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# A description of eleven new species of *Agaricus* sections *Xanthodermatei* and *Hondenses* collected from Tibet and the surrounding areas

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## Abstract

Specimens of *Agaricus* sections *Xanthodermatei* and *Hondenses* were collected in Tibet and the surrounding areas. All specimens were morphologically described and subjected to molecular phylogenetic analysis of the ITS and combined ITS, LSU and *tef-1α* sequence data using Bayesian and Maximum Likelihood methods. Twelve species were identified in this study, eleven of which were new species and one of which was identified in China for the first time. All of the identified species are described and illustrated with photo plates.

**Key words:** Agaricaceae, multigene analysis, phylogeny, taxonomy

## Introduction

*Agaricus* L. (1753: 1171) (Agaricaceae, Agaricales) is a genus containing many edible species, such as *A. bisporus* (J.E. Lange 1926: 8) Imbach (1946: 15) and *A. subrufescens* Peck. (1893: 105) are commercially cultivated worldwide (Zhao *et al.* 2011). Due to their high culinary and medicinal value, *Agaricus* has been well studied by mycologists from Europe and Northern America (Cappelli 1984; Heinemann 1978; Kerrigan 1986, 2016; Møller 1950; Parra 2008, 2013; Pilát 1951; Singer 1986). Before 2000, several studies on *Agaricus* were published describing their morphological features from a number of regions of Asia, such Ceylon (Sri Lanka) (Berkeley 1847; Berkeley & Broome 1870, 1871; Pegler 1986; Petch 1917, 1925) and Tonkin (Vietnam) (Patouillard 1913; Yang 2000). More recently, studies have systematically investigated *Agaricus* in Western China and Southeast Asia using morphological and phylogenetic methods (Chen *et al.* 2015; Thongklang *et al.* 2014; Wang *et al.* 2015; Zhao *et al.* 2011, 2012).

The section *Xanthodermatei* was introduced based on *A. xanthodermus* Genev. (1876: 28) (Singer 1948). This section is characterized by: 1) a negative Schäffer reaction and a bright yellow discoloration in the KOH reaction, 2) a pileus surface and stipe base that show a temporary yellow discoloration when bruised or cut, and 3) a phenolic or iodine-like odor (Parra 2008). However, there were exceptions to these criteria: *A. biannulatus* Mua, L.A. Parra, Cappelli & Callac (2011: 8) and *A. murinocephalus* R.L. Zhao, Desjardin & K.D. Hyde (2013: 189), have neither a yellow discoloration when bruised nor a phenol-like odor (Parra *et al.* 2011; Zhao *et al.* 2012). Furthermore, species in sections *Arvenses* and *Minores* turned yellow when touched or on cutting; however, those taxa were distinguished from sect. *Xanthodermatei* by their more persistent color change, positive Schäffer reaction, anise seed or almond-like odors, and lack of toxic compounds (Parra 2008). Molecular studies using ITS sequence data from samples from

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Europe and North America indicate that this section is monophyletic (Callac & Guinberteau 2005; Challen *et al.* 2003; Geml *et al.* 2004; Kerrigan *et al.* 2005). Later phylogeny studies of *Agaricus* using the ITS sequences of specimens from temperate and tropical areas also indicated that this section is a monophyletic group with 85 supporting BS, composed of two well-supported clades, which are represented by *A. xanthodermus* and *A. hondensis* Murrill (1912: 296), respectively (Zhao *et al.* 2011). The most recent study on this section was based on specimens from Thailand and Pakistan and revealed a new clade in this section. However, this clade was without statistical support (Thongklang *et al.* 2014).

The most recent study on *Agaricus* using multi-gene sequences reconstructed the taxonomic system of this genus (Zhao *et al*. 2016). In this study section *Xanthodermatei*, which was previously recognized to be a monophyletic group, has been re-recognized as a polyphyletic group has been split into two clades, represented by *A. xanthodermus* and *A. hondensis*. Between those two isolated clades, there are new molecularly recognized section *Trisulphurati* and a new section *Crassispori* (Zhao *et al*. 2016). The previous section *Xanthodermatei* was formally split into two sections, *Xanthodermatei* and *Hondenses,* with type species *A. xanthodermus* and *A. hondensis,* respectively (Zhao *et al*. 2016). Morphologically, the species of section *Hondenses* differs from the section *Xanthodermatei* in terms of its lack of distinct yellow discoloration following contact exposure, lack of a strong phenol or iodine smell, and annulus that is often constituted of two different rings (Zhao *et al*. 2016).

In this paper, we report on specimens of *Agaricus* collected in the south of Tibet and the surrounding areas in central and eastern China and northern Thailand. Of the twenty-four collected specimens, eighteen belonged to eleven new species of sections *Xanthodermatei* and *Hondenses*, one was identified for the first time in China, and five specimens remained unnamed as they were lacking some important field features. The new species are described and illustrated in this paper, and the section is discussed.

## Materials and methods

*Sampling*

Specimens were collected in the forests and grassy areas of China and northern Thailand in 2008, 2011, and 2012. Every specimen was photographed *in situ* and gathered and wrapped in aluminium foil or kept separately in a box to avoid mixing and crushing. Odor and color change upon bruising were recorded at the time of collection.

*Morphological Examination*

Descriptions of the macrocharacters, such as the pileus type, lamellae, context, stipe, annulus, and chemical tests were carried out soon after returning from the field, generally following the methods detailed in Largent (1986). The color terminology used followed that of Kornerup & Wanscher (1978) or the Online Auction Color Chart™ (OAC). Specimens were dried overnight in a food drier and then sealed in plastic bags and deposited in Herbarium Mycologicum Academiae Sinicae (HMAS), Beijing and Mae Fah Luang University Herbarium (Herb. MFLU) (http://sweetgum.nybg.org/ih continuously updated).

The micromorphological features of the samples were documented from dried specimens as described by Largent (1986). The anatomy of the pileipellis and partial veil, features of the basidiospores, basidia and cystidia were examined. Measurements of the anatomical features (basidiospores, basidia and cheilocystidia) were given based on at least 20 measurements and include x, the mean of the length by width ± SD; Q, the quotient of the basidiospore length and width; and Qm, the mean of the Q-values ± SD.

*DNA extraction, Polymerase Chain Reaction (PCR) and Sequencing*

Genomic DNA was extracted from dried specimens using the OMEGA bio-tek (E.Z.N.A.™ Forensic DNA Kit, D3591-01, USA). The ITS1, 5.8S and ITS2 regions (ITS1+2) of the nuclear ribosomal DNA repeat unit were amplified using polymerase chain reaction (PCR) with the primers ITS4 and ITS5 (White *et al.* 1990), nLSU-rDNA was amplified using the primers LROR and LR5 (Vilgalys & Hester 1990), and *tef-1α* was amplified using primers EF1-983F and EF1-1567R (Rehner & Buckley 2005). All of the PCR products were sent to a commercial biotech company for sequencing.

*Phylogenetic Analyses*

The datasets were constituted of sequences produced from this study and downloaded from GenBank (Table 1). The

ITS, LSU and *tef-1α* sequence data were initially aligned using Muscle 3.6 with separate default settings (Edgar 2004a,b). They were then manually adjusted without deleted positions and concatenated into a combined dataset in Mesquite (http://mesquiteproject.org/mesquite/mesquite. html). The ITS sequence data were also used separately. The alignments were submitted to TreeBase (No.17244 for ITS+LSU+*tef-1α* and No.17245 for ITS). Maximum likelihood (ML) analyses were performed in raxmlGUI 1.31 (Michalak 2012) with a GTR model, and the starting trees were obtained via stepwise addition, random sequence addition, and TBR branch swapping. The bootstrap values (BS) were obtained from 1,000 replicates. A Bayesian analysis was performed in MrBayes-3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003), with 10,000,000 generations and four chains (one cold, three incrementally heated). Trees were sampled every 100 generations. Trees sampled prior to the searches that reached a split deviation frequency value reaching 0.01 were discarded as the burn-in, and the remaining trees were used to calculate the Bayesian posterior probabilities (PP) of the individual clades.

**TABLE 1.** Species list of *Agaricus* used in this study and GenBank entries. New species are highlighted in boldface.

| Species name | Collection No. | Location | GenBank accession numbers | | | Notes |
|---|---|---|---|---|---|---|
| | | | LSU | ITS | *tef-1α* | |
| Section *Hondenses* | | | | | | |
| *A. biannulatus* | LAPAG611 | Italy, Sardinia | - | JF896229 | - | Type |
| *A. freirei* | CA186 | France, Le Verdon-33 | - | DQ185553 | - | - |
| ***A. grandiomyces*** | ZRL2012611 | China, Tibet, Milin | KR006624 | KM657879 | KR006652 | Type |
| *A. hondensis* | RWK 1938 | USA, California | - | DQ182513 | - | - |
| *A. phaeolepidotus* | CA217 | France, Jézeaux-65 | - | DQ185552 | - | - |
| | CA214 | France, Villandraut-Préchac-33 | - | DQ185551 | - | - |
| ***A. pusillobulbosus*** | ZRL2012627 | China, Tibet, Linzhi | - | KM567888 | KR006654 | Type |
| Section *Xanthodermatei* | | | | | | |
| *A. bisporiticus* | LD2012111 | Thailand, Chiang Rai Prov. | - | KJ575611 | - | - |
| | MCR25 | Pakistan, Punjab | - | KJ575608 | - | Type |
| ***A. brunneogracilis*** | ZRL258 | Thailand, Chiang Mai Prov. | KR006628 | KM657876 | KR006657 | Type |
| *A. californicus* | RWK 1914 | USA, California, Monterey Co. | - | DQ182509 | - | - |
| *A. caribaeus* Pegler | F2530 | France, Martinique, Tartane, pointe rouge | - | JF727856 | - | - |
| *A.* cf. *volvatulus* | F2767 | France, Martinique | - | JF727848 | - | - |
| ***A. daliensis*** | SHY2011071706 | China, Yunnan Prov., Dali | KR006615 | KM657877 | KR006643 | - |
| | SHY2011073114 | China, Yunnan Prov., Dali | - | KM657878 | - | Type |
| *A. endoxanthus* | DEH1114 | USA, Hawaii, Hawaii | - | DQ182528 | - | - |
| *A. endoxanthus* | LAPAG225 | Spain, Madrid, Madrid | - | DQ182511 | - | - |
| *A. endoxanthus* | NTS7 | Thailand, Chiang Rai, Khun Kone W | - | JF514533 | - | - |
| *A. endoxanthus* | ZRL3095 | Thailand, Chiang Mai, Mae Taeng | - | JF691554 | - | - |
| *A. fuscopunctatus* | LD2012115 | Thailand, Chiang Rai Prov. | - | KJ575612 | - | Type |
| *A. fuscopunctatus* | NTF61 | Thailand, Chiang Mai, Kiewtubyoung | - | JF514528 | - | - |

