Phylogeny, diversity and morphological evolution of Amanitaceae

Zhu L. Yang*, Qing Cai and Yang-Yang Cui

Abstract: Fungi of Amanitaceae are very important both economically and ecologically due to their edibility and formation of ectomycorrhizal symbiosis with plants. To date, three genera (*Amanita, Catatrama* and *Limacella* s.l.) and around 1,000 species were described worldwide. However, only about 600 of the described species were accepted as good species. Due to their phenotypic plasticity and morphological stasis, many taxa are not easily recognizable based on merely morphological characters. We studied specimens collected from many parts of the world during the last about twenty years or so by means of morphology and multigene phylogeny. Our observations showed that *Amanita* is very diverse in morphology and the development of basidioma, and, in total, 24 types of mature basidiomata with important morphological features were summarized. *Catatrama* is a unique genus within Amanitaceae with volval remnants on the pileus, which are microscopically similar to those of non-ectomycorrhizal species of *Amanita*. *Limacella* s.l. should be treated as three separate genera, namely *Limacella* s.str., *Myxoderma* and *Limacellopsis*, the last of which was newly erected to accommodate *Limacella guttata* and its allies. In addition, one new species, *Limacellopsis asiatica*, and three new combinations, namely, *Limacellopsis guttata*, *Myxoderma ochraceoluteum* and *M. subillinitum*, were proposed. Judging from an apparent high degree of morphological/anatomical complexity and multi-gene molecular phylogenetic analyses, there are abundant new taxa hidden among the known ones.

Key words: amanitas, morphological evolution, phylogeny, taxonomy

1. Introduction

Fungi of Amanitaceae (Basidiomycetes) are very important both economically and ecologically due to their edibility and formation of mycorrhizal symbiosis with plants (Bas 1969, Yang et al. 1999). Economically, some of amanitas have great economic, dietary, and health values. For example, *Amanita caesarea* (Scop.) Pers., *A. caesareoides* Lj.N. Vassiljeva, *A. hayalyuy* Arora & G.H. Shepard, *A. hemibapha* (Berk. & Broome) Sacc., *A. jacksonii* Pomerl. and *A. tanzanica* Härk. & Saarim., are gourmet mushrooms highly prized in many parts of the world (Jenkins 1986, Härkönen et al. 1994, Breitenbach & Kränzlin 1995, Neville & Poumarat 2004, Shepard et al. 2008, Yang 2015). In contrast, some others, like *A. bisporigera* G.F. Atk., *A. exitialis* Zhu L. Yang & T.H. Li, *A. phalloides* (Vaill.: Fr.) Link and *A. virosa* Bertill., are poisonous or even lethal, causing many problems or deaths annually (Bresinsky & Besl 1985, Jenkins 1986, Wieland 1986, Tulloss et al. 1995, Yang & Li 2001, Neville & Poumarat 2004, Zhang et al. 2010, Cai et al. 2014, Chen et al. 2014, Li et al. 2015, Zhang et al. 2015). Ecologically, most species of Amanitaceae are important ectomycorrhizal (ECM) fungi in the ecosystems and can form ECM relationships with plants of more than ten families (Beeli 1935, Reid 1980, Pegler & Shah-Smith 1997, Wood 1997, Yang et al. 1999), although some species are probably saprophytic (Bas 1969, Wolfe et al. 2012, Tulloss et al. 2014).

Mycologists in the world have studied the systematics and taxonomy of amanitas for over two hundred years. To date, three genera (*Amanita* Pers., *Catatrama* Franco-Mol. and *Limacella* Earle) and over 600 good species of Amanitaceae are known for the family. Several molecular phylogenetic analyses revealed that the genus *Amanita* may be divided into two subgenera and a few sections (Weiss et al. 1998, Drehmel et al. 1999, Oda et al. 1999, Zhang et al. 2004). Due to their phenotypic plasticity, morphological stasis and convergent evolution, many taxa are not easily recognizable based on merely morphological characters (Yang 2011), and the numbers of species and genera of the family are likely to be higher because large parts of the tropics and the subtropics remain little studied. It was suggested that *Catatrama* is a member of Amanitaceae (Moncalvo et al. 2002), and *Aspidella* E.-J. Gilbert should be regarded as an independent genus within the family (Vizzini et al. 2012). However, multigene phylogenetic analyses are still wanted in order to understand their relationships.

Our understanding of morphological evolution in the family remains rudimentary. Moreover, more and more “genera” with sequestrate basidiomata (Bougher 1999, Bougher & Lebel 2002) were proven to be members of *Amanita* (Justo et al. 2010). Yet the phylogenetic relationships between the genera in the family have not been fully clarified, although previous studies showed that sequestrate forms have evolved independently several times from their ancestors (Justo et al. 2010).

Our aims are to study the phylogeny, to understand the relationships of the genera of Amanitaceae, and the diversity of species, and to elucidate the morphological evolution within the family Amanitaceae.

2. Materials and methods

In the last twenty years, we have been collecting samples of Amanitaceae from many parts of southwestern, central, southeastern, northeastern and northwestern China. In addition, specimens were also collected from East Asia (Japan), Europe (Germany), North America (Canada and USA) and Africa (Benin) by us. Additional collections, including types, collected from Africa (Burundi, Madagascar, Malawi, Tanzania and Zambia), Europe (Netherlands), North and Central America (USA and Costa Rica), Oceania (Australia and New Zealand), southeast Asia (Bangladesh, Malaysia, India and Sri Lanka), were obtained on loan. Those collections are deposited in various herbaria including the Herbarium of the Cryptogamics, Kunming Institute of Botany, Chinese Academy of Sciences (HKAS), Herbarium of Institute of Microbiology, Chinese Academy of Sciences (HMAS), Mycological Herbarium of Guangdong Institute of Microbiology (GDGM), Herbarium of Mycology, Jilin Agricultural University (HMJAU), the Private Herbarium Rooseveltensis Amanitarum (RET) and many other herbaria outside of China.

For morphological study, standard methods were employed (Bas 1969, Yang 1997, Yang et al. 2004). For molecular phylogenetic analyses, sequences were generated from samples for three nucDNA regions, namely partial 28S nuc rDNA sequence (nLSU), genes for translation elongation factor 1-*α* (*tef1α*) and the second largest subunit of RNA polymerase II (*rpb2*), following the methods by CAI et al. (2014). Together with additional sequences from GenBank, molecular phylogenetic analyses of Amanitaceae, including the putative four genera (*Amanita, Aspidella, Catatrama* and *Limacella*), were conducted. *Melanoleuca verrucipes*, *Pluteus romelii* and *Volvariella gloiocephala* were selected as out groups (GARNICA et al. 2007). Taxon information and GenBank accession numbers for the sequences used in the molecular phylogeny of Amanitaceae were listed in table 1. Quotation marks were placed around the names in the cladogram and the table due to their original submission as *Limacella* taxa or their taxonomic uncertainty.

The generic name *Amanita* is abbreviated as "*A.*", *Aspidella* as "*Asp.*", *Catatrama* as "*C.*", *Limacella* as "*L.*", *Limacellopsis* as "*Lim.*" and *Myxoderma* as "*M.*". In the part of taxonomy, the taxa are arranged in alphabetic order.

3. Results

3.1. Molecular phylogenetic relationships of Amanitaceae

A phylogenetic tree obtained from maximum likelihood (ML) analysis on the sequences of nLSU, *rpb2* and *tef1α* is shown in figure 1. Five major clades, namely *Amanita*-clade, *Catatrama*-clade, *Limacella* s.str. clade, *Limacella* I-clade and *Limacella* II-clade, were inferred within Amanitaceae with relatively high statistic supports. The monophyly of Amanitaceae, consisting of above clades, was verified. Although the phylogenetic relationships among the clades were largely unresolved, the close relationships between the clades *Catatrama* and *Limacella* s.str. was highly supported.

3.2. Morphology of Amanitaceae

Over 2,000 collections were examined for comparison. Macro-morphological characters, such as, the color of the pileus and the stipe, the form and the shape of the volval remnants on the surfaces of the pileus and on the base of the stipe, and the color and the position of the annulus on the stipe, are useful for the recognition of species of *Amanita*. Microscopical characters, like the size and the shape of basidiospores and the common presence or absence of clamps, and the structure of the volval remnants on the pileus and the base of the stipe are consistent and important characters for the delimitation of species.

