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## *Amanita amplivelata*, (Amanitaceae, Agaricales), a remarkable new Eurasian species of the section *Vaginatae*

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### Abstract

*Amanita amplivelata* is introduced as a new species, based on numerous collections from geographically distant areas of Europe and the Near East (Bulgaria, the Czech Republic, France and Türkiye). This new species is likely ectomycorrhizal with *Populus spp.* in natural poplar stands, urban settings, and plantations. Detailed description and illustrations of its morphological features are presented. Phylogenetic analysis of nrITS and combined nrITS, nrLSU and TEF-1 $\alpha$  sequences placed it in a separate stirp in Clade 5 of section *Vaginatae*. The ample, saccate volva with a peculiar microscopic architecture confirms relatively close phylogenetic relationships with *A. crocea* and *A. dryophila*. The distinction of the new species from other phylogenetically related or morphologically similar taxa is outlined.

**Key words:** *Amanita* subgenus *Amanita*, *Amanitopsis*, DNA barcoding, phylogeny, taxonomy

### Introduction

*Amanita* section *Vaginatae* (Fries 1854: 2) Quélet (1872: 65), harboring the so-called ‘ringless’ *Amanita* species, is estimated to be the largest section of the genus *Amanita* Persoon (1797: 65), comprising at least 236 species worldwide (Tulloss *et al.* 2016). The existence of considerable and partly hidden diversity in this section is corroborated by numerous recent studies from different parts of the world (*e.g.*, Tang *et al.* 2015, Cui *et al.* 2018, 2023, Kiran *et al.* 2018, Thongbai *et al.* 2018, Saba *et al.* 2019, Codjia *et al.* 2023). The most obvious morphological peculiarity of this section, *i.e.*, the lack of an annulus, led to the recognition in the past of the now obsolete genera *Amanitopsis* Roze (1876: 1) and *Vaginata* (Nees von Esenbeck 1816: 191) Gray (1821: 601). It was, however, shown by numerous phylogenetic studies that the ‘ringless’ species are firmly nested within *Amanita*, where they form a monophyletic

lineage, treated invariably at present at section level (Weiß *et al.* 1998, Drehmel *et al.* 1999, Oda *et al.* 1999, Moncalvo *et al.* 2000, Zhang *et al.* 2004; Cui *et al.* 2018). Later on, it was unambiguously shown that the lack of an annulus is not universal within the section, which now encompasses also a few annulate taxa (Liu *et al.* 2017, Zhang *et al.* 2021). Nowadays, several microscopic characters are used to distinguish species within the section, *e. g.*, the size and the shape of basidiospores and the structure of the volva, including the proportion and the distribution of inflated elements and filamentous hyphae (Contu 1988, 1997, 1999, 2000, 2001, 2003, Yang 1997, 2005, 2015, Neville & Poumarat 2009, Tang *et al.* 2015, Tulloss *et al.* 2016, Liu *et al.* 2017, Cui *et al.* 2018, 2023, Kiran *et al.* 2018, Thongbai *et al.* 2018, Saba *et al.* 2019, Zhang *et al.* 2021, Codjia *et al.* 2023). Recently, it was shown by Hanss & Moreau (2020) that the intact volva tissues of the European *Vaginatae* may feature a rather diverse micro-architecture, which along with other microscopic and macroscopic characters could be useful for conclusively separating otherwise very similar species.

The variability and consequently the unclear limits of taxa in the ringless *Amanita* species led some authors to recognize only a few or even a single, highly polymorphic species (Veselý 1933, Kühner & Romagnesi 1953, Wasser 1992), while others proposed over 20 taxa at species level (Fraiture 1993). Throughout most of the 20<sup>th</sup> century, new species of *Vaginatae* were sparingly introduced by mycologists in Europe (Bataille 1910, Velenovský 1920, Sartory & Maire 1923, Singer 1951, Huijsman 1959, 1962a, b, Rouzeau & Massart 1966, Malençon *et al.* 1968, Piane 1972, Aalto 1974), leading to a necessary comprehensive revision by Tulloss (1994). Meanwhile, Yang (1997) marked an important milestone in the study of East Asian *Vaginatae*, publishing the first monograph of the genus and this group in Asia. In the late 20<sup>th</sup> and in the beginning of the 21<sup>st</sup> century, studies in *Vaginatae* in Europe flourished, relying on a combined approach using macroscopic, microscopic, and ecological data for species distinction. A number of new species were described by different authors throughout the last quarter of the previous and this century (not all of them validly published) and in the early 2000's the number of species recognized in Europe was about 50 (Bon 1975, Lanne 1979, Bas 1982, Moser 1984, Urbonas *et al.* 1986, Knudsen & Borgen 1987, Contu 1988, 1997, 1999, 2000, 2001, 2003, Romagnesi 1992, Contu & Pacioni 1998, Consiglio & Contu 1999, Neville *et al.* 2000, Tulloss & Traverso 2001, Neville & Poumarat 2007, 2009). Still, many of these remained practically unknown outside their *loci classici*, a fact, possibly, at least partly related to the lack of synthetic identification keys since Contu (2003). Later, as it was already noted in different parts of Europe, collections were found that did not match the characters of already described species (Hanss & Moreau 2020, Assyov *et al.* 2021, Ševčíková *et al.* 2021).