*...Continued on next page*

**TABLE 1.** (Continued)

| Species name | Collection No. | Location | GenBank accession numbers | | | Notes |
|---|---|---|---|---|---|---|
| | | | LSU | ITS | *tef-1α* | |
| ***A. gregariomyces*** | ZRL2012624 | China, Tibet, Milin | KR006625 | KM657880 | KR006653 | Type |
| *A. iodosmus* | LAPAG245 | Spain, Burgos, Sinovas | - | DQ182518 | - | - |
| ***A. karstomyces*** | ZRL2011048 | China, Yunan Prov., Qujing | KR006632 | KM657899 | KR006662 | Type |
| *A. laskibarii* L.A. Parra & P. Arrill | LAPAG115 | France, Seignosse-40 | - | AY943975 | - | - |
| *A. malangelus* | ZRL2012628 | China, Tibet, Linzhi | KR006626 | KM657892 | KR006655 | - |
| ***A. melanocapus*** | ZRL2011037 | China, Yunnan Prov. | - | KM657881 | - | Type |
| *A. menieri* | CA162 | France, Soulac sur mer-33 | - | DQ185567 | - | - |
| *A. moelleri* | CA209 | France, Villandraut-Préchac-33 | - | DQ185561 | - | - |
| *A. moelleroides* Guinb. & L.A. Parra | CA215 | France, Bareilles-65 | - | DQ185559 | - | Type |
| *A. murinocephalus* | ZRL3044 | Thailand, Chiang Mai, Mae Taeng | - | JF691555 | - | Type |
| *A. microvolvatulus* | Grinling70109 | Congo, Brazzaville | - | JF514524 | - | Type |
| *A. parvitigrinus* Guinb. & Callac | CA158 | France, Villandraut-Préchac-33 | - | AY899267 | - | Type |
| *A. placomyces* | RWK1918_2 | USA, Pennsylvania, Armstrong Co. | - | AF432879 | - | - |
| | RWK1959 | USA, Pennsylvania, Armstrong Co. | - | DQ182525 | - | - |
| *A. pocillator* Murrill | DUKEJ173 | USA, North Carolina, Durham Co. | - | U85308 | - | - |
| *A. pseudopratensis* | CA73 | France, St Enogat-35 | | DQ185558 | - | - |
| ***A. tytthocarpus*** | ZRLWXH3077 | China, Fujian Prov., Wuyishan | KR006618 | KM657889 | KR006645 | Type |
| ***A. sinoplacomyces*** | ZRL2012008 | China, Yunnan Prov., Kunming | KR006620 | KM657883 | KR006648 | Type |
| | ZRL2012009 | China, Yunnan Prov., Kunming | - | KM857884 | - | - |
| | ZRL2012027 | China, Yunnan Prov., Puer | - | KM657885 | - | - |
| | ZRL2012028 | China, Yunnan Prov., Puer | - | KM657886 | - | - |
| | ZRLAG2101 | China, Sichuan Prov. Chengdu | KR006617 | KM657887 | KR006649 | - |
| ***A. tibetensis*** | ZRL2012580 | China, Tibet, Linzhi | KR006629 | KR006604 | KR006659 | - |
| | ZRL2012585 | China, Tibet, Milin | KR006633 | KM657895 | KR006658 | Type |
| | ZRL2012617 | China, Tibet, Milin | KR006631 | KM657897 | KR006661 | - |
| *A. tollocanensis* Callac & G. Mata | MATA688/ CA235 | Mexico | - | AY703913 | - | Type |

*...Continued on next page*

**TABLE 1.** (Continued)

| Species name | Collection No. | Location | GenBank accession numbers | | | Notes |
|---|---|---|---|---|---|---|
| | | | LSU | ITS | *tef-1α* | |
| *A. xanthodermus* | CA15 | France, Lommoye-78 | - | AY899271 | - | - |
| | LAPAG387 | Spain, Soria | KR006609 | KM657923 | KR006638 | - |
| | LAPAG461 | - | KR006612 | KM657925 | - | - |
| *A. xanthodermulus* Callac & Guinb. | CA160 | France, Villandraut-Préchac-33 | - | AY899273 | - | Type |
| *A. xanthosarcus* Heinem. & Gooss.-Font. | Goossens5415 | RD Congo, Panzi, Kivu | - | JF514523 | - | Type |
| *A.* sp. | ZRL2012474 | China, Tibet, Bomi | KR006622 | KM657893 | KR006650 | - |
| *A.* sp. | ZRL2012582 | China, Tibet, Milin | KR006623 | KM657894 | KR006651 | - |
| *A.* sp. | ZRL2012616 | China, Tibet, Milin | KR006630 | KM657896 | KR006660 | - |
| *A.* sp. | ZRL2012629 | China, Tibet, Linzhi | KR006627 | KM657890 | KR006656 | - |
| *A.* sp. | ZRLWXH3092 | China, Fujian Prov., Sanming | KR006619 | KM657891 | KR006646 | - |
| *A.* sp. | F2715 | France, Martinique, Tartane, pointe rouge | - | JF727847 | - | - |
| *A.* sp. | NTF58 | Thailand, Chiang Mai, DSPNP | - | JF514527 | - | - |
| Section Incertae Sedis | | | | | | |
| ***A. nigrogracilis*** | ZRL2012014 | China, Yunnan Prov., Kunming | KR006621 | KM657882 | KR006647 | Type |
| Section *Trisulphurati* | | | | | | |
| *A. trisulphuratus* | LAPAF7 | Togo, Plateaux | KR006605 | KM657924 | KR006634 | - |
| Section *Biverlares* | | | | | | |
| *A. bisporus* | LAPAG446 | Spain, Burgos | KR006611 | KM657920 | KR006640 | - |
| *A. bitorquis* | LAPAG429 | - | KR006610 | KM657926 | KR006639 | - |
| Section *Chitonioides* | | | | | | |
| *A. gennadii* (Chatin & Boud.) P.D. Orton | LAPAG257 | Spain, Burgos | KR006606 | KM657922 | KR006635 | - |
| Section *Nigrobrunnescentes* | | | | | | |
| *A. biberi* Hlaváček | LAPAG687 | Hungary | KR006614 | KM657919 | KR006642 | - |
| *A. padanus* Lancon. | WZR2012903 | China, Xinjiang | KR006616 | KM657903 | KR006644 | - |
| Section *Sanguinolenti* | | | | | | |
| *A. bohusii* Bon | LAPAG562 | Spain, Madrid | KR006613 | KM657928 | KR006641 | - |
| *A. sylvaticus* Schaeff. | LAPAG382 | Spain, Burgos | KR006608 | KM657929 | KR006637 | - |
| Out group (Section *Agaricus*) | | | | | | |
| *A. campestris* | LAPAG370 | Spain, Madrid | KR006607 | KM657927 | KR006636 | - |

## Results

*The ITS dataset*

Because the LSU and *tef-1α* sequence data could not be obtained from all specimens, a separate ITS analysis with all samples was carried out. The 69 specimens clustered into 47 species of sections *Xanthodermatei* and *Hondenses*, one species of section *Agaricus*, one species of section *Chitonioides*, two species of section *Bivelares*, one species of section *Trisulphurati*, two species of section *Nigrobrunnescentes* and two species of section *Sanguinolenti*. All samples were close to section *Xanthodermatei* according to the phylogenetic analysis (Zhao *et al.* 2011). *Agaricus campestris* L. (1753: 1173) from section *Agaricus* was chosen as the outgroup as it was at the farthest position from section *Xanthodermadei* based on a previous study (Zhao *et al.* 2011). The alignment contained 678 total characters after excluding the ambiguous regions, of which 437 were constant characters, 76 were variable and parsimony-uninformative characters, and 165 were parsimony-informative characters. The ML tree and Bayesian trees were almost identical, except for the topology of the sections outside of sections *Xanthodermatei* and *Hondenses*. The Bayesian tree is shown in Figure 1.

In the phylogenetic tree, *A. trisulphuratus* Berk. (section *Trisulphurati*) was found to be between sections *Xanthodermatei* and *Hondenses*, and these two sections were supported with values of 1/87 and 0.71/27 (PP/BS), respectively.

