

Saproamanita, a new name for both *Lepidella* E.-J. Gilbert and *Aspidella* E.-J. Gilbert (*Amaniteae*, *Amanitaceae*)

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Abstract: The genus *Amanita* has been divided into two monophyletic taxa, *Amanita*, an ectomycorrhizal genus, and *Aspidella*, a saprotrophic genus. The controversies and histories about recognition of the two genera based on trophic status are discussed. The name *Aspidella* E.-J. Gilbert is shown to be illegitimate and a later homonym of *Aspidella* E. Billings, a well-known generic name for an enigmatic fossil sometimes classified as a fungus or alga. The name *Saproamanita* is coined to replace *Aspidella* E.-J. Gilbert for the saprotrophic Amanitas, and a selection of previously molecularly analyzed species and closely classified grassland species are transferred to it along with selected similar taxa. The type illustration for the type species, *S. vittadinii*, is explained and a subgeneric classification accepting *Amanita* subgen. *Amanitina* and subgen. *Amanita* is proposed. Validation of the family name, *Amanitaceae* E.-J. Gilbert dating from 1940, rather than by Pouzar in 1983 is explained.

Key words:

Agaricales
Agaricomycotina
Basidiomycota
fungi
mushroom
fossil
Ediacaran
nomenclature
phylogeny
monophyly
mycorrhizas
controversy

Article info: Submitted: 17 March 2016; Accepted: 17 May 2016; Published: 1 June 2016.

INTRODUCTION

The genus *Amanita* Pers. 1797 (nom. cons.), belonging to the *Amanitaceae* E.-J. Gilbert 1940 of the pluteoid clade (or suborder *Pluteineae* Aime *et al.*; Dentinger *et al.* 2016) as circumscribed by Matheny *et al.* (2006) and Justo *et al.* (2011), is simultaneously one of the most famous and infamous of all fungal and mushroom genera. It includes the classical and fairy tale toadstool, the fly agaric, *Amanita muscaria* (L.) Lam. 1783, also renowned for its hallucinogenic properties. Additionally, it includes the highly toxic, often fatal Death Angels and Death Caps in the *Amanita phalloides* (Fr.) Link 1833 and *A. virosa* Bertill. 1866 species complexes. Added to these notorieties are the facts that several species are prized edible species and one spectacularly showy species, *A. caesarea* (Scop.) Pers. 1801, earlier known as Kaiserling, was named after the Roman Caesars who apparently relished it. *Amanita* is also iconic because of its recognisability as some possess a complete complement of agaric tissues, which has led to use of its morphological silhouette to label anatomical features for mushrooms, e.g. for *A. virosa*, the pileus, lamellae, stipe, annulus and volva all being present. These facts are not new; but cumulatively, as

was the case for features previously defining *Coprinus s. lat.*, (Redhead 2001, Redhead *et al.* 2001), they have imparted an emotional inertia to adopting segregate genera.

Several attempts to split off separate genera from *Amanita* were made or supported by some authors in the first half of the 20th century based upon morphological or anatomical characteristics (e.g. Clements & Shear 1931, Earle 1909, Gilbert 1925, 1940, Güssow & Odell 1927, Konrad & Maublanc 1924–27, 1930, Murrill 1914, Singer 1936, Smith & Gruber 1949), but virtually all of these segregate genera, except *Amanitopsis* Roze 1876 (e.g. Groves 1962) were rejected and synonymized by authors in the latter half of the century and early 21st century (e.g. Bas 1969, Horak 2005, Ito 1959, Knudsen & Vesterholt 2012, Kühner & Romagnesi 1953, Moser 1983, Shaffer, 1968, Singer 1951, 1962, 1975, 1986, Smith *et al.* 1979) except for the type studies by Horak (1968) where most were re-described, illustrated and keyed as ‘distinct’ genera for comparative purposes, and Clements & Shear (1931) synonymized *Lepidella* E.-J. Gilbert 1925 with *Lepiota*. The name *Amanitopsis* itself was even successfully proposed for conservation against *Vaginarius* Roussel 1806 and *Vaginata* Gray 1821 (Hawksworth 1984, Rogers 1953, Wiersema *et al.* 2015). *Amanitopsis*, which was largely characterized by the absence of an annulus, was ultimately

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placed in generic synonymy simply on the basis of anatomical and morphological features. However, taxa based on these separate genera were often recognized at subgeneric ranks albeit with modified circumscriptions.

