

Last chance to know? Using literature to explore the biogeography and invasion biology of the death cap mushroom *Amanita phalloides* (Vaill. ex Fr. :Fr.) Link

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Abstract

The biogeography of fungi is poorly understood and a species in a novel location may be an introduction or an endemic newly identified within its native range. Using the literature of *Amanita phalloides* as a case study, we aim to illustrate both the limited utility of the historical record in establishing ectomycorrhizal (EM) species as introduced or invasive, and the difficulty of using modern records to establish a current biogeography. *Amanita phalloides*, the death cap mushroom, is deadly. It is a notorious fungus with a rich literature. Historical records can be used to explore the species' distribution in North America, where the earliest publication on *A. phalloides* dates to 1834, and four different authors identified it as growing in California, Minnesota, Pennsylvania, North Carolina, and Maryland before 1910. In contrast, by mid-century field guides listed *A. phalloides* as rare on the West Coast and absent from the East Coast. In modern literature *A. phalloides* is described as a recently introduced and currently invasive species. The contradictions raise two questions: First, is *A. phalloides* an exotic to North America, and second, can early records be used to delineate the native distribution of any other less infamous EM fungus? We argue that confusion on the introduced status and biogeography of *A. phalloides*, and perhaps other fungi, is the direct result of shifting species concepts. When publications include an explicit species concept they can be used to establish *A. phalloides* as an introduction, for example on the East Coast of North America and in Australia. When species concepts are vague the literature is not useful and cannot be used to determine *A. phalloides* as an introduction, for example on the West Coast of North America or in Asia.

Abbreviation: EM – ectomycorrhizal

Introduction

Research on the invasion biology of fungi has focused primarily on plant pathogenic fungi. Infamous examples of introduced and invasive plant pathogens include chestnut blight (*Cryphonectria parasitica*), Dutch elm disease (*Ophiostoma ulmi*), and white pine blister rust (*Cronartium ribicola*). Rather less is known about the introduction or invasion of nonpathogenic fungi. Careful work has been done with a few species, for example the saprobe *Clathrus archeri* (Parent and Thoen 1986; Parent et al. 2000) and the ectomycorrhizal fungus *Amanita muscaria*

toma ulmi), and white pine blister rust (*Cronartium ribicola*). Rather less is known about the introduction or invasion of nonpathogenic fungi. Careful work has been done with a few species, for example the saprobe *Clathrus archeri* (Parent and Thoen 1986; Parent et al. 2000) and the ectomycorrhizal fungus *Amanita muscaria*

(Sawyer et al. 2001; Bagley and Orlovich 2004). Fungi associated with plants have been moved when trees are planted for agriculture (Garrido 1986; Dunstan et al. 1998) and edible mushrooms, especially truffles, have been cultivated on plantations outside their native range (Sogg 2000; Yun and Hall 2004). Scant attention is paid to the ecological consequences of transporting non-pathogenic fungi across continents (but see Ville-neuve et al. 1991; Chapela et al. 2001; Diez 2005). Monitoring efforts aimed at tracking the dispersal of introduced fungi to native forests are rare in America, but more common in Europe and Australia (for example, the Australian fungimap.rbg.vic.gov.au).

Ectomycorrhizal (EM) fungi function as obligate symbionts of plants (Frank 1885, Trappe 2005). The association is often assumed to be a mutualism but may range across a continuum of parasitism to mutualism (Egger and Hibbett 2004; Jones and Smith 2004). In nature ectomycorrhizal (EM) fungi form species-rich communities in which an individual fungus may colonize multiple trees (Horton and Bruns 1998; Kennedy et al. 2003), and an individual tree may associate with multiple fungi (Bruns 1995).

A notorious species of EM fungus is *Amanita phalloides*, or the death cap or death cup mushroom. It is fatally poisonous and according to folklore an *A. phalloides* mushroom was used by Agrippina to kill the Emperor Claudius so that her son Nero might be Caesar (Benjamin 1995). More recently *A. phalloides* has killed a spate of individuals in California (Rattanvilay et al. 1982; Freedman 1996a, b; Zevin et al. 1997; Hoffman 2004). Because *A. phalloides* is deadly it attracts a great deal of attention and a rich literature records *A. phalloides*' distribution in North America.

