Mycosphere Essay 8: A review of genus Agaricus in tropical and humid subtropical regions of Asia

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Mycosphere 7 (4): 417–439 (2016) www.mycosphere.org ISSN 2077 7019
Article
Doi 10.5943/mycosphere/7/4/3

Mycosphere Essay 8: A review of genus *Agaricus* in tropical and humid subtropical regions of Asia

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Karunarathna SC, Chen J, Mortimer PE, Xu JC, Zhao RL, Callac P, Hyde KD 2016 – Mycosphere Essay 8: A review of genus *Agaricus* in tropical and humid subtropical regions of Asia. Mycosphere 7(4), 417–439, Doi 10.5943/mycosphere/7/4/3

Abstract

The genus *Agaricus* includes both edible and poisonous species, with more than 400 species worldwide. This genus includes many species, which are enormously important as sources of food and medicine, such as the button mushroom (*Agaricus bisporus*) and the almond mushroom (*Agaricus subrufescens*). This paper reviews the genus *Agaricus* in tropical and humid subtropical regions of Asia, including the history, characteristics, pertinent morphological and organoleptic taxonomic traits, molecular phylogeny and taxonomy advances, toxicity and edibility. This review includes *Agaricus* species that are known to be highly valued as edible and medicinal mushrooms, and provides a comprehensive checklist of species described from the tropical and humid subtropical regions of Asia until the end of 2015.

Keywords – check list – edible mushroom– medicinal mushroom – molecular phylogeny – poisonous mushroom

Introduction to the genus *Agaricus*

The history of the denomination of the genus *Agaricus* is relatively complex and is reported in detail in the monograph of Parra (2008), from which we briefly resume here the last major nomenclatural events. Donk (1962) proposed "*Agaricus* L. ex Fries" as "*nomen conservandum*" with "*Agaricus campestris* Linnaeus ex Fries" as the conserved type. In the 2006 ICBN edition (Vienna Code 2006), the starting point for the nomenclature of fungi is *Species plantarum* (Linnaeus, 1753) and, accordingly, the name of the genus is *Agaricus* L. (1753). This name has priority over two homotypic synonyms, which are *Psalliota* (Fr.) P. Kumm. (1871) and *Pratella* (Pers.) Gray (1821). There are about 6000 records with the name of "*Agaricus*" in Index Fungorum (Index Fungorum 2016). This is due to the fact that in the past, many species were designated as *Agaricus* added because the species had lamellae.

Submitted 24 June 2016, Accepted 19 July 2016, Published online 26 July 2016
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Agaricus L. is a large and well-known edible mushroom genus that also includes a small number of species that are toxic if eaten (Kerrigan et al. 2006, Zhao et al. 2012a, Bau et al. 2014). *Agaricus* species are saprotrophic fungi and often gregarious in woods, forests, gardens, on roadside, fields, pasture-land, grass-land, rubbish dumps, manure heaps and alluvial soils. *Agaricus* can be found from sea level up to the vegetation limit in mountainous areas (Cappelli 1984), and also occurs in some arid areas (Xu et al. 1998; Lebel & Syme 2012; Lebel 2013).

According to Bas (1991), the number of *Agaricus* species worldwide is close to 400. Zhao et al. (2011) recognized 386 species in the genus, and from this publication to the end of 2015, 48 new species have been introduced. This includes 18 species new from Thailand (Chen et al. 2012, 2015, Zhao et al. 2012a, b, Karunarathna et al. 2014, Thongklang et al. 2014a, Ariyawansa et al. 2015, Liu et al. 2015), four from China (Li et al. 2014, Gui et al. 2015), one from Sri Lanka (Liu et al. 2015), 16 from Europe (Parra et al. 2011, 2014, Parra 2013), and nine new sequestrate species from Australasia (Lebel & Syme 2012, Lebel 2013). Accordingly, the total number of species is presently 434, and includes 200 tropical species. Even though the genus *Agaricus* is well-known as important edible mushrooms, the taxonomy and delimitation of the species within the genus is very complex (Cappelli 1984).

Taxonomic monographs and other taxonomic studies of *Agaricus* species are mostly from the Americas, Australia, Europe, India and New Zealand (Murrill 1912, 1918, 1941, Hotson 1938, Schäffer & Mø11er 1938, Smith 1944, Møller 1950, 1952, Pilát 1951, Huijsman 1960, Orton 1960, Bohus 1975, 1990, 1995, Heinemann 1978, 1986, Freeman 1979a, b, Pegler 1983, 1990, Cappelli 1984, Kerrigan 1985, 1989, Wasser 1989, Callac et al. 1993, Alberto & Wright 1994, Grgurinovic 1997, Saini et al. 1997, Valenzuela et al. 1997, Alberto 1998, Esteve-Raventós 1998, Flower et al. 1997, Mitchell & Walter 1999; Nauta 1999, 2000, Peterson et al. 2000, Lanconelli 2002, Parra 2003, 2008, 2013, Lacheva & Stoichev 2004, Natarajan et al. 2005, Geml et al. 2007, Ludwig 2007).

The most commonly referenced monographs on tropical *Agaricus* are those of Heinemann (Heinemann 1953–1996, especially those of 1978 and 1980). Heinemann's 1978 and 1980 treatments of *Agaricus* ranked species traditionally included in the genus at the subgeneric level. He added two predominantly subtropical and tropical subgenera, *Lanagaricus* Heinem. and *Conioagaricus* Heinem.

With DNA sequencing and rapidly expanding databases of genetic and taxonomic information, researchers are developing new, efficient tools for the identification and classification of fungi (Geml et al. 2004). Phylogenic analyses based on ribosomal DNA sequences are now widely exploited to deduce evolutionary relationships among agaric taxa (Challen et al. 2003, Kerrigan et al. 1999, 2006, 2008, Geml et al. 2004, Zhao et al. 2011). The concept (or delimitation) of sections initially described from temperate species has further evolved in recent years (Parra 2008, Parra 2013), but these changes may not be sufficient to incorporate tropical diversity. Up until 2010, most reports concerning the systematics and phylogeny of *Agaricus* species were based on European and North American taxa, and failed to include those originating in Asia.

Pertinent morphological and organoleptic taxonomic traits in *Agaricus*

The sporocarp of *Agaricus* is generally described as having a white to brown more or less yellowish or rufescent pileus; free lamellae with a regular trama when young, later becoming irregular and producing a dark brown spore print; and partial veil which forms a ring on the stipe. Basidiospores are smooth with a compound wall and not visibly pseudoamyloid.