Early molecular based phylogenetic analyses based upon DNA sequence data independent of the morphology at first provided strong support for a close relationship between the various subgeneric components of *Amanita* (Weiß *et al.* 1998, Drehmel *et al.* 1999, Moncalvo *et al.* 2000b) and *Amanita* was confirmed as closest to *Limacella* Earle 1909 among sampled taxa in a broader survey of agarics first reported at meetings (Moncalvo *et al.* 1996, 1997) and eventually published (Moncalvo *et al.* 2000a). However, specific inclusion of a suspected saprotrophic, prairie-inhabiting North American taxon by Moncalvo *et al.* (2002), identified as *Amanita armillariiformis* Trueblood & D.T. Jenkins 1990 (Redhead det., GenBank AF261437 & AF261436 = DAOM 184734 & 216919), suggested that those two samples represented a distinct evolutionary lineage characterized by its trophic status and separated from an otherwise well-documented ectomycorrhizal genus *Amanita*. The family *Amanitaceae sensu* Moncalvo *et al.* (2002a) was recognizable as consisting of *Amanita s. str.* (Clade 55/117), including the sequestrate taxon *Torrendia pulchella* Bres. 1902, and which was distinguished from both the prairie inhabiting taxon identified as “*A. armillariiformis*”, and the genus *Limacella* (that also seemed to include the genus *Catatrampa* Franco-Mol. 1991). Analysis of additional samples and species (*Amanita vittadinii* (Moretti) Vittad. 1826 from Italy [Neville 99.10.23.06], *Amanita nauseosa* (Wakef.) D.A. Reid 1966 from North Carolina, and *A. armillariiformis* from USA were investigated by Vilgalys, Ganley, Drehmel & Moncalvo (unpublished) at Duke University in 2007 that supported the recognition of a non-mycorrhizal clade. This preliminary investigation suggested that the *A. armillariiformis* samples from Alberta, Canada used in the Moncalvo *et al.* (2002) publication differed from *A. armillariiformis* as represented by a paratype and two other Orson K. Miller collections (OKM 18830 & OKM18505) [VTMH 646, 3502, 3503]. Subsequently Justo *et al.* (2010) conducted an investigation of sequestrate *Amanitaceae* and synonymized *Torrendia* Bres. 1902 along with the sequestrate genus *Amarrendia* Bougher & T. Lebel 2002 with *Amanita*, renaming *Torrendia pulchella* as *Amanita torrendii* Justo 2010 (non *Amanita pulchella* Imai 1933). In their analysis *A. armillariiformis* clustered with a second species, *A. nauseosa*, presumably represented by an Australian sample (GenBank AY194984) and separated from the ectomycorrhizal species. Additional sequences of grassland species of *Amanita* were generated by Wolfe and deposited in GenBank in 2010 by R. Tulloss, B. Wolfe and A. Pringle and used in the analyses by Wolfe *et al.* (2012a, b) on the trophic status and phylogeny of *Amanita* species and subgeneric groups. Vizzini *et al.* (2012) and Vizzini & Contu (2013) built upon the publications and data supplied by Wolfe *et al.* (2012a, b) with the addition of a second sample of *A. vittadinii*. They adopted a different philosophical position on the taxonomy in the family and proposed that the suspected saprophytic species in a basal clade be recognized as distinct generically from the ectomycorrhizal genus *Amanita*, typified by *A. muscaria*. They adopted the generic name *Aspidella* E.-

J. Gilbert 1940 that appeared to be legitimate and available (Donk 1962) as typified by *Aspidella vittadinii* (Moretti) E.-J. Gilbert 1940 (syn. *Amanita vittadinii*). At that time although the name “*A. pruitii*” had appeared in their analyses, it was not a validly published name and therefore not available for transfer to *Aspidella*. Tulloss *et al.* (2014) considered the separation of *Aspidella* from *Amanita* as being problematic for an unexplained reason when they formally named the presumed saprophytic *Amanita*, *A. pruitii* A.H. Sm. ex Tulloss *et al.* 2014, which had been the invalid species name that had been used as a label in GenBank in 2010 (HQ625011) and in the published phylograms by Wolfe *et al.* (2012), Vizzini *et al.* (2012), and Hess & Pringle (2014). Notably, in the most detailed molecular investigation of the phylogeny of *Amanitaceae* based on four gene regions (nuclear and mitochondrial large and small units) by Wolfe *et al.* (2012) and re-analysis of the nuclear LSU by Hess & Pringle (2014), the non-ectomycorrhizal “*Amanita*” species clustered together and sister to the main *Amanita* clade, adding support for recognizing two genera, one ectomycorrhizal and the other non-ectomycorrhizal. Consequently Redhead & Vizzini (2015) transferred the epithet *pruitii* to *Aspidella* to supply an available combination for the genus when it is differentiated from *Amanita*.

