CHAPTER ONE

LITERATURE REVIEW

ARMILLARIA (FR.:FR.) STAUDE: TAXONOMY, SPECIES CONCEPTS AND PHYLOGENETIC RELATIONSHIPS

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INTRODUCTION

Species of *Armillaria* (Fr.:Fr.) Staude (Basidiomycotina, Agaricales, Tricholomataceae) are best known as pathogens that cause the disease Armillaria root rot. These are widely distributed throughout the tropical, sub-tropical and temperate regions of the world (Hood *et al.* 1991). The impact of *Armillaria* spp. in these areas is intensified by their ability to survive as pathogens, saprobes or necrotrophs on a wide variety of woody plants (Gregory *et al.* 1991, Hood *et al.* 1991, Kile *et al.* 1991, Fox 2000).

Armillaria has had a confused and controversial taxonomic history. Much of this confusion arose from the historical use of a morphological species concept to delineate species. In many cases, the paucity of clear morphological discontinuities between isolates made it difficult for taxonomists to decide whether or not they should be classified as different species. *Armillaria mellea*, for example, was assumed to be a single, highly pleomorphic species, subsuming many isolates currently known to represent distinct species (Singer 1956). This controversy was largely resolved by the adoption of the biological species concept and the subsequent identification of various biological species in Europe, North America and Asia (Korhonen 1978, Anderson and Ullrich 1979, Ota *et al.* 1998b). Most of the biological species are now also equated with taxonomic species defined in terms of their basidiocarp morphology.

The study of *Armillaria* taxonomy is particularly important because of the relevance of Armillaria root rot to commercial forestry and agriculture. Analysis of the phylogenetic relationships among *Armillaria* spp. is also important for a number of reasons. First, knowledge of the evolutionary lineages of these species often yields valuable insights into their taxonomy. Phylogenetic analysis can also be used to determine whether or not species were introduced or are native to a region or continent. Finally, from a basic science perspective, understanding the evolutionary history of the genus is an important goal in itself.

The aim of this review is to provide an overview of the taxonomic history of *Armillaria*. In addition, species concepts that have been applied to *Armillaria* taxonomy are discussed and

current knowledge pertaining to the phylogenetic relationships among species in the genus is reviewed. Overall, the intention is to provide a foundation for studies that follow in this thesis.

TAXONOMIC HISTORY OF THE GENUS *ARMILLARIA*

The taxonomy of *Armillaria* has plagued many fungal taxonomists ever since its recognition as tribe within *Agaricus*. The taxonomic history of *Armillaria* dates back to the 1700's with reference to *Agaricus melleus* by Danish botanist Martin Vahl (Vahl 1787), now accepted as *Armillaria mellea* (Vahl.: Fr.) P. Kummer and the type species of the genus. In the following Century, Swedish mycologist Elias Fries first introduced *Armillaria*, in his *Systema Mycologicum*, by subdividing the genus *Agaricus* into various tribes (sub-genera) that included *Agaricus* tribus *Armillaria* (Fries 1821). At this stage Fries included twelve *Agaricus* species, one of them being *Ag. melleus*. Four years later Fries abandoned *Armillaria* and transferred the species to the tribe *Lepiota* (Fries 1825). However, in 1838 Fries again re-established the tribe *Armillaria* in *Agaricus* but sub-divided it into three groups: Tricholomata subannulatae, Clitocybae annulatae, and Collybiae annulatae; with 24 species in total (Fries 1838). In 1854 Fries again abandoned the tribe *Armillaria* (Fries 1854). Fries later re-established the tribe in 1874 and maintained the 1838 arrangement (despite the fact that several authors had raised *Armillaria* to genus level) but added six additional species (Fries 1874).

Three independent authors accepted Fries's tribe, *Armillaria*, at the generic level in the mid 1800's. Staude (1857) was first to raise the tribe to genus level but did not transfer the species epithets to *Armillaria;* instead, he maintained the name *Agaricus* for the four species that were included. Later in 1871, Kummer gave *Armillaria* genus status and included eight species with their species epithets transferred to *Armillaria* (Kummer 1871). Quélet (1872) was thought to be the authority for *Armillaria* and authors for many years cited *Armillaria* (Fr.) Quél as the generic name. Quélet's status as authority was, however, rejected based on the fact that Staude (1857) and Kummer (1871) preceded him (Singer 1951, Donk 1962).

The validity of *Armillaria* (Fr.:Fr.) Staude (Staude 1857) versus *Armillaria* Kummer (Kummer 1871) has caused much debate in the past. Singer (1951, 1955a,b, 1986) proposed Kummer as the legitimate authority by arguing that Staude was unaware of difference between tribe and genus, and that he did not intend to give *Armillaria* genus status, and did not make any

combinations in *Armillaria*. According to Singer (Singer 1955b), the wording of Kummer (1871) led to the establishment of a genus rather than just raising the Friesian tribe to generic status. Various authors rejected Singer's interpretation, arguing that Staude had met all the requirements for a valid description (Donk 1962, Watling *et al.* 1982, Volk and Burdsall 1995). *Armillaria* (Fr.:Fr.) Staude is, therefore, accepted as legitimate and *A. mellea* (Vahl.:Fr.) Kummer {= *Agaricus melleus* Vahl} serves as the type species for the genus (Watling *et al.* 1982).

The genus name *Armillariella* (Karst.) Karst. is frequently encountered in older taxonomic and plant pathology literature. Karsten introduced this name in 1879 when he erected *Armillaria* section *Armillariella* and later, in 1881, raised it to generic rank (Karsten 1879, Karsten 1881). Three Finnish species were included in this genus with *Arm. mellea* (Vahl:Fr.) Karst. {= *Ag. melleus* Vahl} assumed to be the type species (Karsten 1881, Donk 1962, Watling *et al.* 1982). *Agaricus melleus* Vahl (as *A. mellea* (Vahl.:Fr.) Kummer) is, however, widely accepted as the type species for *Armillaria* (Fr.:Fr.) Staude (Watling *et al.* 1982). The genus name *Armillariella* Karst. was, therefore, considered as an obligate synonym of *Armillaria* (Fr.:Fr.) Staude (Watling *et al.* 1991). However, according to Burdsall and Volk (1993) the genus name *Armillariella* can be ignored and replaced by the name *Armillaria*.

SPECIES CONCEPTS

A species concept represents an abstract idea regarding the variables that delimit species. From such an idea a set of operational criteria can be derived that enable investigators to categorise organisms. These criteria may include morphological similarity, ability to interbreed and reproduce, ecological adaptation, ancestry and descent relationships, or genetic cohesion (Rojas 1992). The application of such criteria to distinguish among species is complicated by the fact that organisms often differ on some of these dimensions but not in others (e.g. they display morphological discontinuity but no reproductive isolation). Decisions as to which criteria should be given preference are often a function of an investigator's philosophical predisposition. However, philosophical preferences must sometimes be set aside in view of the fact that some criteria are not applicable to all organisms (e.g. asexual organisms can not be differentiated based on their ability to interbreed). A single universal species concept can, therefore, not be uniformly imposed in taxonomy (Endler 1989, Davis 1996, Hull 1997).

Species concepts have been reviewed many times in the past (e.g. Mishler and Donoghue 1982, Luckow 1995, Mallet 1995, Hull 1997, Mayden 1997). In a review by Mayden (1997), 22 species concepts were listed from taxonomic literature. These concepts can be arranged in three broad classes: definitions that entail similarity between organisms (morphological and phenotypic); those that invoke evolutionary processes (biological species, evolutionary species, species mate recognition); and phylogenetic or lineage based concepts (Hull 1997; Perkins 2000). In the case of fungi, it has been suggested that species be defined based on a combination of at least one concept from each of the three main categories (phenotypic cohesiveness, reproductive isolation and common evolutionary descent) (Petersen and Hughes 1999).

Species concepts most eminent in fungal systematic literature are the morphological species concept, biological species concept and phylogenetic (diagnostic and genealogical) species concept. These concepts have contributed significantly to the current understanding of fungal diversity and resulted in the discovery of many previously undetected species. The conceptual basis, operational criteria and limitations of these concepts and their relation to general fungal taxonomy were extensively discussed in several recent reviews (Harrington and Rizzo 1999, Petersen and Hughes 1999, Taylor *et al.* 2000). In the current review, a broad theoretical background is presented of these species concepts with regard to holobasidiomycetes, after which the focus is narrowed to their history and use in *Armillaria* taxonomy.

The Morphological Species Concept

Until the middle 20th century, the morphological species concept was the basis for fungal classification (Brasier 1997). Various definitions of a morphological species were proposed (e.g. Du Rietz 1930, Simpson 1943). One of these defines a species as "... a community, or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name." (Regan 1926). Thus, from a strictly morphological point of view, a species in basidiomycetes is a group of organisms congruent in the characteristics of their basidiocarp macro- and micro-morphology.

The application of basidiocarp morphology in species recognition presents various limitations. These are, however, resolved to some extent by employing additional phenotypic characters such

as vegetative mat characteristics, growth rate at different temperatures, secondary metabolite production, isozymes and immunology (Pantidou *et al.* 1983, Bruns *et al.* 1991, Kohn 1992, Guarro *et al.* 1999, Harrington and Rizzo 1999). Species are then defined as groups of organisms with a cluster of phenotypic characters more similar within groups than between groups (Sneath 1976). When overall phenotypic similarity is the primary criterion for defining species, without taking lineage with common descent into account, the concept is phenetic (Sneath 1976, Mayden 1997). The phenetic species concept is, however, considered to be synonymous with the morphological species concept (Mayden 1997).

The majority of fungal species are diagnosed by means of their morphological or phenotypic characters (Taylor *et al.* 2000). Currently, the morphological species concept also forms the basis for new fungal descriptions, as is required by the International Code of Botanical Nomenclature (St. Louis Code)[1]. The utility of the morphological species concept can partially be attributed to its long history and wide use. The fact that so many taxa have already been described in terms of their morphological characteristics allows for comparisons to be drawn between existing taxa as well as between new and existing and/ or described taxa (Taylor *et al.* 2000). However, taxa showing clear evidence of evolutionary divergence (e.g. having lost the ability to interbreed) are often morphologically indistinguishable (Taylor *et al.* 2000). Consequently these taxa, although potentially differentiated in terms of criteria derived from other species concepts, are regarded as conspecific from the perspective of the morphological species concept.

MORPHOLOGICAL SPECIES CONCEPT IN *ARMILLARIA*

The morphological species concept has dominated *Armillaria* taxonomy since the recognition of species within the tribe, and later genus, by Fries (1821). Using the criteria set by this concept, any agaric with white spores, annulus and broadly attached gills were regarded as a species of *Armillaria* (Volk and Burdsall 1995). The acceptance of *A. mellea* Vahl: Fr. as type of the genus (Watling *et al.* 1982), however, narrowed *Armillaria* spp. to agarics with white spores, decurrent to adnate gills and diploid vegetative mycelium, that are wood inhabiting (parasitic or saprophytic) and produce black to reddish-brown rhizomorphs either in the field or in culture

[1] http://www.bgbm.fu-berlin.de/iapt/nomenclature/code/SaintLouis/0000St.Luistitle.htm

(Watling *et al.* 1991, Volk and Burdsall 1995). Adhering to this circumscription has meant that most of the species previously included in the genus have now been transferred to other genera (Volk and Burdsall 1995). Presently the genus includes at least 36 morphological species (Volk and Burdsall 1995) (Table 1), some which are depicted in Fig. 1.

Recognition of morphological species

Recognition of *Armillaria* spp. by means of basidiocarps requires analyses of qualitative and quantitative characteristics of both their macro- and micro-morphology. Although a large variety of characters are available from these structures, many of them are not useful for species recognition due their low interspecific variation. Morphological characters found to be important in species delineation include ornamentation and structure of the stipe and pileus, annulus characteristics, location of pigments, basidiospore size and ornamentation and presence or absence of clamp connections (Bérubé and Dessureault 1988, Watling *et al.* 1991). Data pertaining to the basidiocarp morphology for species currently accepted in *Armillaria* are given in Table 2.

Practical and theoretical limitations of the morphological species concept

As is the general case with basidiomycete taxonomy, the recognition of *Armillaria* spp. based on basidiocarp morphology is beset with practical and theoretical limitations. Some of these limitations are outlined below:

- Basidiocarps of *Armillaria* spp. are ephemeral and produced at irregular intervals (Fox *et al.* 1994); consequently they are not readily available during surveys.
- Qualitative and quantitative characteristics are not always linked to the genetic attributes of a specimen but may be influenced by environmental factors, for example the dimensions and colour of the basidiocarps of *A. luteobubalina* that vary depending on the meteorological conditions (Kile and Watling 1981). In some cases, such environmentally determined phenotypic variation may result from the genetic or physiological block of a single enzyme (Petersen 1977).
- Morphological and genetic changes are sometimes not symmetrically linked. Small changes in the genome may lead to enormous changes in morphology; conversely large

genomic changes may yield small morphological changes (Mishler 1985). Some species, for example *A. ostoyae* and *A. gemina*, produce basidiocarps with identical morphology (Bérubé and Dessureault 1989). Speciation may, therefore, have occurred, but with little or no selection pressure for morphological change; consequently pleisomorphic morphological or phenotypic characters may be retained in sibling or cryptic species (Miller *et al.* 1994, Mayden 1997, Taylor *et al.* 1999).