In the last decade, taxonomic studies in the European *Vaginatae* have focused on the use of molecular data and particularly on nrITS sequences for resolving the taxonomy of the group (Malysheva & Kovalenko 2015, Vizzini *et al.* 2016, Loizides *et al.* 2018, Hanss & Moreau 2020). A number of type materials were sequenced or molecularly characterised epitypes were selected (Vizzini *et al.* 2016, Hanss & Moreau 2020, 2023, Moreau *et al.* 2023). Those steps provided grounds for rapid advancement of the knowledge on section *Vaginatae* and led to the recognition of several new taxa from Europe (Hanss & Moreau 2020, 2023, Crous *et al.* 2021, 2023, Ševčíková *et al.* 2021, Illescas & Plaza Canales 2022, Illescas 2023, Migliozi & Donato 2022a,b, Plaza Canales 2022, Migliozi & Di Palma 2024). During our studies in the genus *Amanita*, we came across one striking, yet apparently undescribed species of ringless *Amanita*, which was often collected during field surveys in different parts of Europe and in the Near East. Supported by both phylogenetic evidence and morphological characteristics, this taxon is introduced as a new species herein.

## Materials and methods

### *Materials*

The materials used in this study were collected in different parts of Bulgaria, the Czech Republic, France and Türkiye. After being documented in the field, the collections were wrapped individually in aluminium foil and transferred to the laboratory, where they were dried at 40 °C. The holotype of the new taxon, as well as paratypes from Bulgarian localities, are deposited in the Mycological Collection of the Institute of Biodiversity and Ecosystem Research (SOMF); an isotype and paratypes are available in the Herbarium of the Lille University (LIP). The Turkish specimens, along with an isotype and paratypes of Bulgarian origin are in the fungarium of Osmaniye Korkut Ata University and are noted in the text below by the abbreviation “FBozok”. The specimens from the collection from the Czech Republic are deposited in the fungarium of the Mycological Department of the National Museum of the Czech Republic in Prague (PRM) with a duplicate in the fungarium of the Botanical department in the Moravian Museum in Brno (BRNM). An

additional French collection is deposited at the herbarium of the Conservatoire Botanique National des Pyrénées et de Midi-Pyrénées, Bagnères-de-Bigorre (BBF). The geographical coordinates of the collections cited in the text below refer to the WGS84 system.

### *Morphological studies*

The description of the macromorphology is derived from field notes and photographs taken *in situ*. Colour codes in the description follow Kornerup & Wanscher (1978). Colour names employed in other parts of the text are vernacular designations rather than colour chart entries. The description of the shape of the volva follows the classification in Fraiture (1993).

The principles and methods used for microscopy follow Bas (1969). Olympus BX-50, Nikon Eclipse 220 and AmScope T360B compound light microscopes with a magnification of 100×, 400×, and 1000× were used to examine the microscopic features. Preparations for microscopy were obtained from dried material. Sections made with a Ranvier microtome or otherwise extracted fragments were mounted in water, 10 % KOH, ammoniacal Congo Red, or reinflated in 3 % KOH and observed in aqueous Congo Red, or alternatively reinflated in “ramollisseur GDS” and mounted in SDS Congo Red (after Cléménçon 1999), or in ammoniacal Congo Red with phloxin in order to better see the structures. Melzer’s reagent following the recipe in Kirk *et al.* (2008) was used for the testing of the so called “K-K” (or “Kotilová-Kubičková”) reaction, which reveals the presence of amyloid particles in the tramal tissues in *Amanita* (Neville & Poumarat 2004, Hanss & Moreau 2020). Aqueous Cotton Blue (5 %) was used to test the cynophilous properties of the hyphae. Macrochemical tests were performed with 10 % NH<sub>4</sub>OH, 5 % KOH, 10 % phenol, and tincture of guaiac was applied to all parts of the fresh basidoma.