At this time the mushroom is abundant in both the urban landscapes and undisturbed forests of California (personal observations), but the literature conflicts on whether or not *A. phalloides* is native. *Amanita phalloides* was recorded in California as early as 1880 (Harkness and Moore 1880). In later publications *A. phalloides* is described as a newly introduced and invasive species (e.g. Saylor 1984a, b). Is *A. phalloides* native, as the 1880 record would suggest, or introduced? California is a biodiversity hotspot

(Stein et al. 2000) and if *A. phalloides* is an exotic species it would be invading into a complex fungal community. A similar story can be told for *A. phalloides* on the East Coast; early reports (Schweinitz 1834; Taylor 1897; McIlvaine and MacAdam 1902) give way to later descriptions of *A. phalloides* as introduced and invasive (Tanghe 1983).

As humans continue to facilitate species' migrations across continents the biogeography of organisms is shifting. Mycorrhizal fungi are no exception and yet examples of invasive EM taxa are rare. How can early records be used to delineate the native distribution of *A. phalloides* and other (and especially less charismatic) EM fungi? By using the literature of *A. phalloides* as a case study we aim to illustrate both the utility of the historical record in establishing EM species as introduced or invasive and the difficulty of describing the past and present biogeography of mushrooms.

Materials and methods

By focusing on the historical literature of *A. phalloides* in North America, and modern literature of *A. phalloides* across the globe, we aimed to discover when *A. phalloides* was first described from North America, when *A. phalloides* was first described as an introduction to North America, and the current distribution of the species. Mycologia is the official publication of the Mycological Society of America and by searching through published indexes we compiled a list of every Mycologia article which carries the words *Amanita phalloides*. Forty Mycologia records spanned 1909–1999. Additional articles were gathered from a variety of sources, including amateur publications and field guides. Very early records were found by searching the shelves of the Marian Koshland Bioscience and Natural Resources Library at the University of California, Berkeley and the Botany Libraries of the Harvard University Herbaria. We did not focus on the early medical literature; early mushroom deaths were often attributed to *A. phalloides* but these reports rarely included a description of the fungus in question and more than one species of *Amanita* is poisonous (Litten 1975). On the East

Coast of North America deaths attributed to *A. phalloides* might have been caused by, for example, *A. virosa*, and on the West Coast of North America mushroom deaths may have been caused by *A. ocreata*. The current distribution of the mushroom was described using modern literature, found on the shelves of the same libraries and also using the CABI Bioscience Bibliography of Systematic Mycology. We used current field guides in our work, however, field guides may be problematic. First, the picture and description are not always drawn from the same specimen, and discrepancies between pictures and descriptions are easy to find; second, descriptions may originate outside of the region covered by the field guide; finally, in most cases authors do not collect voucher specimens and so species' identifications cannot be verified. We approached all field guides with suspicion and focused on other publications with careful descriptions. Finally, we contacted mycologists in South America, Japan, China and Australia for their personal observations. An annotated bibliography of the literature is available upon request.

Results

A. phalloides in North America: historical records and current distribution

Concepts of *A. phalloides*

A description of *A. phalloides*' past and present biogeography is inextricably linked to the variability and accuracy of the species concept. Historical descriptions of the mushroom are only useful when compared to a modern description of *A. phalloides*. In current literature the death cap mushroom is described as having a 3.5–15 cm wide yellow-olive to green-olive cap, often with darker streaks or striations on the cap, white gills, a white stipe (stem) with a flaring ring, and a bulbous base encased in a white volva (cup) (Arora 1986). However, the species concept has changed with time. Written descriptions begin as early as 1727 with Vaillant (1727). Vaillant (1727) used the phrase name "*Fungus phalloides, annulatus, sordide virescens, et patulus*"; his is clearly the modern *A. phalloides*. Vaillant (1727) is widely cited by later authors,

though they used different names, e.g. *Agaricus bulbosus* (Bulliard 1780), *Amanita viridis* (Persoon 1797; Persoon 1801), or *Hypophyllum virosom* (Paulet 1793). Fries (1821) cited Vaillant but called the species *Agaricus phalloides*, and in contrast to Vaillant his descriptions lumped *A. phalloides* with white species, e.g. *Amanita verna*. Although Fries included white species in his description he emphasized the green-capped mushrooms, writing that *A. phalloides* was "*subinde fusco et viridi varius*" or "often dark and variably green". Fries kept to a broad concept of *Agaricus phalloides* throughout his publications (Fries 1836–1838; Fries 1857). Link (1833) gave the species its current binomial, *Amanita phalloides*. Subsequent authors recognized *A. phalloides* as distinct from mushrooms with white caps, for example Berkeley (1860), who recognized *A. phalloides* as distinct from the white *A. verna* and the yellow *A. mappa* (now known as *A. citrina*). By the late 19th Century the European concept of *A. phalloides* was codified and a well-known and widely distributed book by Ricken (1915), "Die Blätterpilze," gives a modern description.

