by Malloch (1973) and subsequently by Сухомилин *et al.* (2007), Isiloglu *et al.* (2010), Voitk *et al.* (2015), Loizides *et al.* (2016), and Taskin *et al.* (2016). All these frequently overlooked but important traits, provide sufficient grounds for mycologists to redefine most taxa in the genus morphologically, provided they have enough fresh, molecularly confirmed reference material to work with.

Diverse ecological niches and biogeographical patterns

To this day, the precise ecology of morels remains uncertain, though it is abundantly clear that not all species share the same trophic habits (see Table 3). Although in the past morels were assumed to be mostly saprotrophic (Ower 1982, Hobbie *et al.* 2001), a strong link between morels and trees is now widely accepted and the formation of mycorrhizae-like structures has been reported for some species (Buscot & Roux 1987, Buscot 1992, Dahlstrom *et al.* 2000). Yellow morels generally appear to be more abundant in temperate northern and continental regions, where they are usually associated with broadleaved trees, while black morels are more widespread in southern and Mediterranean regions, where they are mostly associated with conifers (Taskin *et al.* 2010, 2012, Loizides *et al.* 2016). However, frequently associated trees such as *Fraxinus excelsior* or *Olea europaea* (*Oleaceae*) do not form ectomycorrhizal, but do form arbuscular mycorrhizal, associations and a facultatively biotrophic or endophytic lifestyle has also been suggested (Robert 1865, Tedersoo *et al.* 2010). An endophytic mode of nutrition is further supported by studies sampling the endophytes of cheatgrass (*Bromus tectorum*), which confirmed the presence of at least two *Morchella* species (*M. sextellata*, *M. snyderi*) colonising the stems of this grass (Baynes *et al.* 2012).



Figure 3: Young ascocarps of *Morchella importuna* (Mel-10), the most likely species equating to the iconic *M. elata* Fr. Photograph © M. Loizides.

Ecological specializations and biogeographic patterns can vary greatly among species. For example, the recently described *Morchella arbutiphila* Loizides, Bellanger & P.-A. Moreau, appears to be confined to the Mediterranean basin where it is exclusively associated with *Arbutus*, but the cosmopolitan *M. tridentina* Bres. is present in at least four continents and linked to no less than 15 tree-hosts (Loizides *et al.* 2015, 2016). *Morchella steppicola* Zerova, the earliest diverging species in the Esculenta clade, occurs exclusively in temperate grasslands and steppic meadows of central Eurasia and Eastern Europe (Yatsiuk *et al.* 2016), while *M. dunensis* (Castañera, J.L. Alonso & G. Moreno) Clowez, is a dune specialist found on fixed coastal and inland dunes across the Mediterranean basin and all along the Atlantic coast (Loizides *et al.* 2016). *Morchella galilaea* Masaphy & Clowez, is remarkable in being the only (probably strictly) autumnal morel species known so far (Taskin *et al.* 2015). *Morchella rufobrunnea* Guzmán & F. Tapia, sometimes also fruiting in autumn, may additionally have a dual saprotrophic/endophytic lifestyle, frequently found on treeless, disturbed substrates and woodchips, but also under olive trees (Loizides *et al.* 2015).

A small number of late-diverging lineages

within the Distantes clade (*Morchella eximia* Boud., *M. exuberans* Clowez, Hugh Sm. & S. Sm., *M. importuna* M. Kuo, O'Donnell & T.J. Volk, *M. sextelata* M. Kuo, and *M. tomentosa* M. Kuo), are facultative or obligate pyrophiles and can fruit in vast numbers in the first and second springs following a forest fire. The precise mechanisms for this behaviour are not yet quite understood, but are thought to be linked to both sterilized surfaces and moribund trees (Greene *et al.* 2010). Interestingly, this highly specific ecological niche is not seen in yellow morels of the *Morchella esculenta* clade and may be a relatively recent adaptation of black morels in hot and dry localities, to cope with local disturbance phenomena such as forest fires (Du *et al.* 2012b, Loizides *et al.* 2016).