The measurements of microscopic features were obtained from digital photographs with the aid of Piximètre v. 5.10 software. Measurements of basidiospores are derived from the assessment of a minimum of 30 randomly chosen, mature and normally developed spores from a studied specimen, mounted in 10 % KOH. The spore dimensions (length—L, width—W and quotient—Q) in the description are reported with their minimum, maximum and average values; “Q<sub>av</sub> =” refers to the average spore quotient and is shown as the range of minimum and maximum average values from among the studied specimens; ditto for L<sub>av</sub> and W<sub>av</sub> which are the average lengths and average widths for a collection. The abbreviations “n=”, “m=”, and “p=” stand for the total number of spores measured, the number of specimens and number of fruitbodies from which they were derived, respectively. For the remaining microscopic elements composite minimum and maximum, or representative values are provided. The types of subhymenium follow Bas (1969) and were reproduced and numbered from 1 to 5 in Hanss & Moreau (2020).

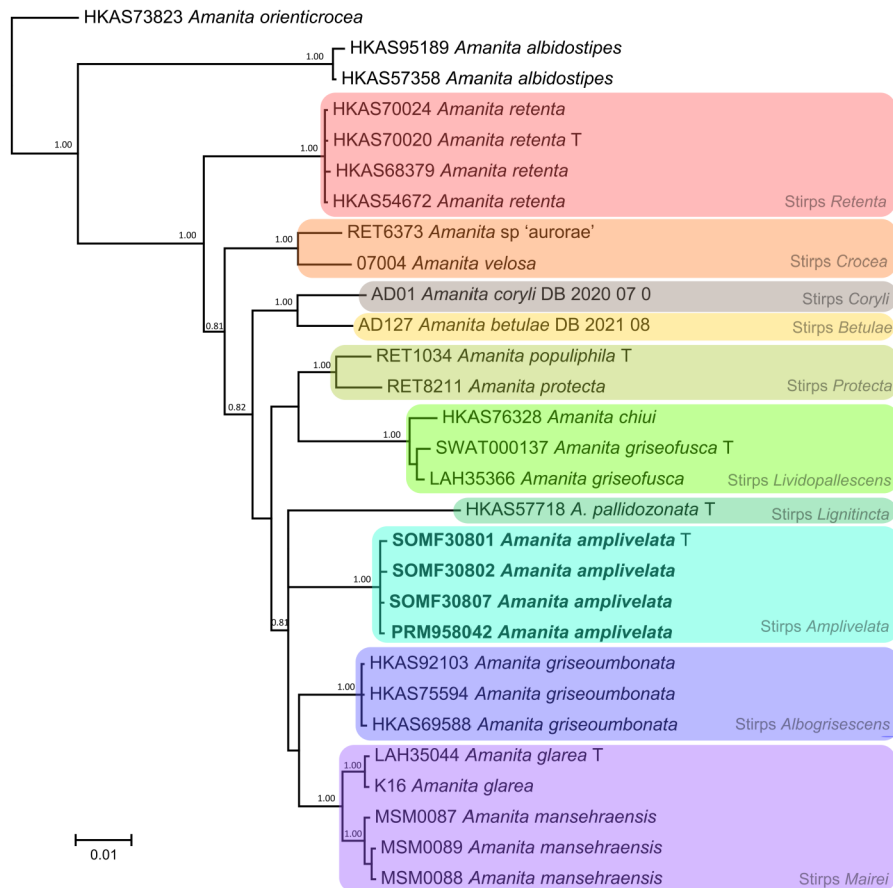
### *DNA extraction, amplification and sequencing*