Overlooked by all earlier authors, in particular mycologists, including ourselves, the name *Aspidella* E.-J. Gilbert 1940 is illegitimate, being a later homonym of *Aspidella* E. Billings 1872, typified by *Aspidella terranova* E. Billings 1872, an enigmatic and famous fossil genus from the Ediacaran period (Boyce & Reynolds 2008, Burzynski & Narbonne 2015, Gehling *et al.* 2000, O'Brien & King 2004, Retallack 2015). Although *Aspidella* E. Billings may eventually universally or unequivocally be recognize as *Animalia* (Narbone 2005), it has been classified as an alga, as bacterial colonies, and a basal group to the fungi, even as a type of lichen (i.e. a fungus), or even as a new kingdom, *Vendobionta* (Misra 2010) and it remains a puzzling fossil genus. The classification of *Aspidella* as either a lichenized or non-lichenized fungus (Petersen *et al.* 2003, Retallack 1994, 2014) or as an alga (under the now synonymous names *Charnia* Ford and *Charniodiscus* Ford (Ford 1958) places the name *Aspidella* E. Billings within the kingdom of names governed by the *International Code of Nomenclature for algae, fungi, and plants* (McNeill *et al.* 2012). Applying Arts 11.8 (Note 5), 45, and 54, *Aspidella* E.-J. Gilbert 1940 is interpreted as a later homonym under the ICN and hence illegitimate (Art. 53.1). Specifically for Art. 54.1 (a, b), even if later applied to a group covered by other codes of nomenclature; having once been classified as either an alga, fungus, or plant, a name such as *Aspidella* Billings, makes illegitimate any later homonym. Although this overlooked homonymy may appear to be unfortunate, it is in fact convenient because *Aspidella* E. Billings is so famous that it has occupied and saturated the scientific literature and databases. With a movement afoot to create a unified *BioCode* regulating the nomenclature of all organisms (Greuter *et al.* 2011, Hawksworth 2011), supporting a competing homonymous name for any organism is counterproductive to scientific communication. Additionally, conservation of *Aspidella* E.-J. Gilbert is unlikely

to succeed because of the overwhelming presence in the literature of the the fossil generic name (T. May, pers. com.).

Splitting *Amanita* into two molecularly monophyletic genera, *Amanita* and *Saproamanita* nom. nov. (see below) along the lines of trophic status is preferred by us as a means of conveying this basic information. The two genera have been supported molecularly in studies by Moncalvo *et al.* (2002), Justo *et al.* (2010), Wolfe *et al.* (2012), Vizzini *et al.* (2012) and Hess & Pringle (2014). In the most thorough analysis of the phylogeny of *Amanitaceae* by Wolfe *et al.* (2012a) using four gene regions (nuclear and mitochondrial LSU and SSU rRNA) there is support for both a clade of ectomycorrhizal *Amanita* and a sister clade containing the non-ectomycorrhizal species formerly named in *Amanita*. Support for the former was high (100 % and 1.00 for maximum likelihood bootstrap and Bayesian posterior probability respectively) while the latter was present but at a lower level (66 % and 0.93).

Notably, support for the “clade” of non-ectomycorrhizal taxa was weaker and may indicate that the ectomycorrhizal genus *Amanita* arose from within the non-ectomycorrhizal clade and that the later may have more diverse range of trophic status. We note, for example, that several non-forest host plants that are primarily herbaceous may form ectomycorrhizas and could occur in open areas, e.g. *Bistorta vivipara* (formerly *Polygonum viviparum*, *Polygonaceae*; Sanchez *et al.* 2009) and *Kobresia myosuroides* ([sometimes classified as *Carex myosuroides*, *Cyperaceae*; Global Carex Group. 2015, Starr *et al.* 2015] Ammarellou *et al.* 2009, Davey *et al.* 2015, Gardes & Dahlberg 1996, Kohn, & Stavoski 1990, Massicotte *et al.* 1998, Moreau *et al.* 2006, Muthukumar *et al.* 2004, Peintner & Dämmrich 2012). No known representatives of *Poaceae* form ectomycorrhizas (Wang & Qiu 2006). For now, we are satisfied that only two genera, *Amanita* and *Saproamanita*, should be recognized rather than three or four, and simply flag taxa in the *A. inopinata* clade as decomposers of unidentified carbon sources (Wolfe *et al.* 2012b).

Others may differ in opinion (see Acknowledgements) as to whether the generic name *Amanita* should apply to all species in the clade that we here recognize as tribe *Amaniteae* R. Maire ex Killerman 1928 in *Amanitaceae* E.-J. Gilbert 1940, excluding the *Pluteaceae* Kotl. & Pouzar 1972. We note, however, that recognizing two genera, *Amanita* and *Saproamanita*, follows all suggested guides of new taxa in the publication by Vellinga *et al.* (2015) and further note that most of the supporting evidence comes from the detailed study by Wolfe *et al.* (2012); those authors differ in opinion to ours as to the desirability of separating two genera and declined our invitation to be co-authors. For a detailed discussion on the various classifications and nomenclature regarding the tribe *Amaniteae* see Neville & Poumarat (2004). For a more detailed higher level classification see Dentinger *et al.* (2016).