The taxonomic system of *Agaricus* is complex, and several treatments have been proposed by different mycologists based on their judgments of how significant each morphological characteristic is in the recognition of species and sections in the genus (Møller 1950, Pilat 1951, Konrad & Maublanc 1952, Kühner & Romagnesi 1953, Moser 1967–1983, Heinemann 1978, Wasser 1980, Cappelli 1984, Kerrigan 1986, Singer 1986, Parra 2008, 2013). All recent systematic treatments of the genus used four taxonomically relevant characteristics: 1) macrochemical reactions: Schaeffer’s cross-reaction – a chemical test with aniline and concentrated Nitric acid; and the alkali test (application of strong alkali, either NaOH or KOH); 2) basidiosporocarp colour change when bruised or cut; 3) odour, which requires that the researcher smelling the samples is trained beforehand (Heinemann 1987); 4) the structure of the annulus, which can be superous or inferous, simple or double, has more recently been recognized as a crucial characteristic.

Some characteristics that are generally not pertinent at the sectional level remain useful at the species level, although in certain cases traits such as the pileus colour or the microscopic features are sometimes more variable within species than between species. However, at the species level and within certain sections the following traits remain useful for species identification: pileus colour, aspect of on pileus (squamules), base of the stipe (marginate bulbous), spore size, cheilocystidia (catenulate), vacuolar pigment in the pileipellis hyphae and also habit, habitat or the geographic/climatic distribution.

Molecular phylogeny and taxonomy advances in *Agaricus*

Molecular phylogeny based on the internal transcribed spacers (ITS1 and ITS2) segments of the nuclear ribosomal DNA region of *Agaricus* was first carried out by Mitchell & Bresinsky (1999). This phylogeny gives a base to identify species and to develop their classification. It is also helpful to detect species that possess interesting traits such as edibility, ability to fruit on compost, odour and other biochemical properties, which are generally shared by members of the same section. Based on ITS data, *Agaricus* sect. *Bivelares* (previously named *A.* sect. *Duploannulati*) and *A.* sect. *Xanthodermatei*, have been phylogenetically reconstructed using temperate specimens from North America and Europe (Challen et al. 2003, Kerrigan et al. 2006, 2008). *Agaricus* sect. *Bivelares* includes edible species such as *A. bisporus* (J.E. Lange) Imbach and *A. bitorquis* (Quél.) Sacc., which are both cultivated, while species of *A.* sect. *Xanthodermatei* are confirmed or suspected to be toxic. Some species or varieties were reported as being new to science based on morphological, molecular and/or biological data (Callac et al. 1993, 2003, Callac & Guinberteau 2005, Geml et al. 2007, Kerrigan et al. 2008, Lebel 2012, Lebel & Syme 2013).

All the classical temperate sections are monophyletic except *A.* sect. *Spissicaules* and *A.* sect. *Sanguinolenti*. The latter appeared as a paraphyletic group comprising three clades in the ITS phylogenetic analyses of Zhao et al. (2011). Recently, Parra et al. (2014) has shown that one of these three clades that already contained *A. pattersoniae* Peck and *A. boisseletii* Heinem. corresponded to *A.* sect. *Nigrobrunnescentes*, since the type species of the section, *A. nigrobrunnescens*, belongs to this clade. Many species belonging to *A.* sect. *Sanguinolenti* (e.g. *A. padanus* Lancon.) were transferred to section *Nigrobrunnescentes*; moreover *A. caballeroi* L.A. Parra, G. Muñoz & Callac, a new species described from Spain (Parra et al. 2014) also belongs to this section. The two other clades representing subsections *Bohusia* and *Sylvatici* remain in *A.* sect. *Sanguinolenti*. With these recent research findings, *Agaricus* species of temperate areas are now distributed in nine sections that are all represented in Figure 1, except the section *Nigrobrunnescentes*. Future investigation will be needed to characterize the tropical clades that have not yet been resolved, except *A.* sect. *Brunneopicti* also represented in Figure 1.

The first phylogenetic analysis including tropical *Agaricus* species was based on ITS data and published by Zhao et al. (2011). The authors aimed to examine the extent to which the current system of classification is appropriate for tropical species. The analysis included 38 temperate species representing the eight classical sections of the genus, and 86 putative species of *Agaricus* from tropical areas of Africa, Asia and the Americas, but mostly from northern Thailand. Samples of approximately 50 putatively novel species from a small area of northern Thailand were included. It was shown that (i) only about one-third of tropical species belong to the classical sections based on temperate species, and that therefore the systematics of the genus needed to be expanded; (ii) most of the remaining two-thirds of tropical species grouped in 11 clades generally exclusively neotropical (Americas) or palaeotropical (Africa + Asia), suggesting that secondary species diversification had occurred separately in these two areas; (iii) in contrast, several clades of classical sections contained both American and African or Asian species along with temperate