Tab 1: Taxon information and GenBank accession numbers for the sequences used in the molecular phylogeny of Amanitaceae. GenBank accession numbers for the sequences generated in this study are in boldface.

Taxon	Herbarium ID	GenBank accession numbers		
		nLSU	*rpb2*	*tef1-α*
Ingroup				
Amanita caesarea	RET 036-2	KF877205	KF877042	KF877105
Amanita aff. *fritillaria*	HKAS 57649	KJ466480	KJ466645	KJ481980
Amanita manicata	HKAS 90174	**KT833801**	**KT833818**	**KT833831**
Amanita manicata	PDD 99110	**KT833802**	---	**KT833832**
Amanita muscaria	HMJAU 4585	**KT833803**	---	**KT833833**
Amanita phalloides	HKAS 75773	JX998060	KJ466612	JX998000
Amanita prairiicola	RET 266-2	HQ539727	---	---
Amanita pruittii	RET 343-2	HQ539729	---	---
Amanita sp.	HKAS 77339	KJ466482	KJ466647	KJ481981
Amanita subglobosa	HKAS 58837	JN941152	JQ031121	KJ482004
Amanita thiersii	DPL 7272	HQ539752	---	---
Amanita virgineoides	HKAS 79691	KJ466495	KJ466663	KJ481996
Amanita vittadinii	RET 277-1	HQ539757	---	---
Catatrama costaricensis	DAOM 211663	**KT833804**	**KT833819**	**KT833834**
Catatrama sp.	GB556	KP311385	---	---
Catatrama sp.	TBGI 14057	**KT833805**	**KT833820**	---
Catatrama sp.	TBGI 14256	**KT833806**	**KT833821**	---
Limacella delicata	ZT Myc55818	**KT833807**	**KT833822**	**KT833835**
Limacella glioderma	HKAS 90169	**KT833808**	**KT833823**	**KT833836**
Limacella glioderma	MB 000750/HKAS 86624	**KT833809**	**KT833824**	**KT833837**
Limacella glioderma	MB 102389/HKAS 86626	**KT833810**	**KT833825**	**KT833838**
'*Limacella glioderma*'	E. C. Vellinga 2241	AY176452	---	---
'*Limacella glioderma*'	E.C. Vellinga 2456	AY176454	---	---
'*Limacella glischra*'	VIGB 505	AY612843	---	---
'*Limacella illinita*'	SFSU HDT 54917	HQ539764	---	---
Limacellopsis asiatica	HKAS 76497	**KT833811**	**KT833826**	**KT833839**
Limacellopsis asiatica	HKAS 82561	**KT833812**	**KT833827**	**KT833840**
Limacellopsis guttata	MB 100157/HKAS 86628	**KT833813**	**KT833828**	**KT833841**
Myxoderma illinitum	HKAS 90168	**KT833814**	**KT833829**	**KT833842**
Myxoderma ochraceoluteum	HKAS 90170	**KT833815**	**KT833830**	**KT833843**
Myxoderma subillinitum	HKAS 84245	**KT833816**	---	**KT833844**
Myxoderma subillinitum	HKAS84246	**KT833817**	---	---
Outgroup				
Pluteus romellii	ECV 3201	AY634279	AY786063	AY883433
Volvariella gloiocephala	PBM2272	AY745710	---	---
Melanoleuca verrucipes	PBM 2289	DQ457687	DQ474119	GU187726

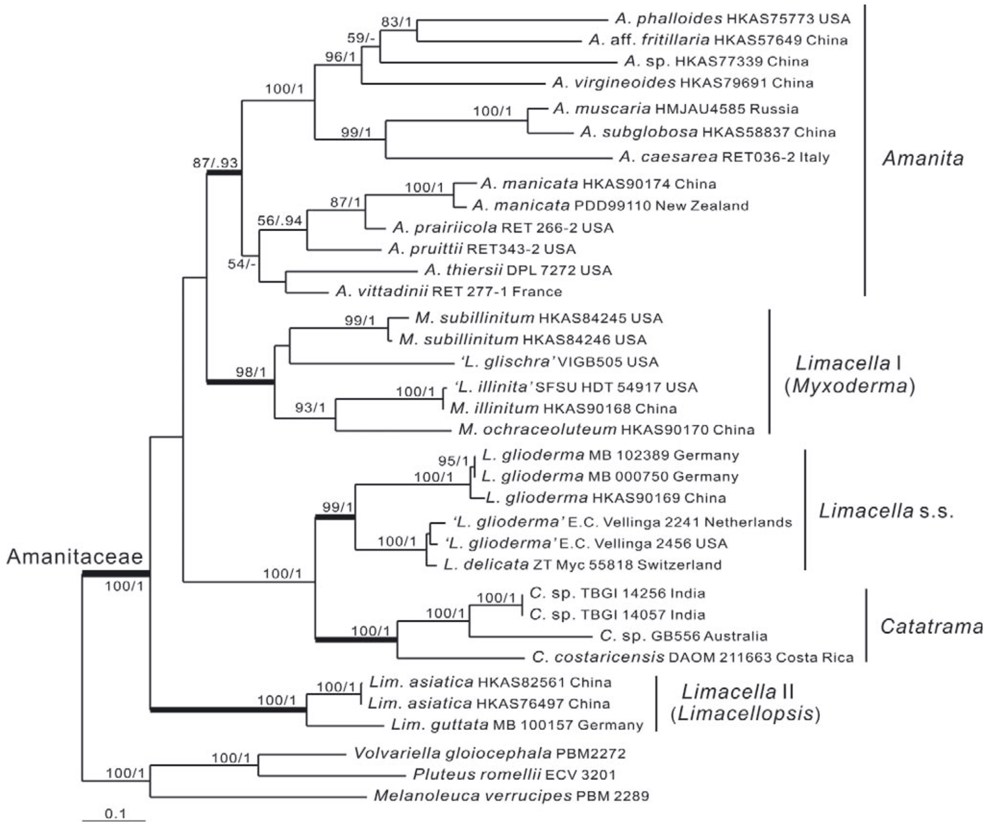

Fig. 1: Phylogeny of Amanitaceae resulted from maximum likelihood analyses of nLSU, *rpb2* and *tef1α.* Maximum parsimony bootstraps over 50 % and Bayesian posterior probabilities over 0.90 are shown.

Features of Amanitaceae

The common features for Amanitaceae are the free lamellae, bilateral lamellar trama (Fig. 3C), inflated terminal cells in trama (Fig. 3B), colorless thin-walled smooth to echinulate basidiospores, inflated subglobose cells in the subhymenium (Figs. 2C, and 3C), and the more or less gelatinized pileipellis (Figs. 3A, 4A, 5C, 6A, 7, 8 and 9). There are no volval remnants on the viscid to glutinous pileus of mature basidiomata in *Limacella* s.str.*, Limacella* I and *Limacella* II. On the contrary, there are volval remnants on the slightly to strongly gelatinized pileus of *Amanita* and *Catatrama*. For some species of *Amanita*, the volval remnants may be largely or entirely retained on the base of the stipe when basidiomata become mature. The squamules on the lower part of the stipe of *Catatrama* might well be volval remnants based on the literature (Franco-Molano 1991, Vrinda et al. 2000) and our observations.

The subclavate to long clavate terminal cells (Fig. 3B) in the trama of a few *Amanita* sections and *Catatrama* are much more differentiated than those in *Limacella* s.str*.*, *Limacella* I and *Limacella* II and *Amanita* sect. *Lepidella.* The basidiospores of *Amanita* are generally smooth, although minute warts were observed on some basidiospores within a few taxa of the genus (Corner & Bas 1962, Bas 1969, Yang 1997). In *Limacella* s.str*.*, *Limacella* I and *Limacella* II, some species possess smooth basidiospores, while others have asperulate basidiospores (Figs. 3D, 5A, 6B and 9B). In a few species, both smooth and asperulate basidiopsores were observed (Fig. 4B, and 9B). Distinctly warted basidiospores were observed in *C. costaricensis* Franco-Mol., with warts up to 1.5 µm in height (Fig. 2C). No true cystidia were observed in Amanitaceae.