In addition to monophyly, our rationale for recognizing two genera lies with the future of mycological investigations well outside the scope of traditional taxonomy. Metagenomic studies reply upon generic level associations with trophic strategies; *Amanita* is most often coded as ectomycorrhizal (ECM) in such studies. It would be disadvantageous to label saprotrophic *Amaniteae* with the generic name *Amanita* and far more informative to separately label them *Saproamanita* to distinguish them from *Amanita* in future large scale

environmental studies (e.g. Azul *et al.* 2010, Buée *et al.* 2009, Dance 2008, Marmeisse *et al.* 2013, Martin & Martin 2010, May & McMullan-Fisher 2012, Orgiazzi *et al.* 2012, Sato *et al.* 2012, Tsujino *et al.* 2009). Agaricologists tend to be focussed on basidiome features and infrequently compare their taxonomic systems and viewpoints to that of phylogenetic investigations and the taxonomy of other fungal groups such as yeasts, smuts, *Glomeromycetes*, *Pleosporales*, or corticioid fungi, etc. , and consequently the broader picture is often obscured. Finally, we note that it was not surprising to look back in time and notice that an unusually high number of basionyms were coined in combinations with the generic names *Lepiota*, *Armillaria*, or *Lepidella* rather than in *Amanita*.

TAXONOMY

***Saproamanita* Redhead, Vizzini, Drehmel & Contu, nom. nov.**

Mycobank MB816353

Etymology: ancient Gr. σαπρός (*saprós*) - decay and *Amanita* (f.).

Replaced name: *Lepidella* E.-J. Gilbert, *Bull. Soc. mycol. Fr.* **41**: 303 (1925); nom. illegit. (Art. 53.1), non *Lepidella* Tiegh. 1911 (*Loranthaceae*).

Type species: *Saproamanita vittadinii* (Moretti) Redhead *et al.* 2016 (syn. *Agaricus vittadinii* Moretti 1826, *Amanita vittadinii* (Moretti) Vittad. 1826, *Armillaria vittadinii* (Moretti) Locq. 1952, *Aspidella vittadinii* (Moretti) E.-J. Gilbert 1940, *Lepidella vittadinii* (Moretti) E.-J. Gilbert 1925, *Lepiota vittadinii* (Moretti) Qué. 1873).

Synonyms: *Aspidella* E.-J. Gilbert in Bresadola, *Icon. mycol.* **27** (suppl. 1, fasc. 1): 63 (1940); nom. illeg. (Art. 53.1), non *Aspidella* E. Billings 1872 (fossil. Classified in various extant kingdoms as an alga, animal, bacterium, fungus or in an extinct Kingdom, *Vendobionta*).

Gilbertia Donk, in litt. “1934”; nom. inval. (Arts. 29, 36.1) , cited by Gilbert (1940) as unpublished. See also Donk (1962) and Neville & Poumarat (2004).

Amanita subgen. *Lepidella* Beauseigneur, *Contrib. Étude Fl. Mycol.*: 38 (1926); as “Gilbert”.

Amanita subgen. *Aspidella* E.-J. Gilbert, *Comment. Amanites, Notul. Amanites* [suppl.] XXX: [3] (1941) nom. and stat. nov. based on an illegitimate basionym (Art. 58.1)

Amanita sect. *Aspidella* Pomerleau, *Nat. can.* **93**: 844 (1966); replacement name at a different rank, based on an illegitimate basionym (Arts. 36.2, 38.1, 41.5, 58.1).

Amanita sect. *Lepidella* Corner & Bas *Persoonia* **2**: 244 (1962); without attribution; replacement name at a different rank based on an illegitimate basionym (Arts 36.2, 38.1, 41.5, 58.1).

Amanita subsect. *Vittadiniae* Bas, *Persoonia* **5**: 346 (1969).

Amanita ser. *Vittadiniae* (Bas) Neville & Poumarat, *Fungi Europaei* **9**: 510 (2004).

The genus *Saproamanita* is here recognized as the “Free-living *Amanita*” clade depicted in Wolfe *et al.* (2012b: fig. 2) and Vizzini *et al.* (2012: fig. 2) in both consisting of the least inclusive clade containing *S. armillariiformis* and *S. thiersii* and characterized by the ability to decompose litter (Wolfe *et al.* 2012b) in the absence of a vascular plant host.

Although the generic name *Saproamanita* is a new name for the validly published but illegitimate generic name *Lepidella*, and is therefore automatically typified by *S. vittadinii*, the taxonomic delimitation differs from previous applications of *Lepidella* by Gilbert (1925), Gilbert & Kühner (1928), Konrad & Maublanc (1924–27) and Beauseigneur (1925), or of *Aspidella* by Gilbert (1940), or at the infrageneric levels of subgenus by Beauseigneur (1926) and Veselý (1933, 1934) or of section *Lepidella* by Corner & Bas (1962) and Bas (1969). The concept of *Saproamanita* here accepted is most similar to that of *Amanita* subsect. *Vittadinae* Bas 1969 which was characterized in part by volval elements dominated by cylindrical to slender clavate inflated cells together with elongated stipes with volval elements mostly scattered mid stipe and growth in open fields and steppes, but perhaps excluding the forest inhabiting taxa with more bulbous stipes such as *Amanita bubalina* Bas 1969.