The puzzle of transcontinental species

So far, 34 *Morchella* species have been shown to be present in Europe, 32 are known to occur in Asia, and 21 are known from North America. Sixteen species have been molecularly confirmed from more than one continent, whilst at least seven species, four of them belonging to post-fire lineages, appear to have a more or less global distribution (see Fig. 4 & Table 3). Considering the high levels of endemism and provincialism

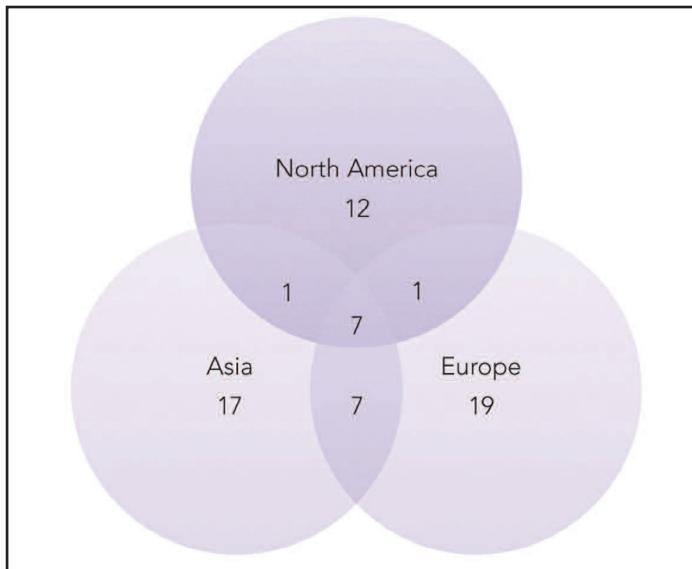


Figure 4: Global *Morchella* diversity including transcontinental species.

seen within the genus, how is it then that at least a quarter of morel species are found in two or more continents? The answer to this paradox, is for the moment not quite clear.

Early phylogenetic and biogeographical studies postulated that these apparently disjunct transcontinental occurrences, are the result of recent anthropogenic introductions from North America (Taskin *et al.* 2010, 2012, O' Donnell *et al.* 2011). Subsequent studies, however, have questioned this hypothesis, arguing that most transatlantic species occurring also in Europe are found in undisturbed native habitats and may be the result of refugia from the Pleistocene glaciation (Loizides *et al.* 2016). Indeed, the percentage of transcontinental species is consistently high in all large-scale biogeographical studies carried out so far, ranging between 33 and 45% of all *Morchella* species documented in China, Cyprus and Turkey. With the exception of the ruderal *Morchella galilaea* and *M. importuna*, frequently reported from greenhouses, gardens and landscaping sites, no apparent anthropogenic dispersal appears to have occurred for most other transcontinental species, the majority of which are strongly associated with native flora (Loizides *et al.* 2015, 2016). Perhaps more importantly, the ancestral *Morchella anatolica* seems to be restricted to the Mediterranean basin and is apparently absent from North America, making the recent introduction of this species to Europe highly unlikely. Long distance spore dispersal

(LDD) has been suggested as the most likely expansion mechanism for the opportunistic post-fire lineages, fruiting prolifically over short periods of time and over long distances, where forest fires randomly occur (Du *et al.* 2012a, Loizides *et al.* 2016). Whether the transcontinental tree-associated species are the result of LDD or refugia, however, remains an open question, and more studies are needed to decipher the complex evolutionary history of these widespread lineages.

Tying up loose ends – which is *Morchella elata*?