In section *Hondenses*, specimens ZRL2012611, ZRL2012627 and ZRL2012014 formed distinct branches that were separate from *A. biannulatus, A. freirei* Blanco-Dios (2001: 28), *A. hondensis* and *A. phaeolepidotus* F.H. Møller (1952: 204).

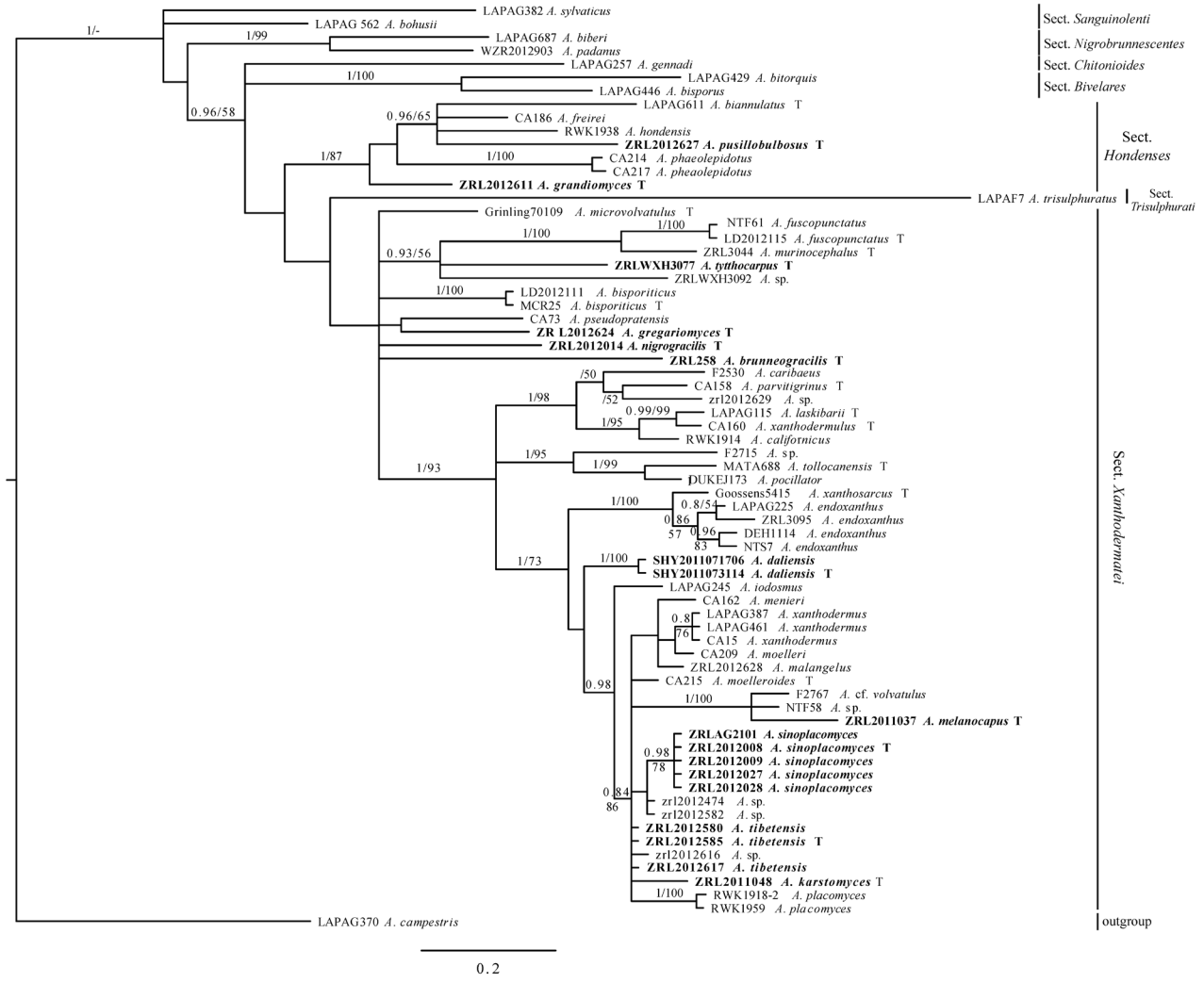


**FIGURE 1.** Phylogenesis of *Agaricus* generated from MrBayesian analysis of the ITS sequences, rooted with *A. campestris*. Bootstrap values (BS>50) and Bayesian posterior probabilities (PP>0.8) are given at the internodes.

In section *Xanthodermatei,* specimens ZRLWXH3092, ZRLWXH3077, ZRL258 and ZRL2012624 were found on distinct branches and were clearly separated from *A. microvolvatulus* Heinem. (1971: 6), *A. fuscopunctatus* Thongklang, J. Chen, Callac & K.D. Hyde (2014: 1227), *A. murinocephalus*, *A. bisporiticus* Nawaz, Callac, Thongklang & Khalid (2014: 1224) and *A. pseudopratensis* (Bohus) Bohus (1971: 81). Specimens SHY2011071706 and SHY2011073114 clustered together as one species, with strong PP/BS support. Specimen ZRL2012628 is a sister to the branch composed of *A. menieri* Bon, *A. xanthodermus* and *A. moelleri* Wasser. Specimen ZRL2011037 clustered with *Agaricus* aff. *volvatulus* Heinem. & Gooss.-Font. (F2767) and *Agaricus* sp. (NTF58), but they have 12 different base pairs in their ITS and thus represent a different species. Specimens ZRLAG2101, ZRL2012008, ZRL2012009, ZRL2012027 and ZRL2012028 clustered together and represent one species, with 0.97/78 PP/BS support. Specimens ZRL2012474, ZRL2012582, ZRL2011048, ZRL2012580, ZRL2012585, ZRL2012616 and ZRL2012617 nested around *A. placomyces* Peck, and their phylogenetic positions are unresolved.

*The combined dataset*

These data included ITS, LSU and *tef-1α* sequences from 69 samples (Table 1), with *A. campestris* as the outgroup taxon (Zhao *et al.* 2011). The alignment contained 2086 total characters after excluding the ambiguous regions, of which 1579 characters were constant, 168 were variable characters and were parsimony-uninformative and 339 were characters that were parsimony-informative. The topologies produced by the ML and Bayesian analyses are identical, and the Bayesian tree is shown in Fig. 2.

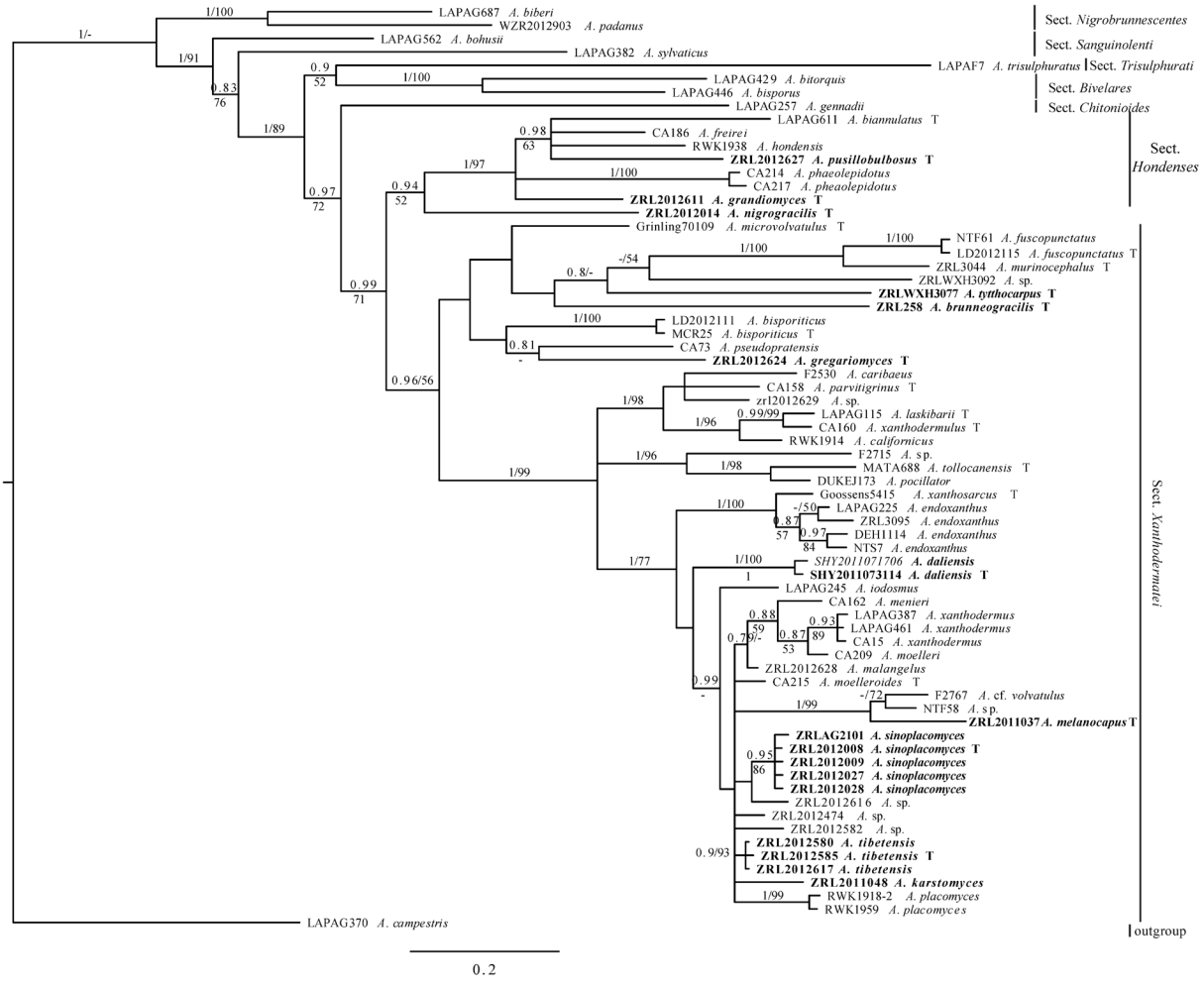


**FIGURE 2.** Phylogenesis of *Agaricus* generated from MrBayesian analysis of the combined 3 genes sequences, rooted with *A. campestris*. Bootstrap values (BS>50) and Bayesian posterior probabilities (PP>0.8) are given at the internodes.