The generic features

The features for the five clades or genera of Amanitaceae can be summarized as follows based on our observations on the collections.

Amanita: The pileus is slightly to strongly viscid, with distinct volval remnamts. Stipe is dry, fibrillose to squamulose, usually with distinctly volval remanants on the base of the stipe; the annulus is present or absent; the stipe base is subcylindrical to bulbous. The pileipellis is an ixo-cutis composed of slightly gelatinized repent filamentous hyphae. Basidiospores are asperulate to warted.

Catatrama: The pileus is slightly viscid, with distinct volval remnants. The stipe is dry, fibrillose to squamulose. Distinctly volval remanants on the base of the stipe were not observed. A rudimental annulus is present. The base of the stipe is subcylindrical. The pileipellis is an ixo-cutis composed of slightly gelatinized repent filamentous hyphae. Basidiospores are asperulate to warted.

Limacella s.str.: The pileus is viscid to slightly viscid. The stipe is dry or slightly viscid, and with fibrillose to incomplete ring-like, non-geletinized volval remnants under a rudimentary annulus or an appressed annulus zone. The base of the stipe is subcylindrical to attenuate downwards, barely enlarged. The pileipellis is an ixotrichoderm composed of

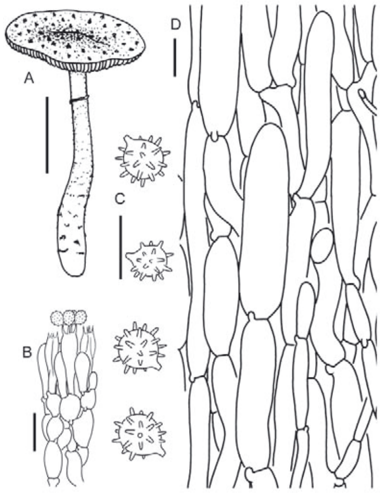

Fig. 2: *Catatrama costaricensis* (Puntarenas, Costa Rica, paratype, NY). A. Basidioma; B. Basidia and subhymenium; C. Basidiospores; D. Vertical section of a volval remnant on the pileus. Bars: A = 3 cm, B = 20 µm, C = 10 µm, D = 20 µm.

subcylindrical terminal cells; inflated cells in short chains are absent. Basidiospores are smooth to asperulate.

Limacella I: The pileus is glutinous to viscid. The stipe is glutinous to strongly viscid, without volval remnants on the surface of the stipe. The annulus is usually strongly gelatinized if present. The base of the stipe is subcylindrical to attenuate downwards, barely enlarged. The pileipellis is an ixotrichoderm composed of subcylindrical terminal cells; inflated cells in short chains are absent.

Limacella II: The pileus is slightly viscid. The stipe is dry or only slightly viscid, glabrous or fibrillose under a large dry persistent membraneous annulus. The base of the stipe is slightly enlarged. The pileipellis is an ixotrichoderm composed of inflated cells in short chains, and upwards attenuate terminal cells.

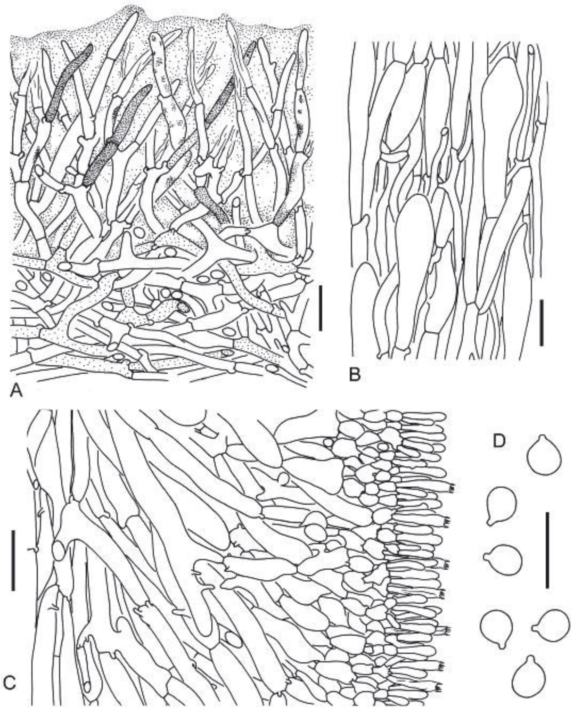

Fig. 3: *Limacella glioderma* (Tübingen, Germany, HKAS 31576). A. Pileipellis; B. Trama of stipe; C. Lamellar trama, subhymenium and hymenium; D. Basidiospores. Bars: A–C = 20 μm, D = 10 μm.

Morphology in *Amanita*

The morphological diversity in the genus *Amanita* is very prominent in comparison with many other agaric genera. Depending on the species, the margin of the pileus is either smooth or striate; the lamellulae are truncate or attenuate; the stipe is annulate or not; the base of the stipe is subcylindrical or bulbous; the trama of the stipe is hollow or solid when mature; the basidiospores are amyloid or non-amyloid, and clamp connections are absent or present. Generally speaking, all these features reflect the phylogenetic relationships among the species.

3.3. Taxonomy of *Limacella* s.l.

Based on the phylogenetic analysis and morphological features, *Limacella* s.l. should be divided into three genera, namely *Limacella* s.str., *Myxoderma* Kühner (corresponding to *Limacella* I) and a new genus (corresponding to *Limacella* II), as described below.

Limacella Earle, Bull. New York Bot. Gard. 5: 447 (1909)

Type: *Limacella delicata* (Fr.) Earle ex Konrad & Maubl. 1926 (≡ *Agaricus delicatus* Fr. 1821)

Diagnosis: Pileus viscid to slightly viscid. Stipe dry or slightly viscid, and with fibrillose to incomplete ring-like, non-geletinized volval remnants under a rudimentary annulus or an appressed annulus zone. Pileipellis an ixotrichoderm composed of subcylindrical terminal cells; inflated cells in short chains absent.

Limacella delicata (Fr.) Earle ex Konrad & Maubl. 1926 (≡ *Agaricus delicatus* Fr. 1821)

Basionym: *Agaricus delicatus* Fr., Syst. mycol. (Lundae) 1: 23 (1821) ≡ *Lepiota delicata* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 136 (1871).

Specimen examined: Switzerland: Canton Zürich, at Brugg, in alluvial forest rich in *Fraxinus excelsior*, on humus-rich soil, 14 IX. 2003, P. A. Moreau s.n. (ZT Myc55818).

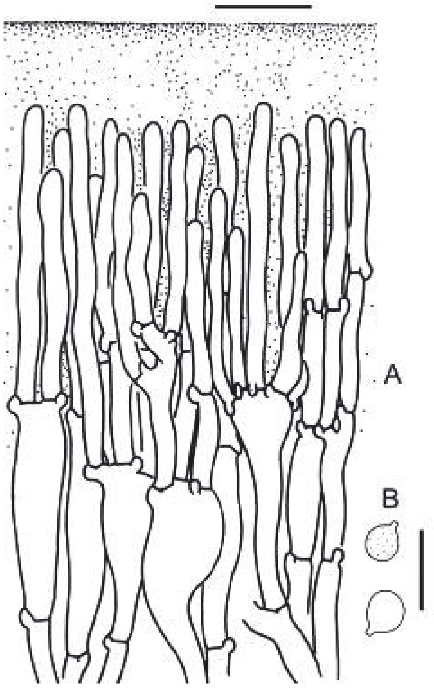

Fig. 4: *Limacella delicata* (Zurich, Switzerland, ZT Myc55818). A. Pileipellis; B. Basidiospores. Bar: A = 20 µm; B = 10 µm.

Limacellopsis Zhu L. Yang, Qing Cai & Yang Y. Cui, gen. nov.

MycoBank: MB814582

Synonyms: *Limacella* subsect. *Pseudoannularia* Contu, Bolm Soc. broteriana, 2a série 65: 82 (1992); *Limacella* sect. *Amanitellae* Gminder, Z. Mykol. 60(2): 386 (1994).

Type: *Limacellopsis guttata* (Pers.) Zhu L. Yang, Qing Cai & Yang Y. Cui [≡ *Agaricus guttatus* Pers. 1793]

Etymology: "*Limacellopsis*" similar to *Limacella*.