- Convergent or parallel evolution may result in species with similar morphology but without sharing a common ancestor (Brasier 1997, Petersen and Hughes 1999).

In view of these problems, a large repertoire of methods has been developed to delineate *Armillaria* spp., either in combination with or as an alternative to basidiocarp morphology (Table 3).

The Biological Species Concept

The primary tenet of the biological species concept is reproductive isolation between groups of organisms (Mayr 1942, Dobzhansky 1970). Species are defined "as groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1942). In this concept, phenotypical and ecological differences are subordinated to interbreeding. Consequently if two populations are interfertile, which implies that they share the same gene pool, they are regarded as representing the same biological species, irrespective of variation in other characteristics (Petersen and Hughes 1999).

Evidence for intersterility groups (biological species) is provided by sexual compatibility between isolates using mating tests. Intersterility is governed by genetic factors that have an epistatic effect to the sexual incompatibility genes between different species (Chase and Ullrich 1990a, b). Thus, intersterility factors provide a mechanism for restricting gene-flow between species by overriding the effect of mating compatibility (Chase and Ullrich 1990a). Consequently isolates from different intersterility groups will not mate, even though they belong to different sexual compatibility groups. Sexual compatibility and intersterility are expressed by clearly identifiable phenotypic attributes (dikaryon formation or diploidization), which renders mating studies an effective means to determine intersterility groups.

Application of the biological species concept in homobasidiomycete taxonomy has proven to be most enlightening, in many cases revealing taxa previously considered to be a single species or representing complexes of species (Clémençon 1977, Vilgalys and Miller 1983, Fries 1984, Hallenberg 1985, Stenlid and Karlsson 1991, Vilgalys 1991, Hallenberg *et al.* 1994, Petersen 1995, Gordon and Petersen 1997, Aanen and Kuyper 1999, Miller and Methven 2000). The biological species concept has also been extensively applied to basidiomycete taxonomy, where its success is attributed to the various characteristics of these fungi that make mating studies relatively easy to conduct (Boidin 1986). Traits considered to be most eminent are their strong outbreeding mating systems and development of absolute intrinsic sterility barriers that often accompany speciation (Petersen and Hughes 1999). By virtue of these properties, holobasidiomycetes are amenable to the biological species definition and interfertility tests have become standard practice in delineating species of these fungi.

BIOLOGICAL SPECIES CONCEPT IN *ARMILLARIA*

The Biological Species Concept was introduced in *Armillaria* taxonomy only during the late 1970's with mating studies among putative isolates of *A. mellea* (*sensu lato*) (Hintikka 1973, Korhonen 1978, Ullrich and Anderson 1978). This species had been viewed in earlier literature as a single taxon with highly variable basidiocarp morphology, rhizomorph production and morphology, pathogenicity, a broad host range and world-wide distribution (Singer 1956, Gibson 1961, Raabe 1966, 1972). Mating tests and, therefore, species delineation based on the biological species concept were, however, possible only after the sexual system of *A. mellea sensu lato* had been elucidated.

Early researchers observed that mycelia from monospore cultures, basidiocarp tissue and vegetative material of *A. mellea* have single nuclei in their hyphal tips and lack clamp connections (Kniep 1911, Motta 1969, Korhonen and Hintikka 1974). In contrast, higher homobasidiomycetes generate dikaryotic vegetative mycelia after anastomosis between sexually compatible monokaryotic hyphae, and clamp connections are observed that retain the dikaryon. These unique features of *A. mellea* have influenced its taxonomy in two ways: 1) The presence of a single nucleus and absence of clamp connections led researchers to consider the sexual system of *A. mellea* (*sensu lato*) as homothallic, asexual or homomictic (Kniep 1911, Burnett 1956, Raper 1966). 2) In mating studies with other basidiomycetes, the formation of clamp

connections is used instead of fruiting as criterion for sexual compatibility between strains. The absence of clamp connections in *A. mellea* precludes the use of this criterion. It is probably because of these two factors that mating tests were not used in *Armillaria* until the work of Hintikka (1973) was published. This is despite the fact that they had been employed in various other basidiomycetes e.g. *Fomes pinicola* (Mounce and MacRae 1938) and *Auricularia auricula* (Duncan and MacDonald 1967) for many years.

Hintikka (1973) observed that monospore cultures made from a single basidiocarp of *A. mellea* had profuse white aerial mycelia. In contrast, cultures made from rhizomorphs, mycelial fans on wood and basidiocarps were crustose and dark brown with aerial mycelia usually lacking. In crosses made between the monospore isolates the culture morphology was transformed to those of the vegetative cultures in accordance with a tetrapolar (bifactorial) mating system. Hintikka (1973) also suggested that, because a single nucleus is present in monospore isolates, the single nucleus in the vegetative mycelium of *A. mellea* should be diploid. These observations were later confirmed (Ullrich and Anderson 1978, Anderson and Ullrich 1982) and paved the way for the use of mating tests in *A. mellea sensu lato*.

Mating tests were first conducted among isolates of *A. mellea* from Europe by Korhonen (1978) and North America by Ullrich and Anderson (1978) and later Anderson and Ullrich (1979). Results of these tests revealed the presence of five intersterility groups in the *A. mellea* complex in Europe (Korhonen 1978) and ten groups in North America (Anderson and Ullrich 1979). Both research groups concluded that reproductive isolation between the sympatric intersterility groups was complete. This characteristic meets the criteria of the biological species concept (Mayr 1942) and the intersterility groups in Europe and North America were, therefore, equated with biological species (Korhonen 1978, Anderson and Ullrich 1979).

The discovery of biological species within the *A. mellea* complex resulted in its extensive use in *Armillaria* taxonomy. Consequently, at least 31 biological species are currently known from different parts of the world, many of which correspond to morphological species (Table 4). Seven biological species occur in Europe, all equated with morphological species (Korhonen 1978, Guillaumin *et al.* 1985, Roll Hansen 1985, Termorshuizen and Arnolds 1987, Zolciak *et al.* 1997). In North America, ten biological species have been found, of which only one (NABS X) is not described in terms of basidiocarp morphology (Anderson and Ullrich 1979, Anderson 1982, Anderson 1986, Morrison *et al.* 1985a, Motta and Korhonen 1986, Bérubé and Dessureault

1988, Bérubé and Dessureault 1989, Volk *et al.* 1996). At least ten biological species occur in Asia, with all but one (NAG E) linked to morphological species (Terashita and Chuman 1989, Cha and Igarashi 1994, 1995b, 1996, Cha *et al.* 1994, 1995, Mohammed *et al.* 1994a, Ota *et al.* 1998b). Australasian isolates representing the morphological species *A. hinnulea, A. luteobubalina, A. limonea, A. novae-zealandiae* and *A. pallidula* are intersterile and these species consequently also represent different biological species (Kile and Watling 1988). Only four biological species have been reported from Africa, of which two represent morphological species (Mohammed and Guillaumin 1993, Mohammed *et al.* 1994b, Abomo-Ndongo and Guillaumin 1997).

Recognition of biological species

Identification of biological species in *Armillaria* is based on either sexual or interspecific somatic incompatibility tests depending on the sexual system of isolates being studied. Most species have a heterothallic bifactorial (tetrapolar) mating system (Korhonen 1978, Ullrich and Anderson 1978, Kile and Watling 1988); it is therefore possible to employ sexual compatibility tests for routine use in species recognition (e.g. Proffer *et al.* 1987, Dumas 1988, Blodgett and Worrall 1992, Harrington and Rizzo 1993). Homothallic sexual systems have, however, been reported for a few species including *A. ectypa, A. heimii, A. mellea* (from Africa) and *A. mellea* subsp. *nipponica* (Cha and Igarashi 1995b, Abomo *et al.* 1997, Zolciak *et al.* 1997). These species produce diploid mycelium from their basidiospores (Fig. 2), which render them unsuitable for mating tests. It was, therefore, suggested that interspecific somatic incompatibility tests be conducted as a means to delineate biological species (Abomo- Ndongo and Guillaumin 1997). In both tests, pre-zygotic reproductive isolation mechanisms allow for a visual evaluation based on the culture morphology (Brasier 1987).

Identification of biological species in *Armillaria* with a heterothallic bifactorial (tetrapolar) mating system (Fig. 2) is usually based on the haploid-haploid sexual compatibility interaction between reference and unknown strains. Sexual compatibility between strains belonging to the same species is dependent on allelic differences at two unlinked mating type loci (e.g. *A* and *B*). Crosses between such isolates may, therefore, display one of the following interactions (Korhonen 1978):

1) Compatible ($A \neq B \neq$) for example (A_1B_1 x A_2B_2): Border between the mating mycelia disappears. Anastomosis takes place, cells become heterokaryotic followed by diploidization. The culture morphology is transformed from the haploid (white, cottony) to the diploid (crustose, brown) type (Fig. 3). This reaction is taken as evidence for conspecificity between the reference strain and the unknown isolate.
2) Incompatible ($A=$, $B=$) for example (A_1B_1 x A_1B_1): The haploid culture morphology is maintained and mycelia grow side by side.
3) Hemicompatible common A ($A=$, $B \neq$) for example (A_1B_1 x A_1B_2): A barrage zone between the confronting mycelia is observed; some of the submerged hyphae have partially disintegrated septa.
4) Hemicompatible common B ($A \neq B=$) for example (A_1B_1 x A_2B_1): Similar to incompatible interaction.

Strains belonging to different biological species display the same interaction as incompatible strains of the same species. Thus, while compatible interactions generally provide conclusive evidence of conspecificity, the converse conclusion cannot be drawn from incompatible interactions. This raises the possibility that conspecific sympatric species might erroneously be regarded as different species due their shared alleles at the mating type loci.

Diploid-haploid mating tests are useful for species identification when monospore (haploid) cultures are not available for the unknown isolates (Korhonen 1978, Anderson and Ullrich 1982). These tests are functionally equivalent to the "Buller phenomenon" where a compatible dikaryotic mycelium donates nuclei to the monokaryotic counterpart during mating (Raper 1966, Anderson and Ullrich 1982). In a compatible mating between heterothallic *Armillaria* isolates the diploid nuclei are transferred to the haploid isolate and subsequently displace the haploid nuclei (Rizzo and Harrington 1992, Rizzo and May 1994, Carvalho *et al.* 1995) or occasionally recombine with the haploid nuclei (Guillaumin *et al.* 1991, Carvalho *et al.* 1995). A compatible mating interaction in this test is judged by the transformation of the haploid culture morphology to that of the diploid culture (Korhonen 1978). Although diploid-haploid mating tests are regularly used for species identification (e.g. Gregory 1989, Mohammed *et al.* 1994a, Tsopelas 1999), diploidization is slow (Korhonen 1978, 1983) and results are often ambiguous (Siepmann 1985, Shaw and Loopstra 1988).

An alternative to diploid-haploid pairings in sexual compatibility tests is to induce somatic segregation of diploids with the use of Benomyl (Anderson 1983, Anderson and Yacoob 1984).

The artificial haploids are then used in a similar fashion to haploid-haploid tests. This method has been used in some studies (e.g. Proffer *et al.* 1987, Mwangi *et al.* 1989) but its success is not guaranteed (Holdenrieder 1986).

Species recognition based on interspecific somatic incompatibility tests employs diploid-diploid crosses between reference and unknown isolates of *Armillaria*. This method should, however, not be confused with intraspecific somatic incompatibility tests that use crosses between diploid isolates of the same species to distinguish between genotypes in population studies (Korhonen 1978, Kile 1983, Harrington *et al.* 1992). In intraspecific somatic compatibility tests, isolates of different genomic entities produce a demarcation line of faint hyaline mycelium at the confrontation point (Korhonen 1978). Interspecific somatic incompatibility between isolates, on the other hand, is determined by the formation of a black pigmented demarcation line between the confronting mycelia of different biological species (Mallett and Hiratsuka 1986, Mallett *et al.* 1989). This black demarcation line is often not clear and may be enhanced with L-DOPA (L-β-3,4-dihydroxyphenylalanine) (Hopkin *et al.* 1989). Isolates that do not produce the demarcation line are regarded as conspecific.

Practical and theoretical limitations of the biological species concept

The biological species concept is mechanistic in the sense that species are conceived as participants in an evolutionary process and not the end-points of evolution (Luckow 1995). The mechanistic paradigm, of which the biological species concept is a representative, is hampered by theoretical flaws that are related to its dependence on the biology of a particular organism under investigation and dependence on observation of process rather than pattern (Luckow 1995). Its major theoretical shortcoming, however, is its *a priori* decision to focus on a specific causal agent of speciation with disregard for the potential contribution of other factors (Donoghue 1985, Luckow 1995). It ignores the fact that reproductive isolation is but a single node in a complex web of interrelated processes, many of which may be regarded as both the cause and the product of speciation (Cracraft 1989, Endler 1989, Turelli *et al.* 2001). In view of these problems many systematists have rejected the biological species concept (Donoghue 1985, Cracraft 1989, 1997).