DNA sequences from the Bulgarian and the Turkish specimens were obtained in accordance with the protocol described in detail in Bozok *et al.* (2020). Universal oligonucleotide primer pairs were employed for amplification and in the sequencing process as follows: ITS1F and ITS4 for the nrITS region, LR0R and LR5 for nrLSU, and 983F and 1567R for the TEF-1 $\alpha$  locus (White *et al.* 1990, Vilgalys & Hester 1990, Rehner & Buckley 2005). All of the sequences were aligned and edited using the BioEdit Sequence Alignment Editor (Hall 1999) and Sequencher version 5.4.5 (Gene Codes, Ann Arbor, MI, USA). nrITS and nrLSU sequences from the Czech collection were obtained in accordance with the protocol in Borovička *et al.* (2015). The sequence of the French specimen was obtained by the protocol communicated by the MycoSeq project of the Société Mycologique de France/CEFE Montpellier (see also Hanss & Moreau 2020). The extraction of the genomic DNA was carried out using the REDExtract-N-Amp Plant PCR (Sigma-Aldrich, Saint Louis, MO, USA), according to the manufacturer’s instructions. The nrITS region was amplified by PCR using the combinations of primers ITS1F, ITS5, ITS4, ITS4B, and, for problematic cases, ITS2 and ITS3 (White *et al.* 1990, Gardes & Bruns 1993), following Richard *et al.* (2015). The purification and the sequencing in both directions of the amplicons were carried out by EurofinsGenomics (Ebersberg, Germany). The reconstruction and display of the sequences in full length have been realized under Codon Code Aligner 4.1.1 (Codon Code Corp., Centerville, MA, USA).

### *Datasets assembly and phylogenetic analysis*

For the multigene tree, an alignment of nrITS, nrLSU and TEF-1 $\alpha$  regions obtained from 28 collections was carried out by Alvalab. BLASTn (Altschul *et al.* 1990) was used to select the most closely related sequences from the International

Nucleotide Sequence Database Collaboration public database (INSDC, Arita *et al.* 2021). Sequences were first aligned in MEGA 5.0 (Tamura *et al.* 2011) with Clustal W application and then realigned manually as needed to establish positional homology. Aligned loci were loaded in MrBayes 3.2.6 (Ronquist *et al.* 2012), where a Bayesian analysis was performed (three partitions: nrITS, nrLSU, TEF-1 $\alpha$ , two simultaneous runs, four chains, temperature set to 0.2, sampling every 100<sup>th</sup> generation) until the average split frequencies between the simultaneous runs fell below 0.01 after 0.23 M generations. Finally, a full search for the best-scoring Maximum Likelihood tree was performed in RAxML 8.2.12 (Stamatakis 2014) using the standard search algorithm (same partitions, GTRGAMMAI model, 2000 bootstrap replications). The significance threshold was set above 0.95 for posterior probability (PP) and 70 % bootstrap proportions (BP). For the ITS tree, an alignment of 300 sequences was made using the free software BioEdit (Hall 1999). In both cases, the sequences originated from this study or came from our database or were downloaded from GenBank (www.ncbi.nlm.nih.gov/genbank) and UNITE (unite.ut.ee). In both cases the alignment inaccuracies were corrected by Alvalab with the free MEGA5 software (Tamura *et al.* 2011).



**FIGURE 1.** Phylogenetic multigene tree of Clade 5 (as defined in Hanss & Moreau 2020), based on the markers nrITS, nrLSU and TEF-1 $\alpha$ . The sequences of *A. amplivelata* are shown in bold. Figures next to branches indicate Bayesian probability. The notation “T” marks type-derived sequences.