Diagnosis: Pileus slightly viscid. Stipe dry or only slightly viscid, glabrous or fibrillose under a large dry persistent membraneous annulus. Pileipellis an ixotrichoderm composed of inflated cells in short chains, and upwards attenuate terminal cells.

Basidiomata medium-sized to large. *Pileus* convex to plano-convex, smooth, occasionally finely cracked, slightly viscid; margin non-striate, non-appendiculate. *Lamellae* free, crowded, white to cream-colored; lamellulae attenuate to round attenuate. *Stipe* subcylindric, glabrous or fibrillose under the annulus; base somewhat enlarged. *Annulus* present, subapical to superior, skirt-shaped, membranous, persistent. *Lamellar trama* bilateral. *Subhymenium* composed of subglobose to ellipsoid or irregularly shaped cells. *Basidia* clavate. *Basidiospores* globose, subglobose or ellipsoid, inamyloid, non-dextrinoid, colorless, hyaline, thin-walled, smooth to asperulate; apiculus relatively large. *Pleurocystidia* and *cheilocystidia* absent. *Pileipellis* an ixotrichoderm composed of inflated cells in short chains, with upwards attenuate terminal cells. *Stipe trama* composed of longitudinally arranged filamentous hyphae, mixed with long ellipsoid cells and clavate to subclavate terminal cells. All hyphae with clamped septa.

Limacellopsis asiatica Zhu L. Yang, Qing Cai & Yang Y. Cui, sp. nov.

MycoBank: MB814584

Type: China: Sichuan Prov., Hongyuan County, Shuajing Temple, 3300 m, on ground under trees of *Picea*, 12. VIII. 2013, B. Feng 1455 (HKAS 82561).

Basidiomata medium-sized. *Pileus* 6–9 cm in diam., convex to plano-convex, sometimes umbonate, pale yellowish (4A2–3), grayish yellow (4B2–4), yellowish brown (5C7–8, 5B3–4) to pinkish brown (6B2–4), sometimes with grayish brown (6E3) tints, glabrous or cracked, slightly viscid when wet; margin non-striate, non-appendiculate; trama white, unchanging. *Lamellae* free, crowded, white (11A1); lamellulae attenuate to round attenuate, plentiful. *Stipe* 10–17 × 1–1.5 cm, subcylindric, dirty white, grayish to pale yellowish, fibrillose under the annulus; context white; base enlarged, ca. 2–2.8 cm in diam., white. *Annulus* subapical to superior, large, membranous, dirty white to whitish on both surfaces, persistent. *Odor* indistinct.

Lamellar trama bilateral. Mediostratum 30–50 µm wide, composed of abundant subfusiform, ellipsoid to clavate inflated cells (25–95 × 10–30 µm); filamentous hyphae abundant, 3–8 µm wide; vascular hyphae rare. Lateral stratum composed of abundant subfusiform to ellipsoid inflated cells (25–50 × 8–12 µm), diverging at an angle of ca. 30–45° to the mediostratum; filamentous hyphae abundant, 4–6 µm wide; septa often with clamps. *Subhymenium* 25–40 µm thick, with 2–3 layers of subglobose to ellipsoid or irregularly shaped cells (10–25 × 7–12 µm), sometimes mixed with barely inflated elements 2–5 µm in diam. *Basidia* 30–40 × 7–10 µm, clavate, 4-spored; sterigmata 3–4 µm long; basal septa often with clamps. *Basidiospores* [100/4/3] (3.5–)4–6 × (3–)4–5.5(–6) µm, Q = 1–1.1 (–1.18), **Q** = 1.05 ± 0.04, globose to subglobose, inamyloid, non-dextrinoid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. *Pleurocystidia* and *cheilocystidia* absent. *Pileipellis* 75–125 µm thick, an ixotrichodermium composed of more or less inflated, subglobose, ellipsoid to clavate, thin-walled cells (20–50 × 6–13 µm) in chains, with upwards attenuate terminal cells. *Stipe trama* composed of longitudinally arranged, long clavate terminal cells (40–200 × 15–25 µm); filamentous hyphae abundant, 3–10 µm in diam.; vascular hyphae rare. *Annulus* composed of subradially arranged elements; inflated cells abundant, subglobose to ellipsoid, 10–35 × 8–18 µm, colorless, thin-walled, becoming elongated and rare towards the lower surface; filamentous hyphae abundant, 4–8(–10) µm in diam., colorless, thin-walled. All hyphae with clamped septa.

Additional specimens examined: China: Sichuan Prov., Hongyuan County, Shuamalu, 3400 m, 5. VIII. 1996, M.S. Yuan 2425 (HKAS 30864); Gansu Prov., Lintan County, Zhiliguan Forest Park, 3000 m, 10. VIII. 2012, X.T. Zhu 648 (HKAS 76497).

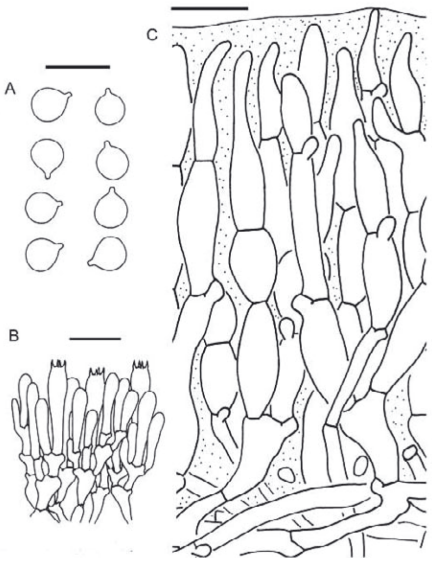

Fig. 5: *Limacellopsis asiatica*. A. Basidiospores (Sichuan, China, HKAS 30864); B. Basidia and subhymenium (Gansu, China, HKAS 76497); C. Pileipellis (HKAS 30864). Bar: A = 10 µm; B–C = 20 µm.

Note: *Limacellopsis asiatica* is characterized by its yellowish brown to pinkish brown pileus, whitish annulus, and globose to subglobose basidiospores with Q= 1–1.1 (–1.18). *Limacellopsis asiatica* was mistakenly regarded as *Lim. guttata* by Yang (2005, 2015). However, the latter species possesses a pileus with a reddish brown pileal center, an annulus with its both surfaces often decorated with brownish droplets, and ellipsoid basidiospores (GMINDER 1994; NEVILLE & POUMARAT 2004). Our observation on a Netherlandish collection of *Lim. guttata* (HMAS 40575) indicated that the basidiospores are ellipsoid, with Q = 1.3–1.63 (–1.75) (Fig. 6B). Molecular phylogenetic analysis (Fig.1) also indicated that the European and the East Asian collections should be treated as different species.

Limacellopsis guttata (PERS.: FR.) Zhu L. YANG, Qing CAI & Yang Y. CUI, comb. nov.

MycoBank: MB814585

Basionym: *Agaricus guttatus* PERS. in HOFFMANN, Naturgetr. Abbild. Beschr. Schwämme (Prague) 3: tab. 22 (1793) ≡ *Agaricus guttatus* PERS.: FR., Syst. Mycol. (Lundae). 1: 27 (1821) ≡ *Lepiota guttata* (PERS.: FR.) QUÉL., Bull. Soc. bot. Fr. 23: 325 (1877) [“1876”] ≡ *Limacella guttata* (PERS.: FR.) KONRAD & MAUBL., Encyclop. Mycol. 14: 70 (1949) [“1948”].

Specimens examined: Germany: Marburg, 6. X. 2007, G. GUTHÖRLEIN s.n. (MB 100157). The Netherlands: Prov. Noord-Holland, under *Fagus*, 18. X. 1964, R.A. MAAS GEESTERANUS 14393 (HMAS 40575).

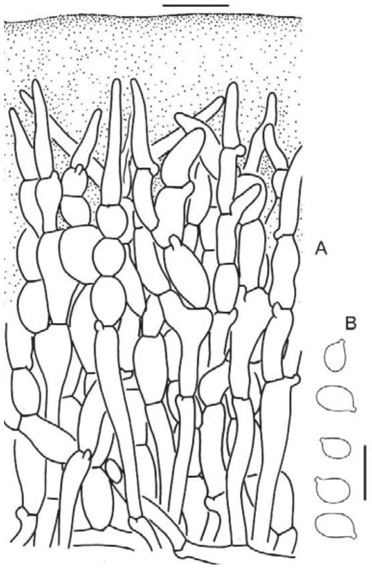

Fig. 6: *Limacellopsis guttata*. A. Pileipellis (Marburg, Germany, MB 100157); B. Basidiospores (Noord-Holland, Netherlands, HMAS 40575). Bar: A = 20 µm, B = 10 µm.