Application of the subgeneric name, *Amanita* subgen. *Lepidella*, for the ectomycorrhizal taxa (e.g. Drehmel *et al.* 1999, Wolfe *et al.* 2012b, Weiß *et al.* 1998, Zhang *et al.* 2004) is no longer appropriate and should be discontinued because the type of that subgeneric name is *S. vittadinii* (syn. *Amanita vittadinii*, *Lepidella vittadinii*, *Aspidella vittadinii*).

Subgeneric names combined with *Amanita*

Note: Some of the names listed below are no longer considered as belonging to either *Amanita* or *Saproamanita*.

Amanita subgen. *Amanita* [autonym]

Conserved type: *Amanita muscaria* (L.: Fr.) Lam. 1783 *fide* Wiersema *et al.* (2015), with corrected authority as permitted by Art. 55.3.

Amanita subgen. *Amanitaria* (E.-J. Gilbert) E.-J. Gilbert 1941.
Basionym: *Amanitaria* E.-J. Gilbert 1940.

Holotype: *Amanita pantherina* (DC.: Fr.) Krombh. 1846 *fide* Donk (1962)

Amanita subgen. *Amanitina* (E.-J. Gilbert 1940) E.-J. Gilbert 1941.

Basionym: *Amanitina* E.-J. Gilbert 1940.

Holotype: *Amanita phalloides* (Vaill. ex Fr.: Fr.) Link 1833 *fide* Donk (1962).

Amanita subgen. *Amanitopsis* (Roze) Barbier 1907.

Basionym: *Amanitopsis* Roze 1876.

Conserved type: *Amanita vaginata* (Bull.: Fr.) Lam. 1783 *fide* Wiersema *et al.* (2015).

Amanita subgen. *Amidella* (E.-J. Gilbert) E.-J. Gilbert 1941.

Basionym: *Amidella* E.-J. Gilbert 1940.

Holotype: *Agaricus volvatus* Peck 1872 (syn. *Amanita volvata* (Peck) Lloyd 1898, *fide* Donk (1962).

Amanita subgen. *Amplariella* (E.-J. Gilbert) E.-J. Gilbert 1941.
Basionym: *Amplariella* E.-J. Gilbert 1940.

Holotype: *Amanita ampla* Pers. 1801 (syn. *Amanita excelsa* (Fr.) Bertill. 1866 *fide* Donk 1962).

Amanita subgen. *Euamanita* Lange 1915, and Singer (1950: 389); nom. inval. (Art. 21.2).

Amanita subgen. *Limacella* (Earle) E.-J. Gilbert 1918.

Basionym: *Limacella* Earle 1909.

Holotype: *Lepiota delicata* (Fr.) Kummer 1871 (syn. *Limacella delicata* (Fr.) Earle ex Konr. & Maubl. 1930; = *Limacella glioderma* (Fr.) Maire 1926 *fide* Donk (1962).

Amanita subgen. *Metraria* (Cooke) Barbier 1907.

Basionym: *Agaricus* subg. *Metraria* Cooke 1891.

Holotype: *Agaricus insignis* Cooke & Masee 1891 (syn. *Metraria insignis* Cooke & Masee ex Saccardo 1891, non *Agaricus (Annularia) insignis* Cooke & Masee 1889; = *Metraria* Cooke & Masee ex Saccardo 1891, see also type studies by Singer (1955) and Horak (1968) and nomenclatural analyses by Donk (1962) and Neville & Poumarat (2004).

Amanita subgen. *Peplophora* (Quélet.) E.-J. Gilbert 1918.

Basionym: *Amanita* [unranked] *Peplophora* Quélet 1888.

Lectotype: *Amanita muscaria fide* Corner & Bas 1962.

Amanita subgen. *Pseudoamanita* Singer 1936 ex Singer 1950; validated by Singer (1950: 389).

Lectotype: *Amanita muscaria fide* Singer (1951).

Amanita subgen. *Vaginarina* (Forquignon ex Quélet) Singer 1951.

Basionym: *Amanita* [unranked] *Vaginarina* Forquignon ex Quélet 1888.

Lectotype: *Amanita vaginata fide* Singer (*Lilloa* 22: 386, 1951); see also Corner & Bas (1962: 283).

Accepted infrageneric classification of *Amanita*

Considering the four gene phylogeny shown by Wolfe *et al.* (2012b) and the type species for each of the taxon names listed above, three of the above subgeneric names are applicable to taxa within *Amanita* but outside of *Amanita* subg. *Amanita*; namely subg. *Amanitina*, *Amidella*, and *Amplariella*. These names are available, are of equal priority when synonymized, and also are based on three generic names of equal priority. Therefore, we hereby select for the purpose of application of Article 11.5, the following synonymy that hereby establishes priority:

Amanita* subgen. *Amanitina

Synonyms: *Amanita* subgen. *Amidella*

Amanita subgen. *Amplariella*

The family name *Amanitaceae*

One final note on nomenclature requires reconsideration of the family names *Amanitaceae* “Heim ex Pouzar 1983” as it is often cited and *Torrenciaeae* Jülich 1981, now that