In the combined tree (Fig. 2), section *Xanthodermatei* has 0.96/56 PP/BS support and section *Hondenses* has 1/97 PP/BS supports. Nearly all of the identified species were identical in the ITS and combined trees (Fig. 1; 2), except for the position of ZRL2012014 and a new branch with one species composed of samples ZRL2012580, ZRL2012585

and ZRL2012617 with 0.9/93 PP/BS support (Fig. 2). Samples ZRL2012474, ZRL2012582, ZRL2012616 and ZRL2011048 clustered around *A. placomyces,* as in the ITS tree.

Finally, five samples were unnamed: ZRLWXH3092 and ZRL2012629 could not be identified because the specimens were not sufficiently fresh, while ZRL2012474, ZRL2012582 and ZRL2012616 could not be clearly identified due to their unclear phylogenetic positions and morphological characteristics.

## Taxonomy

### Section *Hondenses*

**1 *Agaricus grandiomyces*** J.L. Zhou & R.L. Zhao, *sp. nov.* (Fig. 4: A–E)
MycoBank NO.: MB 812313

Diagnosis: this species is characterized by its triangular and curved brown to yellowish brown squamules on the cap, stiped rhizomorphs, bulbous base, and ellipsoid basidiospores (5.7–6.5 × 3.8–4.4 µm).

Etymology: the word "grandiomyces" refers to large basidiomata; from 'grandis' (Latin) large.

Material examined: **China, Tibet,** Milin County, Nanyigou Forest Park, N 29°07′45″, E 94°13′10″, elevation 3003.51 m, 29 July 2012, Xin-Yu Dong (*ZRL2012611*, HMAS 275728, HOLOTYPE).

**Pileus** 84 mm in diam., convex; surface covered by squamules, scales sharp triangular, slightly recurved, brown (oac640) at the disc, but fade into yellowish brown (oac683) towards the margin, background white; margin a little incurved and sterile overhang. **Context** 7 mm thick at the disc, white and fleshy. **Lamellae** free and crowded; with 3 series of plural-lamellulae, 8 mm broad broad, slightly ventricose, and dark brown; edge entire. **Stipe** 11 mm (apex)–19 mm (base) × 180 mm (length); cylindrical with a bulbous base and rhizomorphs; surface smooth and silky above annulus, and covered with white fibrils below annulus; hollow. **Annulus** single, membranous, 10 mm in diam., superior, pendant-shaped; upper side white and smooth, lower side white with a yellow tone (oac 676) at the edge. **Odor** not iodine-like, but pleasant. Changing to yellow after bruising occurs on the stipe surface.

**Macrochemical reactions** KOH reaction yellow. Schäffer's reaction negative.

**Basidiospores** (Fig. 4–D) (5.3–)5.7–6.5 × (–3.5)3.8–4.4 µm [x = 6.0 ± 0.3 × 4.0 ± 0.2 µm, Q = 1.4–1.6, Qm = 1.5 ± 0.1, n = 20 basidiospores]; ellipsoid, few broadly ellipsoid; smooth, thick-walled; light brown when young and brown when mature. **Basidia** are 16.7–17.4 × 4.5–5.8 µm, hyaline, smooth, clavate, and 4-spored. **Cheilocystidia** are not observed. **Pleurocystidia** absent. **Pileipellis** (Fig. 4-E) a cutis composed of hyphae 3.2–7.1 µm wide; smooth, not constricted at the septa; containing brown vacuolar pigments.

**Habitat** solitary under *Picea* trees.

**Notes:** This species, along with *A. pusillobulbosus* (see the next species in this article), *A. freirei*, *A. hondensis*, and *A. phaeolepidotus,* form the *Hondenses* section in the phylogenetic tree (Fig. 1). *Agaricus pusillobulbosus* and *A. hondensis* are easily separated from the new species as they lack dark scales on their pileus (Kerrigan 1986). *Agaricus phaeolepidotus* has a similar cap, but has cheilocystidia and an annulus with a collar-like ridge on the lower side (Cappelli 1984). *Agaricus freirei* in this clade also has brown scales on the cap; however, its strong iodine smell, larger basidiospores and cheilocystidia allow it to be distinguished from the new species (Blanco-Dios 2001; Guinberteau 2009). *Agaricus bukavuensis* Heinem. & Gooss.-Font. was first collected in the Congo (Heinemann & Goossens-Fontana 1956). It has medium to large fruiting bodies and large scales on the pileus. However, it differs from *A. grandiomyces* in that it has wider basidiospores and a rough and subperonate annulus. *Agaricus rosoeocingulatus* has an almond smell, but has cheilocystidia and a reddish brown cap (Heinemann 1978).

**2 *Agaricus pusillobulbosus*** S.Y. Su & R.L. Zhao, *sp. nov.* (Fig. 5: K–M)
MycoBank NO.: MB 812318

Diagnosis: this species can be recognized by its small basidiomata, medium grayish white cap, super superior and fragile annulus, stipe with a bulbous base, and broadly ellipsoid to ellipsoid basidiospores (5.1–5.9 × 3.5–4.4 µm).

Etymology: the word "pusillobulbosus" refers to the small basidiomata and bulbose base; from 'pusillus' (Latin) small, and 'bulbus' (Latin) bulb.

Material examined: **China, Tibet**, Linzhi county, Bayi town, Cypress King Garden, N 29°37′21″, E 94°24′07″, elevation 3059.32 m, 31 July 2012, Sheng-Yu Su (*ZRL2012627*, HMAS 275732, HOLOTYPE).


**FIGURE 3. A–E.** Morphology of *A. brunneogracilis* (ZRL258 HOLOTYPE): A–C. Basidiomata; D. Basidiospores; E. Pileipellis hyphae. **F–K.** Morphology of *A. daliensis* (F–J. SHY2011073114, HOLOTYPE; K SHY2011071706): F. Pileipellis hyphae; G. Basidiospores. H–K. Basidiomata. Scale bar A–C, H–K = 10mm; D–G = 10 µm.


**FIGURE 4. A–E**. Morphology *A. grandiomyces* (ZRL2012611, HOLOTYPE): A–C. Basidiomata; D. Basidiospores; E. Pileipellis hyphae. **F–K**. Morphology of *A. gregariomyces* (ZRL2012624, HOLOTYPE):F. Basidiospores; G,I–K. Basidiomata, J shows the yellowing staining on the pileus, K shows annulus characters; H. Pileipellis hyphae. Scale bar A–C,G, I–K = 10 mm; D–F = 10 µm; H = 5 µm.


**FIGURE 5. A–G**. Morphology of *A. karstomyces* (ZRL2011048, HOLOTYPE): A–C. Basidiomata; D. Basidiospores; E–G. Cheilocystidia. **H–J.** Morphology of *A. malangelus* (ZRL2012628): H–I. Basidiomata; J. Basidiospores. **K–M.** Morphology of *A. pusillobulbosus* (ZRL2012627, HOLOTYPE): K–L. Basidiomata; M. Basidiospores. Scale bar A–C, H–I, and K–L = 10 mm; D–G and J = 10 µm; M = 20 µm.

**Pileus** 44 mm in diam. plane with a subumbonate centre; surface grayish white (oac907), dry, and covered with fine fibrils, light grey (oac905); centre light brown (oac850); margin split and straight. **Context** 5 mm thick at the disc, white and fleshy. **Lamellae** free and crowded; appearing as 5 series of plural-lamellulae, 3 mm broad, dark brown; edge entire. **Stipe** 9 mm (apex)–14 mm (base) × 68 mm (length); cylindrical with a bulbous base; surface is white, smooth and silky, narrow; hollow. **Annulus** single, membranous, white, and located at the apex of stipe (super superior); split and covers the lamellae, and smooth at the upper and lower sides. **Odor** not iodine-like, but pleasant. Changing to slightly yellow upon touching and cutting the stipe.

**Macrochemical reactions** KOH reaction yellow. Schäffer's **reaction** negative.

**Basidiospores** (Fig. 5-M) 5.1–5.9 (6.9) × (3.1) 3.5–4.4 (5.1) µm [x = 5.5 ± 0.3 × 4.0 ± 0.2 µm, Q = 1.2–1.6, Qm = 1.4 ± 0.1, n = 20 basidiospores], broadly ellipsoid to ellipsoid, occasionally elongated, smooth, thick-walled, and brown. **Basidia** 20.0–22.5 × 5.8–7.1 µm, hyaline, smooth, clavate, and 4-spored. **Cheilocystidia** are not observed. **Pleurocystidia** likewise absent. **Pileipellis** a cutis composed of hyphae 3.9–7.1 µm in diam; long cylindrical, smooth, and hyaline, and some constricted at the septa.