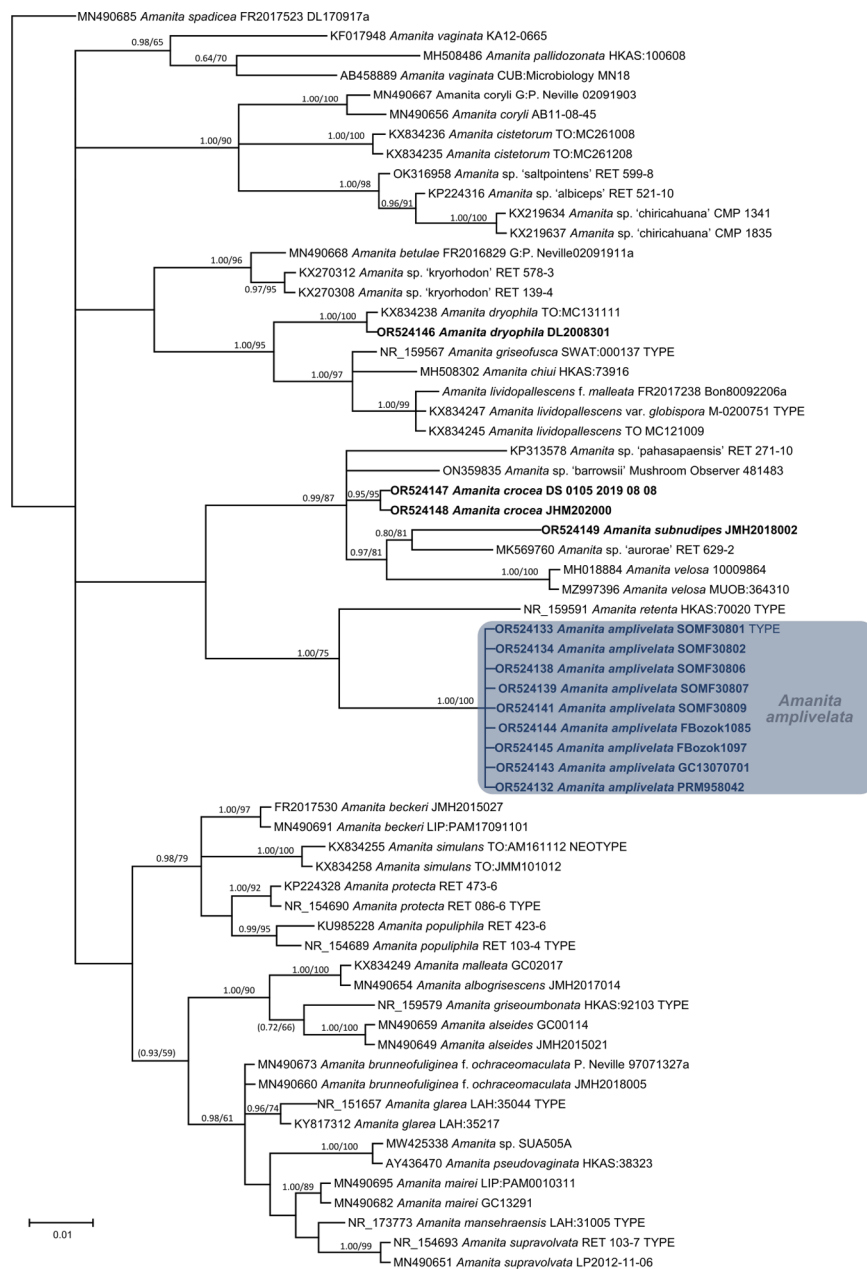
## Results

### Analyses of DNA sequences

We obtained sequences of the nrITS region from a total of 14 collections of the new species proposed below. Those sequences are completely identical to each other in comparison of the ITS1-5.8S-ITS2 alignment. For four collections nrLSU reads were produced, which are also completely identical in their common part. Two collections yielded sequences of the TEF-1 $\alpha$  locus.

A Bayesian analysis of the dataset of nrITS, nrLSU and TEF-1 $\alpha$  produced the phylogenetic tree presented in Figure 1. The tree is rooted by sequences of *A. orienticrocea* Zhu L. Yang, Y.Y. Cui & Q. Cai (in Cui *et al.* 2018: 90) and *A.*

*albidostipes* Y.Y. Cui, Q. Cai & Zhu L. Yang (in Cui *et al.* 2018: 90), two species assigned to stirp *Spadicea* that could be eventually included in Clade 5 of *Amanita* section *Vaginatae* (as defined in Hanss & Moreau 2020). The analysis resolved ten major, well-supported clades, which could be informally assigned to the rank of stirp following Tulloss & Yang's (2023) provisional classification. Of these, the stirps *Albogrisescens*, *Coryli*, *Crocea*, *Lividopallescens*, *Mairei*, and *Protecta* were already outlined by Hanss & Moreau (2020). Four more lineages were resolved, which may be similarly treated as stirps, namely *Amplivelata*, *Betulae*, *Lignitincta*, and *Retenta*. Stirp *Lignitincta* harbours *A. pallidozonata* Y.Y. Cui, Q. Cai & Zhu L. Yang, in Cui *et al.* (2018: 93). Stirp *Retenta* includes *A. retenta* Y.Y. Cui, Q. Cai & Zhu L. Yang (in Cui *et al.* 2018: 95). Finally, the species introduced below, *A. amplivelata* *sp. nov.* resides in a fully supported clade, which represents a new stirp, *Amplivelata*, appearing in between the similarly well-supported clades between the stirps *Albogrisescens* (represented in Fig. 1 by *A. griseoumbonata* Y.Y. Cui, Q. Cai & Zhu L. Yang in Cui *et al.* 2018: 90) and *Lignitincta*. Pairwise comparison of the nrITS sequences of *A. amplivelata* and the closely related species as inferred by the multilocus analysis show that they are considerably divergent from one another (sequences from the holotypes compared). The difference between *A. amplivelata* and *A. pallidozonata* is 36 substitutions and 13 indels (89.98 % similarity) and from *A. griseoumbonata*, 21 substitutions and 10 indels (93.85 % similarity), on pairwise alignments of 489 and 501 positions respectively.