Practical problems with the biological species concept arise when sympatrically defined biological species are considered in allopatric terms. The European species, *A. cepistipes* (= *A. bulbosa*, EBS B), is reproductively isolated from its European counterparts (Korhonen 1978). This species is fully interfertile with the North American NABS XI and is, therefore, conspecific with it (Morrison *et al.* 1985a, Banik and Burdsall 1998). It is, however, also partially interfertile with two North American biological species, *A. sinapina* (NABS V) and NABS X (Anderson *et al.* 1980, Anderson 1986, Bérubé *et al.* 1996). The reproductive barriers between these allopatric intersterility groups are, therefore, not complete. Partial interfertility between these intersterility groups may be associated with recent speciation or with taxa in the process of speciation through geographic isolation, host specialisation or adaptation to changing environmental conditions without development of genetic isolation mechanisms (Boidin 1986). The ability to interbreed could, therefore, be ascribed to a retained ancestral trait (plesiomorphy) (Rosen 1978, 1979, Bremer and Wanntorp 1979, Donoghue 1985, Davis 1997). The occurrence of such reactions during mating tests poses a serious problem in assigning anonymous isolates unequivocally to a biological species.

It is possible that species might remain fully interfertile despite their being morphologically, ecologically or phylogenetically distinct e.g. *Auricularia* (Duncan and MacDonald 1967, Duncan 1972) and *Lentinula* (Hibbett *et al.* 1995, Petersen 1995). Intersterility is governed by relatively simple genetic determinants (Hallenberg 1988, Chase and Ullrich 1990a, b, Hallenberg and Larsson 1992) and are not necessarily linked to morphological, phenotypic, genetic and ecological traits (Petersen and Bermudes 1992). Divergence in these traits may, therefore, precede the emergence of reproductive barriers. The genetic basis for intersterility between biological species is, however, not well understood in most basidiomycetes, including *Armillaria*.

A further practical problem is the fact that the relational nature of biological species in terms of diagnosable characters makes it difficult to assign anonymous isolates to species, without the aid of a battery of tester isolates. Live mating monokaryotic/ haploid reference strains representing a biological species must, therefore, be readily available from culture collections. Currently testers for the North American Biological Species (NABS) are available from the American Type Culture Collection (Anderson 1986). However, mating tests yield better results with fresh strains and some haploid strains may become dark and crustose with age and are, therefore, not suitable for mating tests (Harrington *et al.* 1992). An additional problem posed by the relational nature

of the biological species concept is the fact that some species (e.g. *A. gallica*, *A. cepistipes* and *A. calvescens*) produce rather crustose haploid cultures whereas other species (e.g. *A. mellea*) may generate cottonous diploid mycelium that complicates interpretation of mating tests (Guillaumin *et al.* 1991, Harrington *et al.* 1992).

In addition to the problems outlined above, concern exists about the ability of mating tests to provide evidence of true interfertility (i.e. the ability to produce viable monokaryotic progeny) since mating is only the first step towards reproduction (Mueller and Gardes 1991, Harrington and Rizzo 1999). However, stable dikaryon formation between two monokaryotic hyphae and subsequent repetitive coupled nuclear division are considered to indicate close genetic relationships (Boidin 1986). The recognition of species is also complicated by the fact that intersterility barriers between populations might not always be an indication of species boundaries, but in some cases may be regarded as a species' propagation strategy, in particular when genetic differences between intersterility groups are small (Hallenberg and Larsson 1992, Hallenberg *et al.* 1994, 1996).

Phylogenetic Species Concepts

Phylogenetic species concepts represent a diverse set of species concepts, all of which have their historical roots in Hennig's (Hennig 1966) phylogenetic systematics and later work by Rosen (Rosen 1978, 1979). Phylogenetic systematics defines the boundary between species as the interface between reticulated (tokogenetically related) and hierarchic (phylogenetically) descendent systems (Fig. 4) (Hennig 1966). From this perspective, the main focus of a phylogenetic species concept should be to recognize the boundary between the two systems. This is accomplished by determining the hierarchical ancestry and descendent structures among organisms and then interpreting and incorporating these structures in terms of a classification system (Davis 1996, 1999).

Phylogenetic species concepts comprise at least four different versions. These include the diagnostic species concept (Eldredge and Cracraft 1980, Nelson and Platnick 1981, Cracraft 1983, Nixon and Wheeler 1990, Wheeler 1990), monophyletic (autapomorphic) species concept (Donoghue 1985, Mishler and Donoghue 1982, Mishler and Brandon 1987, de Queiroz and Donoghue 1988, 1990a), a combination of the first two concepts (McKitrick and Zink 1988), and

the genealogical concordance species concept (also known as the genealogical species concept) (Baum and Donoghue 1995, Baum and Shaw 1995). Concepts within the body of the phylogenetic species concept differ significantly in their assumptions, criteria used for species diagnoses and adherence to the Hennigian phylogenetic systematic principles.

Phylogenetic species concepts such as the diagnostic and genealogical concordance species concepts view species as biological entities at the end point of evolution and are, therefore, considered historical species concepts (Luckow 1995). History based concepts are "theory neutral" in terms of evolutionary process; what matters is pattern, not process. Species recognition is therefore solely based on character evidence of ancestry. Other versions such as the monophyletic species concept employ a combination of historical and mechanistic approaches (Luckow 1995). These concepts give primacy to monophyly (an historical attribute) as grouping criterion and then rank taxa based on a speciation mechanism (e.g. reproductive isolation) believed to give rise to and maintaining the lineage (Donoghue 1985, Mishler and Donoghue 1982, Mishler and Brandon 1987).

A major source of conflict between advocates of different phylogenetic species concepts is their disagreement on the conceptualisation of monophyly (see Davis 1999 for an in depth discussion on this issue). Hennig (1966) defined monophyletic groups as "... a group of species descended from a single ('stem') species, and which includes all species descended from this species." Hennig (1966) also gave a second definition that states that "A monophyletic group is a group of species in which every species is more closely related to every other species than to any species that is classified outside this group." Monophyly in Hennigian terms is thus applicable at the phylogenetic level and refers to a specific relationship between at least two species. Some authors have, however, extended monophyly to the level of individual organisms (Donoghue 1985, Baum 1992) or populations (Mishler 1985, de Queiroz and Donoghue 1988).

Phylogenetic species concepts most prominent in contemporary systematic literature include the diagnostic species concept and the genealogical concordance species concept (Baum 1992, Davis 1996). These concepts have been the subject of numerous discussions and critical comparisons in the past (e.g. Baum and Donoghue 1995, Luckow 1995, Davis 1996, 1997). Application and limitations of these concepts in fungal taxonomy were discussed in depth and advocated with examples from various genera in recent reviews by Harrington and Rizzo (1999) and Taylor *et al.* (2000). These concepts have not received, however, much attention in *Armillaria* taxonomy.

The current review will therefore be limited to a broad overview of the general principles underlying these two types of phylogenetic species concepts.

DIAGNOSTIC SPECIES CONCEPT

The diagnostic species concept (*sensu* Hull 1997) was developed and promoted by authors that include Eldredge and Cracraft (1980), Nelson and Platnick (1981), Cracraft (1983), Nixon and Wheeler (1990), Wheeler and Nixon (1990), Davis and Nixon (1992). In terms of this concept, a species is "the smallest aggregation of populations (sexual) and lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon and Wheeler 1990). A phylogenetic species, within this context, is thus a group of organisms among which there is a reticulated ancestry and descent structure (tokogenetic relationship) and forms the basal diagnosable element among the hierarchy (phylogenetic relationship) of taxa within a classification system.

The diagnostic species concept is consistent with Hennig's (Hennig 1966) view that a single species is not monophyletic; a species can only be monophyletic with another species (Luckow 1995, Davis 1999). As mentioned above, species in this concept are minimal basal phylogenetic elements with reticulated structure within the species. If they were to be monophyletic, this would imply that phylogenetic structure (hierarchic) exist within a species. Consequently, monophyly in terms of this species concept is not applicable for delimiting species. Key to the diagnostic species concept is constant characters or character states as evidence for divergence between species and phylogenetic pattern (Davis and Nixon 1992).

Recognition of diagnostic species

Proponents of the diagnostic species concept see species as the result of speciation; pattern and not process is of importance in this concept (Cracraft 1983). Pattern reflects common ancestry and evolutionary history and is observed by assessing the inherited attributes of organisms. Inherited attributes are considered to represent either traits or characters (Nixon and Wheeler 1990, Davis and Nixon 1992). Traits are properties that are not fixed in a population and are, therefore, not present in all comparative individuals (semaphoronts) among a terminal lineage.

Traits do not reliably reflect historical relationships among organisms (Davis and Nixon 1992). Characters, in contrast, are fixed properties within a population and are therefore present in all comparative individuals in a terminal lineage. Fixed characters provide evidence for hierarchic descent (Davis and Nixon 1992). These characters need not be monomorphic but can represent the original or transformed states of a character (Davis and Nixon 1992). The nature of characters is not taken into account and can be any unique combination of derived (apomorphic) or primitive (pleisomorphic) characters. Characters are obtained from any of the comparable intrinsic attributes of organisms (Cracraft 1983, 1989, Harrington and Rizzo 1999).

One method for discovering diagnostic species is through "population aggregation analysis" (Davis and Nixon 1992). This method distinguishes traits from attributes by means of pattern variation analyses within local populations. Populations with fixed characters are then aggregated and assigned to a diagnostic species. Davis and Nixon (1992) indicated several sources of error that include incorrect homology assessment, undersampling of attributes, individuals or populations, incorrect delimitation of populations and parallel fixation. Most of these can, however, be avoided through rigorous study of characters and populations (Harrington and Rizzo 1999).

Genealogical Concordance Species Concept

The genealogical concordance species concept (GCSC) was derived from the monophyletic species concept (Mishler and Donoghue 1982, Donoghue 1985, de Queiroz and Donoghue 1988, 1990a) that gives primacy to shared historical relationships between organisms as the attribute that unites them in a species. The GCSC was first proposed by Avise and Ball (1990) and further developed and promoted as the genealogical species concept by Baum and Shaw (1995). This concept defines species as "basal, exclusive groups of organisms" (Baum and Shaw 1995)

The GCSC adopted a variation of the second definition of monophyly provided by Hennig (Davis 1999). Baum and Shaw (1995) follow earlier views (Donoghue 1985, de Queiroz and Donoghue 1988) extending the concept of monophyly to a level that relates to relationships between individual organisms and not only between species. Monophyly at this level is equated with the term exclusivity (de Queiroz and Donoghue 1990b) where "an exclusive group is one whose members are more closely related to each other than they are to any organism outside the

group" (Baum and Donoghue 1995). Davis (1999), however, pointed out that that the term "exclusivity" in the context of the GCSC refers to a group of organisms whose members have gene copies that are more closely related to each other than to any gene copies of organisms outside the group.

Exclusive genealogical relationships are determined by means of coalescence patterns of gene genealogies of individual organisms from different populations (Baum and Shaw 1995). This approach stems from ideas adopted from "coalescence theory" whereby the transmission pathway of gene lineages is traced back in time to the point where they coalesce with their most recent common ancestor (MRCA) (Hudson 1990, Maddison 1995). In the GCSC, individuals with gene lineages that coalesce to a single lineage, the MRCA of the genealogy, constitute an exclusive genealogical relationship (Baum and Shaw 1995). In the light of coalescence theory, Baum and Donoghue (1995) have redefined genealogical species as "a basal group of organisms all of whose genes coalesce more recently with each other than with those outside the group."

Recognition of genealogical species

The GCSC invokes phylogenetic analysis of gene sequence data to construct gene trees representing the gene genealogy of organisms. Gene sequences are obtained from individuals sampled from different populations and often only portions of the genes are used. Genes, or gene regions, to be employed in phylogenetic analyses are not specified but a prerequisite is that they should not be recombining within the species (Baum and Shaw 1995).

Gene trees generated from single loci and species trees often do not correspond in their topological patterns. Reasons for this phenomenon include ancient divergence among gene lineages in contrast to a more recent divergence among species, use of paralogous genomic regions, and recombination through horizontal transfer or hybridisation between species (Hudson 1983, 1992, Nei 1987, Takahata 1989, Wu 1991, Doyle 1992, Maddison 1995, 1997, Brower *et al.* 1996). It is, therefore, suggested that genealogical concordance among multiple loci from the same set of individuals be used to delimit species (Baum and Donoghue 1995, Baum and Shaw 1995). Species limits in this approach are determined at the point of transition from incongruity to congruence in a consensus gene tree (Taylor *et al.* 2000) (Fig. 5). Alternatively, multi-loci

sequence data are combined and the point of transition determined at the branching node in the combined gene tree with high statistical support (Kroken and Taylor 2001).

PHYLOGENETIC RELATIONSHIPS AMONG *ARMILLARIA* SPP.

The phylogenetic relationships among the Northern Hemisphere *Armillaria* spp. have received much attention and are consequently well resolved. Collectively, a number of studies suggest that the Northern Hemisphere species reside in at least five major clusters. Based on overall similarity and differences among taxa in terms of morphological and ecological characteristics, Korhonen (1995) identified these as the *A. ostoyae*, *A. gallica*, *A. mellea*, *A. ectypa* and *A. tabescens* clusters (in this review the *A. ectypa* and *A. tabescens* clusters will be referred to as the "exannulated cluster"). Assessing the relationships between taxa within these clusters is, however, complicated by the fact that many researchers have concentrated only on those species that are of specific interest to them. In contrast to the Northern Hemisphere species, the phylogenetic relationships among the Southern Hemisphere species have not received much attention and virtually nothing is known about them in this regard. One of the reliable conclusions that can be drawn, however, is that the Southern Hemisphere species can be sorted into two clusters: an African cluster and an Australasian cluster. The four Northern Hemisphere and two Southern Hemisphere clusters are discussed in turn below.