Despite all the progress in *Morchella* phylogenetics and systematics, the identity of *Morchella elata* ironically remains unresolved. Originally described from a burned fir forest in Sweden (Fries 1822), *M. elata* represents the archetypal morel species and this binomial has indeed been indiscriminately applied to dozens of black morels throughout the years. The post-fire ecology explicitly mentioned in Fries' original description ("praecipue locis humidis adustis" = chiefly in damp, scorched places), fortunately limits the candidate species to just a handful, with Mel-10, presently known as *Morchella importuna* (Fig. 3), being the most likely candidate (Richard *et al.* 2015). The latter is a facultatively pyrophilic species, also known to occur in urban habitats such as gardens, landscaping sites or woodchips. Although it was originally described as a "North-American endemic" (Kuo *et al.* 2012), it was later revealed to have a far more widespread distribution stretching over three continents (see Table 3), suggesting the highly probable existence of an earlier European name for this transcontinental lineage. Since no molecular data could be obtained from the two-century-old holotype (Richard *et al.* 2015), the identity of *M. elata* will need to be resolved through epitypification, preferably from Scandinavia, from where the species was originally described.

The status of a number of phylogenetically close and poorly understood lineages within the *Morchella purpurascens* complex (Mel-19, Mel-20, Mel-34, Mel-38), also needs to be carefully



Fig. 5. *Morchella tridentina*, a cosmopolitan member of the Distantes clade, showing distinct rufescence (reddening) of the ascocarps and its unique for the clade non-darkening ridges. Under *Olea europaea*, Cyprus, March 2016. Photograph © Geoffrey Kibby.

looked at, integrating phylogenetic and morphological analyses, to establish whether the small molecular differences between these clades (or subclades) correspond to specific morphological, ecological, or biogeographical patterns. Updated morphological descriptions based on contemporary polythetic taxonomical models, are urgently needed for most other taxa, to enable mycologists to recognize these species by non-molecular means. Large-scale integrative studies, especially from refugia hotspots, would greatly help in answering critical questions regarding species diversity and biogeography, but also concerning the genus' evolutionary history. Last but not least, some classical, validly named taxa currently remaining as 'ghost species', need to be satisfactorily resolved. These include widely applied binomials such as *M. rotunda*, *M. crassipes*, *M. hortensis*, *M. vaporaria*, *M. umbrina*, *M. rigida* and *M. norvegiensis* (the latter probably a prior synonym for the recently

described *M. eohespera*/Mel-19). Clarifying the status of these old binomials via topotypic epitypification, would not only simplify the proposal of new taxa, avoiding further synonymy, but also acknowledge and honour, where appropriate, the contribution of early pioneers to the systematic study of this remarkable genus.