Myxoderma Kühner, Le Botaniste 17: 145 (1926)

Synonym: *Limacella* sect. *Lubricae* H.V. Sm. ex Contu, Bol. Soc. Brot. 2a série 65: 81 (1992)

Type: *Myxoderma illinitum* (Fr.) Kühner 1926 (≡ *Agaricus illinitus* Fr. 1818)

Diagnosis: Pileus glutinous to viscid. Stipe glutinous to strongly viscid, with neither annulus nor volval remnants on the surface of stipe; annulus usually strongly gelatinized if present. Pileipellis an ixotrichoderm composed of subcylindrical terminal cells; inflated cells in short chains absent.

Myxoderma illinitum (Fr.: Fr.) Kühner, Le Botaniste 17: 145 (1926)

Basionym: *Agaricus illinitus* Fr., Observ. mycol. (Havniae) 2: 8 (1818) ≡ *Agaricus illinitus* Fr.: Fr., Syst. mycol. (Lundae) 1: 23 (1821) ≡ *Lepiota illinita* (Fr.: Fr.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 326 (1872) ≡ *Amanitella illinita* (Fr.: Fr.) Maire, Ann. Mycol. 11(4): 337 (1913) ≡ *Limacella illinita* (Fr.: Fr.) Maire, Treb. Mus. Ciènc. nat. Barcelona, sér. bot. 15(no. 2): 85 (1933).

Specimens examined: China: Jilin Prov., Chibei District, Changbaishan, 2. VIII. 2008, Z.L. Yang 5087 (HKAS 54183); Heilongjiang Prov., Mudanjiang City, Muling Town, Daling, 1. IX. 2015, Q. Cai 1476 (HKAS 90168).

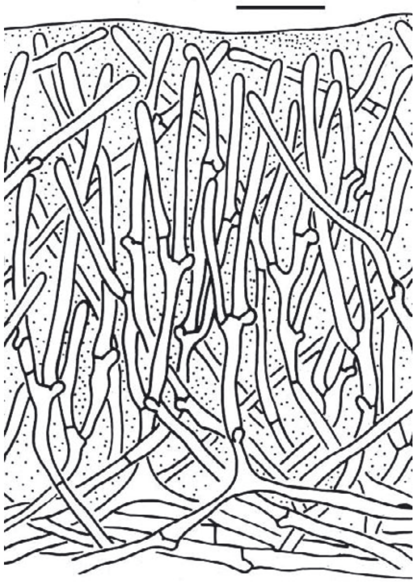

Fig. 7: Pileipellis of *Myxoderma illinitum* (Jilin, China, HKAS 90168). Bar: 20 µm.

Myxoderma ochraceoluteum (P.D. ORTON) Zhu L. YANG, Qing CAI & Yang Y. CUI, comb. nov.

MycoBank: MB814598

Basionym: *Limacella ochraceolutea* P.D. ORTON, Notes Roy. Bot. Gard. Edinburgh 29(1): 106 (1969).

Specimens examined: China: Yunnan Prov., Kunming, Kunming Botanical Garden, on ground under subtropical mixed forest, 9. X. 2012, Z.L. YANG 5644 (HKAS 77301); same location, 21. VIII. 2013, Q. CAI 991 (HKAS 90170); same location, 8. VII. 2014, Z.L. YANG 5785 (HKAS 82684).

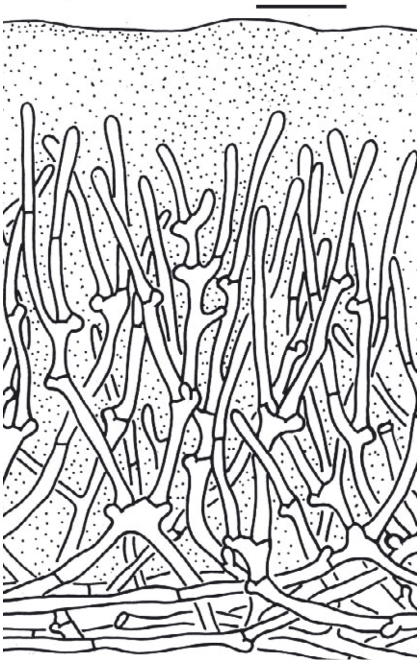

Fig. 8: Pileipellis of *Myxoderma ochraceoluteum* (Yunnan, China, HKAS 77301). Bar: 20 µm.

Myxoderma subillinitum (GUZMÁN) Zhu L. YANG, Qing CAI & Yang Y. CUI, comb. nov.

MycoBank: MB814613

Basionym: *Limacella subillinita* GUZMÁN, Boln. Soc. mex. Micol. 8: 89 (1974).

Specimens examined: USA: Florida, Gainesville, on ground in broad-leaved forest, 7. X. 2012, Z.W. GE 3407 (HKAS 84245); Gainesville, on ground in broad-leaved forest, 8. X. 2012, Z.W. GE 3408 (HKAS 84246).

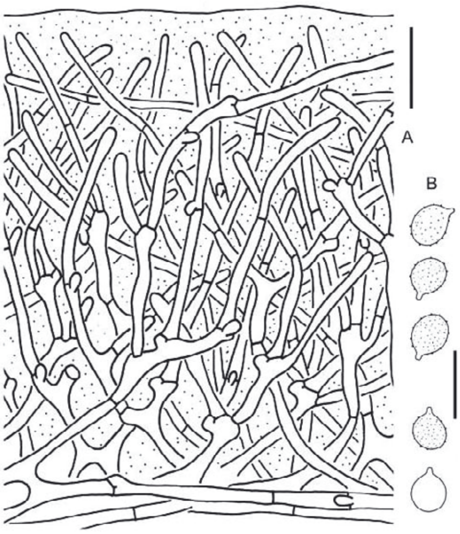

Fig. 9: *Myxoderma subillinitum* (HKAS 84246). A. Pileipellis; B. Basidiospores. Bars: A = 20 µm; B = 10 µm.

4. Discussion

4.1. Circumscription of Amanitaceae and relationships among the genera

Historically, several genera, *Amanita*, *Limacella*, *Pluteus* Fr., *Rhodotus* Maire, *Termitomyces* R. Heim and *Volvariella* Speg., were arranged in the family Amanitaceae (Singer 1936, Moser 1967). However, Kühner (1980), Pouzar (1983) and Singer (1986) included only *Amanita* and *Limacella* s.l. in the family. Moncalvo et al. (2002) indicated that *Amanita*, *Catatrama* and *Limacella* s.l. were grouped together, but with weak bootstrap support based on the analysis of the DNA sequences of the single molecular marker, nLSU. The monophyly of Amanitaceae, consisting of *Amanita*, *Catatrama*, *Limacella* s.str., *Myxoderma* and *Limacellopsis*, was verified for the first time in our study. Although the phylogenetic relationships among the five genera were largely unresolved, the close relationships between *Catatrama* and *Limacella* s.str. was highly supported (Fig. 1). Recently, Amanitaceae was treated in the family Pluteaceae (Cannon & Kirk 2007). However, our multi-gene analyses indicated that the sister relationship between Pluteaceae and Amanitaceae was not supported (data not shown).

Within Amanitaceae, the genera possess their own morphological characters. Specifically, *Limacella* s.str., *Myxoderma* and *Limacellopsis* have glabrous pileus, while *Catatrama*, mainly distributed in tropical and subtropical regions, and *Amanita*, a nearly cosmopolitan genus, possess strongly developed volval remnants on the pileus and/or on the basal part of the stipe. The pileipellis structures of *Limacella* s.str. and *Myxoderma* are nearly identical, both composed of gelatinized narrow subcylindrical terminal cells, and, thus, *Myxoderma* (Kühner 1926) was rarely regarded as an independent genus even though it was validly published (Donk 1962). However, both genera can be easily separated by the following characters: taxa of *Limacella* s.str. possess a dry surface of the stipe, which is covered with squamules and decorated with a rudimentary annulus, while taxa of *Myxoderma* have a gelatinized surface of the glabrous stipe without annulus. Although *Limacellopsis* also has a gelatinized pileal surface, the structure of the pileipellis, composed of inflated cells in chains and upwards attenuate terminal cells (Figs. 5C and 6A), is clearly different from those of *Limacella* s.str. (Figs. 3A and 4A) and *Myxoderma* (Figs. 7–9). For the necessary rearrangement of the remaining species in *Limacella* s.l., more studies should be conducted.