Early views: *W.A. Murrill and morphological variability of A. phalloides (1832–1940)*

Early descriptions of *A. phalloides* in North America include Schweinitz (1834), Peck (1897), Taylor (1897), Herbst (1899), McIlvaine and Macadam (1902), Clements (1910) and Coker (1917). These mycologists based their identifications on European books, which typically included short descriptions in Latin (e.g. Fries 1821) and more rarely color plates (e.g. Bulliard 1780). It is not likely that any of the mycologists would have possessed European material of *A. phalloides*. American authors described the mushroom as growing in various states, but used a species concept that is more variable than the European conception of the late 19th Century. For example Taylor (1897) described the mushroom as common in Maryland and either white, brown or green, but noted "I have not yet found the green-capped variety sometimes figured in European works" (Figure 1). In Pennsylvania, Herbst (1899) described *A. phalloides* as "shining white or sometimes light fuscous" and "found in nearly every open woods in the Lehigh valley and the state"; there is no emphasis on the green



Figure 1. Concepts of the ectomycorrhizal fungus *Amanita phalloides*. (a) From Berkeley's 1860 book *Outlines of British Fungology*. The mushroom is drawn with the partial veil intact; there is no annulus on the mushroom stem. (b) From Taylor's 1897 *Student's Hand-Book of Mushrooms of America*. Note color and spots on the mushroom cap. (c) From Murrill's 1916 description in the journal *Mycologia*, an article titled "Illustrations of Fungi – XXV". Note color. (d) The mushroom currently recognized as *Amanita phalloides* in both Europe and North America. From McKnight and McKnight's Peterson Field Guide *Mushrooms*. Note color and streaks of olive on cap. Compare to Figure 1a at left.

form. McIlvaine and Macadam (1902) described *A. phalloides* as "common and variable", cap color is listed as white or yellow, becoming green and occasionally variegated or even black. Pre-saging what would become accepted taxonomy, these authors (1902) wrote that an inexperienced mycologist might "mistake its different forms for distinct species". McIlvaine and Macadam (1902) also wrote that "it is remarkable that the form with a greenish pileus, which seems to be common enough in Europe, does not occur here". Clements (1910) wrote of *A. phalloides* as common in Minnesota and "usually white, more rarely olive, brown or yellow". Coker (1917) monographed the *Amanitas* of North Carolina and described *A. phalloides* as having 'usually a smoky black or smoky brown cap center, varying to much lighter brownish straw'.

In California, *A. phalloides* was listed in the *Catalogue of the Pacific Coast Fungi* compiled by Harkness and Moore (1880). However no description or distribution was given by the authors; the mushrooms were apparently collected from San Rafael, Marin County.

William A. Murrill, a mycologist employed by the New York Botanical Garden, wrote extensive descriptions of *A. phalloides* in the early part of the 20th Century and his works are emblematic

of the confusion over color in the species. In 1909, Murrill described *A. phalloides* as white, however, he also stated that "other forms will require color" (Murrill 1909). In that publication Murrill gave *A. phalloides* the common name of "Destroying Angel", currently the name is used to describe any of several pure white and deadly *Amanita* species (e.g. *A. virosa*), but not *A. phalloides*. Again in 1910 Murrill described *A. phalloides* as having "many forms and colors" (Murrill 1910) and, in 1913, Murrill gave a full description of the species and also published a color plate (Figure 1). In that publication Murrill renamed the species *Venenarius phalloides* and described the mushroom as "pure-white to yellow, yellowish-green, green, gray, brown, or blackish".

Mycologists' descriptions were accepted by the American medical community, as illustrated by a paper published by Ford and Clark in 1914 on the "properties of poisonous fungi". Ford and Clark (1914) described *A. phalloides* as "varying from brownish amber to yellow" and went on to say that "colors of the pileus... are important, but are not as a rule regarded as of specific value. In Europe the pileus is usually greenish in color, but in America the greenish color is rarely seen".