The "*Armillaria ostoyae* cluster"

The "*Armillaria ostoyae* cluster" (Fig. 6) includes three species: *A. ostoyae*, *A. gemina* and *A. borealis*. These species are morphologically related by their thick annulus, more or less equal shape of the stipe and distinct dark scales (Gregory and Watling 1985, Bérubé and Dessureault 1989, Korhonen 1995). Phylogenetically these species are more closely related to one another than to other Northern Hemisphere *Armillaria* spp. (Anderson *et al.* 1989, Anderson and Stasovski 1992).

The three species in this cluster are distinct in their ITS and IGS-1 sequence data (Anderson and Stasovski 1992, Chillali *et al.* 1998a) and were separated into three respective rDNA classes based on their rDNA RFLP profiles (Anderson *et al.* 1989). Furthermore, they show variation in

terms of their geographic distribution: *A. borealis* is confined to Europe, *A. gemina* to North America and *A. ostoyae* is transcontinentally distributed between Europe, Japan and North America (Kile *et al.* 1994, Ota *et al.* 1998a). Some authors have therefore suggested that *A. ostoyae* is ancestral to *A. gemina* by virtue of its broader distribution (Miller *et al.* 1994, Piercey-Normore *et al.* 1998) and it is for the same reason probably ancestral to *A. borealis*.

The "*Armillaria gallica* cluster"

The "*Armillaria gallica* cluster" (Fig. 6) represents the largest group of Northern Hemisphere species and includes *A. calvescens*, *A. cepistipes*, *A. gallica*, *A. jezoensis*, *A. nabsnona*, *A. sinapina*, *A singula* and NABS X. Morphologically these species, with the exception of NABS X for which the basidiocarp morphology is not known, are related by virtue of their thin delicate annulus and more bulbous or clavate stipes (Korhonen 1995). A combination of various phylogenetic studies based on ITS (Chillali *et al.* 1998b), IGS-1 (Anderson and Stasovski 1992, Terashima *et al.* 1998a), DNA-DNA hybridisation (Miller *et al.* 1994) and amplification of sequences with arbitrary primer pairs (SWAPP) (Piercey-Normore *et al.* 1998) supported their grouping and the conclusion that they share a common ancestor. The relationships between the species within this cluster are, however, not well resolved.

Analysis of rDNA operon sequence data revealed that the European and North American biological species in this cluster are separated into two rDNA classes (Anderson *et al.* 1989). The one rDNA class included *A. gallica, A. cepistipes* and *A. calvescens,* based on their shared 0.4 Kbp (Kilobase pair) insertion at 5' end of rDNA operon, while the second class included *A. sinapina*, *A. nabsnona* and NABS X (Anderson *et al.* 1989). Subsequent DNA-DNA hybridisation and IGS-1 sequence analyses, however, could not resolve the relationships between taxa within the two classes and therefore did not support their dichotomy (Anderson and Stasovski 1992, Miller *et al.* 1994). Recently, Piercey-Normore *et al.* (1998) showed that the morphologically similar species *A. gallica* and *A. calvescens* are more closely related to each other than to the other species in this cluster. It was also suggested that *A. gallica* might be the ancestor to *A. calvescens* based on the broad distribution of the former species in Europe, North America and Japan in contrast to that of the latter species, which is restricted to North America. The two Asian species, *A. singula* and *A. jezoensis*, are closely related and form a monophyletic group with *A. sinapina* and *A. cepistipes* isolates from Japan (Terashima *et al.* 1998a).

The "*Armillaria mellea* cluster"

Armillaria mellea is the only member of this cluster and is distinct from the rest of the annulated Northern Hemisphere *Armillaria* spp. based on morphological and molecular characteristics. Representatives of this species cluster are characterised by the complete lack of clamp connections at the base of their basidia, prominent annulus, honey coloured caps and robust appearance of their basidiocarps (Motta and Korhonen 1986, Bérubé and Dessureault 1989). At the molecular level, this species is differentiated from other *Armillaria* spp. by a shorter IGS-1 region (Harrington and Wingfield 1995, Terashima *et al.* 1998a) and a 2.5 Kbp insertion in their rDNA operon (Anderson *et al.* 1989).

Phylogenetic studies indicate that this species is distantly related to the rest of the annulated *Armillaria* spp. from the Northern Hemisphere (Anderson and Stasovski 1992, Miller *et al.* 1994, Chillali *et al.* 1998b, Piercey-Normore *et al.* 1998). Consequently, some authors suggested that *A. mellea* is a basal species to the annulated species from the Northern Hemisphere (Miller *et al.* 1994, Piercey-Normore *et al.* 1998). The relationships between *A. mellea* and the annulated *Armillaria* spp. from the Southern Hemisphere have, however, not been investigated and a final conclusion can thus not be drawn.

Members of the "*Armillaria mellea* cluster" display considerable intraspecific variation. Differences are observed in their sexual systems with homothallic forms occurring in Africa and Japan, and heterothallic forms in Europe and North America (Hintikka 1973, Ullrich and Anderson 1978, Abomo-Ndongo *et al.* 1997, Ota *et al.* 1998a). Isolates from Europe and North America were differentiated based on differences in RFLP (restriction fragment-length polymorphism) patterns of the rDNA operon (Anderson *et al.* 1989) and RAPD (randomly amplified polymorphic DNA) profiles (Ota *et al.* 2000). The African and Japanese *A. mellea* are divergent from the heterothallic forms but are genetically similar and it was suggested that they originated in Japan (Ota *et al.* 2000). Phylogenetic studies based on ITS and IGS-1 sequence data showed that members of this cluster can be separated into four distinct geographic lineages representing Europe, western and eastern North America and Asia (Coetzee *et al.* 2000b). In view of the high diversity in *A. mellea,* it was suggested that *A. mellea* is in the process of speciation as a result of genetic isolation due to geographic barriers (Coetzee *et al.* 2000b).

The "Exannulated cluster"

The "Exannulated cluster" includes *A. tabescens* and *A. ectypa* (Fig. 6). Both species are characterised by their complete lack of an annulus. *Armillaria ectypa*, however, is homothallic and a rare species in Europe, growing specifically in peat bogs (Zolciak *et al.* 1997). In contrast, *A. tabescens* is heterothallic (Darmono *et al.* 1992) and more widely distributed, occurring in Europe, Japan and North America[2] (Volk and Burdsall 1995).

Phylogenetic studies have shown that *A. tabescens* and *A. ectypa* are distantly related to the annulated species of *Armillaria* (Anderson and Stasovski 1992, Miller *et al.* 1994, Chillali *et al.* 1998b). Miller *et al.* (1994) suggested that *A. tabescens* is the oldest species and that it gave rise to the genus. These authors did not, however, include *A. ectypa* in their study. In a more resent study, Chillali *et al.* (1998b) suggested that *A. tabescens* is more closely related to *A. mellea* and that *A. ectypa* is the basal species to *Armillaria*. The narrow distribution of *A. ectypa*, however, renders the conjecture that this species is ancestral to *Armillaria* highly improbable.

The "African cluster"

The "African cluster" includes *A. fuscipes* and *A. heimii* (Fig. 6). A distinguishing feature of this cluster is the fact that their 5S gene is in an inverted orientation relative to that of other *Armillaria* spp. (Coetzee *et al.* 2000a). The two species residing in this cluster were considered synonymous by some authors and the name *A. heimii* was given preference (Mohammed and Guillaumin 1993). A recent study by Coetzee *et al.* (2000a), however, separated isolates thought represent *A. heimii* into two monophyletic lineages based on their IGS-1 sequence data. The authors subsequently suggested that the one lineage be named A. *fuscipes* and the second *A. heimii*. The phylogenetic relationship between these species and the rest of the *Armillaria* spp. is currently unknown.

[2] The name *A. monadelpha* (Morgan) was erroneously used for this fungus in North America where it was thought to be intersterile with *A. tabescens* from Europe (Volk and Burdsall 1995).

The "Australasian cluster"

The Australasian cluster includes the more common species reported from Australia and New Zealand (Fig. 6). These species include *A. fumosa*, *A. hinnulea*, *A. pallidula*, *A. novae-zelandiae*, *A. limonea* and *A. luteobubalina* (Podger *et al.* 1978, Kile and Watling 1981, 1983, 1988, Pearce *et al.* 1986, Hood 1989). Information pertaining to the phylogenetic relationships of these species to one another and to those from the Northern Hemisphere is not currently available from the literature. Hypotheses regarding the relationships of some species can, however, be formulated based on their distribution and morphological characteristics.

Armillaria novae-zelandiae has been reported from Australia and New Zealand, while *A. limonea* has been reported from New Zealand. Both species were also found on *Nothofagus* trees in South America by Singer (Singer 1969). These trees formed a continuous forest from Australia and New Zealand through Antarctica to South America when these landmasses were part of Gondwanaland (Poole 1987). It is therefore likely that *A. novae-zelandiae* and *A. limonea* have a Gondwanean origin and that they represent the ancestors of the species in the Australasian clade.

Armillaria luteobubalina is broadly distributed in eastern and western Australia (Kile and Watling 1981, 1983, Pearce *et al.* 1986) and may be ancestral to the Australian species, *A. fumosa* and *A. pallidula*. *Armillaria pallidula* was reported from only one location in Queensland in Australia (Kile and Watling 1988) and may therefore have a relatively recent origin within the Australasian cluster. *Armillaria hinnulea* resembles the Northern Hemisphere *A. cepistipes* (synonym *A. bulbosa*) in basidiocarp morphology and is the only species with clamp connections in the sub-hymenial layer of its basidiocarps (Kile and Watling 1983). Hence, *A. hinnulea* is probably closely related to the Northern Hemisphere species.

CONCLUSIONS

This review shows that *Armillaria* is a highly diverse genus comprising several biological and morphological species. Much information is available regarding their distribution and their relationships to one another. The following conclusions are drawn from the reviewed studies:

- Species identification is possible through a variety of morphological, biochemical and DNA-based methods.

- All three major categories of species concepts (the morphological, biological and phylogenetic species concepts) have been employed in fungal taxonomic literature. The morphological species concept and the biological concept have made a major contribution to the current understanding of species within the genus *Armillaria*. Both concepts are, however, subject to certain limitations and the use of a single concept makes unequivocal identification of species problematic. The phylogenetic species concept, although widely used in fungal taxonomy, has not received much attention in *Armillaria* taxonomy. It may provide a valuable means for species delineation and identification.

- The phylogenetic relationships among species from the Northern Hemisphere are well resolved. In contrast, nothing is known about the relationships among species from the Southern Hemisphere and their relationship with those from the Northern Hemisphere.

- The distribution of *Armillaria novae-zelandiae* and *A. limonea* suggest that the Southern Hemisphere species might have a Gondwanean origin. It is therefore postulated that the Southern Hemisphere *Armillaria* spp. might be very old and may have given rise to the Northern Hemisphere species.

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TABLE 1: Species currently accepted in the genus *Armillaria* (Fr.:Fr.) Staude and their distribution (adopted from Watling *et al.* 1991 and Volk and Burdsall 1995).

Species	Species
1. *A. affinis* (Singer) Volk & Burdsall. Central America, Carribbean	20. *A. melleo-rubens* (Berk. & M.A.Curtis) Sacc. Central America.
2. *A. borealis* Marxmüller & Korhonen. Europe	21. *A. montagnei* (Singer) Herink. South America, Europe.
3. *A. calvescens* Bérubé & Desurr. Eastern North America.	22. *A. nabsnona* Volk & Burdsall. Western North America.
4. *A. camerunensis* (Henn.) Volk & Burdsall. Africa.	23. *A. novae-zelandiae* (G.Stev) Herink. Australia, New Zealand, New Guinea, South America.
5. *A. cepistipes* Velen. Europe, North America, Japan.	24. *A. omnituens* (Berk.) Sacc. India.
6. *A. duplicate* (Berk.) Sacc. India.	25. *A. ostoyae* (Romagn.) Herink. (= *A. obscura* (Shaeff.) Herink, *Armillariella polymyces* (Pers.) Singer & Clémençon). Europe, North America, Japan.
7. *A. ectypa* (Berk.) Emel. Europe.	26. *A. pallidula* Kile & Watling. Australia.
8. *A. fellea* (Hongo) Kile & Watling. New Guinea.	27. *A. pelliculata* Beeli. Africa.
9. *A. fumosa* Kile & Watling. Australia.	28. *A. procera* Speg. South America.
10. *A. fuscipes* Petch. India, Africa†	29. *A. puiggarii* Speg. South America.
11. *A. gallica* Marxmüller & Romagn.(= *A. lutea* Gillet, *A. bulbosa* (Barla) Kile & Watling). Europe, Japan, North America.	30. *A. sinapina* Bérubé & Dessur. Japan, North America.
12. *A. gemina* Bérubé & Dessur. Eastern North America.	31. *A. singula* Cha & Igarashi. Japan.
13. *A. griseomellea* (Singer) Kile & Watling. South America.	32. *A. sparrei* (Singer) Herink. South America.
14. *A. heimii* Pegler. Africa†	33. *A. tabescens* (Scop.) Emel. Europe, North America, Japan
15. *A. hinnulea* Kile & Watling. Australia, New Zealand.	34. *A. tigrensis* (Singer) Volk & Burdsall. South America
16. *A. jezoensis* Cha & Igarashi. Japan.	35. *A. viridiflava* (Singer) Volk & Burdsall. South America, Europe?
17. *A. limonea* (G.Stev) Boesewinkel. New Zealand.	36. *A. yungensis* (Singer) Herink. South America.
18. *A. luteobubalina* Watling & Kile. Australia.	
19. *A. mellea* (Vahl.:Fr.) P.Kumm. Asia, Africa, Europe, North America.	† Synonymy proposed by Kile and Watling (1988) and Chandra and Watling (1981)

TABLE 2: Basidiocarp morphology of some *Armillaria* spp.