Torrendia is considered to be synonymous with *Amanita* as it appeared to be necessary to conserve *Amanitaceae* against *Torrendiaceae*. When Jülich (1981) published the name *Torrendiaceae* independent of the *Amanitaceae*, he attributed the name *Amanitaceae* to Roze (1876a, b) but Roze spelled the family name Amanitées and therefore it was not a validly published name (Art. 18.4). Heim (1934) also used the name “Amanitaceae” but did not supply any description or reference to one, and therefore the name was still not validated (Art. 39.1). Overlooked by all later authors was the validation by Gilbert (1940: 63) where he published “FAMILLE: AMANITACEAE (vel *Amanitoideae*)”. The subfamily name *Amanitoideae* Gaümann (1926; as “Unterfamilie. Amaniteae”) with a German description was a valid name (Arts. 18.4, 39.1) with a correctable termination. Hence, Gilbert (1940) inadvertently validated the family name *Amanitaceae* E.-J. Gilbert as a replacement name at a new rank as is permitted under Arts 6.10, 41.1 and 41.2, and solely attributable to Gilbert (Art. 49.2). Consequently the publication of *Amanitaceae* by Pouzar (1983) was unnecessary and superfluous and the name *Torrendiaceae* 1981 is much younger than *Amanitaceae* 1940.

Classification within the family

Family: *Amanitaceae* E.-J. Gilbert 1940

Subfamily: *Amanitoideae* Gaümann 1926 (as “*Amaniteae*”)

Tribe: *Amaniteae* R. Maire ex Killermann 1928

Amanita Pers. 1797

subgen. *Amanita* (type: *A. muscaria*)

subgen. *Amanitina* (E.-J. Gilbert) E.-J. Gilbert 1941 (type: *A. phalloides*)

Saproamanita Redhead *et al.* 2016 (type: *S. vittadinii*)

Limacella Earle 1909

Catatrampa Franco-Mol. 1991

Species included in *Saproamanita*

The reclassification listed below is based on phylogenetic analyses of samples by Moncalvo *et al.* (2002), Justo *et al.* (2010), Wolfe *et al.* (2012), and Vizzini *et al.* (2012), and for selected species (marked with *) based upon anatomical, morphological and ecological similarity to molecularly placed taxa.

Saproamanita ameghinoi* (Speg.) Redhead, Vizzini, Drehmel & Contu, **comb. nov.

Mycobank MB816474

Basionym: *Armillaria ameghinoi* Speg., *An. Mus. nac. Hist. nat. Cienc. Córdoba* **28**: 276 (1899).

Saproamanita armillariiformis (Trueblood & D.T. Jenkins) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

Mycobank MB816354

Basionym: *Amanita armillariiformis* Trueblood & D.T. Jenkins, *Mycologia* **82**: 120 (1990).

Saproamanita codinae (Maire) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

Mycobank MB816355

Basionym: *Lepidella codinae* Maire, *Treb. Mus. Cienc. nat. Barcelona, sér. bot.* **15**(2): 85 (1933).

Saproamanita flavofloccosa* (Nagas. & Hongo) Redhead, Vizzini, Drehmel & Contu, **comb. nov.

Mycobank MB816475

Basionym: *Amanita flavofloccosa* Nagas. & Hongo, *Trans. Mycol. Soc. Japan* **25**: 367 (1984).

Saproamanita foetidissima* (D.A. Reid & Eicker) Redhead, Vizzini, Drehmel & Contu, **comb. nov.

Mycobank MB816476

Basionym: *Amanita foetidissima* D.A. Reid & Eicker, *Mycol. Res.* **95**: 83 (1991); holotype in K indicated on p. 84.

Saproamanita grallipes (Bas & de Meijer) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

Mycobank MB816356

Basionym: *Amanita grallipes* Bas & de Meijer, *Persoonia* **15**: 345 (1993).

Saproamanita inopinata (D.A. Reid & Bas) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

MB816357

Basionym: *Amanita inopinata* D.A. Reid & Bas, *Notes R. bot. Gdn Edinb.* **44**: 506 (1987).

Saproamanita lilloi* (Singer) Redhead, Vizzini, Drehmel & Contu, **comb. nov.

Mycobank MB816477

Basionym: *Amanita lilloi* Singer, *Lilloa* **25**: 245 (1952) [“1951”].

Saproamanita manicata (Berk. & Broome) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

Mycobank MB816358

Basionym: *Agaricus manicatus* Berk. & Broome, *Trans. Linn. Soc. London* **27**: 150 (1870) [“1871”].

Saproamanita nana* (Singer) Redhead, Vizzini, Drehmel & Contu, **comb. nov.

Mycobank MB816478

Basionym: *Amanita nana* Singer, *Bot. Mater. Otd. Sporov. Rast.* **5**(4-6): 85 (1941).

Saproamanita nauseosa (Wakef.) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

Mycobank MB816359

Basionym: *Lepiota nauseosa* Wakef., *Bull. Misc. Inf., Kew* **1918**: 230 (1918).