The discussion of color gives an insight into the contrast between American and European views of *A. phalloides*. While American mycologists clearly felt that the cap color of *A. phalloides* could be quite variable and was rarely green, in Europe *A. phalloides* was described as variable but typically green. For example, one of the principle works consulted by Herbst (1899, see preface) was Rev. M. J. Berkeley's *Outlines of British Fungology* (1860). While Herbst (1899) wrote of *A. phalloides* as a white (occasionally fuscous) mushroom, according to Berkeley *A. phalloides* is "variously coloured, often greenish". In contrast to Herbst's (1899) description, Berkeley's figure of the mushroom is a perfect modern conception of the species (Figure 1).

The difference between American and European mycologists is also illustrated by the comments of Jakob E. Lange, an experienced Danish mycologist who traveled extensively in the United States and Canada in the fall of 1931. Unlike Murrill (1909; 1910; 1913), Ford (1909, with Clark in 1914), and others (Overholts and Overholts 1916; Rosen 1926), Lange thought that *A. phalloides* "seems to be almost unknown in America, while it is very common with us" (Lange 1934). This is a particularly important reference as it was written by a European mycologist with extensive knowledge of the European species *A. phalloides*. Lange did not think that the European species grew in America. That opinion and the problematic nature of earlier American descriptions suggest that *A. phalloides* did not grow in North America at the time of his visit.

In fact American mycologists of the 19th and early 20th century seem to have used the name *A. phalloides* for a variety of species. Detailed records for the West Coast are absent, but on the East Coast at least it seems unlikely that the European *A. phalloides* grew at this time.

Mid-Century: A. H. Smith and the dismissal of A. phalloides as an American Species (1940–1970)
The view of *A. phalloides* as absent from North America was the consensus among American mycologists at mid-century: Murrill's descriptions were discredited and mycologists including Alexander H. Smith (1958, 1975) and Rolf Singer (1959) concluded that *A. phalloides* is green, and

not white, brown, gray or black. Smith (1958) was particularly influential and wrote "it now appears that the true *A. phalloides* is not known from eastern North America". Smith's concept of the species is illustrated in a later publication, *A Field Guide to Western Mushrooms* (1975). In that book Smith described *A. phalloides* as "olive fuscous on the disc to paler olive or olive yellow over the marginal area". When formally describing the species *Amanita aestivalis* Singer (1959) described *A. phalloides* as of a "green color".

A few mycologists allude to the controversy, for example Emmons (1962) acknowledged that the question of whether or not *A. phalloides* is found in America was "moot"; and Isaacs and Tyler (1963) stated "the occurrence of *Amanita phalloides* (Vaill. ex Fr.) Secr. in North America has been disputed for some years".

Ironically, this may be the period in which *A. phalloides* was introduced and established in North America, at least to the East Coast of North America. On the West Coast Isaacs and Tyler (1963) described a specimen putatively identified as *A. phalloides* in Ashland, OR. The cap was olivaceous and a screen for toxins determined that the mushroom had some (but not all) of the kinds of amanitin poisons; however Smith examined the specimen and doubted that it was *A. phalloides* (Isaacs and Tyler 1963).

Even if he doubted the Oregon collection, Smith made "the first reliable reports of *A. phalloides* from the West Coast of North America" in his field guides (discussed in Ammirati et al. 1977). From 1958 to 1996 Smith published various editions of a guide titled *The Mushroom Hunter's Field Guide*. In the first edition, Smith wrote of *A. phalloides* as occurring "rarely, in California" (Smith 1958). In 1966 and 1973 Smith wrote "a species close to *Amanita phalloides* is rare in California and southern Oregon" (Smith 1966; Smith 1973).

At mid-century we also find the first descriptions of *A. phalloides* as an introduced species, but from South America: Herter (1934) gives a careful account of the mass occurrence of *A. phalloides* in oak plantations in Uruguay; his publication is titled "La aparición del hongo venenoso *Amanita phalloides* en Sudamérica". Singer (1953) also comments that in the urban centers of South America "since the host

frequently determines the fungous flora, one is likely to find, side by side with native elements, species unwittingly introduced by man” and as an example wrote “we find commonly species of the genus *Suillus* in [pine] plantations, even *Amanita phalloides* and *A. muscaria*”.