Species	*A. affinis*	*A. borealis*	*A. calvescens*	*A. camerunensis*	*A. cepistipes*
References	Singer 1989 (in Latin)	Gregory and Watling 1985	Bérubé and Dessureault 1989	Hennings 1895 (in Latin)	Motta and Korhonen 1986 (as *A. bulbosa*)
Pileus					
Size (mm)	29-31	(18-)28-50	20-100	5-10	50-70(90)
Shape	convex, obtuse, soon applanate; *centre* sub-depressed	convex almost campanulate then plano-convex	globose, convex then plano-convex, sometimes mammilate	plano-convex	plano-convex
Color	brown	yellow-brown with honey-coloured tinge towards the disk; *centre* faintly bay or purplish	tan to brown	reddish-brown	tan to pinkish-brown; *centre* paler than rest of the pileus
Surface	almost nude, translucent; striate; smooth or subsulcate; subviscid; *centre* minute brown scales	black to dark brown rather ephemeral floccules; hygrophanous	finely fibrillose, almost denuded; dry	small dark squamules	black scales; dry; *centre* black scales more densely than rest
Margin		incurved at first; smooth; minutely striate	straight; sometimes with striations	inrolled at first then plane; somewhat striate	inrolled then down-turned; entire; striate
Lamellae	decurrent; crowded; horizontal; pale-brown, then brown (pale deep-brown)	subdecurrent to adnate; white, slightly tinged pinkish at first but bruising pinkish cream or with age unevenly pink	subdecurrent to sometimes strongly decurrent; close; thick; sinuate; cream, light brown when old	sinuate-adnate, barely decurrent; close; pale	attached to slightly decurrent; distant; thick at point of attachment to stipe, narrower to the margin, broad; white to pale pinkish buff
Stipe					
Size (mm)	42-43x+/-4 (at apex mostly 3 diam)	55-65 x 6-7	40-90x5-20	10-20x2-3	70-100x15 (at apex)
Shape	cylindrical, rarely slightly attenuate at apex	cylindrical, slightly bulbous or clavate	clavate, often bulbous	-	clavate when young, later more or less equal
Context texture	-	fluffy fleshy	fibrous	-	fibrous
Flesh	-	hollow in over mature basidiocarps	-	stuffed	slightly stuffed

TABLE 2 (continued)

Species	*A. affinis*	*A. borealis*	*A. calvescens*	*A. camerunensis*	*A. cepistipes*
Annulus	slightly membranaceous (not arachnoid); white	thick; double; white to cream; floccose	thin; submembranaceous; white to cream	thick; membranaeous; floccose	cortinate; evanescent
Basidiospores					
Size (µm)	(6.5-)7-8(-9)x(4.5-)4.7-5.5(-6)	(6.4-)6.8-8(-9.2)x4.4-5.7	8.5-10x5-7	7-8	8.4-12x6-7.2
Shape	ellipsoid, some ovoid	broadly ellipsoid to elongate-ellipsoid	broadly elliptical to ovate, apiculate	subglobose	broadly elliptical to ovate, distinct apiculus
Colour	white-cream in mass; non-amyloid, hyaline	white in mass; non-amyloid, hyaline	ivory in mass; non-amyloid	hyaline	ivory in mass; non-amyloid, hyaline
Ornamentation	smooth	smooth	smooth	smooth	smooth
Wall	up to 0.5um when matured	slightly thickened	-	-	-
Basidia					
Size (µm)	24-26.8x5.5-7.2	24-30x6-7	-	-	-
Shape	-	elongate clavate	clavate	clavate	clavate
Clamp-connections	absent	present	present	-	present
Hymenophoral trama	bilateral	bilateral	bilateral	-	bilateral
Subhymenial tissue - nuclei	-	-	binucleate	-	binucleate
Pigments	often inside cell walls	in cell walls and vacuoles	in cell walls	-	-
Habit	caespitose	loosely grouped	single or fasciculate groups	-	-
Rhizomorphs *in vitro*	-	-	cylindrical, monopodial branches	-	-

TABLE 2 (continued)

Species	*A. fumosa*	*A. fuscipes*	*A. gallica*	*A. gemina*	*A. heimii*
References	Kile and Watling 1983	Petch 1909, Chandra and Watling 1981, Pegler 1986	Marxmüller 1987	Bérubé and Dessureault 1989	Pegler 1977
Pileus					
Size (mm)	20-120	25-60	40-130(-170)	20-100	10-25
Shape	convex expanding to plano-convex	broadly convex to applanate; *center* slightly umbonate, rarely umbilicate	at first campanulate, then convex	broad, hemispherical-campanulate or obtusely-parabolic, then convex and finally plane, sometimes mammilate	convex, applanate to umbonate
Colour	grey to hazel	yellowish-brown to brown or whitish; *centre* pale brown or whitish	yellowish brown to pinkish brown	dark to very dark brown	cream to orange; *centre* darker brown
Surface	*centre* densely covered with brown to fuscous black fibrillose squamules	glabrescent; *centre* covered with minute brown squamules	indistinct squamules, deep brown, olivaceous fibrils	distinct black scales; dry; *centre* scales more dense	brown squamules; dry; *centre* squamules crowed
Margin	initially incurved	finally recurved; striate	inrolled then irregular, undulate or lobbed; subtranslucent, striate when matured	inrolled then down-turned; entire; striate	incurved
Lamellae	decurrent to subdecurrent; fairly crowded; pliable; ivory-pale cream, yellowish cream or pale cinnamon with age	subdecurrent; rather crowded; narrow, 3-4mm broad; white	subdecurrent to sometimes strongly decurrent; close; thick; sinuate; cream, light brown when old	adnate to slightly decurrent, sinutate when matured; rather close; thick; cream when young, later greyish orange to cinnamon	adnate, with decurrent tooth; subdistant; pale cream; two lengths
Stipe					
Size (mm)	55-130x5-14	30-100x50-90	60-150	50-80x5-10	25-45x2-3
Shape	usually elongated, enlarging downwards to more or less clavate base	slender, curved, cylindrical	clavate to cylindrical	clavate, later more or less equal	cylindrical

TABLE 2 (continued)

Species	*A. fumosa*	*A. fuscipes*	*A. gallica*	*A. gemina*	*A. heimii*
Context texture	cartilaginous, fibrous	-	fibrous	fibrous	
Flesh	stuffed	solid	-	-	hollow
Annulus	thin; membranaceous; white; generally evanescent; floccose below	thick; floccose below	cortinate; arachnoid; whitish; evanescent	thick, membranaceous, white and brown	membranaceous; whitish; evanescent; floccose below
Basidiospores					
Size (µm)	6.5-8.5(-9.5)x(4-)4.5-6 (-6.5)	6-8.3x4.5-6.5	7.5-8.5x4.5-5	8.2-10x5.2-7	7.2-9x(4.4)5-5.5
Shape	elongated-ellipsoid; apiculated	broadly ellipsoid but somewhat angled in outline	obtuse ellipsoid	broadly elliptical to ovate, apiculated	obvoid to angular, apiculated
Colour	almost white in mass, non-amyloid	non-amyloid, hyaline	-	ivory in mass; non-amyloid	non-amyloid, hyaline to tinged slightly honey
Ornamentation	smooth	smooth (but can be very slightly roughened)	smooth	smooth	smooth to very faintly irregular
Wall	moderately thick	slightly thickened	thin	-	thin, thicken slightly with age
Basidia					
Size (µm)	35-47.5x7.5-9	22-31x5-7.5	(20)30-45(-55)x(5)6-8	-	20-30x7.5-8
Shape	clavate	clavate	clavate	clavate	clavate
Clamp-connections	absent	absent	present	present	(not seen)
Hymenophoral trama	bilateral	slightly bilateral	-	bilateral	bilateral
Subhymenial tissue	-	-	binucleate	binucleate	-
Pigments	in vacuoles	-	in cell walls and vacuoles	in cell wall	-
Habit	caespitose (5-20)	caespitose (6-9)	solitory	single, commonly in large fasciculated groups	fasciculate
Rhizomorphs *in vitro*	cylindrical, dichotomous branches	-	cylindrical, monopodial branches	cylindrical, monopodial branches	cylindrical, monopodial branches

TABLE 2 (continued)

Species	*A. hinnulea*	*A. jezoensis*	*A. limonea*	*A. luteobubalina*	*A. mellea*
References	Kile and Watling 1983	Cha *et al.* 1994	Stevenson 1964, Podger *et al.* 1978, Hood 1992	Podger *et al.* 1978, Bougher and Syme 1998	Watling *et al.* 1982, Motta and Korhonen 1986
Pileus					
Size (mm)	20-80(-120)	47-68	80-130	40-70(-100)	up to 90
Shape	subumbonate to broadly convex becoming plano-concave or regularly depressed	hemispherical-convex to convex when young, then plano-convex to plane, sometimes slightly umbonate	convex at first, becoming almost plane, waved at edges	convex at first, becoming expanded and subumbonate to umbonate, sometimes concave	convex , becoming plano-convex or plane
Colour	various shades of brown	dark yellowish-brown or strong brown; *centre* sometimes reddish	lemon yellow	lemon-yellow to honey-brown; *center* at first dark brown	weak yellow to dark honey
Surface	brown to fuscous black squamules; at most subviscid with age; hygrophanous; *centre* particularly squamulose	reddish-brown to brownish yellow fine fibres; dry; *centre* fine fibres or small dark brown to dusky-red scales	dark brown tufted scales, more sparsely towards the margin; dry	dark brown squamules, dense at disk, sparse towards the margin	silky fibrils or minute darker scales
Margin	sometimes distinctly striate	inrolled at first, then acute or slightly incurved later; striate	strongly down-rolled	strongly inrolled; dentate, occasionally striate	entire; striate
Lamellae	sinuate to subdecurrent; subcrowded; fleshy; pliable	sinuate, subdecurrent; close; thick; white when young, then reddish brown to pink; crenate	sinuate to subdecurrent; moderately crowded; cream white becoming stained pinkish fawn	subdecurrent, less frequently distinctly decurrent; crowded; white to pallid, becoming brownish cream or pinkish brown	emarginate, slightly decurrent, slightly sinuate; white to ivory, spotted rust-colour with age; slightly marginate
Stipe					
Size (mm)	30-70(-100)x4-9	39-61x7-11	100-150x10-15	40-100(-120)x7.5-12(-15)	85-145, 4.5-8.0, 0.8-10
Shape	cylindrical tapering towards a bulbous to sub-bulbous base	cylindrical, clavate to subclavate	slightly bulbous at base	slightly thickened towards the base, sometimes sub-bulbose	clavate
Context texture	cartilaginous	fibrous	tough	tough	fibrous

TABLE 2 (continued)

Species	*A. hinnulea*	*A. jezoensis*	*A. limonea*	*A. luteobubalina*	*A. mellea*
Flesh	stuffed	solid when young, stuffed when old	solid	solid	stuffed then hollow
Annulus	arachnoid; grey to brown; evanescent, forming annular zone	thin; submembrananceous; white; fibrillate	arachnoid; white above, dark brown below	moderately thick; membranaceous; yellow; persistent; floccose	thick; double; membranaceous; pale above, citron yellow below; persistent; flocci below
Basidiospores					
Size (µm)	6-8.5(-9)x(3.5-)4-6(-6.5)	6.3-10.3x4.8-6.3	6.5-9x3.5-5.0	(5-)6.5-7.5(-8)x4.5-5.5(-6)	6.0-70.0x8.4-12.0
Shape	ellipsoid to ovoid	broadly elliptical to ovate, apicululated		broadly ellipsoid, broad apiculus	broadly ellipsoid to ovate, apiculated
Colour	white in mass; non-amyloid, hyaline	white in mass; non-amyloid, hyaline	white in mass; non-amyloid,	ivory white in mass; non-amyloid	ivory in mass; non-amyloid, hyaline
Ornamentation	faintly and irregularly sculptured	smooth	finely roughened	smooth	smooth
Wall	relatively thick		moderately thick	moderately to slightly thick	thin or slightly thickened
Basidia					
Size (µm)	21-47x5-9	39.1-44.1x6-7.8	-	20-35(-40)x5-10	25.5-37.8x6.5-8.5
Shape	clavate-cylindrical	clavate	-	-	clavate
Clamp-connections	absent	present	-	absent	absent
Hymenophoral trama	bilateral	bilateral	bilateral	subregular to slightly divergent	slightly bilateral
Subhymenial tissue – nuclei	-	binucleate	-	-	uninucleate
Pigments	-	-	-	-	in vacuoles
Habit	solitary or in small fasciculate groups	solitary to caespitose	caespitose	single to subcaespitose	caespitose
Rhizomorphs *in vitro*	cylindrical, monopodial branching	cylindrical, monopodial branching	-	cylindrial to flattened, sparsely-branching	belt shape, dichotomous branching