**Habitat** solitary in *Cypress* forests.

**Notes:** This species is a small mushroom with a grayish white cap, no squamules, a bulbous stipe, a thin and superior annulus and wide basidiospores. *Agaricus freirei* and *A. hondensis* are phylogenetically close to this new species. However, *A. freirei* has dark colored scales and much narrower basidiospores (Blanco-Dios 2001; Guinberteau 2009). In contrast, *A. hondensis* is more similar to *A. pusillobulbosus,* as both have a light cap and a bulbous stipe; however, the former has much larger basidiomata, a tough and thick annulus, and ellipsoid to elongate basidiospores, all of which can be used to distinguish it (Kerrigan 1986).

## Section *Xanthodermatei*

**1** ***Agariucs brunneogracilis*** R.L. Zhao & K.D. Hyde, *sp. nov.* (Fig. 3: A–E)
MycoBank NO.: MB 812310

Diagnosis: this species is characterized by slender basidiomata, a cap completely covered with grayish brown scales, a long clavate and smooth stipe, a movable annulus, a lack of phenolic or iodine-like odor, and elongated ellipsoid basidiospores (5.9–6.9 × 3.2–3.8 µm).

Etymology: the word "brunneogracilis" refers to the brown pileus and slender habit; from 'brunneus' (Latin) brown, and 'gracilis' (Latin) slender.

Material examined: **Thailand, Chiang Mai Prov.**, Mae Taeng Dist., Ban Pha Deng Village, N 19°17′04″, E 98°44′47″, elevation 900 m, 30 June, 2008, Rui-Lin Zhao (*ZRL258* MFLU HOLOTYPE; HMAS 275738, ISOTYPE).

**Pileus** 22 mm in diam., plane; surface covered with fibrillose squamules, entirely grayish brown (5E3); edge straight. **Context** 1.5 mm thick at the disc, white, and fleshy. **Lamellae** free and crowded; 5 series of plural-lamellulae, 2 mm broad, pink to brownish orange (6C3) or brown; edge entire. **Stipe** 1.5 (apex)–2 mm (above the base)–5 mm (base) × 60 mm (length); elongated clavate, with rhizomorphs at the base; surface white, smooth and silky; hollow. **Annulus** single but thick (1 mm thick), movable, 1 mm broad; upper side white and smooth, lower side white, floccose and subperonate. **Odor** not iodine-like, but pleasant. No color change on touching the stipe, slightly yellow at the base of the stipe on cutting.

**Macrochemical reactions:** KOH reaction yellow. Schäffer's reaction negative.

**Basidiospores** (Fig. 3-D) 5.9–6.9 × 3.2–3.8 µm [x = 6.4 ± 0.3 × 3.4 ± 0.2 µm, Q = 1.7–2.1, Qm = 1.9 ± 0.1, n = 20 basidiospores], elongated ellipsoid, occasionally cylindrical, smooth, thick-walled, light brown when young and brown when mature. **Basidia** 13.6–15.4 × 6–7 µm, hyaline, smooth, clavate, and 4-spored. **Cheilocystidia** not observed. **Pleurocystidia** absent. **Pileipellis** (Fig. 3-E) a cutis composed of hyphae 4–8 µm wide, long clavate, cylindrical, smooth, containing light brown to brown vacuolar pigments.

**Habitat** solitary in forests.

**Notes:** This species is phylogenetically close to *A. murinocephalus*, but *A. murinocephalus* has a pileus covered in greyish brown (5F5) to black scales, which are only present at the disc, and a distinctly visible white background and a truncate umbo (Zhao *et al.* 2012). *Agaricus microvolvatulus* is another similar species, but it has smaller and rounder basidiospores (4.2–4.8 × 2.8–3 µm, Heinemann 1978; 4.5–6 × 2.9–3.8µm, Q=1.62–1.67, Thongklang 2014) and a volva-like or abrupt bulbous stipe base (Heinemann 1978, Thongklang 2014).

**2 *Agaricus daliensis*** H.Y. Su & R.L. Zhao, *sp. nov.* (Fig. 3: F–K)
MycoBank NO.: MB 812311

Diagnosis: this species is characterized by large basidiomata, dot-like brown to smoky black scales on the white background of the cap, a stipe surface that changes to reddish brown when touched and small ellipsoid to elongate basidiospores (4.3–5.1 × 2.7–3.2 µm).

Etymology: the word "daliensis" refers to the place where the holotype was collected.

Material examined: **China, Yunnan Prov.**, Dali, 17 July 2011, Hong-Yan Su (*SHY2011071706*, HMAS 275739); 31 July 2011, Hong-Yan Su (*SHY2011073114*, HMAS 254643, HOLOTYPE).

**Pileus** 85–120 mm in diam., convex, plano-convex, some subunbonate; margin slightly flared and irregularly grooved; scales small, dot-like, dense at disc, distantly spaced at the margin, arranged concentrically to some degree, brown (oac640) to smoky black (oac902) against a white background; edge decurved to incurved, exceeding into white lace-like around cap. **Context** white and fleshy. **Lamellae** free and crowded; with 5–7 series of plural-lamellulae, pink to brown; edge entire. **Stipe** 15 mm (apex)–25 mm (base) × 200 mm (length); cylindrical or slightly long clavate; surface white, dry and smooth; hollow. **Annulus** double, membranous, pendant, more than 40 mm in diam., superior; upper layer white and smooth; lower layer white, slightly flocculent or attached light brown granulose. **Odor** unknown. Changing to reddish brown upon touching the stipe surface; changing to yellow at the base of stipe upon cutting.

**Macrochemical reactions:** KOH reaction unknown. Schäffer's reaction negative.

**Basidiospores** (Fig. 3-G) 4.3–5.1(–5.7) × 2.7–3.2 µm [x = 4.8 ± 0.4 × 2.9 ± 0.1 µm, Q = 1.5–1.9, Qm = 1.7 ± 0.2, n = 20 basidiospores], ellipsoid to elongate, smooth, thick-walled, brown. **Basidia** 13.2–16.1 × 3.9–5.6 µm, hyaline, smooth, clavate, and 4-spored. **Cheilocystidia** not observed. **Pleurocystidia** absent. **Pileipellis** (Fig. 3-F) a cutis composed of hyphae 4.5–12.9 µm in diam. and has cylindrical cells that are often broadly clavate, ellipsoid and constricted at the septa near apex, smooth, containing light brown to brown vacuolar pigments.

**Habitat** solitary or scattered.

**Notes:** The features of the pileus and basidiospores of this species are quite similar to those of *A. moelleri* [=*A. praeclaresquamosus* A.E. Freeman (1979: 90) =*A. meleagris* (Jul. Schäff.) Pilát (1951: 106)] collected from Northern America and Europe (Cappelli 1984; Kerrigan 1986; Freeman 1979). However, this new species differs in its cylindrical to slightly clavate stipe and in its lack of cheilocystidia. *Agaricus daliensis* is similar to *A. iodosmus* Heinem. (1965: 399) [= *A. xanthodermus* var. *pilatianus* Bohus (1971: 80)] in that it has dark grey squamules on its pileus and a cylindrical stipe; however, the latter known species has larger basidiospores (5.5–7 × 4.5–5.5 µm) (Heinemann 1990). Molecular data also demonstrates that these are distinct species.

**3 *Agaricus gregariomyces*** J.L. Zhou & R.L. Zhao, *sp. nov.* (Fig. 4: F–K)
MycoBank NO.: MB 812314

Diagnosis: this species can be recognized by its medium to large basidiomata, a cap completely covered by grayish brown fibrillose squamules, a bulbous stipe base, a reddish yellow tone on touching and cutting, and elongated basidiospores (5.62–6.3 × 3.52–4.0 µm).

Etymology: the word "gregariomyces" refers to the gregarious habit; from 'gregarius' (Latin).

Material examined: **China, Tibet**, Milin County, Pai Town, Gongbujiangda Natural Reserve, N 29°46′18″, E 94°43′51″, elevation 3351.10 m, 31 July 2012, Sheng-Yu Su (*ZRL2012624*, HMAS 254645, HOLOTYPE).

**Pileus** 50–100 mm in diam., campanulate or conic when young, then convex with umbo, plano-convex or plane when mature; surface dry, covered with grayish brown (8E2) fibrils, radially ranked, breaking up into fibrillose scales towards the margin, with some recurved; edge decurved. **Context** 3–7 mm thick at the disc, white and fleshy. **Lamellae** free and crowded; with 8 series of plural-lamellulae, 6–9 mm broad, reddish-brown to dark brown; edge entire. **Stipe** 5–12 mm (apex)–18–20 mm (base) × 50–90 mm (length); cylindrical with a bulbous base; surface white and smooth; hollow. **Annulus** complex, 6–11 mm wide; first composed of 2 membranous layers and filled with heavy fibrillose hair between them, then shrinking into one membranous layer with a thickened edge; upper and lower sides smooth, white, sometimes with yellow tone. **Odor** not iodine-like, but pleasant. Changing to yellow and then reddish yellow, finally becoming blackish brown after bruising the stipe; slightly reddish yellow on cutting at the disc and base of the stipe.
**Macrochemical reactions** KOH reaction yellow. Schäffer's reaction negative.

**Basidiospores** (Fig. 3-F) 5.6–6.3(–6.7) × (3.1–) 3.5–4.0(–4.3) µm [x = 6.1 ± 0.2 × 3.7 ± 0.1 µm, Q = 1.6–1.9, Qm = 1.7 ± 0.1, n = 20 basidiospores], elongate, smooth, thick-walled, light brown when young and dark brown when mature. **Basidia** 20.0–22.5 × 5.8–7.1 µm, hyaline, smooth, clavate and 4-spored. **Cheilocystidia** not observed.