Current opinion: A. phalloides as a European immigrant (1970–Present)

Tanghe and Simons (1973) and Ammirati, Thiers and Horgen (1977) were the first to describe unambiguous specimens of *A. phalloides* with a European morphology from the East and West Coasts of North America. Tanghe and Simons (1973) detailed collections from New York, New Jersey, Delaware and Virginia; the description leaves no doubt that the authors have found the European *A. phalloides*. Mushrooms were found growing with a variety of tree species, both native (e.g. *Pinus strobus* and *P. taeda*) and introduced (*Picea abies*). Ammirati et al. (1977) described *A. phalloides* as “a common species in California” often collected under the endemic *Quercus agrifolia*. In a separate publication, Tanghe (1983) compiled a useful chronology of its appearance in various states and wrote that the first authenticated eastern North American collection was in 1967 in Laurel, MD.

After 1970 *A. phalloides* was increasingly described as a European immigrant. In a guidebook to North American mushrooms, Miller (1979) described *A. phalloides* as growing “mostly under European trees or plantations”. Tanghe’s (1983) article is titled, “Spread of *Amanita phalloides* in North America” and Saylor (1984a) published an article titled “*A. phalloides* in California: This preliminary report suggests that it is a relative newcomer to the state”. Smith and Weber (1996) concluded “the picture of its distribution in North America is changing with every passing mushroom season”.

The current distribution of A. phalloides in North America

In California, Ammirati et al. (1977) collected *A. phalloides* from Sonoma, Napa, Marin, Alameda, San Mateo and Santa Cruz Counties – all of these are within the San Francisco Bay Area. Thiers (1982) treated *Amanita* in the first installment of “The Agaricales of California” and gave

a similar distribution. Biek (1984) listed additional locations in Northern California, including Shasta County. Saylor (1984b) described the mushroom as growing north to Mendocino County and South to Santa Barbara County, and according to him it also grew east to the Sierra foothills of Butte County. We have been collecting *A. phalloides* since 2002 and our focus has been California (Figure 2). Specimens are identified using morphology as a guide and the ITS molecular marker as confirmation (the ITS1 marker is invariant in *A. phalloides* collected from across Europe and North America and ITS2 includes a single insertion–deletion, data not shown). We have no specimens of the mushroom from north of Mendocino County. We also have collections of *A. phalloides* from Seattle, Washington and Vancouver Island, British Columbia, Canada, but not from central or eastern Canada. There are sporadic reports of the mushroom growing elsewhere on the West Coast, including Portland, Oregon.

On the East Coast Tanghe (1983) reported the mushroom as growing in Pennsylvania, Virginia, Maryland, Delaware, perhaps Massachusetts, New Jersey, New York and Rhode Island; this distribution is repeatedly listed by other authors (e.g. Lincoff 1981; Jenkins 1986). There have been no systematic surveys of the fungus on this coast in the last 20 years, but we hold authenticated specimens from Pennsylvania and New Jersey.

There are also two reports of *A. phalloides* from Mexico (Villegas et al. 1982; Aroche et al. 1984), but Aroche et al. (1984) concluded that mushrooms described as *A. phalloides* in Mexico differ from the European *A. phalloides*, and more recently the Mexican specimens were described as a new species, *A. arocheae* Tulloss, Ovrebo & Halling (1992), also occurring in Colombia. However, it is not clear if the species described in the first report is indeed *A. arocheae*, and not *A. phalloides*.

The current biogeography of A. phalloides outside of North America

What is known of the species outside of North America can mimic the history of the species in North America, for example in New Zealand



Figure 2. Current distribution of the death cap mushroom *Amanita phalloides* in California. Verified collections are held from counties marked with grey. The fungus is reported from counties with dots.

there is a historical record of *A. phalloides* (Hooker 1855) but currently the mushroom is considered an introduction (Ridley 1991). In other countries the presence or absence of *A. phalloides* is controversial: there are historical records of *A. phalloides* in Japan (Imai 1938, Kawamura 1964), and a modern field guide of Japanese mushrooms includes *A. phalloides* in its descriptions (K. Maruyama, personal communication), but a number of Japanese mycologists do not think *A. phalloides* grows on the islands (K. Maruyama, T. Oda, personal communications). Often the fine scale distribution of the mushroom is unknown. Here we summarize current knowledge of *A. phalloides*' biogeography outside of North America. We base our summary on the available literature. As we have just concluded that the literature is fraught with

error, we are careful to distinguish those sources with complete species descriptions from publications (especially field guides and lists of species) that do not provide descriptions. When species descriptions were provided we compared them to the modern concept of *A. phalloides* (Figure 3).