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Species	Synonyms	Ecology/tree associations	Biogeographical distribution	References
Rufobrunnea clade				
<i>Morchella anatolica</i>	<i>M. lanceolata</i>	Uncertain, perhaps saprotrophic	Spain, Turkey	Isiloglu <i>et al.</i> 2010; Clowez 2012; Richard <i>et al.</i> 2015
<i>Morchella rufobrunnea</i>		Saprotrophic, but probably also facultatively biotrophic or endophytic, found on disturbed ground, wood mulch and under <i>Olea</i>	Australia, Cyprus, Israel, Mexico, USA	Guzmän & Tapia 1998; Kuo 2008; Masaphy <i>et al.</i> 2009; Loizides 2011; O'Donnell <i>et al.</i> 2011; Kuo <i>et al.</i> 2012; Elliott <i>et al.</i> 2014; Loizides <i>et al.</i> 2011; 2015; 2016
Esculenta clade				
<i>Morchella americana</i>	<i>M. americana</i> var. <i>elongata</i> , <i>M. californica</i> <i>M. claviformis</i> <i>M. esculentoides</i> <i>M. populina</i>	Probably biotrophic or endophytic, associated with <i>Fraxinus</i> , <i>Ulmus</i> , <i>Populus</i> , <i>Quercus</i> and <i>Acer</i>	Canada, France, Germany, Turkey, USA	Taşkin <i>et al.</i> 2010; 2012; O'Donnell <i>et al.</i> 2011; Clowez 2012; Kuo <i>et al.</i> 2012; Richard <i>et al.</i> 2015
<i>Morchella castaneae</i>	<i>M. brunneorosea</i> , <i>M. brunneorosea</i> var. <i>sordida</i>	Reported with <i>Castanea</i> , <i>Fraxinus</i> and <i>Populus</i>	Spain	Clowez 2012; Richard <i>et al.</i> 2015
<i>Morchella dunensis</i>	<i>M. esculenta</i> f. <i>dunensis</i> <i>M. esculenta</i> f. <i>sterilis</i> <i>M. andalusiae</i> ,	Probably saprotrophic as well as facultatively biotrophic or endophytic, found on sand dunes and under <i>Malus</i>	Cyprus, Spain, Turkey	Castañera & Moreno 1996; Taşkin <i>et al.</i> 2010; 2012; Clowez 1997; 2012; Loizides <i>et al.</i> 2011; 2016
<i>Morchella esculenta</i>	<i>M. esculenta</i> var. <i>aurantiaca</i> , <i>M. esculenta</i> var. <i>brunnea</i> , <i>M. esculenta</i> var. <i>ruboris</i> , <i>M. ochraceoviridis</i> , <i>M. ovalis</i> , <i>M. ovalis</i> var. <i>minor</i> <i>M. pseudoumbrina</i> <i>M. pseudoviridis</i> <i>M. crassipes</i> ? <i>M. rotunda</i> ?	Mostly associated with <i>Fraxinus</i> , <i>Malus</i> , <i>Populus</i> , <i>Quercus</i> and <i>Ulmus</i>	Belgium, China, Czech Republic, France, Netherlands, Norway, Spain, Sweden, Switzerland, Turkey	Persoon 1794; Fries 1822; Krombholz 1834; Boudier 1897; Jacquetant 1984; Taşkin <i>et al.</i> 2010; 2012; O'Donnell <i>et al.</i> 2011; Du <i>et al.</i> 2012a; 2012b; Clowez 1997; 2012; Loizides <i>et al.</i> 2011; 2016; Richard <i>et al.</i> 2015
<i>Morchella fluvialis</i>	-	Found in riparian forests of <i>Fraxinus</i> , <i>Alnus</i> and <i>Ulmus</i>	Spain, Turkey	Taşkin <i>et al.</i> 2010; 2012; Clowez 1997; 2012; Richard <i>et al.</i> 2015
<i>Morchella galilaea</i>	-	Uncertain, reported under a wide diversity of vegetation, including greenhouses	Africa, China, Hawaii, India, Israel, Java, New Zealand, Turkey	Masaphy <i>et al.</i> 2009; O'Donnell <i>et al.</i> 2011; Taşkin <i>et al.</i> 2010; 2012; Clowez 2012; Du <i>et al.</i> 2012a; 2012b; Richard <i>et al.</i> 2015; Loizides <i>et al.</i> 2016
<i>Morchella palazonii</i>	-	Reported under <i>Quercus ilex</i> and <i>Fraxinus angustifolia</i>	Spain	Clowez <i>et al.</i> 2015

Table 3: Morel species molecularly confirmed to be present in Europe, including currently confirmed synonyms, putative ecology and known distribution. Names are arranged alphabetically within their clades.

<i>Morchella steppicola</i>	-	Probably saprotrophic or endophytic, found in steppic meadows and dry grasslands	Germany, Hungary, Serbia, Slovakia, Ukraine, Uzbekistan	Zerova 1941; O'Donnell <i>et al.</i> 2011; Kuo <i>et al.</i> 2012; Richard <i>et al.</i> 2015; Yatsiuk <i>et al.</i> 2016
<i>Morchella vulgaris</i>	<i>M. acerina</i> , <i>M. anthracina</i> , <i>M. conica</i> var. <i>pygmaea</i> <i>M. lepida</i> , <i>M. robiniae</i> , <i>M. spongiosa</i> , <i>M. vulgaris</i> var. <i>aucupariae</i>	Likely biotrophic or endophytic, associated with <i>Acer</i> , <i>Crataegus</i> , <i>Fraxinus</i> , <i>Sorbus</i> and <i>Ulmus</i>	France, Spain	Persoon 1801; Fries 1822; Gray 1821; Clowez 2012; Richard <i>et al.</i> 2015