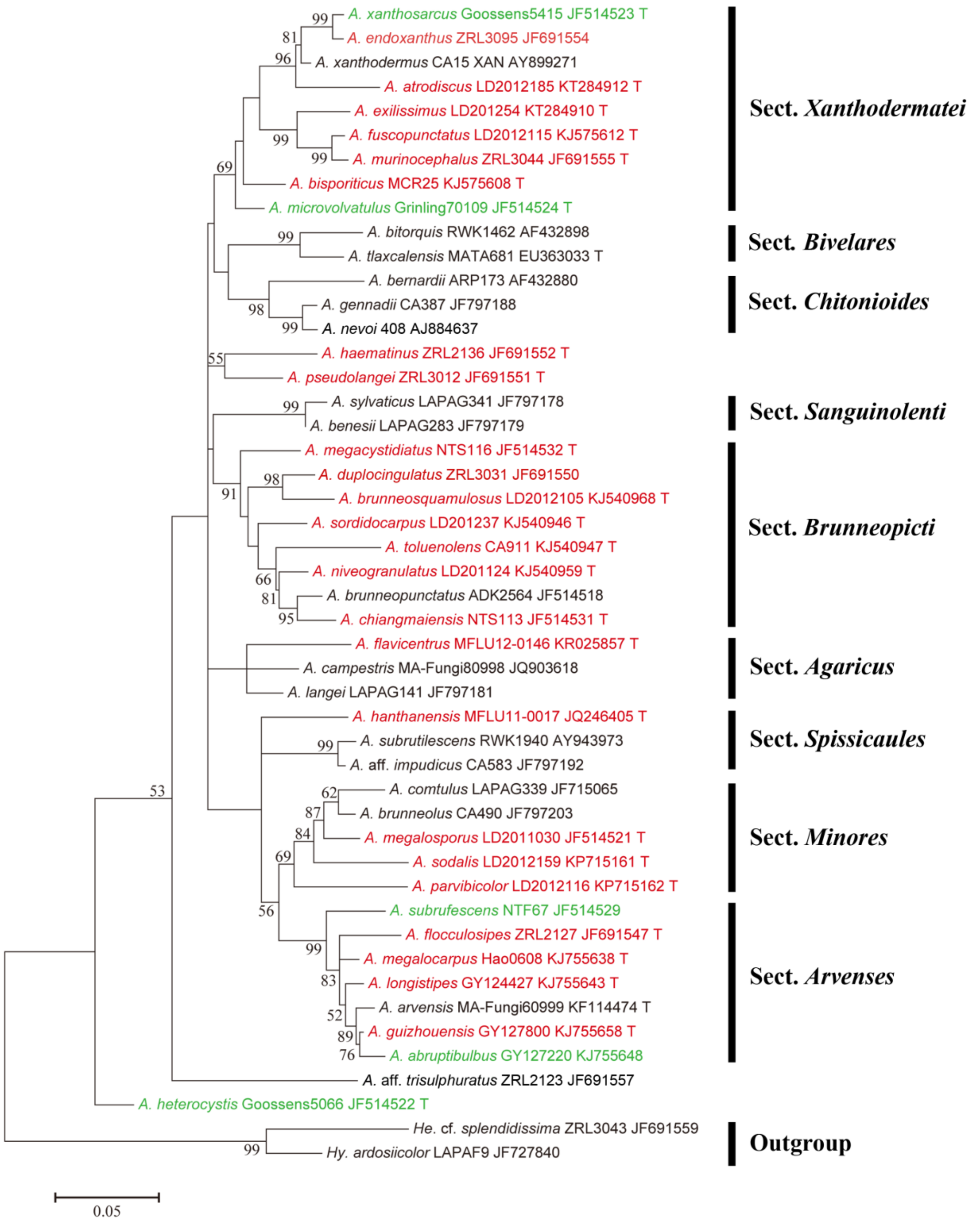

Fig. 1 ML phylogram based on ITS1+2 sequences showing 29 species of *Agaricus* described or reported from tropical and humid subtropical regions of Asia, which have been sequenced before 2016. Species originally described from this region are indicated in red while those only reported are in green. T = type specimen (a recent epitype in the case of *A. arvensis*). *A. brunneopunctatus* has been recently proposed to replace the illegitimate name *A. brunneopictus*. The two outgroup species are *Heinemannomyces* cf. *splendidissima* Watling and *Hymenagaricus ardosiicolor* (Heinem.) Heinem. Eight classical sections and the palaeotropical section *Brunneopicti* are shown. For each sample the species name, the sample number, and the GenBank accession number are indicated.

species. Seven of the 11 tropical clades were statistically well supported and numbered from TR I to TR VII. It was hypothesized that clade TR I might represent *A.* sect. *Brunneopicti.*

This first investigation of tropical species has been followed by several studies using both morphological approaches and phylogenetic analyses based on ITS1+2 sequence data. These studies focused on tropical species in different groups such as the *A.* sections *Xanthodermatei*, the *A.* sect. *Arvenses* and the clade TRI. Based on collections from Thailand, two new species *A. megacystidiatus* Karun., Guinb. & K.D. Hyde and *A. chiangmaiensis* Karun., Guinb. & K.D. Hyde belonging to the clade TRI have been described (Karunarathna et al. 2014, Figure 1). More recently, Chen et al. (2015) confirmed that this clade corresponds to *A.* sect. *Brunneopicti*. The reconstructed section included 16 species grouped in four strongly supported subclades and two isolated branches. Only the six species of one of these clades exhibit punctiform squamules with remains of the veil on the pileus and stipe, which initially characterized this section. In addition, the new name *A. brunneopunctatus* L.J. Chen, Callac & L.A. Parra was introduced to replace the illegitimate name *A. brunneopictus* Berk. & Broome of the type species and four of the 16 species were described as new to science, *A. brunneosquamulosus* L.J. Chen, R.L. Zhao, K.D. Hyde & Callac, *A. niveogranulatus* L.J. Chen, R.L. Zhao, Callac & K.D. Hyde, *A. sordidocarpus* L.J. Chen, Callac & K.D. Hyde, and *A. toluenolens* Callac, L.J. Chen & K.D. Hyde (Figure 1). Studies on *A.* sect. *Xanthodermatei* including Thai and Pakistani tropical samples revealed five new species (*A. atrodiscus* L.J. Chen, Callac, R.L. Zhao & K.D. Hyde, *A. bisporiticus* Nawaz, Callac, Thongklang & Khalid, *A. exilissimus* L.J. Chen, Callac, R.L. Zhao & K.D. Hyde, *A. fuscopunctatus* Thongklang, L.J. Chen, Callac & K.D. Hyde, and *A. murinocephalus* R.L. Zhao, Desjardin & K.D. Hyde) and *A. microvolvatulus* Heinem., which was originally described from Africa, was reported from Thailand (Zhao et al. 2011; Thongklang et al. 2014a, Ariyawansa et al. 2015). Similarly, Gui et al. (2015) reported eight species of *Agaricus* section *Arvenses* from highland subtropical Southwest China and three of them (*A. guizhouensis* Y. Gui, Zuo Y. Liu & K.D. Hyde, *A. longistipes* Y. Gui, Zuo Y. Liu, Callac, L.A. Parra & K.D. Hyde, and *A. megalocarpus* Y. Gui, Zuo Y. Liu, Callac, L.A. Parra & K.D. Hyde) were described as new to science (Fig. 1). However, for certain species the correct classification remains uncertain (*A. hanthanaensis* Karun. & K.D. Hyde, Sri Lanka, Liu et al. 2015) or unresolved (*A. haematinus* K.D. Hyde & R.L. Zhao and *A. pseudolangei* K.D. Hyde & R.L. Zhao, Ariyawansa et al 2015). We predict that the species richness of somewhat forgotten or new tropical sections will increase in coming years.

Toxicity and unknown edibility

Agaricus is a genus of saprobic mushrooms that includes economically important species such as *A. bisporus*, the button mushroom (Savoie et al. 2013, Thawthong et al. 2014). There has been significant ecological, nutritional and medicinal interest in the genus (Dai et al. 2009, 2011), yet the extent of its diversity remains poorly known, particularly in subtropical and tropical areas (Zhao et al. 2011). Excellent edible frequently consumed species belong to the sections *Agaricus*, *Arvenses, Bivelares*, *Nigrobrunnescentes* and *Sanguinolenti*, nevertheless, heavy metal accumulation (cadmium, lead and mercury) has been reported in species of *A.* sect. *Arvenses* (Kalac & Svoboda 2000). In the five remaining sections most species are toxic or their edibility is generally unknown for different reasons; for example, they may be unattractive (unpleasant odour, small basidiosporocarps) or simply too rare, hard to identify, or recently recognized.