TABLE 2 (continued)

Species	*A. montagnei*	*A. nabsnona*	*A. novae-zelandiae*	*A. ostoyae*	*A. pallidula*
Reference	Singer 1956, 1970	Volk *et al.* 1996	Stevenson 1964, Kile and Watling 1983, Hood 1992	Bérubé and Dessureault 1988	Kile and Watling 1988
Pileus					
Size (mm)	40-81	40-70	30-100(-150)	50-100	45-90
Shape	convex; *center* umbonate	convex later plane	subumbonate to umbonate becoming plano-convex and later often depressed; *center* sumbumbonate to umbonate	hemispherical-campanulate or obtusely parabolic, later convex and finally plane	campanulate, then convex to subumbonate later plano-convex or slightly depressed
Color	olive melleous, later yellowish	orange brown, paler towards the margin	olive-buff to olive-brown	dark to very dark brown	yellowish buff to pale fulvous, darker towards the centre
Surface	ochre brown squamules	smooth; hygrophanous; *centre* sometimes short dark fibrils when young	small reddish brown squamules; viscid; hygrophanous	distinct dark scales all over, more dense at centre; dry	fulvous or tawny scales, irregularly and sparsely distributed at first, disappearing with age
Margin	declivous; glubrescent; later slightly striate, eventually sulcate	somewhat incurved; translucent striate to furrowed	initially incurved; striate	at first inrolled then down- turned; sometimes striate	inrolled
Lamellae	initially arcuate-decurrent, later adnate-decurrent; close; broad; whitish, eventually pale yellow	adnate to subdecurrent; subdistant; white to cream, pinkish-tan when aged, brownish patches may develop	sinuate, subdecurrent; subcrowded; white to ivory, becoming cream, yellowish or pinkish tints when age	adnate to slightly decurrent becoming sinuate when matured; rather close; thick where attached to stipe, thinner towards margin; white or cream when young, greyish orange, cinnamon later	subdecurrent, decurrent in large basidiocarps; fairly crowded; relatively thick; pliable; pale tawny, somewhat mottled
Stipe					
Size (mm)	120-220x5-11	80-100x 4-5	50-120(-150)x4-9(-13)	50-200	52-64x20-24

TABLE 2 (continued)

Species	*A. montagnei*	*A. nabsnona*	*A. novae-zelandiae*	*A. ostoyae*	*A. pallidula*
Shape	subequal	-	elongate expanding from mid-point downwards to semi-bulbous or bulbous base	cylindrical	usually elongated, clavate or bulbous, more cylindrical in larger basidiocarps
Context texture	fibrous	fibrous	cartilaginous	fibrous	cartilaginous
Flesh	stuffed then hollow	-	stuffed	-	stuffed
Annulus	thick; double; membranaceous; white; persistent; flocci below	sometimes persist as an evanescent cortina, difficult to observe	thin; membranaceous; dark brown; evanescent	thick; membranaceous; white and brown	thin; cortinate; pale; persistent; darker floccules below
Basidiospores					
Size (µm)	6.2-9.0x4.5-6.5	(6-)8-10x5.5-6.5	7-8(-8.5)x4.5-5.0(-5.5)	5.5-7x8-11	4.4-6.3x5.6-10
Shape	ovoid-ellipsoid	ovoid to subglobose	ellipsoid to elongate-ellipsoid, broad apiculus	broadly elliptical to ovate, apiculate	elongate to broadly ellipsoid, broad prominent apiculus
Colour	pure white in mass; non-amyloid	white in mass; non-amyloid, hyaline	nearly white in mass	white in mass, non-amyloid	cream in mass; non-amyloid, hyaline
Ornamentation	smooth	smooth	smooth or very slightly roughened	smooth	smooth
Wall	thin to medium-thick	somewhat thick at maturity	moderately thick	-	moderately to distinctly thick
Basidia					
Size (µm)	-	25-35x5.5-6.0	24-45x6-9		42.5-55x4-5.5
Shape	clavate	clavate	clavate	clavate	elongate-clavate
Clamp-connections	absent	present	absent	present	absent
Hymenophoral trama	regular to subbilateral	regular	bilateral	strongly bilateral	bilateral
Subhymenial tissue- nuclei	-	-	-	binucleate	-
Pigments	-	-	-	in cell walls	-
Habit	-	gregarious, but not caespitose	solitary or fasciculate	fasciculate	-
Rhizomorphs *in vitro*	-	-	belt shape, dichotomous branches	belt shaped, dichotomous branches	cylindrial to flattened, sparsely-branched

TABLE 2 (continued)

Species	*A. procera*	*A. puiggarii*	*A. sinapina*	*A. singula*	*A. sparrei*
References	Singer 1969, 1970	Singer 1956, 1970	Bérubé and Dessureault 1988, Cha *et al.* 1994	Cha *et al.* 1994	Singer 1956, 1969
Pileus					
Size (mm)	49-65(-85)	(11-)21-100(-175)	20-60	24-38	18-66
Shape	convex; *centre* depressed often with umbo in depression	semiglobose, then convex; *center* depressed but with subumbonate elevation, or more distinctly umbonate	conical-campanulate to campanulate, convex then plano-convex; *center* occasionally mammilate	convex to hemispherical when young, later plano-covex to plane; *centre* obtusely umbonate	convex-subcampanulate, then flatter-convex, often subumbonate
Colour	greyish; *centre* ochraceous	"indian buff" to honey colour; *centre* deeper brown	pale to dark brown with reddish tinges	yellow to brownish yellow; *centre* pale yellow to very pale brown	varying from pale coloured to deep olive
Surface	viscid; hygrophanous; *centre* spinulose-flocconous small scales	small concolorous scales, later darker brown squamules; dry; hygrophanous; *centre* dark brown squamules	brown scales; usually dry; sometimes hygrophanous	dark reddish-brown to very dark gray tufts of fine fibers; dry; *centre* fibers concentrated	smooth or rugose; viscid;
Margin	sulcate and transparently striate	uplifted when aged; transparently striate when matured	decurved; sometimes with striations	inrolled at first then acute later; translucent-striate	upturned; transparently striate
Lamellae	sinuate-decurrent or short-decurrent; close or subclose; rather broad; pure white, pallid with age	adnate, the adnato-decurrent or adnate with decurrent tooth; subclose; narrow to rather broad; varying from white to brown pallid, edge tends to be brown-spotted	sinuate, subdecurrent to sometimes strongly decurrent; close; thick; cream to cinnamon when old	subdecurrent; close; thick at apex, thin towards the margin; cream when young, light brown later	adnate, irregularly decurrent tooth, or subdecurrent; moderately close to close; relatively rather broad and often ventricose when aged; crisp or forked but not intervenose; ocher whitish to cream
Stipe					
Size (mm)	37-58x4.5-9(-12)	25-70(-170)x2-8 above, 2-18 below	47-68x5-8	42-60x4-6	as long or longer than size of pileus
Shape	equal or tapering downwards, or slightly tapering upwards	equal with bulbous base, later sometimes ebulbose or tapering downwards	clavate	cylindric, clavate	cylindrical or tapering upwards

TABLE 2 (continued)

Species	*A. procera*	*A. puiggarii*	*A. sinapina*	*A. singula*	*A. sparrei*
Context texture	fleshy	fragile	fibrous	fragile	fleshy
Flesh	solid	solid	solid when young, stuffed when old	solid when young, slightly hollow later	solid
Annulus	thick; membranaceous; persistent	subcortinoid to thin membranaceous; white; fibrils below	thin; sometimes membranaceous; whitish above, yellowish below; fibrous	thin; membranaceous; white to cream	thin; white; not persistent
Basidiospores					
Size (µm)	6.5-11.7x4.5-7.3	6.5-11x6.5-7.3	5.9-8x8.2-10	6.2-10.6x3.6-6.2	(7.3-)8-12x(4.5-)5.3-7.3 [2]
Shape	ellipsoid to ovoid;	subcylindrical to ovoid-ellipsoid	broadly elliptical to ovate, apiculated	broadly elliptical to ovate, apiculated	ellipsoid or cylindrical
Colour	pure white in mass; non-amyloid, hyaline	pure white in mass; non-amyloid, hyaline	ivory in mass; non-amyloid	cream in mass; non-amyloid, hyaline	pure white in mass
Ornamentation	smooth	smooth	smooth	smooth	rarely roughened
Wall	slightly thick	thin to slightly thickened	-	-	first thin, later gradually thickening
Basidia					
Size (µm)	23-38x6.5-11.7	40-47x7.3-8.8	37.9-44.9x7.2-9.4	33-37.8-5.4-7.5	30-44x6.7-8
Shape	-	clavate	clavate	clavate	clavate
Clamp-connections	present	present	present	present	absent
Hymenophoral trama	bilateral	bilateral	bilateral	bilateral	subparallel or very slightly interwoven
Subhymenial tissue- nuclei	-	-	binucleate	binucleate	-
Pigments	-	-	in cell walls	-	-
Habit	caespitose or densely fasciculate	fasciculate to caespitose	small fasciculate groups	solitary	fasciculate in large bunches
Rhizomorphs *in vitro*	-	-	cylindrical, monopodial branching	cylindrical, monopodial branching	-

TABLE 2 (continued)

Species	*A. tabescens*	*A. tigrensis*	*A. viridiflava*	*A. yungensis*
References	Singer 1970	Singer 1970	Singer 1989 (in Latin)	Singer 1970
Pileus				
Size (mm)	(25-)40-70(-100)	(11-)21-127(-175)	30-64	34-64
Shape	convex, sometimes slightly depressed in age around a slight umbo, or exumbonate, often sulcate	semiglobose or convex, later flattened, in larger basidiocarps subumbonate to umbonate	campanulate-convex the convex, later sometimes subapplanate; *centre* umbonate	semiglobate then applanate; *center* +/- depressed or subumbilicate to subumbonate
Colour	light brownish yellow; *centre* stramineous buff	pale ochraceous or yellow later dark honey; *centre* sometimes deeper brown	olive to olive-blackish	pale-brown to dark-brown
Surface	smooth; subhygrophanous	rugulose to subrugulose; somewhat subviscid, later dry; subhygrophanous or hygrophanous; *centre* concolorous scales, later darker brown	fibrillose; not viscid; hygrophanous; *center* generally rugulose, fibrillose	slightly fibrillose; not viscid; *center* blackish dotted squamulose
Margin	-	upturned with age	-	striate when matured
Lamellae	irregularly decurrent; subclose; broad; arcuate; whitish later dark cream, or flesh-pallid, sometimes brown-spotted	adnate, or sometimes adnexed, with subdecurrent to decurrent tooth, or adnato-decurrent to sinuate decurrent; close or subclose; narrow to rather broad; white to cinnamon-white, tending to become fulvous-brown spotted	decurrent; crowded; moderately broad; white then pale-yellow	decurrent; close or subclose; narrow; arcuate; beige
Stipe				
Size (mm)	(35-)60-150x(3-)4-11	25-90(-170)x2-18	80-125x9-11.5	25-65x3.5-12
Shape	tapering towards base or at least with thickened apex and tapering base	equal with bulbous base, later subequal or slightly ventricose with bulbous base, at times tapering down	subequal or tapering towards the base	equal or tapering upwards

TABLE 2 (continued)

Species	*A. tabescens*	*A. tigrensis*	*A. viridiflava*	*A. yungensis*
Context texture	flexous	-	-	-
Flesh	solid or stuffed, sometimes hollow when aged	solid, later stuffed or hollow	solid, later stuffed	solid
Annulus	absent	membranous or thin-membranous; white; persistent	thick; membranaceous; yellow; persistent	thick; cortinoid; whitish
Basidiospores				
Size (µm)	7.7-8.8x5.2-6	9.3-11x6.5-7.3	6.2-8.5x4.5-5.5(-6)	7-9x4-5.3
Shape	short-ellipsoid or somewhat ovoid	ellipsoid	ellipsoid	ellipsoid, ovoid, or short-cylindric
Colour	white in mass; non-amyloid	pure white; non-amyloid, hyaline	cream-yellowish in mass	pure white in mass; non-amyloid, hyaline
Ornamitation	smooth	smooth	smooth	smooth
Wall	-	somewhat thick	thickened	-
Basidia				
Size (µm)	30-40x8-9	40-47x7.3-8.8	(16-)21.8-31.8x(6-)6.7-9(-10)	20-32x5.3-8.7um
Shape	clavate, elongated when matured	clavate, strongly elongated when matured	-	-
Clamp-connections	-	not always present	present	sometimes
Hymenophoral trama	somewhat bilateral	subregular-subbilateral to more distinctly bilateral	subregular-bilateral	bilateral
Subhymenial tissue	-	-	-	-
Pigments	-	in vacuoles	-	-
Habit	fasciculate or caespitose	fasciculate to caespitose	-	-
Rhizomorphs *in vitro*	-	-	-	-

TABLE 3: Phenotypic and genotypic characters used to differentiate *Armillaria* spp. in conjunction with or instead of basidiocarps (sexual compatibility studies are dealt with under the biological species concept and are therefore not included in this table).