Elaた clade

<i>Morchella arbutiphila</i>	-	So far strictly associated with <i>Arbutus andrachne</i>	Cyprus, Turkey	Taşkin <i>et al.</i> 2010; 2012; Loizides <i>et al.</i> 2016
<i>Morchella conifericola</i>	-	Reported with <i>Pinus</i> , <i>Cedrus</i> and <i>Abies</i>	Turkey	Taşkin <i>et al.</i> 2012; 2016
<i>Morchella deliciosa</i>	<i>M. deliciosa</i> var. <i>elegans</i> , <i>M. deliciosa</i> var. <i>incarnata</i> , <i>M. conica</i> var. <i>flexuosa</i> , <i>M. conica</i> var. <i>nigra</i> , <i>M. conica</i> var. <i>violetipes</i> , <i>Morilla deliciosa</i>	Associated with conifers, mostly <i>Larix</i> , <i>Picea</i> and <i>Pinus</i>	France, Sweden, Turkey	Taşkin <i>et al.</i> 2010; 2012; Clowez 2012; Richard <i>et al.</i> 2015
<i>Morchella disparilis</i>	-	Probably biotrophic or endophytic, found under <i>Cupressus</i> and <i>Arbutus</i>	Cyprus	Loizides <i>et al.</i> 2016;
<i>Morchella dunali</i>	<i>M. fallax</i>	Associated with <i>Pinus brutia</i> and evergreen <i>Quercus</i> spp., rarely also with <i>Cistus</i>	Cyprus, France, Spain, Turkey	Boudier 1897; Taşkin <i>et al.</i> 2010; 2012; Loizides <i>et al.</i> 2011; 2016; Moreau <i>et al.</i> 2011; Clowez 2012; Richard <i>et al.</i> 2015; Loizides 2016
<i>Morchella eohespera</i>	<i>M. norvegiensis</i> is probably a priority synonym of this taxon	Uncertain, reported under mixed vegetation	France, Canada, China, Germany, Sweden, Switzerland, JUSA	Du <i>et al.</i> 2012b; Beug & O'Donnell 2011; Richard <i>et al.</i> 2015 Voitk <i>et al.</i> 2016
<i>Morchella eximia</i>	<i>M. anthracophila</i> , <i>M. carbonaria</i> , <i>M. septimelata</i>	Strictly pyrophilic, found in 1–2-year-old burned coniferous forests	Argentina, Australia, Canada, China, Cyprus, France, Spain, Turkey, USA	Boudier 1909; Jacqueman 1984; Taşkin <i>et al.</i> 2010; 2012; O'Donnell <i>et al.</i> 2011; Kuo <i>et al.</i> 2012; Du <i>et al.</i> 2012b; Richard <i>et al.</i> 2015; Loizides <i>et al.</i> 2016
<i>Morchella eximioides</i>	-	Uncertain, originally reported under deciduous trees	China, Norway	Jacqueman 1984; Du <i>et al.</i> 2012b; Richard <i>et al.</i> 2015
<i>Morchella exuberans</i>	<i>M. capitata</i>	Strictly pyrophilic, found in 1–2-year-old burned coniferous forests	China, Cyprus, Sweden, Turkey, USA	Taşkin <i>et al.</i> 2010; 2012; O'Donnell <i>et al.</i> 2011; Du <i>et al.</i> 2012a; 2012b; Loizides <i>et al.</i> 2016

Table 3 continued.