Saproamanita pleropus* (Kalchbr. & MacOwan) Redhead, Vizzini, Drehmel & Contu, **comb. nov.

Mycobank MB816479

Basionym: *Agaricus (Lepiota) pleropus* Kalchbr. & MacOwan, in Kalchbrenner & Cooke, *Grevillea* **9**: 17 (1880); as “*pteropus*”, a typographical error correctable under Art. 60.1, Ex. 2; corrected by Kalchbrenner (1881), Reid (1975), and Reid & Eicker (1991); and incorrectly ‘corrected’ by Saccardo (1887) as *Lepiota* “*pteropoda*”.

Saproamanita praeclara* (A. Pearson) Redhead, Vizzini, Drehmel & Contu, **comb. nov.

Mycobank MB816480

Basionym: Lepiota praeclara A. Pearson, *Trans. Brit. mycol. Soc.* **33**: 288 (1950).

***Saproamanita praegraveolens** (Murrill) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

MycoBank MB816481

Basionym: Lepiota praegraveolens Murrill, *Bull. Torrey bot. Club* **66**: 153 (1939).

Saproamanita prairicola (Peck) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

MycoBank MB816360

Basionym: Amanita prairicola Peck, *Bull. Torrey bot. Club* **24**: 138 (1897).

Saproamanita pruitii (A.H. Sm. ex Tulloss *et al.*) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

MycoBank MB816361

Basionym: Amanita pruitii A.H. Sm. ex Tulloss *et al.*, *Amanitaceae* **1**(1): 2 (2014).

***Saproamanita roseolescens** (A. Pearson & Stephens) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

MycoBank MB816482

Basionym: Lepiota roseolescens A. Pearson & Stephens, *Trans. Brit. mycol. Soc.* **33**: 288 (1950).

***Saproamanita savannae** (Tulloss & Franco-Mol.) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

MycoBank MB816362

Basionym: Amanita savannae Tulloss & Franco-Mol., *Mycotaxon* **105**: 318 (2008).

Saproamanita silvifuga (Bas) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

MycoBank MB816363

Basionym: Amanita silvifuga Bas, *Persoonia* **5**: 356 (1969).

Saproamanita singeri (Bas) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

MycoBank MB816364

Basionym: Amanita singeri Bas, *Persoonia* **5**: 364 (1969).

Saproamanita subcaligata (A.H. Sm. & P.M. Rea) **comb. nov.**

MycoBank MB816365

Basionym: Armillaria subcaligata A.H. Sm. & P.M. Rea, *Mycologia* **36**: 128 (1944).

Saproamanita thiersii (Bas) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

MycoBank MB816366

Basionym: Amanita thiersii Bas, *Persoonia* **5**: 382 (1969); nom. nov. for *Amanita alba* Thiers 1957 non Lam. 1783.

Saproamanita vittadinii (Moretti) Redhead, Vizzini, Drehmel & Contu, **comb. nov.**

MycoBank MB816367

Basionym: Agaricus vittadinii Moretti, *Giorn.Fis., Chim., Stor. nat. med. Arti* **2**: 66 (1826).

Notes on the name *Agaricus vittadinii*

Bas (1969: 349) selected as the lectotype for *Agaricus vittadinii*, "pl. I" published by Moretti (1826b), which is a publication that is generally separately cited from Moretti (1826a) (e.g. Neville & Poumarat 2004) even though the latter is typically cited as the publication with the protologue. Therefore, there is a question about the status of "pl. I" (=Tab. 1) being original material as used in Arts 9.2, 9.11, and 9.12 (McNeill *et al.* 2012) and therefore its eligibility for lectotypification as generally accepted (e.g. Vizzini *et al.* 2012).

Giuseppe Moretti (1782–1853) was a well-known botanist in his day (Bianchi *et al.* 1959) who contributed to the *Flora Italica* series. In 1826 he decided to publish discussions as supplements to *Flora Italica* under the heading "Il botanico Italiano ossia discussioni sulla Flora Italica" and he simultaneously published each of these discussions twice, each with 5-part notes entitled "I. Piante nuove", "II. Piante non peranco indicate come indigene d'Italia", "III. Osservazioni intorno ad alcune specie onde rettificarne la sinonimia", "IV. Memorie originali", and "V. Piante dubbie". He published three issues of these five-part supplements (or discussions) in near duplicate format in the journal *Giornale di fisica, chimica, storia naturale, medicini ed arti, Pavia* (Decade Secunda) and also published them as inserts distributed with the journal, each entitled "Il Botanico Italiano ossia discussioni sulla Flora Italica" (sometimes shortened in later citations as 'Botanico Italiano'), as numbers I, II, and II. This same title was used within the journal (referred here as 'Giornale') for the three contributions (each being the five named parts), in 1826 in vol. **9**(1): 65–82; (2); 154–166; (3): 238–250. This explanatory level of detail is significant because Stafleu & Cowan (1981) in listing "6303" under G. Moretti stated that the articles are "To be cited from journal." Stafleu & Cowan (1981) listed the 'Botanico Italiano' separate as having pages [1]–44 and three plates, and the three parts do have consecutive pagination and plate numbering, but evidence suggests the three parts have three different publication dates.