**Pleurocystidia** absent. **Pileipellis** (Fig. 3-H) a cutis composed of hyphae 3.9–7.1 µm in diam., long cylindrical, smooth, constricted at the septa, and containing brown pigments.

**Habitat** gregarious on grassland.

**Notes:** *Agaricus gregariomyces* is phylogenetically distant from most known species from section *Xanthodermatei*, and its closest relative is *A. pseudopratensis* from Europe, which also has a reddish tone on cutting. However, *A. pseudopratensis* has cheilocystidia and less elongated basidiospores (Q=1.42–1.65); macromorphologically its squamules are only concentrated at the disc.

**4 *Agaricus karstomyces*** R.L. Zhao, *sp. nov.* (Fig. 5: A–G)
MycoBank NO.: MB 812315

Diagnosis: this species can be recognized by its medium to large basidiomata, a pileus covered with dark brown to dark brown grey dot-like squamules, a lack of phenolic or iodine-like odor and elongated basidiospores (5–6.5 × 3–3.5 µm).

Etymology: the word "karstomyces" refers to its environment which has a large amount of limestone; from 'karst'.

Material examined: **China, Yunnan Prov.**, Shizong County, Yingwu Mountain Forest Park, N 24°38′24″, E 104°08′49″, elevation 2350.83 m, 29 June 2011, Jie Chen (*ZRL2011048*, HMAS 254644, HOLOTYPE).

**Pileus** 90–120 mm in diam., plano-convex, plane, deeply split; covered with squamules, appressed, dot-like, dense at the disc and becoming more sparse towards the margin; dark brown to dark brown grey (oac647) and lighter towards the edge; edge straight. **Context** 6 mm thick at the disc, white with a grey tone at the centre of the pileus, fleshy. **Lamellae** free and crowded; more than 6 series of plural-lamellulae, 8 mm in broad, ventricose, pink when young, brown to dark brown when mature, edge entire. **Stipe** 8–13 mm (apex) –13–15 mm (base) × 120–140 mm (length); cylindrical to long clavate; surface dry and smooth or slightly fibrillose, white; hollow. **Annulus** single, membranous, 8 mm in diam.; pendant, large, white; lower side floccose. **Odor** pleasant. Not discoloring on touching, although the stipe turns slightly yellow on cutting.

**Macrochemical reactions** KOH reaction yellow. Schäffer's reaction negative.

**Basidiospores** (Fig. 5-D) 5–6.5 (–7) × 3–3.5 (–4) µm [x = 5.9 ± 0.5 × 3.3 ± 0.3 µm, Q = (1.4–)1.7–2.3, Qm = 2 ± 0.3, n =20 basidiospores], elongate to cylindric, smooth, brown, thick-walled. **Basidia** 13–17 × 5–6 µm, hyaline, smooth, 4-spored. **Cheilocystidia** (Fig. 5 E–G) clavate, pyriform to subspherial, 11–18 × 6–9 µm, with 2 elements (14–16 µm in diam.) occasionally observed in chain. **Pleurocystidia** absent. **Pileipellis** a cutis composed of hyphae of 5–7 µm wide and up to 14 µm in diam.; terminal cells long-clavate to clavate, smooth, slightly constricted at septa, containing brown vacuolar pigment. Annulus composed of a cylindrical cell, slightly constricted at the septa, 4–5 µm wide, hyaline.

**Habitat** scattered in grassland.

**Notes:** This species was collected from Karst mountain, Yingwushan in the Yunnan Province and is close to *A. deardorffensis* nom. prov. (from America) in terms of its phylogeny (Kerrigan 2015). *Agaricus karstomyces* differs from *A. deardorffensis* by the following: 1) on cutting, the latter has a strong yellow discoloration at the base of stipe, while *A. karstomyces* becomes slightly yellow at the middle of the stipe, and 2) *A. deardorffensis* has narrower basidiospores (Q = 1.39) and cheilocystidia, which are similar to the basidia in shape and size.

*Agaricus karstomyces* is similar to *A. sinoplacomyces* in its medium to large basidiomata, large annulus, cap characteristics and spore size and shape. *Agaricus karstomyces,* however, differs in its equal clavate stipe, lack of or faint yellow discoloration on cutting, and cheilocystidia.

This new species is quite similar to *A. placomyces* in the field; however, *A. placomyces* has more robust basidiomata and wider basidiospores (Heinemann 1986; Freeman 1979).

**5 *Agaricus malangelus*** Kerrigan nom. prov. (Fig. 5: H–J)

Material examined: **China, Tibet,** Linzhi county, Cypress King garden, N 29°37′21″, E 94°24′07″, elevation 3059.32 m, 31 July 2012, Guang-Ping Li (*ZRL 2012628*, HMAS).

**Pileus** 40 mm in diam., rectangular, plane; covered in large scales, recurved, mostly black brown to black (oac625), cracked and revealed white flesh; edge decurved. **Context** 10 mm-thick at the disc, white and fleshy. **Lamellae** free and crowded; 7 mm broad, light pink to brown; edge entire. **Stipe** 13 mm (apex)–22 mm (base) × 95 mm (length); cylindrical with sub-bulbous base; surface white, dry and smooth; hollow. **Annulus** single, thick on the edge (up to 4 mm in thickness), pendant, 12 mm in diam.; upper side white and smooth, lower side slightly brown and flocculent. **Odor** indistinct. Changes to reddish brown on touching at the surface of the stipe and slightly yellow at the base of stipe on cutting.

**Macrochemical reactions** KOH reaction yellow. Schäffer's reaction negative.

**Basidiospores** (Fig. 5-J) 4.9–6.8 × 3.9–4.9 µm [x = 4.8 ± 0.3 × 3.7± 0.3 µm, Q = 1.2–1.5, Qm = 1.3 ± 0.1, n = 20 basidiospores], broadly ellipsoid to ellipsoid, smooth, thick-walled, brown. **Basidia** 16.9–18.1 × 4.4–6.8 µm, hyaline, smooth, clavate, 4-spored. **Cheilocystidia** not observed. **Pleurocystidia** absent. **Pileipellis** a cutis composed of hyphae of 3.1–6.2 µm wide, long clavate, smooth and not constricted at the septa, walls hyaline, containing light-brown vacuolar pigment.

**Habitat** solitary under Cypress trees.

**Notes:** This Chinese specimen morphologically matches *A. malangelus* (Kerrigan 2016). There are only two base pair differences in the ITS sequences between this type and the Chinese specimens. Molecular data shows that this species is close to *A. menieri, A. moelleri, A. xanthodermus* and *A. placomyces*. The colored pileus clearly differentiates this species from *A. xanthodermus*, while *A. malangelus* has broadly ellipsoid to ellipsoid basidiospores. These are quite different from the basidiospores of *A. menieri, A. moelleri*, and *A. placomyces*, which are typically ellipsoid to elongated ellipsoid (Parra 2003; Cappelli 1984; Kerrigan 1986; Nauta 2001; Freeman 1979). *Agaricus iodosmus* Heinem.(1965: 399) also has a dark cap; however, it has larger basidiospores (6–7 × 4.8–5.1 µm) than those of *A. malangelus*, and cheilocystidia are present (Heinemann 1978).

**6 *Agaricus melanocapus*** R.L. Zhao *sp. nov.* (Fig. 6: A–F)
MycoBank NO.: MB 812316

Diagnosis: this species can be recognized by its small basidiomata, a pileus covered with dark brown to nearly black minutely fibrillose squamules, a double annulus and small ellipsoid to elongate basidiospores (3.7–4.9 × 2.6–3.2 µm).

Etymology: the word "melanocapus" refers to the black brown pileus, from 'melano' (Latin) black and 'caput' (Latin) head.

Material examined: **China, Yunnan Prov.**, Shizong County, Yingwu Mountain Forest Park, N 24°38′24″, E 104°08′49″, elevation 2350.83 m, 28 June 2011, Rui-Lin Zhao (*ZRL2011037*, HMAS 275734, HOLOTYPE).

**Pileus** 40 mm in diam., parabolic when young and becoming convex when mature, slightly subumbonate; surface dry with fine fibrillose squamules that are generally dot-like, dark brown (oac 637) to nearly black (oac 626), dense at the disc and covering the whole cap; edge straight. **Context** 5 mm thick at disc, white and fleshy. **Lamellae** free and crowded; with 5 series of plural-lamellulae, 5 mm broad, slightly ventricose, pink when young and brown when mature; edge entire. **Stipe** 6 mm (apex)–10–12 mm (base) × 90 mm (length); cylindrical to subclavate, with a bulbous base; surface white, smooth and silky; hollow. **Annulus** double-layered; with a white, upper layer membranous and white; up to 15 mm wide, lower layer fragile, easily torn, some remnants remain attached at the edge of the pileus, crenate, some remain on the lower side of the upper layer, (floccose) and some remain near the stipe bracelet-like (white). **Odor** indistinct, not iodine-like. Pileus bruising slightly rubescent, and stipe base turns yellow where cut.

**Macrochemical reactions** KOH reaction yellow. Schäffer's reaction negative.

**Basidiospores** (Fig. 6-E) 3.7–4.9(5.6) × 2.6–3.2 µm [x = 4.6 ± 0.4 × 2.9 ± 0.2 µm, Q = 1.4–1.8, Qm = 1.6 ± 0.2, n =20 basidiospores], ellipsoid to elongated, smooth, translucent, thick-walled, light brown when young and brown when mature. **Basidia** 12.5–15.0 × 3.7–5.0 µm, hyaline, smooth, clavate, 4-spored. **Cheilocystidia** not observed. **Pleurocystidia** absent. **Pileipellis** (Fig. 6-F) a cutis composed of hyphae 4–18 µm wide; ellipsoid to long clavate, smooth, and always constricted at septa; walls hyaline, containing brown vacuolar pigment. **Annulus** composed of long cylindrical hyphae, 4–10 µm in diam., with no constriction at the septa, smooth, mostly light yellowish brown and some hyaline.