<i>Morchella fekeensis</i>	-	Mostly associated with <i>Pinus</i>	Turkey	Taşkin <i>et al.</i> 2010; 2012; 2016
<i>Morchella importuna</i>	<i>M. elata</i> , <i>M. hortensis</i> <i>M. pragensis</i> and <i>M. vaporaria</i> are all likely earlier names for this widespread species	Facultatively pyrophilic, found in 1-2-year-old burned forests, disturbed ground, wood mulch, but also under <i>Malus</i>	Canada, China, Cyprus, Finland, France, Germany, Spain, Switzerland, Turkey, USA	Taşkin <i>et al.</i> 2010 ; 2012 ; O'Donnell <i>et al.</i> 2011 ; Kuo <i>et al.</i> 2012 ; Du <i>et al.</i> 2012a ; 2012b ; O'Donnell 2014 ; Loizides <i>et al.</i> 2016
<i>Morchella kakiicolor</i>	<i>M. quercus-ilicis</i> <i>f. kakiicolor</i>	Associated with <i>Castanea</i> <i>sativa</i>	Spain	O'Donnell <i>et al.</i> 2011; Clowez 2012; Richard <i>et al.</i> 2015; Loizides <i>et al.</i> 2015
<i>Morchella magnispora</i>	-	Mostly reported from coniferous forests	Turkey	Taşkin <i>et al.</i> 2010; 2012; 2016
<i>Morchella mediterraneensis</i>	-	Mostly reported from coniferous forests	Spain, Turkey	Taşkin <i>et al.</i> 2010; 2012; 2016
<i>Morchella pulchella</i>	-	Uncertain, reported with both broadleaved and coniferous trees	China, France, Turkey	Taşkin <i>et al.</i> 2010; 2012; Clowez 2012; Du <i>et al.</i> 2012b; Richard 2015
<i>Morchella purpurascens</i>	<i>M. elata</i> var. <i>purpurascens</i> <i>M. conica</i> var. <i>purpurascens</i> <i>M. conica</i> var. <i>crassa</i>	Associated with <i>Pinus</i> and other conifers	China, Denmark, France, Norway, Sweden, Turkey	Krombholz 1834; Boudier 1897; Jacquetant 1984; Jacquetant & Bon 1985; Taşkin <i>et al.</i> 2010; 2012; Clowez 2012; Du <i>et al.</i> 2012b; Richard <i>et al.</i> 2015
<i>Morchella semilibera</i>	<i>M. gigas</i> , <i>M. gigas</i> var. <i>tintinnabulum</i> , <i>M. hybrida</i> , <i>M. undosa</i> , <i>M. varisiensis</i> , <i>M. esculenta</i> var. <i>crassipes</i> , <i>Phallus gigas</i> , <i>P. undosus</i> , <i>P. crassipes</i> , <i>Eromitra gigas</i> , <i>Mitrophora hybrida</i> , <i>M. hybrida</i> var. <i>crassipes</i> , <i>Ptychoverpa gigas</i> , <i>Helvella hybrida</i>	Reported with <i>Castanea</i> , <i>Fraxinus</i> , <i>Malus</i> and <i>Ranunculus</i>	Czech Republic, France, Germany, India, Italy, Netherlands, Turkey	Taşkin <i>et al.</i> 2010; 2012; O'Donnell <i>et al.</i> 2011; Clowez 2012; Du <i>et al.</i> 2012a; Moreau <i>et al.</i> 2014; Richard <i>et al.</i> 2015
<i>Morchella tridentina</i>	<i>M. quercus-ilicis</i> , <i>M. frustrata</i> , <i>M. elatoides</i> , <i>M. elatoides</i> var. <i>elegans</i> , <i>M. conica</i> var. <i>pseudoeximia</i>	Most likely biotrophic or endophytic, associated with <i>Abies</i> , <i>Arbutus</i> , <i>Castanea</i> , <i>Corylus</i> , <i>Fraxinus</i> , <i>Olea</i> , <i>Pinus</i> , <i>Pseudotsuga</i> , <i>Quercus</i> etc.	Argentina, Armenia, Chile, Cyprus, France, India, Italy, Spain, Turkey, USA	Bresadola 1898; Jacquetant 1984; Röllin & Anthoine 2001; Barseghyan <i>et al.</i> 2012; Taşkin <i>et al.</i> 2010 ; 2012; O'Donnell <i>et al.</i> 2011; Clowez 2012; Kuo <i>et al.</i> 2012; Richard <i>et al.</i> 2015; Loizides <i>et al.</i> 2015; 2016; Loizides 2016

Table 3 continued.

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