Characters	**Differentiate:**
Phenotypic	
1. Morphology of mycelium and rhizomorphs (in many cases this is not unique for a specific species but can be used to differentiate between two species with similar basidiocarp morphologies).	• North America: *A. gemina* from *A. ostoyae*, *A. calvescens* and *A. sinapina* (Bérubé and Dessureault 1988, 1989) • Europe: all species except *A. cepistipes* and *A. galllica* (Rishbeth 1982, 1986, Zolciak *et al.* 1997, Tsopelas 1999). • Africa: *A. mellea*, *A. heimii*, interspecific somatic compatibility group (SIG) III and SIG IV (Mohammed *et al.* 1989, 1994b, Mwangi *et al.* 1989) • Australia: *A. novae-zelandiae*, *A. hinnulea*. *A. fumosa* and *A. luteobubalina* are the same but different from the other species (Kile and Watling 1983). • New Zealand: *A. limonea* and *A. novae-zelandiae* (Shaw *et al.* 1981)
2. Response to temperature	• Europe: all species, especially *A. tabescens* and *A. mellea* (Rishbeth 1982, 1986) • Africa: *A. mellea*, *A. heimii*, (SIG) III and IV (Mohammed *et al.* 1994b)
3. Response to phenolic acids and terpens	• Europe: *A. mellea*, *A. ostoyae*, *A.cepistipes* and *A. tabescens* (Rishbeth 1986)

TABLE 3 (continued)

Characters	Differentiate:
4. Isozyme and protein profiles	• North America: *A. ostoyae, A. calvescens, A. sinapina, A. nabsnona* and *A. gallica* (Morrison *et al.* 1985b, Lin *et al.* 1989) • Europe: all species (Wahlström *et al.* 1991, Bragaloni *et al.* 1997) • Africa: *A. mellea, A. heimii* and SIG III (Agustian *et al.* 1994, Mwenje and Ride 1997) • Japan: *A. ostoyae, A. gallica, A. jezoensis, A. singula* and *A. sinapina* (Cha and Igarashi 1995a, Matsushita *et al.* 1996)
5. Mono- and polyclonal antibodies	• Europe: all species (Lung-Escarmant and Dunez 1979, 1980, Lung-Escarmant *et al.* 1985, Fox and Hahne 1989).
Genotypic	
6. DNA/DNA hybridization	• North America: *A. cepistipes, A. mellea* and *A. ostoyae* (Jahnke *et al.* 1987)
7. DNA base composition (mol % G+C)	• North America: *A. mellea* and *A. cepistipes* (Motta *et al.* 1986)
8. Restriction fragment length polymorphisms (RFLP's)	
8.1 mitochondrial DNA (mtDNA)	• North America: all species (Anderson *et al.* 1987, Smith and Anderson 1989) • Europe: *A. cepistipes, A.ostoyae* and *A. mellea* (Jahnke *et al.* 1987)

TABLE 3 (continued)

Characters		Differentiate:
8.2	whole cell nuclear DNA (nDNA)	• North America: all species (Anderson *et al.* 1987)
8.3	complete ribosomal nDNA operon (rnDNA)	• North America: *A. mellea*, *A. ostoyae* and *A. gemina*. *Armillaria gallic* and *A. cepistipes* similar but distinct from other species. *Armillaria sinapina*, *A. nabsnona* and NABS X similar but distinct from other species (Anderson *et al.* 1989) • Europe: *A. mellea*, *A. gallica*, *A. ostoyae*, *A. borealis*, *A. cepistipes* and *A. tabescens* (Anderson *et al.* 1989, Schulze *et al.* 1995)
8.4	PCR generated rnDNA intergenic spacer region (IGS-1)	• North America: all species except *A. gallica* and *A. calvescens* (Harrington and Wingfield 1995, Banik *et al.* 1996, Volk *et al.* 1996, White *et al.* 1998) • Europe: all species (Harrington and Wingfield 1995, Pérez Sierra *et al.* 1999) • Africa: *A. fuscipes* and *A. heimii* (Coetzee *et al.* 2000a) • Japan: all species (Terashima *et al.* 1998b)
8.5	PCR generated rnDNA internal transcribed spacer (ITS)	• Europe: *A. mellea*, *A. tabescens* and *A. ectypa* (Chillali *et al.* 1998a) • Africa: *A. mellea*, *A. heimii* and SIG III (Chillali *et al.* 1997)

TABLE 3 (continued)

Characters		Differentiate:
9.	Interspecific DNA sequence character differences	
	9.1 IGS-1	• North America: *A. ostoyae*, *A. gemina*, *A. borealis*, *A. mellea*, *A. tabescens* and *A. nabsnona*. Few differences between *A. sinapina*, *A. cepistipes*, *A. gallica*, *A. calvescens* and NABS X (Anderson and Stasovski 1992, Coetzee *et al.* 2000b) • Europe: *A. borealis*, *A. mellea*, *A. tabescens* and *A. ostoyae*. Few differences between *A. gallica* and *A. cepistipes* (Anderson and Stasovski 1992, Coetzee *et al.* 2000b) • Africa: *A. fuscipes* and *A. heimii* (Coetzee *et al.* 2000a) • Japan: all species (Terashima *et al.* 1998a)
	9.2 ITS	• North America: *A. mellea* and *A. tabescens* (Anderson and Stasovski 1992) • Europe: *A. mellea*, *A. tabescens* and *A. ectypa*. Single nucleotide differences between *A. borealis*, *A. ostoyae*, *A. cepistipes* and *A. gallica* (Anderson and Stasovski 1992, Chillali *et al.* 1998b)

TABLE 4: Biological species and corresponding morphological species of *Armillaria* in Europe, North America, Japan and Africa.

Morphological species	Biological species			
	Europe	**North America**	**Japan**	**Africa**
A. borealis	A			
A. calvescens		NABS[a] III		
A. cepistipes	B	NABS XI	NAG[b] D	
A. ectypa	*[c]			
A. gallica	E	NABS VII	NAG A	
A. gemina		NABS II		
A. heimii				SIG[d] II
A. jezoensis			H	
A. mellea	D	NABS VI	NAG Am	SIG I
A. nabsnona		NABS IX	NAG B	
A. ostoyae	C	NABS I	NAG C	
A. sinapina		NABS V	F	
A. singula			G	
A. tabescens	*	*	T[e]	
Undescribed		NABS X	NAG E	SIG III SIG IV

[a] NABS: North American Biological Species

[b] NAG: Nagasawa

[c] Asterisk denotes intersterility groups without vernacular.

[d] SIG: Somatic Incompatibility Group

[e] Compatible with European strains of *A. tabescens* but not with North American strains (Ota *et al.* 1998b).

[3] http://www.uoguelph.ca/~gbarron/index.htm
[4] http://www.hiddenforest.co.nz
[5] http://morwellnp.pangaean.net

Figure 1. Basidiocarps of commonly found *Armillaria* spp. 1) *A. calvescens*, 2) *A. cepistipes*, 3) *A. fumosa*, 4) *A. fuscipes*, 5) *A. gallica*, 6) *A. gemina*, 7) *A. hinnulea*, 8) *A. jezoensis*, 8) *A. jezoensis*, 9) *A. limonea*, 10) *A. luteobubalina*, 11) *A. mellea*, 12) *A. nabsnona*, 13) *A. novae-zelandiae*, 14) *A. ostoyae*, 15) *A. pallidula*, 16) *A. sinapina*, 17) *A. singula*, 18) *A. tabescens*. (Photo credits. TJ Volk: 1, 2, 5, 6, 12, 14, 16, 18. GS Ridley: 7. JY Cha: 8, 17. G. Barron[3]: 9. C. Shirley[4]: 4. C. Harris[5]: 10. Armillaria Root Disease Handbook Figure 1.2: 3, 15.).

[3] http://www.uoguelph.ca/~gbarron/index.htm
[4] http://www.hiddenforest.co.nz
[5] http://morwellnp.pangaean.net

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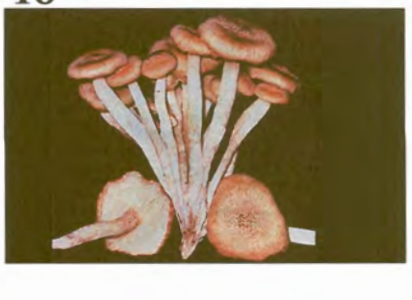


Figure 2. Life cycle of *Armillaria* spp. with different mating systems. A) Heterosexual bifactorial (tetrapolar) mating compatibility system (genotypes are arbitrarily chosen); B) Non-heterosexual mating system. ●: diploid nuclei, ○: haploid nuclei. (Redrawn and expanded from Fig. 6, Ota *et al.* 1998)

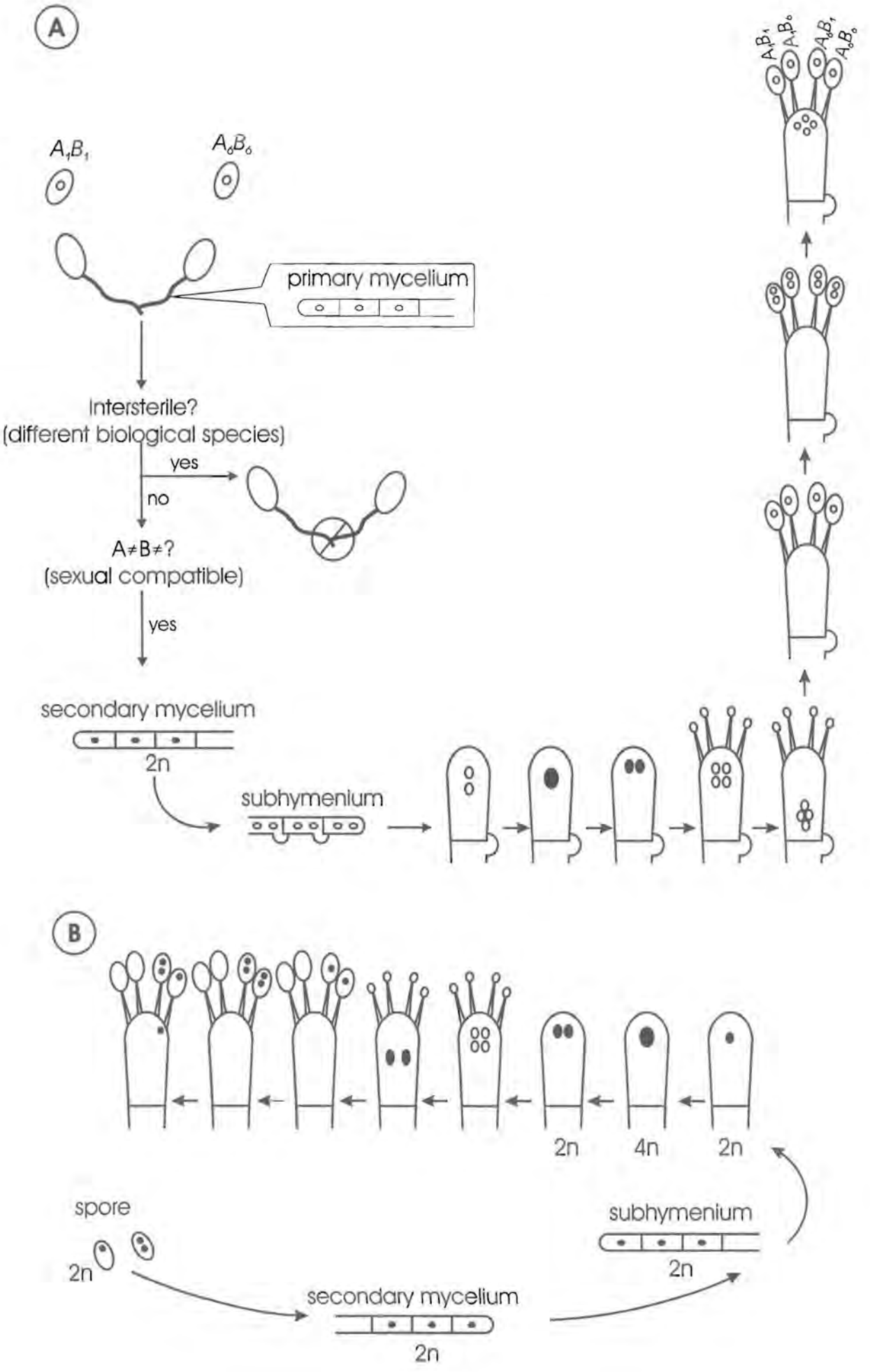


Figure 3. Haploid – haploid mating interaction between two sexually compatible isolates. The culture morphology of the haploid isolates is white with abundant aerial mycelium (left and right pictures). The culture morphology of the compatible isolates changes to brown and crustose after successful diploidization (middle picture).