The structures of the pileipellis and the volval remnants on the pileus of *Catatrama* were largely unknown. Our observations on the paratype of *C. costaricensis* indicated that the pileipellis is a slightly gelatinized cuticle consisting of radially repent slightly gelatinized filamentous hyphae, and the volval remnants on the pileus consist of more or less vertically arranged ellipsoid to subfusiform inflated cells mixed with scattered filamentous hyphae (Fig. 2D), all of which are very similar to those in *A.* subsect. *Vittadiniae*. In addition, there are relatively abundant clavate to long clavate terminal cells in the trama of the stipe, a unique character as also observed in the other genera of Amanitaceae. Surprisingly, although the taxa of both *Catatrama* and *Amanita* possess volval remnants on the pileal surface and/or on the basal part of the stipe, and even share similar pileipellis and volval structures, they are not closely related as sister groups (Fig. 1).

Most species of Amanitaceae possess smooth basidiospores. The surfaces of the basidiospores are finely asperulate in some species of *Limacella* s.str. and *Limacellopsis* (Smith 1945, Gminder 1994, Neville & Poumarat 2004). It is interesting to note that the echinulate warts become much more evident in *Catatrama* than in *Limacella* s.str. and *Limacellopsis* (Figs. 2C, 3D, 4B, 5A, 6B and 9B). The size of the warts on the surfaces of the basidiospores should be a useful character in the taxonomy in *Catatrama*, which was regarded as monotypic (Franco-Molano 1991, Vrinda et al. 2000) but should be treated as a genus consisting of more than a single species based on our morphological and molecular-phylogenetic studies (Fig. 1).

In the family Amanitaceae, species of *Limacella* s.str., *Myxoderma* and *Limacellopsis* are probably all non-mycorrhizal (Hutchison 1988, Horak 2005, Wolfe et al. 2012). Bas (1969) reported that some species of *A.* sect. *Lepidella*, particularly in its subsection *Vittadiniae*, are probably non-mycorrhizal. Wolfe et al. (2012) demonstrated that the irreversible loss of genes required for autonomous growth is associated with the evolution of an ectomycorrhizal symbiosis in *Amanita*. Vizzini et al. (2012) treated the non-mycorrhizal or putatively non-mycorrhizal species in an independent genus, namely *Aspidella*, typified by *Asp. vittadinii* (Moretti) E.-J. Gilbert, while the ectomycorrhizal taxa were arranged in *Amanita*. Our data indicated that *Amanita* in its broad sense (including *Aspidella*) is a natural group, a view also held by Tulloss et al. (2014). It is unknown whether *Catatrama* species are mycorrhizal partners or not. If *Catatrama* species are non-mycorrhizal, only a single transition from free-living saprotrophic precursors to ectomycorrhizal symbiosis was evolved within *Amanita* in the whole family.

Phylogeny and diversity of *Amanita*

To date, about 1,000 species were described worldwide in *Amanita*, the largest genus in Amanitaceae. However, only about 600 of the described species were accepted as good species. Tulloss (2005) estimated that there are 900–1,000 species of *Amanita* in the world. For more than 20 years since 1994, species of *Amanita* in China were extensively collected and studied (Yang 1994, 1997, 2005). Over 30 new species of Amaniatceae were formally described from China. Recently 130 taxa were recorded in China (Deng et al. 2014, Li & Cai 2014, Li et al. 2015, Yang, 2015). Here, we use the study of *Amanita* in China as an example to show how little we know about the species diversity of this genus in the world.

In the last few years, besides morphological characterization of species of *Amanita*, we have generated DNA sequences from a large number of collections made from many parts of China. To our surprise, our molecular analyses revealed that even in such a relatively *Amanita*-well-studied country, there are still at least 70 additional new phylogenetic species, occupying about 35 % of the total 200 taxa in China, let alone the vast tropical regions in the world, where little studies on *Amanita* and other groups of fungi have been done. Due to their phenotypic plasticity, many species of *Amanita* cannot be easily recognized based on merely morphological characters. Judging from that an apparent high degree of a morph-species often corresponds to more than one phylogenetic species, there are abundant new taxa hidden among the known ones. The documented *Amanita* species may only represent the tip of the iceberg in terms of the resources of Amanitaceae in the world. In the near future, it is necessary to accelerate the discovery and documentation of fungal species of the family relying on both morphological and molecular data (Yang 2011).

Morphological evolution in Amanitaceae

The presence of clavate to long clavate terminal cells in the trama, termed as acrophysalides by Bas (1975), is unique to Amanitaceae (Bas 1969, Yang & Oberwinkler 1999). Such inflated terminal cells are much easier to be distinguished in the trama of the stipe than in that of the pileus. However, the degree of differentiation of inflated terminal cells and filamentous hyphae in the stipe trama are different in the genera of Amanitaceae. Inflated terminal cells and filamentous hyphae in *Limacellopsis*, *Myxoderma*, *Limacella* and *A.* sect. Lepidella are generally less perfectly differentiated than those in the species of *Catatrama* and other sections of *Amanita* (Bas 1969, our observations). Bas (1969) considered that the lower degree of differentiation in species of *A.* sect. *Lepidella* and in *Limacella* (in its broad sense) must be regarded as primitive compared with the highly differentiated tissue in the stipes of most *Amanita* species. Taking the phylogeny of the family into consideration (Fig. 1), this point of view is probably right.

The basidiospores of *Amanita* are generally smooth, although minute warts were observed on some basidiospores within a few taxa (Corner & Bas 1962, Bas 1969, Yang 1997). In *Limacella* s.str., *Limacellopsis* and *Myxoderma*, some species possess smooth basidiospores, while others have asperulate basidiospores. In a few species, both smooth and asperulate basidiopsores were observed. Distinctly warted basidiospores were observed in *C. costaricensis*, with watrts up to 1.5 µm in height (Fig. 2C).

It is Bas (1975) who suggested that the sequestrate *Torrendia pulchella* Bres. must have a close relationship with *Amanita* due to several morphological common features observed by Malençon (1955). Bougher & T. Lebel (2002) reported another sequestrate genus *Amarrendia* Bougher & T. Lebel and several species of *Torrendia* Bres. Justo et al. (2010) concluded that the genera *Amarrendia* and *Torrendia* are synonyms of *Amanita*. It is, thus, quite evident that convergent evolutions in the family are challenges for morphology-based taxonomy. Morphological evolution of sequestrate *Amanita* species was schematically illustrated by Yang (2011). Taking into consideration the development of basidioma, particularly the position of the primordium of the basidioma in the nodulus, the presence or absence of the annulus, the shape of the lamellulae, the elongation pattern and the trama consistency of the stipe, and the diverse forms of the volval remnants on the mature basidioma (Bas 1969, Yang & Oberwinkler 1999), the diversity of agaricoid *Amanita* species in connection with morphological evolution may be summarized in Fig. 10.