In *A.* sect. *Spissicaules*, *A. litoralis* (Wakef. & A. Pearson) Pilát is edible. However, *A. bresadolanus* Bohus is regarded as toxic causing gastro-intestinal syndrome. Other species are suspect and also difficult to identify.

Species of *A.* sect. *Minores* are not popular because they are hard to identify, even for experts, and they are generally small. However, it can be noted that intoxication by such species has not been reported and that they generally have a pleasant almond-like odour, as do species of the closely related *A.* sect. *Arvenses*. *Agaricus brunneolus* (I.E. Lange) Pilát (syn. *A. porphyrizon* P.D. Orton) is one of the relatively large and sometimes abundant species of this section which is consumed in Europe (Cappelli 2011).

Species of *A.* sect. *Chitonioides* are sometimes eaten, although certain species can exhibit an unpleasant odour that disappears with cooking, such as *A. bernardii* Quél. which is widely consumed and highly prized by many families in certain places of Denmark. Bernard (1882) reported that *A. bernardii* is edible and sold at the market in La Rochelle (France). Møller (1950) pointed out that it is often eaten and is not toxic, even though many people do not like it because of its unpleasant smell, and because it is tough and somewhat indigestible.

The edibility of species of *A.* sect. *Brunneopicti* (Chen et al. 2015) is generally unknown except for the two species *A. subsaharianus* L.A. Parra, Hama & De Kesel and *A. bingensis* Heinem., which are consumed in Africa (Hama et al. 2010, Pegler 1977). This section contains species with odours ranging from pleasant bitter almond-like smells, to unpleasant odours similar to phenol or the solvents used in marker pens. Species exhibiting these kinds of unpleasant odours are potentially toxic, similar to the species of *A.* sect. *Xanthodermatei*, which give off similar odours.

Species of the *A.* sect. *Xanthodermatei* are recognized or suspected to be toxic. They are characterized by a negative Schäffer's reaction, a positive KOH reaction (yellow), an odour of phenol (sometimes faint or absent), and a yellow (sometimes absent or reddish) discoloration when cut or bruised (Kerrigan et al. 2006, Parra 2013, Thongklang et al. 2014a). Despite their potential or recognized toxicity, some species of this section are regularly eaten and tolerated by some people from Eastern Europe and Russia (Pilat 1951, Bohus 1974, Kerrigan et al. 2006, Parra 2008) or Spain (Parra 2008) without gastro-intestinal symptoms. Genevier (1876) reported that *A. xanthodermus* Genev. was sold in the markets of Nantes and noted three *A. xanthodermus* poisoning cases, of which one was serious. Menier (1893) noted that *A. menieri* Bon was not tasty, and though not much prized, it was eaten in Siant-Brevin. Spegazzini (1919) pointed out *A. iodoformicus* Speg. (a synonym of *A. xanthodermus*) is edible, despite its strong odour and taste of iodoform perceivable even in dried specimens. Regarding the edibility of *A. phaeolepidotus* F.H. Møller, Pilat & Ušak (1961) mentioned it is a good edible fungus. Genevier (1876) and Jordan (2000) indicated that some people can eat *A. xanthodermus* and *A. placomyces* Peck without any ill-effects at all, while Passecker (1930) reported that inhabitants of Rosemberg, Austria, cultivate *A. xanthodermus* by cutting the stipes and planting the caps of *A. xanthodermus* in gardens, after which basidiomes appear in the following year which are collected and eaten without any problem; moreover Passecker (1930) cultivated *A. xanthodermus* mycelia artificially and noted that the mycelia smelled of phenol. Bon (1987) and Jordan (2000) reported that eating *A. xanthodermus* can cause alarming symptoms including coma, vomiting or diarrhea, but recovery is complete within a few days. According to Walton (1986) three families suffered by consuming *A. xanthodermus*. First detected in *A. xanthodermus* (Gill & Strauch 1984), the phenol is also the major volatile component in *A. moelleri* Wasser (syn. *A. praeclaresquamosus* A.E. Freeman) (Wood et al. 1998) and likely responsible for the poisonous symptoms. In the medical poison center in Marseille, France, 20% of poisonings by identified mushrooms are due to ingestion of species of *A.* sect. *Xanthodermatei* (De Haro et al. 1999).

Agaricus species having high value as edible and medicinal mushrooms

The main cultivated species are in section *Bivelares* and *Arvenses*, while it remains difficult to cultivate species of sections *Sanguinolenti*, *Nigrobrunnescentes* and *Agaricus* because mycelium growth rate is generally too slow (Callac 2007). The consumed species in section *Sanguinolenti* (e.g. *A. sylvaticus* Schaeff.) and in section *Nigrobrunnescentes* (e.g. *A. lilaceps* Zeller) are considered very tasty (Wang et al. 2015). Unfortunately, cultivation of *A. lilaceps* on standard substrates has been limited or has failed due a slow mycelium growth rate (Hildén et al. 2013).

In *Agaricus* sect. *Agaricus*, *A. campestris* (the field or meadow mushroom) is widely collected and eaten, but this mushroom is not commercially cultivated on account of its fast maturing and short shelf-life (Grigson 1975). In fact, the cultivation of this species has never been formally reported. Studies reported on *A. campestris* must be carefully considered knowing that this species was in the past frequently confused with other species of *A.* sect. *Agaricus* or even with species of other sections such as *A. bisporus*. This possibly results from the perpetuation of an outdated and incorrect concept confusing samples of different species exhibiting a white pileus. In fact, the colour of the pileus can vary from white to dark brown within the populations of *A. bisporus* (Callac et al. 2002). For example, it is unfortunate that Gray and Flatt (1998) report in their "materials and methods" section of their study: "Plant material. Dried fruiting bodies of mushroom (*A. campestris*) obtained from a commercial source". The antihyperglycemic effects reported by these authors and subsequently by Gallagher et al. (2003), Patrick (2008), and De Silva et al. (2012b) do not concern *A. campestris,* but likely *A. bisporus*.

In *A.* sect. *Bivelares* most species seem edible and cultivatable, but only *A. bisporus* and *A. bitorquis* are commercially cultivated. Species closely related to *A. bisporus* (*A. subfloccosus* (J.E. Lange) Hlaváček and *A. agrinferus* Kerrigan & Callac) have been cultivated on an experimental basis in several laboratories and are regarded as high-quality mushrooms (Noble et al. 1995, Kerrigan et al. 1999, 2008, Callac et al. 2005). Interestingly, *A. cupressicola* Bon & Grilli and many strains of *A. devoniensis* P.D. Orton, the sand dune mushroom, have been successfully cultivated at INRA, France (Callac et al. 2005, Callac 2007).