Isolate 1: haploid **Isolate 1 and 2: diploid** **Isolate 2: haploid**

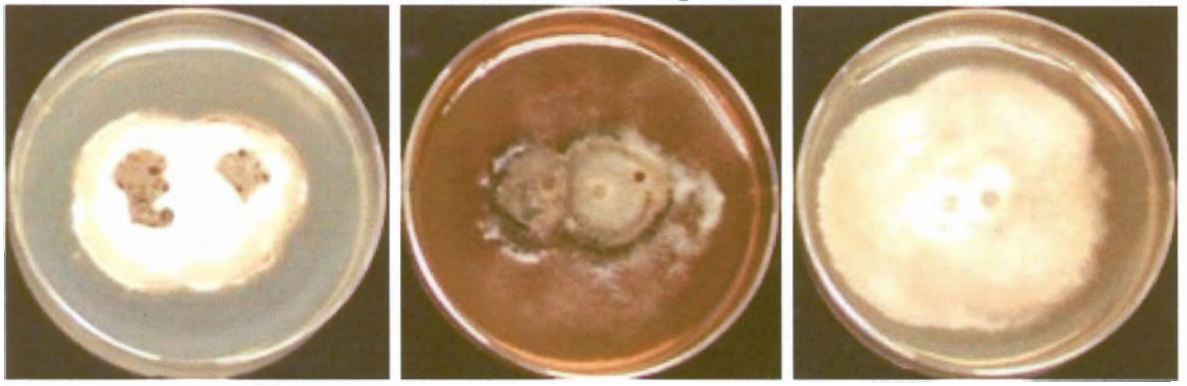


Figure 4. The relationship between reticulated (tokogenetically related) and hierarchic (phylogenetically related) descendent systems. (Redrawn from Fig. 6, Hennig 1966)

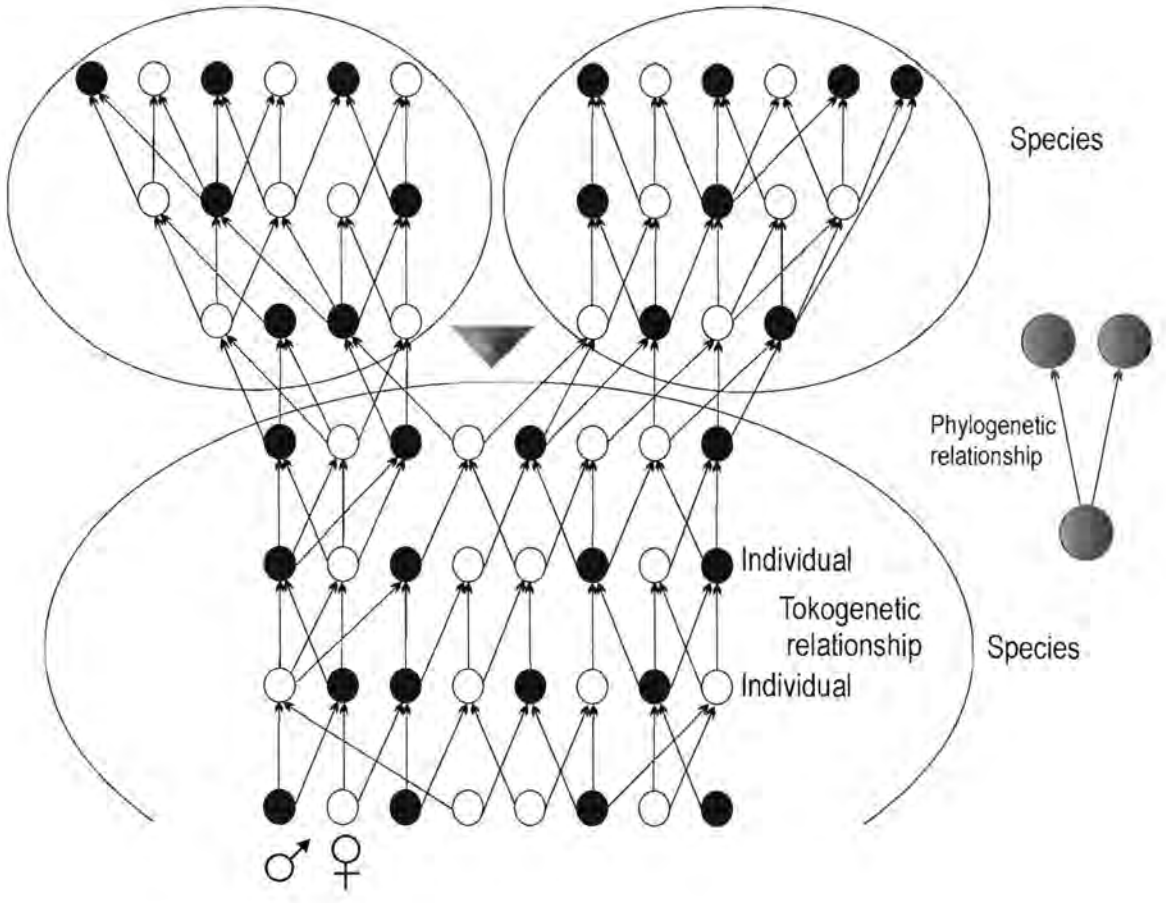
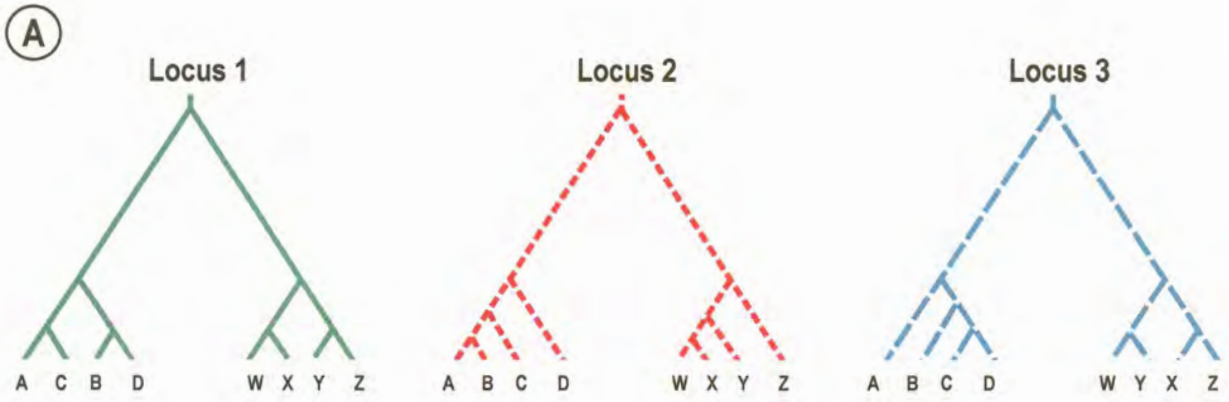


Figure 5. Genealogical concordance among multi-loci data sets. A) Cladograms depicting the genealogy of three individual loci for eight taxa. B) Consensus tree of the three cladograms shows the limit of species at the point of transition from incongruity to concordance among branches. (Redrawn from Fig. 2, Taylor *et al*. 2000)



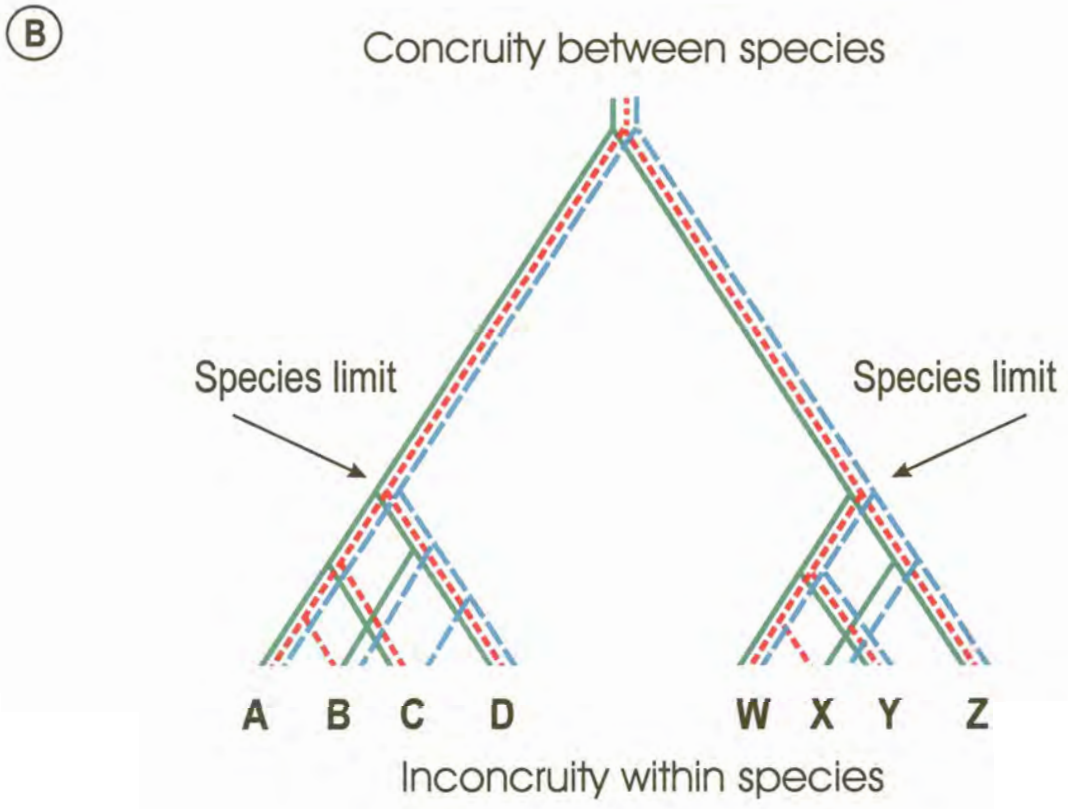
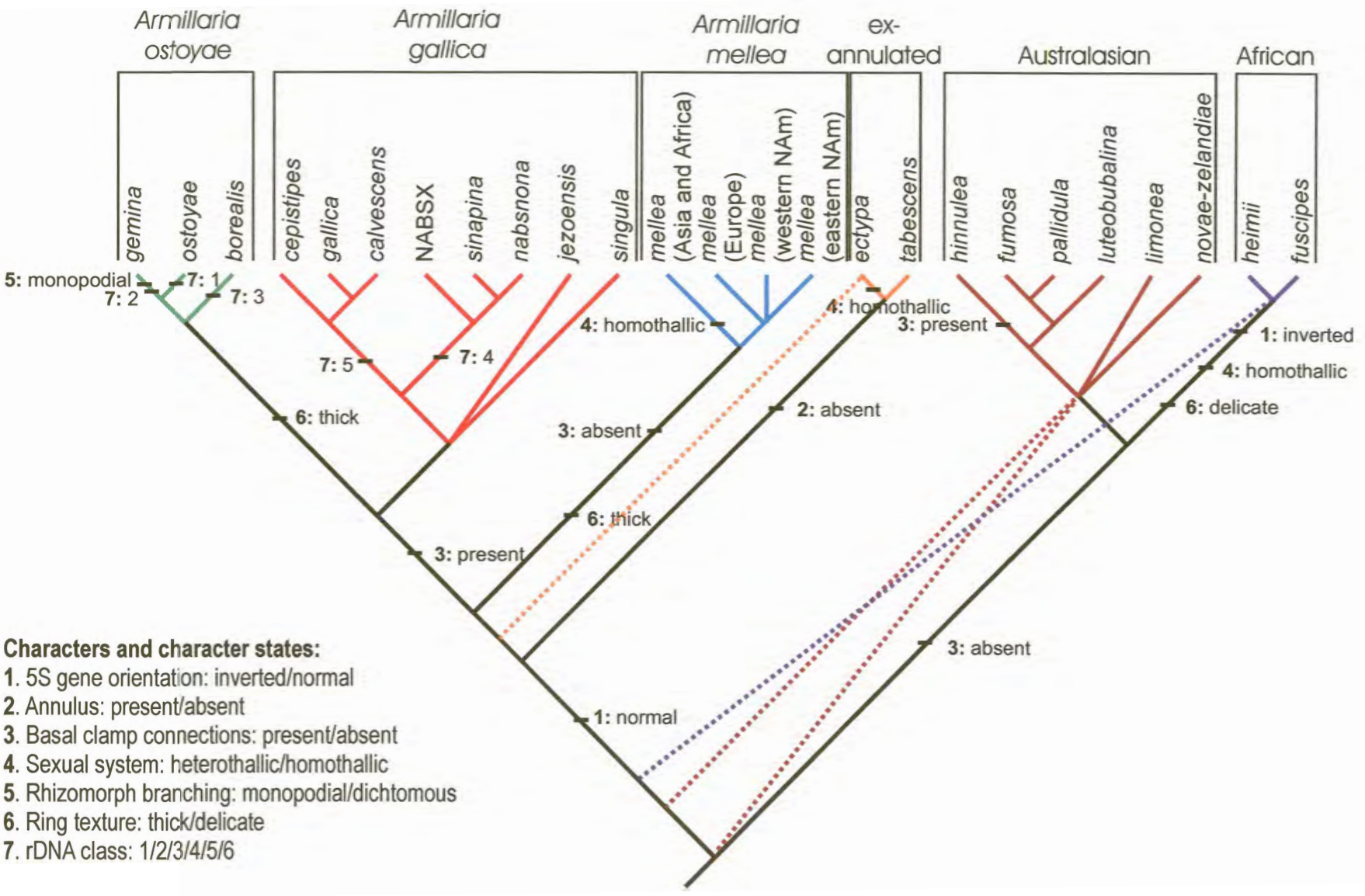


Figure 6. Cladogram showing the phylogenetic relationships among taxa within the species clusters and the relationships among clusters based on morphological and molecular data. Alternative relationships are indicated with a dashed line. Character states that differentiate between clusters or species within the clusters are indicated on the branches.



Characters and character states:

1. 5S gene orientation: inverted/normal
2. Annulus: present/absent
3. Basal clamp connections: present/absent
4. Sexual system: heterothallic/homothallic
5. Rhizomorph branching: monopodial/dichtomous
6. Ring texture: thick/delicate
7. rDNA class: 1/2/3/4/5/6