**Habitat:** solitary under *Rhododendron* trees.

**Notes:** *Agaricus melanocapus* is morphologically similar to *A. endoxanthus*. However, the stipe of *A. melanocapus* has a distinctly bulbous base and lacks cheilocystidia. The ITS sequence data analysis has shown it to be a distinct species from *A. endothanthus*. This species is phylogenetically close to *A.* cf. *volvatulus* (specimen F2767). *Agaricus volvatulus* (Heinemann & Goossens-Fontana 1956, Heinemann 1980, Chen *et al.* 2016) is characterized by a volva-like stipe at its base and abundant cheilocystidia, and thus can be differentiated from *A. melanocapus*. We also compared this new species with the recently published *A. atrodiscus* L.J. Chen, Callac, R.L. Zhao & K.D. Hyde, (Ariyawansa *et al.* 2015) from section *Xanthodermatei* in morphology, and our new species differs from this known species by larger sized basidiospores and bulbous base of stipe."


**FIGURE 6. A–F.** Morphology of *A. melanocapus* (ZRL2011037 HOLOTYPE): A–D Basidiomata, C shows yellow staining at the base of stipe; E. Basidiospores; F. Pileipellis hyphae. **G–K**. Morphology of *A. nigrogracilis* (ZRL2012014 HOLOTYPE): G. Basidiospores; H. Pileipellis hyphae; I–K. Basidiomata. Scale bar A–D = 20 mm; I–K = 10 mm; E–H = 10 μm.

**7** ***Agaricus tytthocarpus*** R.L. Zhao, *sp. nov.* (Fig. 7: A–C)
MycoBank NO.: MB 812320

Diagnosis: this species can be recognized by its small basidiomata, the presence of a pileus covered with grayish brown fibrils, a slender and hollow stipe, an annulus with a serrated edge, and elongated basidiospores (5.5–6.4 × 3.2–3.8 μm).

Etymology: the word "tytthocarpus" refers to the small pileus;from 'tyttho' (Latin) small, and 'caput' (Latin) head.

Material examined: **China, Fujian Prov.**, Wuyishan City, Longjing Mountain, N 27°38′11″, E 117°56′47″, elevation 324.59 m, 4 Sep. 2011, Xiang-Hua Wang (*ZRLWXH3077*, HMAS 275741, HOLOTYPE).

**Pileus** 15–20 mm in diam., conical to convex; surface covered with densely fibrillose, grayish brown (oac868) at the disc, then breaks into small brown scales (not triangle-shaped) towards the margin, white fibrillose near margin; edge straight and sterile overhang, crenate. **Context** thin, white and fleshy. **Lamellae** free and crowded; with 5 series of plural-lamellulae, 4 mm broad and brown; edge entire. **Stipe** 1 mm (apex)–1.5 mm (base) × 30–40 mm (length); cylindrical, curved, with a smooth white surface; hollow. **Annulus** membranous, white, subperonate, 2 mm broad; upper side smooth, lower side thick fibrillose; edge serrate. **Odor** unknown. No color change after touching the stipe. **Macrochemical reactions** KOH reaction unknown. Schäffer's reaction negative.

**Basidiospores** (Fig. 7-B) (4.7)5.5–6.4(7.0) × 3.2–3.8 μm [x = 5.9 ± 0.2 x 3.4 ± 0.2 μm, Q = 1.6–1.9, Qm = 1.7 ± 0.1, n = 20 basidiospores], elongated, smooth, thick-walled, brown to dark brown. **Basidia** 14.6–16.9 × 4.5–5.8 μm, hyaline, smooth, clavate, and 4-spored. **Cheilocystidia** not observed. **Pleurocystidia** absent. **Pileipellis** (Fig. 7-C) a cutis composed of hyphae of 2.6–7.1 μm in diam., long clavate, smooth, with no constrictions at the septa; walls hyaline, containing brown vascular pigment.

**Habitat** scattered in broadleaved forest.

**Notes:** This is a small and slender agaric, and its cap is heavily fibrillose, which is quite rare in this group. Those characteristics also distinguish it from *A. murinocephalus,* which is the closest species in terms of phylogeny.

**8** ***Agaricus sinoplacomyces*** P. Callac & R.L. Zhao, *sp. nov.* (Fig. 7: D–G)
MycoBank NO.: MB 812321

Diagnosis: this species can be recognized by its medium to large basidiomata, a pileus surface covered with pulverulent or fibrillose squamules, a lower annulus surface of annulus with very heavy flocculence, and elongated basidiospores (4.9–5.8 × 2.9–3.3 μm).

Etymology: the word sinoplacomyces refers to the species is recorded from China and similar to *A. placomyces*; from 'sina' (Latin) China.

Material examined: **China, Yunnan Prov.**, Kunming City, Yeya Lake, N 25°07′15″, E 102°51′47″, elevation 2078.94 m, 30 June 2012, Rui-Lin Zhao (*ZRL2012008*, HMAS 275724, HOLOTYPE, and *ZRL2012009*, HMAS 280514); **Yunnan Prov.**, Nanjian county, Wuliang Mountain National Natural Reserve, N 24°49′38″, E 100°26′26″, elevation 2634.48 m, 3 July 2012, Philippe Callac (*ZRL2012027*, HMAS 275727) and Olivier Raspé (*ZRL2012028*, HMAS 280512); **Sichuan Prov.**, Chengdu City, Longquanyi district, N 30°33′32″, E 104°16′20″, elevation 523.78 m, 7 October 2011, Bo Wang (*ZRLAG2101*, HMAS 254646).

**Pileus** 40–100 mm in diam., conical and often truncated when young, then convex and plano-convex to plane when mature, umbonate indistinct or flat, sometimes with a depressed centre; surface covered with fibrillose squamules that break into small squamules towards margin, often pulverulent and sometimes become irregular or mud-cracked after exposure to sunlight, with a dark brown(oac 637) to almost black (oac 626) at the centre, and becomes lighter towards edge, against a white to slightly light brownish-white background that has a red tone upon wetting; margin straight when fresh and decurved after aging and drying. **Context** 5–8 mm thick at the disc, white and fleshy. **Lamellae** free and crowded; with 7 series of plural-lamellulae, 4–6 mm broad, pink to pinkish brown when young, and changing into dark brown when old; edge entire. **Stipe** 7–10 mm (apex)–14–20 mm (base) × 42–150 mm (length); cylindrical with an abruptly bulbous base; surface white, smooth and silky; hollow. **Annulus** large, 15–30 mm in diam., membranous and pendant; upper surface white and smooth, lower surface slightly yellowish brown white (oac900) with very heavy flocculence; often extending 1–2 mm in a downward direction and becoming collar-like, surrounding the stipe loosely. **Odor** not iodine-like, but pleasant. Staining yellow on touching the stipe and distinctly yellow at the base of stipe on cutting.

**Macrochemical reactions** KOH reaction yellow. Schäffer's reaction negative.


**FIGURE 7. A–C.** Morphology of *A. tytthocarpus*sp (ZRLWXH3077 HOLOTYPE): A. Basidiomata; B. Basidiospores; C. Pileipellis hyphae. **D–G.** Morphology of *A. sinoplacomyces* (ZRL2012008 HOLOTYPE): D–E. Basidiomata. F. Basidiospores. G. Pileipellis hyphae. **H–K.** Morphology of *A. tibetensis* (ZRL2012585, HOLOTYPE): H. Basidiospores; I. Pileipellis hyphae (in Congon red); J–K. Basidiomata. Scale bar A, D–E and J–K = 10 mm, B, C and F–I = 10 μm.

**Basidiospores** (Fig. 7-F) (4.4)4.9–5.8(6.2) × (2.6)2.9–3.3(4.0) µm [x = 5.3 ± 0.3 × 3.1 ± 0.1 µm, Q = 1.3–1.9 (2.2), Qm = 1.68 ± 0.1, n = 100 basidiospores], most basidiospores elongated, few ellipsoid or cylindrical; smooth, thick-walled, and brown. **Basidia** 11.5–15.2 × 3.8–6.2 µm, hyaline, smooth, clavate, 4-spored. **Cheilocystidia** not observed. **Pleurocystidia** absent. **Pileipellis** (Fig. 7-G) a cutis comprised of hyphae 3.9–9.6 µm wide, broadly clavated and smooth, containing light brown to brown vacuolar pigments, not constricted at the septa. **Annulus** hyphae 4–8.8 µm in diam., cylindrical to long clavated, hyaline, smooth, and not constricted at the septa.

**Habit** solitary or scattered in the open areas under trees, both *Rhododendron* and Fagaceae trees.

**Notes:** This species is similar to *A. placomyces,* which is mostly distributed in northern and southern America (Heinemann 1978, 1986; Freemen 1979). In the field, both have dark grey dot-like squamules on the pileus, stipes with bulbous bases, and a complex annulus. However, under the microscope, the basidiospores of this new species are found to be ellipsoid to elongated (Q = 1.4–1.9), while those of *A. placomyces* are broadly ellipsoid to ovoid (Q = 1.3–1.4) (from the type specimen by Freeman, 1979). Phylogenetic data also suggest that this new species is distinct from *A. placomyces*, as there are 5 base pair differences in its sequences data. *Agaricus californicus* Peck (1895: 203) has dark grey dot-like squamules on the pileus, and it is often present in deciduous forests (Kerrigan 1986); however, its phenol smell and cylindrical stipe can be used to differentiate it from *A. sinoplacomyces*.