In *A.* sect. *Arvenses* most species seem to be edible, but not all of them are cultivatable, and only *A. subrufescens* Peck. and *A. arvensis* Schaeff. are commercially cultivated. There are reports of cultivation experiments of *A. macrosporoides* Bohus (Bohus 1978, 1987), *A. crocodilinus* Murrill (syn. *A. macrosporus* (F.H. Møller & Jul. Schäff.) Pilát and *A. urinascens* (Jul. Schäff. & F.H. Møller) Singer) (Fermor 1982) and *A. sylvícola* (Vittad.) Peck (Heinemann 1977). *Agaricus flocculosipes* R.L. Zhao, Desjardin, Guinb. & K.D. Hyde was described from northern Thailand, and is expected to be a good edible species that may have potential commercial value for Thailand and other tropical countries. It also has an almond flavor (Zhao et al. 2012b) and some fruit bodies have been obtained through cultivation (Thongklang et al. 2014b). *Agaricus guizhouensis,* which is consumed in China, and *A. megalocarpus* are potentially valuable for cultivation because of their relatively large sized sporocarps. Although *A. longistipes* has smaller sporocarps, it may be of medicinal interest since it is a relative of the robust *A. crocodilinus,* in which analgesic triglycerides have been discovered (Stadler et al. 2005, Gui et al. 2015). *Agaricus augustus* Fr. is mainly collected in Europe and North America, and is highly sought after for its flavor (Boa 2006); however, despite its popularity it has never been successfully cultivated. Wild edible mushrooms in the section *Arvenses* include *A. arvensis*, *A. augustus* and *A. sylvicola*, all of which are collected from the wild for human consumption in Europe and the Americas (Kalač & Svoboda 2000, Wisitrassameewong et al. 2012a, Thongklang et al. 2014b). Nutritional studies have been carried out on *A. augustus, A. crocodilinus* and *A. essettei* Bon (Elliott 1978, Fermor 1982, Geml & Rimoczi 1999, Dabbour & Takruri 2002, Geml & Royse 2002, Barros et al. 2007, Ozturk et al. 2011, Marekov et al. 2012); volatile components responsible for almond or aniseed odours have been identified in several species such as *Agaricus essettei* (Rapior et al. 2002). *Agaricus crocodilinus* has been reported as a potential bioremediation agent (Garcia et al. 2005).

Commercially cultivated species of *Agaricus* and their medicinal potential

Commercially cultivated *Agaricus* species belong to the sections *Bivelares* or *Arvenses*. The species of *A.* sect. *Bivelares* are known to be highly nutritious, an example being *A. bisporus.* This mushroom was first cultivated three and half centuries ago in France, and remains the most widely cultivated species of edible mushrooms, representing about 32% of world production in 1997 and 21% in 2013 (Chang 1999; Challen et al. 2003; Anonymous 2004, Zhang et al. 2015). *Agaricus bisporus* has a broad geographic distribution all along the temperate areas of the north hemisphere. A highly diversified germplasm is available (Callac et al. 2002) and the biology and genetics of *A. bisporus* has been well documented (Savoie et al. 2013). Great attention has been focused on the immune modulating and antitumor properties of *A. bisporus* (Yu et al. 1993, Chen et al. 2006, Ren et al. 2008, Adams et al. 2008, Jeong et al. 2010). This mushroom has potential anti-inflammatory, hypoglycemic and hypocholesterolemic effects due to the presence of high amounts of acidic polysaccharides, dietary fibre, antioxidants (folate, ergothioneine, polyphenol) and vitamins (C, B12, D) (Fukushima et al. 2000, Mattila et al. 2001, Koyyalamudi et al. 2009, Geösel 2011). It also suggests that a high intake of button mushrooms may promote innate immunity against tumors and viruses (Wu et al. 2007, Adotey et al. 2011, De Silva et al. 2012a, b). Lectins are abundant in *A. bisporus* and dehydrated fruiting body extracts of *A. bisporus* have been shown to lower blood glucose and cholesterol levels (Jeong et al. 2010, Yamac et al. 2010, Smiderle et al. 2011, De Silva et al. 2012a). Rats fed with *A. bisporus* fruiting bodies exhibited significant anti-glycemic and anti-hypercholesterolemic effects (Jeong et al. 2010, Volman et al. 2010, De Silva et al. 2013), and significant decrease in plasma total cholesterol (TC) and low-density lipoprotein (LDL) (22.8 % and 33.1 %) accompanied by a significant increase in plasma high-density lipoprotein concentrations. This was observed after oral administration of *A. bisporus* for four weeks in an animal model (Jeong et al. 2010, De Silva et al. 2013). Moreover, this mushroom shows a positive influence on lipid metabolism and liver function.

Another commercially cultivated species of *A.* sect. *Bivelares* is *A. bitorquis* (the pavement mushroom), which is frequently found on hard-packed soils. It was first introduced for cultivation by Poppe (1972) in the 1970s and its cultivation has persisted in regions with hotter climates, including India (Cappelli 1984, Heinemann 1978, Kerrigan 1986). In Spain *A. bitorquis* is grown instead of *A. bisporus* in hot summers as it has a slightly higher growth temperature. However, recent studies have shown that certain strains of *A. bisporus* can also fructify at the relatively high temperature of 25 °C or more (Largeteau et al. 2011).