Europe and North Africa

Amanita phalloides is native to Europe. It grows north to the southern edge of Norway and Sweden (Lange 1974; Eckblad 1981; Neville and Poumarat 2004) and south to Morocco and Algeria (Malençon and Bertault 1970). The western limit of the mushroom is in Ireland (Lange 1974); the eastern limit is unknown but *A. phalloides* is described from Poland and the Balkan States (Lange 1974) and Russia (Neville and Poumarat 2004). The species is also described from



Figure 3. Current biogeography of *Amanita phalloides* according to available literature. Dark green dots are from sources with detailed species descriptions; with these publications it was possible to authenticate the identity of *A. phalloides* and delineate a native range. Principal publications included Lange (1974) and Neville and Poumarat (2004). Light green dots relate to publications with minimal descriptions or descriptions that do not match the current concept of *A. phalloides*, for example Chin (1988). *Amanita phalloides* may or may not be native here. Red dots are drawn from sources which clearly describe *A. phalloides* and provide convincing evidence for its introduced status. Question marks are placed on regions where *A. phalloides* may be found and may be introduced (Madagascar) or is found and may be either native or introduced (California). See text for more information and additional citations.

Italy (Traverso 1998; Galli 2001). It is listed from the Baltic States, Ukraine, Turkey and Armenia (Zerov 1979; Melik-Khachatryan 1980; Urbonas et al. 1986; Peksen and Karaca 2003), but there are no detailed species descriptions from these regions. Accurate and explicit information on its distribution in Europe can be found in the literature (e.g. Lange 1974 for the whole of Europe, and collections related to Lange (1974) are stored in various herbaria, for example the National Herbarium Nederland in Leiden, Netherlands; Krieglsteiner 1991 for Germany; Nauta and Vellinga 1995 for the Netherlands) and also on websites (e.g. the Mycological Herbarium of the University of Oslo, at <http://www.nhm.uio.no/botanisk/sopp>; the British Mycological Society's British Fungi Records Database, at <http://194.203.77.76/fieldmycology/>, and the Swiss

online atlas of fungi at <http://www.wsl.ch/swiss-fungi/welcome-de.ehtml>).

South America

Amanita phalloides was introduced to South America with exotic trees (Herter 1934; Martínez 1945; Singer 1953; Takacs 1961; Valenzuela et al. 1992). The first record of the species comes from Uruguay (Herter 1934), where it was found fruiting in a *Quercus ilex* plantation. In Argentina the mushroom is still associated with exotic species, for example with oak and chestnut in the central part of the country (Hunziker 1983); it does not associate with native plants (C. Barroetaveña, L. Dominguez, personal communications). This is also true in Chile (Valenzuela et al. 1992). Herter (1934) carefully compared his collections to European material, and the records

for Chile were confirmed by the European mycologist Gabriel Moreno (Valenzuela et al. 1992).

Asia and the middle east

Amanita phalloides may or may not grow in Asia outside of the Mediterranean region. It has been reported from Japan but may not grow in Japan, as discussed above. It has been reported from China (Tai 1979; Teng 1996, the latter is a posthumous publication of work done before 1966), but the authenticity of these reports is also in doubt (Z. Yang, personal communication). The fungus was reported as growing in the lowland dipterocarp forests of Sarawak (Chin 1988), but this seems a very unlikely habitat. *Amanita phalloides* has been collected underneath *Pinus kesiya* in India (Rao et al. 1997). But in a critically annotated checklist of the Amanitaceae of India (Bhatt et al. 2003) the authors are equivocal on *A. phalloides* in India, “there are instances in which this species has been exported along with a variety of symbionts, which would make its occurrence in India possible... [but] some Uttaranchal material determined as [*A. phalloides*] proved to be *A. subjunquillea*”. There are also scattered reports of *A. phalloides* in Pakistan and Iran (Ershad 1977; <http://www.nhm.uio.no/botanisk/sopp>). The fungus *A. phalloides* may grow in Asia, but the scant information available does not provide an accurate picture of the species’ distribution in the region.