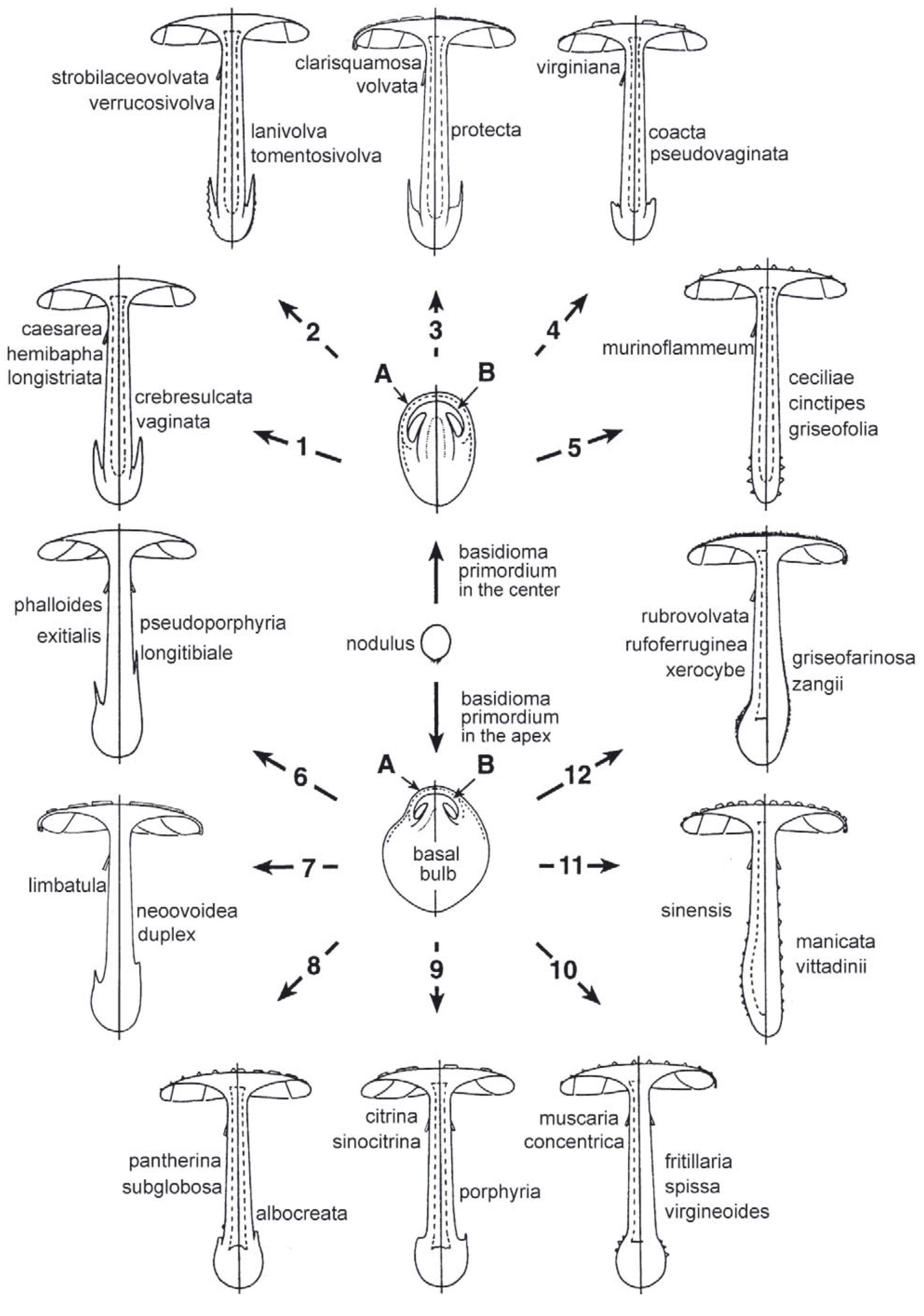

Fig. 10: Diversity of agaricoid *Amanita* species. The epithets of Latin names of some representatives are listed besides the basidioma. A and B indicate the outer and the inner layers of the volva respectively, which were discussed by YANG & OBERWINKLER (1999).

5. Acknowledgements

The senior author thanks Prof. Dr. P. Blanz and Prof. Dr. F. Oberwinkler for the invitation to participate in the symposium, and extends his sincere gratitude to Prof. Oberwinkler for his guidance during his study at the Universität Tübingen, and to Dr. R.E. Tulloss and the late Dr. C. Bas for providing access to many relevant collections and important literature, as well as many illuminating discussions. The authors are grateful to Dr. R. Berndt, Prof. C.C. Chen, Prof. Z.H. Chen, Dr. G. Gates, Dr. Z.W. Ge, Dr. R. Halling, Dr. K. Hosaka, Prof. G. Kost, Prof. T.H. Li, Dr. E. Nagasawa, Dr. F. Popa, Dr. C.K. Pradeep, Prof. B. Tolgor, Dr. M. Weiss, Prof. J. Xu, Dr. N.S. Yorou and Dr. P. Zhang for sending collections on loan or for their kind help. The curators of the herbaria AMH, BO, BPI, CUP, F, FH, FRIM, GDGM, H, HKAS, HMAS, HMJAU, IFP, K, L, MB, MHHNU, NY, PDD, RET, SAPA, TBGT, TF, TMI, TNM, TNS, and TU are acknowledged for their support. Dr. Hong Luo is acknowledged for improving the manuscript. This study was supported by the Joint Funds from the National Natural Science Foundation of China and Yunnan Provincial Government (No. U1302263), and by the Funds for International Cooperation and Exchange of the National Natural Science Foundation of China (No. 31210103919).

6. References

Bas, C. 1969: Morphology and subdivision of *Amanita* and a monograph of its section *Lepidella*. — Persoonia **5**: 285–579.

Bas, C. 1975: A comparision of *Torrendia* (Gasteromycetes) with *Amanita* (Agaricales). — In Bigelow, H.E. & Thiers, H.D. (eds.): Studies on Higher Fungi. — Beih. Nova Hedwigia **51**: 53–60.

Beeli, M. 1935: Flore iconographique des champignons du Congo, Fasc. I. — Bruxelles: Office de Publicité.

Bougher, N. 1999: New species of *Torrendia* (Fungi, Agaricales) from remnant woodlands in the wheat-belt region of Western Australia. — Austral. Syst. Bot. **12**: 145–156.

Bougher, N. & Lebel, T. 2002: Australian sequestrate (truffle-like) fungi XII. *Amarrendia* gen. nov.: an astipitate, sequestrate relative of *Torrendia* and *Amanita* (Amanitaceae) from Australia. — Austral. Syst. Bot. **15**: 513–525.

Breitenbach, J. & Kränzlin, F. 1995: Pilze der Schweiz. Band 4. — Luzern: Verlag Mykologia.

Bresinsky, A. & Besl, H. 1985: Giftpilze, mit einer Einführung in die Pilzbestimmung. — Stuttgart: Wissenschaftl. Verlagsgesellschaft.

Cai, Q., Tulloss, R.E., Tang, L.P., Tolgor, B., Zhang, P., Chen, Z.H. & Yang, Z.L. 2014: Multi-locus phylogeny of lethal amanitas: Implications for species diversity and historical biogeography. — BMC Evol Biol **14**(1): 143.

Cannon, P.F. & Kirk, P.M. 2007: Fungal families of the world. — Wallingford: CAN International.

Chen, Z.H., Zhang, P. & Zhang, Z.G. 2014: Investigation and analysis of 102 mushroom poisoning cases in southern China from 1994 to 2012. — Fungal Divers. **64**: 123–131.

Corner, E.J.H. & Bas, C. 1962: The genus *Amanita* in Singapore and Malaya. — Persoonia **2**: 241–304.

Deng, W.Q., Li T.H., Li P. & Yang, Z.L. 2014: A new species of *Amanita* section *Lepidella* from South China. — Mycol. Prog. **13**: 211–217.

Donk, M.A. 1962: The generic names proposed for Hymenomycetes. II. The generic names proposed for Agaricaceae. — Nova Hedwigia Beih. **5**: 1–320.

Drehmel, D., Moncalvo, J.-M. & Vilgalys, R. 1999: Molecular phylogeny of *Amanita* based on large-subunit ribosomal DNA sequences: implications for taxonomy and character evolution. — Mycologia **91**: 610-618.

Franco-Molano, A. 1991: *Catatrama* (Tricholomataceae), a new genus from Costa Rica. — Mycologia **83**: 501–505.

Garnica, S., Weiss, M., Walther, G. & Oberwinkler, F. 2007: Reconstructing the evolution of agarics from nuclear gene sequences and basidiospore ultrastructure. — Mycol. Prog. **111**: 1019–1029.

Gminder, A. 1994: Die trockenstieligen Arten der Gattung *Limacella* in Europe. — Z. Mykol. **60**: 377–398.

Härkönen, M., Saarimäki, T. & Mwasumbi, L. 1994: Tanzania mushrooms and their uses 4. Some reddish edible and poisonous *Amanita* species. — Karstenia **34**: 47–60.