Agaricus subrufescens, the almond mushroom, is a species of *A.* sect. *Arvenses* which was first discovered in eastern North America and commercially cultivated in USA from 1890 to 1910 (Peck 1893, Kerrigan 2005, Firenzuoli et al. 2008). This species was ‘rediscovered’ and cultivated in Brazil but misidentified as *Agaricus blazei* Murrill (or ABM) or *Agaricus sylvaticus* (misapplied names, Dias et al. 2004). This species is also used as a health food for alternative medicines and cultivated in Asia, mainly in Indonesia, China, Japan, and Taiwan. For taxonomy and synonymy of this taxon we follow Kerrigan (2005), Arrillaga and Parra (2006), Ludwig (2007), Cappelli (2011) and Thongklang et al. (2016). Main synonyms are *A. blazei sensu* Heinemann (1993), *A. bambusae* Beeli var. *bambusae* (1928), *A. rufotegulis* Nauta (1999), *A. brasiliensis* Wasser, M. Didukh, Amazonas & Stamets (2002) nom. illegit., and *A. albopersistens* Zuccher (2006). *Agaricus subrufescens* is a cosmopolitan species reported from the Americas, Oceania (Hawaii) and Europe (Kerrigan 2005), and more recently from Thailand (Wisitrassameewong et al. 2012a), China (Gui et al. 2015) and Africa (Thongklang et al. 2016). This sort of large geographical distribution range is infrequent in the genus *Agaricus* and thus the question of potential interfertility between specimens originating from different continents arose. Kerrigan (2005) reported hybridization between Brazilian and Californian strains, and recently, Thongklang et al. (2014c) showed that samples from Brazil, France and Thailand are amphithallic (i.e. both heterothallic and pseudohomothellic) and interfertile in all pairwise combinations. In addition, Brito de Rocha et al. (2016) found that the sporocarps of certain isolates produce a proportion of heterokaryotic spores giving rise to heterokaryons, which are infertile (i.e. unable to fruit), but can easily cross with homokaryons. Recent genetic analyses revealed a duplication of the ITS in a French isolate suggesting a possible introgression from Asian or African populations (Chen et al. 2016a). A genetic linkage map of *A. subrufescens*, which exhibits a highly conserved macrosynteny with *A. bisporus* was published recently (Foulongne-Oriol et al. 2016). Such a rich available germplasm and so much available information relating to the genetics and biology of *A. bisporus* should facilitate the genetic improvement of *A. subrufescens* in the future.

However, currently, with the exception of a Brazilian-Californian hybrid, strains of *A. subrufescens* that are commercially cultivated in Asia have likely been introduced from Brazil. Thongklang et al. (2014b) showed the successful results of preliminary fruiting test of a Thai wild strain, while Jatuwong et al. (2014) described the development of a Thai-French hybrid strain of *A. subrufescens* recently developed through a joint program between INRA, France and Mae Fah

Luang University. This strain has the potential to grow in northern Thailand, as its optimal growth conditions are 25–30˚C with 91–95 % relative humidity. *Agaricus subrufescens* has many health promoting benefits or medicinal properties such as anti-cancer and tumor suppressive activity, anti-genotoxicity activities, cytokine induction activity, lymphocyte activation activity, antimicrobial activity, anti-allergy effect, and biological responses on the immune system (Wisitrassameewong et al. 2012b). There has also been research on the nutraceutical properties of *A. subrufescens* and the protective effects of β-glucans (Angeli et al. 2006; Mantovani et al. 2007). The same fungus has also been reported to have anti-mutagenic activity (Menoli et al. 2001, Machado et al. 2005), anti-clastogenic properties (Luiz et al. 2003), anti-genotoxic activity (Martins de Oliviera et al. 2002) and anti-tumor effects (Kawagishi et al. 1989, Mizuno et al. 1990, 1999, Lee et al. 2003). *Agaricus subrufescens* has previously been reported to have pharmaceutical potential (Firenzuoli 2008) and is used in cosmetics (Hyde et al. 2010). Under the misapplied name *A. sylvaticus* some research has investigated its effects on cancer and AIDS, and other potential medicinal properties (Gennari 2000a, 2000b, Gennari et al. 2001, Taveira et al. 2008; Fortes et al. 2008, 2009, Fortes and Carvalho 2011, De Silva et al. 2012b, 2013). In spite of these useful properties, the reason *A. subrufescens* has not found wide commercial application is possibly its difficulty of digestion and strong almond flavour (Wisitrassameewong et al. 2012b). Although this is a well-known edible species, we queried northern Thai locals in local markets and concluded that this species is not popularly consumed.

Agaricus arvensis, the horse mushroom, is also a species of *A.* sect. *Arvenses* cultivated in Europe (Galli 2004), where it is produced by mushroom cultivators in France and Holland (Couvy 1974). A recent study, however, indicated that a strain commercialized under this name belongs to the closely related species *A. fissuratus* F.H. Møller (Parra 2013).

A checklist of species reported from tropical and humid subtropical regions of Asia

In Table 1, we listed 84 species of *Agaricus* described before 2016 from tropical and humid subtropical regions of Asia. Historically, 31 species were described in the nineteenth century, mostly (27) from Sri Lanka by the British mycologists M. J. Berkeley and C. E. Broome. These species have relatively short descriptions and only a few of them have been further studied, again by P. Heinemann or D. Pegler. A single species is well known today, *A. endoxanthus* Berk. & Broome, which is distributed in most tropical areas and has even been introduced to tropical niches of temperate regions such as greenhouses (Chen et al. 2016b). In the twentieth century, 31 new species were described including eight, mainly from Singapore, by the Belgium mycologist P. Heinemann. Only one, *A. duplocingulatus*, has been recently reported again, in Thailand (Chen et al. 2015). From 2000 to 2015, 22 new species have been described, mostly (18 species) from Thailand.

Sequence data (ITS) are currently available in GenBank for 24 of the 84 (29 %) species originally described from tropical and subtropical humid areas of Asia. This includes *A. endoxanthus*, *A. duplocingulatus* Heinem. and the 22 new species described from 2000 to 2015. In addition, sequences of specimens collected in this Asian region, but belonging to five species initially described from other continents are also available. Two of them, *abruptibulbus* Peck (1905) and *A. subrufescens* Peck (1894), are cosmopolitan species which have been originally described from North America, then reported from Europe and more recently from subtropical China (Gui et al. 2015). Moreover, *A. subrufescens*, which is one of the rare species of the genus to be distributed in both temperate and tropical areas, has also been reported from Thailand (Wisitrassameewong et al. 2012a). The three remaining species, *A. heterocystis* Heinem. & Gooss. Font., *A. microvolvatulus* and. *A. xanthosarcus* Heinem. & Gooss.-Font., are exclusively tropical and were originally described from tropical Africa by Heinemann (1956, 1971). Zhao et al. (2011) reported Thai samples having ITS sequences identical to their respective African type specimens. Because morphological comparative studies have not yet been done except for *A. microvolvatulus* (Thongklang et al. 2014c), these three species are represented by their African type specimen in the phylogenetic tree of Figure 1. In sum, 29 species from tropical or humid subtropical regions of Asia are represented in the phylogenetic tree of Figure 1: 24 species originally described from these regions, two cosmopolitan species (*A. subrufescens* and *A. abruptibulbus*), and three tropical species distributed in both Africa and Asia (*A. heterocystis, A. microvolvatulus* and. *A. xanthosarcus*). It must be noted that many unnamed species or species newly described since 2016 are not included in this review.