Australia and New Zealand

Amanita phalloides was introduced to Australia (Talbot 1976; Reid 1980; Shepherd and Totterdell 1988; Young 1994; Wood 1997; fungimap.rbg.vic.gov.au; H. Lepp, personal communication) and New Zealand (Taylor 1981; Ridley 1991). Early works on Australian fungi do not list *A. phalloides* as found in Australia (Cooke 1892; McAlpine 1895; Cleland 1934–1935); Cooke was a British mycologist who would have known the European species from Great Britain. In contrast, the fungus is included in two modern field guides (Shepherd and Totterdell 1988; Young 1994) and both describe the mushroom as associated with exotic trees. Extensive and accurate taxonomic treatments of Australian *A. phalloides* are given by

Reid (1980) and Wood (1997). The species’ current distribution includes urban and suburban sites in the southeast and especially Canberra (Australian Capital Territories) and Melbourne (Victoria) (fungimap.rbg.vic.gov.au, Heino Lepp personal communication); the species is also listed as growing in New South Wales (Young 1994).

In New Zealand Hooker’s expedition collected *A. phalloides* in 1841 (Hooker 1855), but the specimen was likely misidentified (Ridley 1991). Ridley (1991) provides a thorough description of the species. Currently the mushroom is restricted to the north of the North Island (Ridley 1991). In both Australia and New Zealand *A. phalloides* associates with exotic flora, for example *Quercus* (but see Ridley 1991).

Africa south of the Sahara

Amanita phalloides is frequently reported from southern Africa (see Walley and Rammeloo 1994 and references therein, also Ryvar den et al. 1994; van der Westhuizen and Eicker 1994; Hallen et al. 2002). In South Africa, the mushroom was reported “from pine woods near Stellenbosch” as early as 1913 (Marloth 1913) and later at a variety of sites including Cape Town, Stellenbosch and Harrismith (Doidge 1950). It is listed as “known throughout the region” in a modern field guide to the mushrooms of Southern Africa (van der Westhuizen and Eicker 1994, see also van der Westhuizen and Eicker 1987). Reid and Eicker (1991) provided a detailed description of *A. phalloides* and considered it as “an introduced species which is now widespread throughout South Africa in pine plantations and in association with exotic trees such as oak (*Quercus* spp.) and poplar (*Populus* sp.)”. Reid is a British mycologist who undoubtedly knows the species well. The mushroom is tentatively listed in a field guide to mushrooms of South Central Africa (Malawi, Zambia and Zimbabwe) (Ryvar den et al. 1994). In this guide, *A. phalloides* is described as rare and introduced, but the ITS DNA sequence data of at least one specimen from Zimbabwe held at San Francisco State University and tentatively named as *A. phalloides* is not *A. phalloides* (data not shown). Apparently *A. phalloides* closely resembles a choice edible of Zambia, *A. zambiana* or *tente* (Pearce 1970).

The fungus is reported as “prevalent throughout East Africa” (Walley and Rammeloo 1994). The British author Pegler (1977) described *A. phalloides* in Tanzania as “only in plantations” and “likely to represent an introduced species” (Pegler 1977). It has also been reported from plantations of exotic trees in Madagascar (P. Laurent, personal communication).

Discussion

A careful reading of the literature offers insights into the biogeography and invasion biology of *A. phalloides* in North America, but only when written descriptions can be confirmed (or refuted) as matches to the modern concept of *A. phalloides*. The history of the mushroom on the East Coast is illustrative: early reports of *A. phalloides* are explicitly rejected by mycologists at mid-century because in America in 1900 a variety of species were collected as *A. phalloides*; by 1950 only the European species was recognized as *A. phalloides*. The difference between early authors (Taylor 1897; McIlvaine and Macadam 1902; Murrill 1909; Murrill 1910; Murrill 1913) and later authors (Smith 1958; Tanghe and Simons 1973; Smith 1975) relates to a shifting species concept (Figure 1), and conflicts in the literature are resolved because unambiguous identifications can be made from historical and current descriptions. When Tanghe (1983) argues for the mushroom as a European immigrant he is convincing; Taylor (1897) did not collect the European *A. phalloides* but Tanghe and Simons (1973) did. The literature will not be as useful for species with a more limited suite of morphological characters, for example many *Cortinarius* or *Inocybe* species, or for morphological species possessing cryptic genetic species, perhaps including *A. muscaria* (Oda et al. 2004).