As has been repeatedly noted in historical literature (Bas 1969, Gilbert 1941, Neville & Poumarat 2004), the description of *Agaricus vittadinii* occurs on pages 4–5 of the 'Botanico Italiano' and simultaneously on pages 66–67 of the 'Giornale' but that the two illustrative plates, one [foldout] on *Agaricus vittadinii* Moretti and the second on the plant *Potentilla grammopetala* Moretti were not included in the 'Giornale' and only occurred in the 'Botanico Italiano'. Reference to the first plate is made on page 4 of the 'Botanico Italiano' as "I. *Agaricus Vittadinii* Nob. Tab. I." whereas on page 66 of the 'Giornale' the same description simply states "I. *Agaricus Vittadinii* Nob." and it lacks reference to "Tab. I.". This anomaly was specifically noted by the bibliographers that same year (Raspail 1826b) under listings Nos 167 & 168 "Il Botanico Italiano" Moretti and No. 182 "Tentamen mycologicum, seu Amanitarum illustratio" Vittadini, and by Vittadini (1826) himself who reproduced the illustration from Moretti with comments in a footnote. Evidence for the simultaneous publication of each part of 'Botanico Italiano' together with each of three bimestrially issues of the 'Giornale' comes from: (1) the separate listings by Raspail (1826a, b) for each part; (2) the mention of illustrations for part one by Raspail (1826a);



Fig. 1. *Agaricus vittadini* illustrated by Moretti (1826b: tab. 1 – selected as lectotype by Bas) and reproduced in Vittadini (1826).



Fig. 2. *Saproamanita vittadinii*. Photographed *in situ* in Italy by Francesco Dovana.

(3) the quartet signature pagination counts [multiples of 4, i.e. 20, 12, and 12 pages] together with type setting of paragraphs on pages differing from the 'Giornale' and beginning each page one; (4) the different bimestri distribution of the issues of the 'Giornale'; and (5) finally the difference in appearances of the first two plates from the third plate which presumably was subject to different handling or storage conditions (cf. Biodiversity Heritage Library scanned copy from the Arnold Arboretum, Harvard University). These facts and evidence indicate that the Tab. 1 depicting *Agaricus vittadinii* published in the 'Botanico Italiano' is original material, just as is the case for *Potentilla grammopetala* depicted on Tab. 2 because they were simultaneously published and distributed together with the 'Giornale'. Therefore, the lectotypification by Bas (1969) of *Agaricus vittadinii* by Tab. 1 (Moretti 1826b) that Bas designated sight unseen, can be accepted. Bas (1969) had seen Vittadini's (1826) reproduction and accepted Gilbert's (1941) indication that it is the same illustration published by Moretti. We can confirm that the illustrations are identical. This illustration representing the lectotype is republished here as our (Fig. 1) comparable to the species in the field (Fig. 2).

ACKNOWLEDGEMENTS

Correspondence and discussions regarding splitting *Amanita* along the lines of trophic statuses has spanned 15 years preceding the publication by Moncalvo *et al.* (2002) and e-mail discussions

by S.A.R. were renewed in 2005 through 2008 with Jean-Marc Moncalvo, Rytas Vilgalys, Austen R. Ganley, Rod Tulloss, Anne Pringle, Benjamin Wolfe, Zhu-liang Yang (Zhu L. Yang), and with S.A.R. and Europeans interested in *A. vittadinii* in 2005: Francesco Bellù, Pierre Neville, Vincenzo Migliozi; and between S.A.R. and A.V. in 2005. In particular opposing viewpoints have been articulated by Anne Pringle and Rod Tulloss with cordial and constructive discussions. In 2008 the subject was placed on hold for four years until 2012 to allow Benjamin Wolfe to complete his studies unhindered. In 2016 discussions were held with Paul M. Kirk and Tom May regarding the status of *Aspidella* E.-J. Gilbert versus *Aspidella* E. Billings, and with John McNeill in 2016 on the statuses and citations of Moretti's two simultaneous publications in 1826, and with P M Kirk and John McNeil and Fred Barrie on the name *Amanitaceae*. To all of these individuals S.A.R. owes a measure of gratitude for contributing ideas, correction of misunderstood features, advice and/or words of caution, in particular that of Rod Tulloss. S.A.R. also thanks Stephen J. Locke for suggesting the succinct name *Saproamanita* and Julian Starr for literature on *Cyperaceae*. A.F. thanks Francesco Dovana for contributing his photograph. Extensive use was made using the following online freely available resources that are very much appreciated: Tulloss & Yang (2016) "Amanitaceae studies", *Index Fungorum*, *Mycobank*, Biodiversity Heritage Library (BHL), *Libri Fungorum*, and Cyberliber.

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