Climate was noted as a major factor in the evolution of *Agaricus* by Zhao et al. (2011). Among the 29 sequenced species, 25 have been described or reported from tropical areas, mainly in Thailand. Among these 25 species, only the cosmopolitan species *A. subrufescens* and the "great traveler" species *A. endoxanthus* are also reported in temperate areas but the latter only because it was introduced to tropical greenhouses (Chen et al. 2016b). Another species, *A. flocculosipes*, is reported from the subtropical region of China. It can be noted that the two non-strictly tropical species *A. subrufescens* and *A. flocculosipes*, both belonging to *A.* sect. *Arvenses*, are also reported from tropical Africa by Zhao et al. (2012b) and Thongklang et al. (2016). Among the remaining 22 species having a known strictly tropical distribution range, 17 belong to the three sections *A.* sect. *Xanthodermatei*, *Minores,* and *Brunneopicti*, one to *A.* sect. *Agaricus,* one to *A.* sect. *Spissicaules*, and the three remaining species are unclassified. This count roughly reflects the phylogenetic diversity and species richness of *Agaricus* in tropical Asia where two traditional sections (*A.* sect. *Xanthodermatei* and *A.* sect. *Minores*) and tropical sections (*A.* sect. *Brunneopicti* and unnamed groups) dominate. Few members of *A.* sect. *Arvenses* are also present but they are not exclusively tropical, except for *A. subtilipes* Thongklang, L.J. Chen, Callac & K.D. Hyde, a new species recently described in 2016 (Thongklang et al. 2016) and thus not included in our checklist.

We, members of Center of Excellence in Fungal Research collected 400 *Agaricus* specimens in a small area of Northern Thailand between May 2005 and October 2015. These samples potentially include more than 70 novel species, indicating that *Agaricus* is a species-rich genus in the tropics as well as in temperate regions (Zhao 2008, Zhao et al. 2011, 2012a, b, Chen et al. 2012, 2015, Karunarathna et al. 2014, Thongklang et al. 2014a, b, 2016, Thongklang 2016). In agreement with the checklist and the tree presented above, no species of *A.* sect. *Bivelares* or *A.* sect. *Chitonioides* and only a few species of *A.* sect. *Agaricus, A. sect. Sanguinolenti* and *A.* sect *Spissicaules*, were found. We did not list all the species originally described from other continents and reported from tropical or humid subtropical Asia, except those that were molecularly confirmed. The reason is that most identification of such species are dubious. For example, some species originally described in Europe such as *A. campestris*, *A. bisporus* and *A. bitorquis* have been inventoried from Thailand in local reports (Zhao 2008, Chandrasrikul et al. 2011). In absence of published detailed descriptions or ITS sequences, these identifications will remain doubtful, given that during ten years of field collecting in Thailand we never found any species which was originally described in Europe. However, the reports of some species originally described from Africa, such as *A. rufolanosus,* are more plausible.

Numerous new species, mostly of *A.* sect. *Xanthodermatei, A.* sect. *Minores* and *A.* sect. *Brunneopicti* remain to be named. However, before describing a new species, we generally expect to have several samples and to know its phylogenetic position. This allows us to take into consideration intraspecific variability and to identify characteristics that are distinct from neighboring species. Certain species of *A.* sect. *Minores* and *A.* sect. *Brunneopicti* would merit investigation of their edibility and cultivability. Some species remain unclassified and certain putative tropical new sections remain to be named. However, new species and sections have been recently proposed in 2016 (Zhao et al. 2016), including, for example, the new *A.* sect. *Amoeni* Callac & Zhao corresponding to the tropical clade TRIII in Zhao et al. (2011). An inventory of *Agaricus* species in tropical and humid subtropical regions of Asia will be a first step towards describing numerous species new to science. Further research could build on the present study by providing DNA sequences and developing the classification of species in tropical regions of Africa and the Americas.

Table 1 *Agaricus* species originally described until end 2015 from tropical and humid subtropical regions of Asia

Country	Species	Reference
China		
Yunnan prov.	*A. dimorphosquamatus* Yu Li	Li 1990
Yunnan prov.	*A. lepiotiformis* Yu Li	Li 1990
Yunnan prov.	*A. compressipes*W.F. Chiu	Wei-Fan 1973
Yunnan prov.	*A. yunnanensis* W.F. Chiu	Wei-Fan 1973
Guizhou prov.	***A. guizhouensis*** Y. Gui et al.	Gui et al. 2015
Guizhou prov.	***A. longistipes*** Y. Gui et al.	Gui et al. 2015
Guizhou prov.	***A. megalocarpus*** Y. Gui et al.	Gui et al. 2015
India		
Bengal	*A. burkillii* (Massee) Sacc. & Trotter	Saccardo & Trotter 1913
	Basionym *Psallota burkillii*	Massee 1907
Calcutta	*A. squalidus* Massee Nom. illegit.	Massee 1912
Bombay	*A. woodrowii* Massee	Massee 1901
	A. fulviceps Berk.	Berkeley 1854
Karnataka	*A. heinemanniensis* K. Natarajan & Purush.	Natarajan & Purushothama 1996
Kerala	*A. basianulosus* Paracer & Chahal	Paracer & Chahal 1963 [1962]
Japan		
	A. semotellus S. Imai.	Imai 1938
	A. comtulellus S. Imai.	Imai 1938
	A. jezoensis S. Imai.	Imai 1938
Bonin Islands	*A. primipilus* Berk. &M. A. Curtis	Berkeley & Curtis 1860 [1858]
Java		
	A. rhinocerotis Jungh.	Junghuhn 1840
	A. inoxydabilis[a] Heinem.	Heinemann 1980
Malaysia		
Penang	*A. inoxydabilis*[a] Heinem.	Heinemann 1980
Sabah	*A.albidoperonatus* Heinem.	Heinemann 1980
Pakistan		
Punjab	***A. bisporiticus***[b] Nawaz et al.	Thongklang et al. 2014a
Philippines		
	A. argyrotectus Copel.	Copeland 1905
	A. boltoni Copel.	Copeland 1905
	A. philippinensis Berk.	Berkeley 1842
	A. merrillii Copel.	Copeland 1905
	A. manilensis Copel.	Copeland 1905
	A. perfuscus Copel.	Copeland 1905
Singapore		
	A. inedulis Heinem.	Heinemann 1980
	A. pleurocystidiatus Heinem.	Heinemann 1980
	A. inoxydabilis[a] Heinem.[a]	Heinemann 1980
	*A. hypophaeus*Heinem.	Heinemann 1980
	A.duplocingulatus Heinem.	Heinemann 1980
	(in Thailand)	Chen et al. 2015
	A.oenotrichus Heinem.	Heinemann 1980
	A. singaporensis Heinem.	Heinemann 1990
	A. tenuiceps Massee	Massee 1914
Sri Lanka		
	A. simulans Berk.	Berkeley 1847
	A. rufo-albus Berk.	Berkeley 1847
	A. crocopeplus Berk. & Broome	Berkeley & Broome 1871
	(in Singapore)	Heinemann 1980
	(in Sri Lanka; subg. *Lanagaricus*)	Peggler 1986
	A. didactylus Berk.& Broome	Berkeley & Broome 1871
	A. spilocephalus Berk.& Broome	Berkeley & Broome 1870 [1871]
	A. lasiophrys Berk. & Broome	Berkeley & Broome 1871
	A. hemilasius Berk. & Broome	Berkeley & Broome 1871
	A. endoxanthus Berk. & Broome	Berkeley & Broome 1871
	(in Thailand)	Zhao et al. 2012a