Horak, E. 2005: Röhringe und Blätterpilze in Europa. — München: Elsevier.

Hutchison, L.J. 1988: Notes on *Limacella illinita* in pure culture. — Mycologia **80**: 111–114.

Jenkins, D.T. 1986: *Amanita* of North America. — Eureka: Mad River Press.

Justo, A., Morgenstern, I., Hallen-Adams, H.E. & Hibbett, D.S. 2010: Convergent evolution of sequestrate forms in *Amanita* under Mediterranean climate conditions. — Mycologia **102**: 675–688.

Kühner, R. 1926: Contribution à l'étude des Hyménomycètes et spécialement des Agaricacées. — Le Botaniste **17**: 5–218.

Kühner, R. 1980: Les Hyménomycètes Agaricoïdes (Agaricales, Tricholomatales, Pluteales, Russulales). Etude générale et classification. — Numéro spécial du Bull. Men. Soc. Linn. Lyon **49e** année: 1–1027.

Li, F. & Cai, Q. 2014: *Amanita heishidingensis*, a new species of *Amanita* sect. *Lepidella* from China. — Mycol. Prog. **13**: 1191–1197.

Li, H.J., Xie, J.W., Zhang, S., Zhou, Y.J., Ma, P.B., Zhou, J. & Sun, C.Y. 2015: *Amanita subpallidorosea*, a new lethal fungus from China. — Mycol. Prog. **14**: 43.

Malençon, G. 1955: Le dévelopment du *Torrendia pulchella* Bres. et son importance morphologénétique. — Revue Mycol. **20**: 81–130.

MONCALVO, J.-M., VILGALYS, R., REDHEAD, S.A., JOHNSON, J.E., JAMES, T.Y., CATHERINE, A.M., HOFSTETTER, V., VERDUIN, S.J.W., LARSSON, E. & BARONI, T.J. 2002: One hundred and seventeen clades of euagarics. — Mol. Phylogen. Evol. **23**: 357–400.

MOSER, M. 1967: Die Röhrlinge und Blätterpilze (Agaricales). — In GAMS, H. (ed.): Kleine Kryptogamenflora, Band II b/2. Basidiomyceten II. Teil. 3. Aufl. — Stuttgart: Gustav Fischer Verlag.

NEVILLE, P. & POUMARAT, S. 2004: Amaniteae: *Amanita*, *Limacella* & *Torrendia*. — Alssio: Edizioni Candusso.

ODA, T.M., TANAKA C. & TSUDA M. 1999: Molecular phylogeny of Japanese *Amanita* species based on nucleotide sequences of the internal transcribed spacer region of nuclear ribosomal DNA. — Mycoscience **40**: 57–64.

PEGLER, D.N. & SHAH-SMITH, D. 1997: The genus *Amanita* (Amanitaceae, Agaricales) in Zambia. — Mycotaxon **61**: 389–417.

POUZAR, Z. 1983: Taxonomic and nomenclatural notes on some families of larger fungi. — Česká Mycol. **37**: 172–176.

REID, D.A. 1980: A monograph of the Australian species of *Amanita* PERS. ex HOOK. (fungi). — Austr. Journ. Bot. Suppl. Ser. **8**: 1–97.

SHEPARD, G.H., ARORA, D. & LAMPMAN, A. 2008: The grace of the flood: classification and use of wild mushrooms among the Highland Maya of Chiapas. — Econ. Bot. **62**: 437–470.

SINGER, R. 1936: Das System der Agaricales I. — Ann. Mycol. **34**: 286–376.

SINGER, R. 1986: The Agaricales in modern taxonomy, 4th edn. — Koenigstein: Koeltz Scientific Books.

SMITH, H.V. 1945: The genus *Limacella* in North America. — Pape. Michigan Acad. Sci. **30**: 125–147.

TULLOSS, R.E. 2005: *Amanita* — distribution in the Americas, with comparison to eastern and southern Asia and notes on spore character variation with latitude and ecology. — Mycotaxon **93**: 189–231.

TULLOSS, R. E., LINDGREN, J. E., ARORA, D., WOLFE, B. E. & RODRÍGUEZ-CAYCEDO, C. 2014: *Amanita pruittii* — a new, apparently saprotrophic species from US Pacific coastal states. — Amanitaceae **1**: 1–9.

TULLOSS, R.E., STEPHENSON, S.L., BHATT, R.P. & KUMAR, A. 1995: Studies on *Amanita* (Amanitaceae) in West Virginia and adjacent areas of the mid-Appalachians. Preliminary results. — Mycotaxon **56**: 243–293.

VIZZINI, A., CONTU, M., ERCOLE, E. & VOYRON, S. 2012: Rivalutazione e delimitazione del genere *Aspidella* (Agaricales, Amanitaceae), nuovamente separato da *Amanita*. — Micol. Vegit. Medit. **27**(2): 75–90.

VRINDA, K.B., PRADEEP, C.K., MATHEW, S. & ABRAHAM, T.K. 2000: *Catatrama* (Tricholomataceae), a genus new to India. — Persoonia **17**: 495–496.

WEISS, M., YANG, Z.L. & OBERWINKLER, F. 1998: Molecular phylogenetic studies in the genus *Amanita*. — Can. J. Bot. **76**: 1170–1179.

WIELAND, TH. 1986: Peptides of Poisonous *Amanita* Mushrooms. — Heidelberg: Springer-Verlag.

WOLFE, B.E., TULLOSS, R.E. & PRINGLE, A. 2012: The irreversible loss of a decomposition pathway marks the single origin of an ectomycorrhizal symbiosis. — PLOS ONE **7** (7): e39597.

WOOD, A.E. 1997: Studies in the genus *Amanita* (Agaricales) in Australia. — Austr. Syst. Bot. **10**: 723–854.

YANG, Z.L. 1994: Studies of the genus *Amanita* from southwestern China (I). — Mycotaxon **51**: 459–470.

YANG, Z.L. 1997: Die *Amanita*-Arten von Südwestchina. — Biblioth. Mycol. **170**: 1–240.

YANG, Z.L. 2005: Flora fungorum sinicorum. Vol. 27 Amanitaceae (in Chinese). — Beijing: Science Press.

YANG, Z.L. 2011: Molecular techniques revolutionize knowledge of basidiomycete evolution. — Fungal Divers. **50**: 47–58.

YANG, Z.L. 2015: Atlas of the Chinese species of Amanitaceae (in Chinese). — Beijing: Science Press.

YANG, Z.L. & LI T.H. 2001: Notes on three white *Amanitae* of section *Phalloideae* (Amanitaceae) from China. — Mycotaxon **78**: 439–448.

YANG, Z.L. & OBERWINKLER, F. 1999: Die Fruchtköperentwicklung von *Amanita muscaria* (Basidiomycetes). — Nova Hedwigia **68**: 441–468.

YANG, Z.L., WEISS, M., KOTTKE, I., OBERWINKLER, F., NEHLS, U., GUTTENBERGER, M. & HAMPP, R. 1999: *Amanita*. — In CAIRNEY, J.W.G. & CHAMBERS, S.M. (eds.): Ectomycorrhizal fungi, key genera in profile. — Berlin: Springer-Verlag.

YANG, Z.L., WEISS, M. & OBERWINKLER, F. 2004: New species of *Amanita* from the eastern Himalaya and adjacent regions. — Mycologia **96**: 636–646.

ZHANG, L.F., YANG, J.B. & YANG, Z.L. 2004: Molecular phylogeny of eastern Asian species of *Amanita* (Agaricales, Basidiomycota): taxonomic and biogeographic implications. — Fungal Divers. **17**: 219–238.

ZHANG, P., CHEN, Z.H., XIAO, B., TOLGOR, B., BAO, H.Y. & YANG, Z.L. 2010: Lethal amanitas of East Asia characterized by morphological and molecular data. — Fungal Divers. **42**: 119–133.

ZHANG., P., TANG, L.P., CAI, Q. & XU, J. 2015: A review on the diversity, phylogeography and population genetics of *Amanita* mushrooms. — Mycology **6**: 86–93.

Address of the authors:

Prof. Dr. Zhu L. YANG*, Dr. Qing CAI & Yang-Yang CUI
Key Laboratory for Plant Diversity and Biogeography of East Asia,
Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China
*Email: fungi@mail.kib.ac.cn