**9 *Agaricus tibetensis*** J.L. Zhou & R.L. Zhao, *sp. nov.* (Fig. 7: H–K)
MycoBank NO.: MB 812322

Diagnosis: this species can be recognized by its small to medium basidiomata, a pileus covered with grey to dark brown squamules, often shell-like at the disc, a slender stipe with a distinct and bulbous base, and ellipsoid basidiospores (6–7 × 4–5 µm).

Etymology: the word "tibetensis" refers to the Tibet Autonomous Region of China, where the holotype was originally collected.

Material examined: **China, Tibet**, Milin County, Nanyigou Forest Park, N 29°07′45″, E 94°13′10″, elevation 3003.51 m, 29 July 2012, Sheng-Yu Su (*ZRL2012585*, HMAS 275725, HOLOTYPE); same location, 28 July 2012, Guang-Ping Li (*ZRL2012580*, HMAS 280513); **Tibet**, Milin County, Pai town, Gongbujiangda Nature Reserve, N 29°46′18″, E 94°43′51″, elevation 3351.10 m, Rui-Lin Zhao (*ZRL2012617*, HMAS 275731).

**Pileus** 25–55 mm in diam., parabolic when young, becoming convex, plano-convex or plane when mature; covered with grey (oac902) to dark brown (oac733) appressed or slightly recurved squamules, which are dense and often shell-like at the disc, dark brown to blackish brown (oac733, oac639, oac640), gradually distantly spaced towards margin, sometimes cracked and revealing white flesh; margin decurved, inrolled. **Context** 2 mm thick at the disc, white and fleshy. **Lamellae** free and crowded; with 5 series of plural-lamellulae, 4 mm broad, pink, taupe brown (oac753) to brown (oac648); edge entire. **Stipe** 5–6 mm (apex)–10–15 mm (base) × 80–120 mm (length); cylindrical with a distinct and bulbous base; surface white, dry and smooth; hollow. **Annulus** single and thick, rigid, pendant or subperonate, superior, 5–10 mm in diam., upper side smooth and white, lower side white to light grey in color and smooth or slightly floccose. **Odor** not iodine-like, but pleasant. Discoloring yellow, then reddish brown on the stipe when touched, and bright yellow at the base of the stipe on cutting.

**Macrochemical reactions** KOH reaction yellow. Schäffer's reaction negative.

**Basidiospores** (Fig. 7-H) 6–7 × 4–5 µm [x = 6.8 ± 0.2 × 4.2 ± 0.2 µm, Q = 1.4–1.75, Qm = 1.6 ± 0.2, n =60 basidiospores], ellipsoid, smooth, thick-walled, and brown. **Basidia** 17–24 × 7–8 µm, hyaline, smooth, clavate, 4-spored. **Cheilocystidia** absent or basidia-like. **Pleurocystidia** absent. **Pileipellis** (Fig. 7-I) a cutis composed of hyphae 5–10 µm wide, long clavate, smooth, constricted at the septa, with hyaline walls, containing a brown vacuolar pigment. **Annulus** composed of hyphae similar to those of pileipellis, except lacking pigments.

**Habit** Solitary or in groups in coniferous forests of *Picea asperata*, *Pinus densata* and *Platycladus orientalis.*

**Notes:** This new species can be distinguished from other species in this section by its small to medium sized basidiomata, pileus covered in small dark brown squamules, thick annulus, and the distinct bulbous base of its stipe. It has a strong yellow discoloration on cutting. All four samples from Tibet were collected from an elevation above 3000 m. This new species is similar to *A. placomyces*, as they both grow associated with coniferous forests; however, *A. tibetensis* has relatively smaller and slender basidiomata and longer basidiospores than those of *A. placomyces* (more robust basidiomata, with basidiospores less than 6 µm in length) (Heinemann 1986; Freeman 1979). *Agaricus tibetensis* is also morphologically similar to *A. sinoplacomyces*; however, *A. sinoplacomyces* was collected from the broadleaf forests and has medium to large basidiomata, smaller basidiospores, and a large and very thin membranous annulus that differs from those of *A. tibetensis*. The molecular analysis suggests that these two are distinct species.

We also compared this new species with *A. deardorffensis* from America (Kerrigan 2016). Although there is only one ITS base pair different between the two, *A. deardorffensis* is a species with an equal stipe, smaller basidiospores and a strong phenol smell, which are distinctive characters.

**Section Incertae Sedis**

***Agaricus nigrogracilis*** R.L. Zhao, *sp. nov.* (Fig. 6: G–K)
MycoBank NO.: MB 812317

Diagnosis: this species can be recognized by its small basidiomata, pileus covered with brown squamulose, and stiped surface that is white fibrillose to fibrillose squamulose. No discoloration occurs on cutting, and elongated basidiospores are present (5.2–5.9 × 2.9–3.4 μm).

Etymology: the word "nigrogracilis" refers to the black squamules on the pileus and slender habit; from 'nigrare' (Latin) be black, and 'gracilis' (Latin) slender.

Material examined: **China, Yunnan Prov.**, Kunming, Yeya Lake Forest Park, N 25°07′15″, E 102°51′47″, elevation 2078.94 m, 30 June 2012, Rui-Lin Zhao (*ZRL2012014*, HMAS 275735, HOLOTYPE).

**Pileus** 35 mm in diam., convex to plano-convex; surface innately fibrillose, becoming appressed squamulose towards the margin, brown (oac 662) with a white background; edge decurved. **Context** 3 mm thick at the disc, white and fleshy. **Lamellae** free and crowded; 4–5 series of plural-lamellulae, 4 mm broad, pink to brown; edge entire. **Stipe** 5 mm (apex)–10 mm (base) × 75 mm (length); long clavate, surface white, dry, silky, and fibrillose to fibrillose-squamulose; hollow. **Annulus** single, membranous, subperonate, 2.5 mm in diam., with a distinct brown edge; upper and lower surfaces smooth and white. **Odor** not iodine-like, but pleasant. Changing slightly yellow on touching the surface of the stipe; not discoloring on cutting.

**Macrochemical reactions** KOH reaction no change or slightly reddish. Schäffer's reaction negative.

**Basidiospores** (Fig. 6-G) (4.6) 5.2–5.9 × 2.9–3.4 μm [x = 5.4 ± 0.3 × 3.2 ± 0.1 μm, Q = 1.5–2.0, Qm = 1.7 ± 0.1, n = 20 basidiospores]; elongated and occasionally ellipsoid, smooth, thick-walled, and brown. **Basidia** 13.1–16.4 × 4.5–5.9 μm, hyaline, smooth, clavate, and 4-spored. **Cheilocystidia** not observed. **Pleurocystidia** absent. **Pileipellis** (Fig. 6-H) a cutis composed of hyphae 3.2–7.8 μm wide, cylindrical, branched, and smooth, some of which are constricted at the branch and contain light brown vacuolar pigments. **Annulus** composed of hyphae 2–6 μm in diam., smooth, long clavoid, hyaline and branched, not constricted at septa; hyphae of the annulus margin contained brown to dark brown vacular pigments.

**Habitat** solitary in forest.

**Notes:** Molecular analysis based on ITS sequence indicates that this is a distinct species in section *Xanthodermatei*; however, the phylogenetic analysis using multi-gene sequences suggests that this species is a member of section *Hondenses*. We performed the sequencing and analysis a second time with the same results, such that we were unable to clearly place this species in any section. Correspondingly, the morphology of this species was also quite different from that of the known species in those sections: it lacked color changes after flesh exposure and had a pleasant odor and a negative KOH reaction. *Agaricus bukavuensis* is a species lacking a color change on cutting, but it has a bulbous stipe and larger basidiospores (5.4–6.9 × 4–4.9 μm) than those of *A. nigrogracilis* (Heinemann & Goossens-Fontana 1956, Heinemann 1978).

## Discussion

The section *Xanthodermatei* was originally thought to be a monophyletic group based on its ITS sequence data (Callac and Guinberteau 2005; Challen *et al.* 2003; Geml *et al.* 2004; Kerrigan *et al.* 2005; Thongklang *et al.* 2014; Zhao *et al.* 2011). However, based on the most recent study on *Agaricus* using multigene sequences, the *Xanthodermatei* section has been split into two sections: *Xanthodermatei* and *Hondenses* (Zhao *et al*. 2016). Here, we adopted the newest taxonomic system of *Agaricus* (Zhao *et al*. 2016). In this study, the statistic supporting each clade in the multigene-based tree was typically hgher than that supporting the single gene sequences. At the species level, most species can be distinguished using ITS sequences, except *A. tibetensis,* which can instead be recognized by its ITS-based phylogeny. However, this species can be identified via multigene data. Thus, multigene sequencing is recommended

for the phylogenetic study of *Agaricus*. It is remarkable that the tropical species are not grouped in a specific subclade within the section *Xanthodermatei*, in contrast there are no tropical species in section *Hondenses*.

Twenty-four specimens were involved in this study, with one from Thailand and all others from China, including the areas surrounding Tibet. They were separated into twelve species, eleven of which were new species. This indicates that the Himalayas and surrounding areas are rich in *Agaricus* biodiversity, with the exception of tropical areas (Zhao *et al.* 2011). *Agaricus malangelus* was first described in the USA. In this study, we extended its distribution range to Tibet. Although their occurrences are distant and isolated, the morphology and phylogeny support this identification. Importantly, climate may also be an important factor determining the species distribution of *Agaricus*.

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