Country	Species	Reference
	(in Malaysia)	Chen et al. 2016b
	A. actinorachis Berk. & Broome	Berkeley & Broome 1871
	(in SriLanka; subg. *Conioagaricus*)	Pegler 1986
	A. tornocephalus Berk. & Broome	Berkeley & Broome 1871
	A. nymphidius Berk. & Broome	Berkeley & Broome 1871
	A. bolorhizus Berk. & Broome	Berkeley & Broome 1871
	(in Sri Lanka)	Pegler 1986
	A. dyspines Berk. & Broome	Berkeley & Broome 1871
	A. lituratus Berk. & Broome	Berkeley & Broome 1871
	A. celidotus Berk. & Broome	Berkeley & Broome 1871
	A. chrysocyclus Berk. & Broome	Berkeley & Broome 1871
	A. lepiotoides Berk. & Broome	Berkeley & Broome 1871
	A. rhodochrous Berk. & Broome	Berkeley & Broome 1871
	A. argineus Berk. & Broome	Berkeley & Broome 1871
	A. microcosmus Berk. & Broome	Berkeley & Broome 1871
	A. plumarius Berk. & Broome	Berkeley & Broome 1871
	A. callipeplus Berk. & Broome	Berkeley & Broome 1871
	(in Sri Lanka)	Pegler 1986
	A. chloroconius Berk. & Broome	Berkeley & Broome 1871
	A. illotus Berk. & Broome	Berkeley & Broome 1871
	A. illotus var. thyranophurus Berk. & Broome	Berkeley & Broome 1871
	A. subcitrinus Berk. & Broome	Berkeley & Broome 1871
	A. erythrospilus Berk. & Broome	Berkeley & Broome 1871
	A. subaeruginosus Berk. & Broome	Berkeley & Broome 1871
	A. stadii (Petch) Cash	Cash, in Trotter 1972
	(basionym: *Psalliota stadii*)	Petch 1925
	A. petchii Pegler nom nov.	Pegler 1986
	(syn. *Psalliota zeylanica* Petch)	Petch 1917
	A. hanthanaensis Karun. & K.D. Hyde	Liu et al. 2015
Thailand		
Chiang Rai	***A. flocculosipes***[c] R.L. Zhao et al.	Zhao et al. 2012b
	(in Guizhou, China)	Gui et al. 2015
Chiang Rai	***A. megalosporus*** J. Chen et al.	Chen et al. 2012
Chiang Rai	***A. bisporiticus***[b] Nawaz et al.	Thongklang et al. 2014a
Chiang Rai	***A. fuscopunctatus*** Thongklang et al.	Thongklang et al. 2014a
Chiang Mai	***A. murinocephalus*** R.L. Zhao et al.	Zhao et al. 2012a
Chiang Mai	***A. megacystidiatus*** Karunarathna et al.	Karunarathna et al. 2014
Chiang Mai	***A. chiangmaiensis*** Karunarathna et al.	Karunarathna et al. 2014
Chiang Mai	***A. niveogranulatus*** L.J. Chen et al.	Chen et al. 2015
Chiang Mai	***A. brunneosquamulosus*** L.J. Chen et al.	Chen et al. 2015
Chiang Mai	***A. sordidocarpus*** L.J. Chen et al.	Chen et al. 2015
Chiang Mai	***A. toluenolens*** Callac et al.	Chen et al. 2015
Chiang Rai	***A. flavicentrus*** Karunarathna & K.D. Hyde	Liu et al. 2015
Chiang Mai	***A. parvibicolor*** L.J. Chen et al.	Liu et al. 2015
Chiang Mai	***A. sodalis*** L.J. Chen et al.	Liu et al. 5015
Chiang Mai	***A. atrodiscus*** L.J. Chen et al.	Ariyawansa et al. 2015
Chiang Mai	***A. exilissimus*** L.J. Chen et al.	Ariyawansa et al. 2015
Chiang Mai	***A. haematinus*** K.D.Hyde & R.L.Zhao	Ariyawansa et al. 2015
Chiang Mai	***A. pseudolangei*** K.D.Hyde & R.L.Zhao	Ariyawansa et al. 2015
Vietnam		
	A. iocephalus Pat., (syn. *A. iocephalusiopsis*)	Patouillard 1913
	A. phaeocyclus Pat.	Patouillard 1913
	A. rhopalopodius Pat.	Patouillard 1913

[a] Described from Java, Malaysia and Singapore
[b] Described from both Thailand and Pakistan
[c] Described from both Thailand and Mayotte Island (Africa)
Available ITS GenBank accession number of species in bold type are indicated in Fig. 1

Acknowledgements

Andrew Stevenson in the World Agroforestry Centre (ICRAF), East and Central Asia Office, Kunming Institute of Botany, Kunming, Yunnan, China is thanked for English editing. Saranyaphat Boonmee and Thatsanee Luangharn (MFLU) are thanked for their assistance in the herbarium. Kevin D. Hyde thanks the Chinese Academy of Sciences, project number 2013T2S0030, for the award of Visiting Professorship for Senior International Scientists at Kunming Institute of Botany. This study was financially supported by Thailand Research Fund grant - Taxonomy, Phylogeny and biochemistry of Thai Basidiomycetes (BRG 5580009), the National Research Council of Thailand (NRCT), projects - Taxonomy, Phylogeny and cultivation of *Lentinus* species in northern Thailand (NRCT/55201020007), Mae Fah Luang University, the project—Taxonomy, Phylogeny and cultivation of *Lentinus* species in northern Thailand (MFU/54 1 01 02 00 48), National Natural Science Funds of China (Project No: 31000013, 31360014 and 31470152), and the Chinese Ministry of Science and Technology, under the 12th 5-year National Key Technology Support Program (NKTSP)2013BAB07B06 integration and comprehensive demonstration of key technologies on Green Phosphate-mountaion Construction. We would also like to thank the CGIAR Research Program 6: Forest, Trees and Agroforestry, for partially funding this work.

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