By 1977 the European *A. phalloides* was found on both coasts, however there is a stark contrast between the literature of the East Coast and the literature from the West Coast. Between Harkness and Moore (1880) and Ammirati et al. (1977) there is scant mention of *A. phalloides* in California, only a note by Smith (1958) of the mushroom as growing “rarely, in California”. The Harkness and Moore (1880) record provides

no description, and in fact the first full description of *A. phalloides* in California belongs to Ammirati et al. (1977). The species was not ignored; between 1911 and 1976 31 collections identified as “*A. phalloides*” were deposited at the University of California at Berkeley, San Francisco State University, and New York Botanical Garden Herbaria. Accessions may not be authentic (Pringle and Nguyen, unpublished data), but given the scant literature available it is not at all clear that *A. phalloides* was introduced to the West Coast of North America. In fact Ammirati et al. (1977) are careful to avoid naming the fungus as an introduction, the mushroom is described only as “a common species in California”. Arora (1986) is similarly cautious, writing of *A. phalloides* as “perhaps an adventitious (but hardly advantageous!) introduction from Europe...”. At this time *A. phalloides* is often assumed to be an introduced and invasive species (Saylor 1984a, b; personal observations), and in fact it is widely distributed on the coast and in the Sierra foothills (Figure 2). However, the hypothesis of *A. phalloides* as invasive to California remains conjecture and cannot be tested with the literature.

Although the literature does not establish *A. phalloides* as an introduction to the West Coast, it does prove *A. phalloides* to be an introduction to the East Coast. A key difference is the explicit refutation of the European *A. phalloides*’ presence on the East Coast; in contrast mycologists in California have collected mushrooms named as *A. phalloides* throughout the 20th Century and have never unambiguously rejected its presence on the West Coast.

The literature on *A. phalloides*’ biogeography outside of North America is scarce, often obscure, and contradictory, and in these aspects is not very different from the American literature. Sadly, poisonings have often alerted mycologists to the presence of *A. phalloides* (e.g. Herter 1934; Valenzuela et al. 1992; both of these publications carefully described the taxonomy and ecology of *A. phalloides* specimens after reports of mushroom poisonings). In some countries, and especially in Argentina, Australia, New Zealand and South Africa, the history and distribution of the mushroom are well understood. In a few cases conflicts between historic

and modern literature mimic the history of the species on the East Coast, for example Hooker's collection of *A. phalloides* in New Zealand in 1841 (Hooker 1855) and the current understanding of *A. phalloides* as an introduction (Ridley 1991). In contrast we have a very poor understanding of whether or not *A. phalloides* grows in Asia, how common or abundant it is in East Africa outside of Tanzania, and if it grows in West or Central Africa.

Authors on at least four continents have concluded that *A. phalloides* is an introduced species, but our limited knowledge of its current biogeography will impede an understanding of *A. phalloides*' future movements. The death cap mushroom has apparently been introduced to the East Coast of North America, several countries in South America, Australia and New Zealand, and South and East Africa, including Madagascar. But a modern collection of *A. phalloides* in a novel location, for example a collection made at the eastern edge of Russia or between Russia and China, could not be classified as an introduction – as we do not know the eastern limit of *A. phalloides* in Russia, or if *A. phalloides* grows in Asia – the collection might simply be the first record of *A. phalloides* from a previously unexplored parcel of its native range. The problem is not unique to *A. phalloides*, as with few exceptions the biogeography of EM species is poorly understood.

Introduced fungi that persist with introduced hosts are distinct from introduced fungi that associate with native flora, and it is fungi that disperse from plantations and establish in native habitats that may put endemics at risk. Although *A. phalloides* appears to associate exclusively with introduced flora in South America, Australia, New Zealand, and South Africa, reports of *A. phalloides* associating with *Eucalyptus* in Algeria and Tanzania (Malençon and Bertault 1970; Pegler 1977), and with *Leptospermum* and *Kunzea* in New Zealand (Ridley 1991) suggest that *A. phalloides* may have invasive potential. In California, where *A. phalloides* is assumed to be an introduction, the fungus is collected in undisturbed forests under the endemic *Quercus agrifolia*.

The world is changing. As humans continue to facilitate species' migrations across continents the biogeography of ectomycorrhizal fungi must

also be shifting, and yet the native ranges of most mushrooms are poorly known. It is literally our last chance to know the endemic habitats of a variety of species, even within Europe and North America. Basic research is needed (Simberloff et al. 2005), and for a few especially charismatic fungi, including *A. phalloides*, a careful reading of the literature may provide needed data.

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