**FIGURE 2.** Phylogenetic tree of Clade 5 (as defined in Hanss & Moreau 2020), based on the nrITS marker. Figures next to branches indicate Bayesian probability and Maximum Likelihood bootstrap proportions, respectively.

The Bayesian tree based on the nrITS marker (Fig. 2) in general retrieved the major subclades of Clade 5 that were already defined in Hanss & Moreau (2020). Later, it placed the selected eight sequences of *A. amplivelata* in a well-defined separate clade, which receives full statistical support, albeit its position in the nrITS inference does not correspond to the placement inferred by the analysis of the multilocus dataset. The suggestion by the BLASTn search (Altschul *et al.* 1990) of the similarity of nrITS sequences of *A. amplivelata* to sequences of the stirp *Mairei*, is not supported by the nrITS inference, where the new species is placed close to accessions falling in the clade corresponding to the *Crocea* stirp. In conclusion, in spite of the incongruence of the topology of the multilocus and nrITS inferences, both phylogenies unambiguously support *A. amplivelata* as a separate and well-defined lineage in Clade 5 of section *Vaginatae*.

The single nrITS phylogeny as presented by Hanss & Moreau (2020) does not resolve the position of *A. amplivelata*, due to the important interspecific variability in the nrITS region in section *Vaginatae*. As in *A. vladimirii* which addressed a similar challenge (Ševčíková *et al.* 2021), the quite isolated phylogenetic position of *A. amplivelata* requires a multilocus analysis to be satisfactorily resolved. The current limit of multigene analysis is the low representation of *Vaginatae* species by LSU or TEF-1 $\alpha$  sequences in public databases.

## Taxonomy

*Amanita amplivelata* Hanss, Assyov, Bozok, Taşkın & Borovička, *sp. nov.* (Figs. 3, 4)  
MycoBank 849891

*Etymology*:—*amplus* (Latin)—ample, and *velum* (Latin)—veil, refers to the well-developed, thick universal veil, which is characteristic for the new species.

*Diagnosis*:—*Amanita amplivelata* differs from *A. crocea* by different colours, variable from one collection to another, *viz.*, silvery grey, mouse grey, greyish ochraceous, buff, olivaceous, rarely whitish; by the white universal veil sometimes stained yellow ochraceous or ochraceous grey on the velar remnants of the pileus and the saccate volva; by the white floccose stipe covering, by the predominantly broadly ellipsoid basidiospores, as well as by its inferred mycorrhizal relationship with trees of Salicaceae, the genus *Populus* in particular.

*Type*:—BULGARIA. Pernik province, between Trun town and Ezdimirtsi village, 42°50'07.6"N, 22°41'28.2"E, elev. *ca* 805 m, forest of *Populus tremula* and *Carpinus betulus*, 5 September 2020, *B. Assyov* (SOMF 30801!, holotype; LIP 0004524!, FBozok 1226!, isotypes; nrITS: OR524133; nrLSU: OR512418; TEF-1 $\alpha$ : OR526520).

*Description*:—*Pileus* up to 15 cm diam, at first campanulate or sometimes hemispherical, then expanding to convex, convex-applanate, in old basidiomata completely applanate or sometimes slightly depressed in the center, sometimes slightly umbonate, dry to viscid, especially in wet weather, in young basidiomata very finely rugulose, later usually more or less smooth, sometimes with an innately fibrillose pattern, pale grey (1B1, 4B1), ash grey (1B2), platinum (1–3D1), pearl grey (3B1), smoke grey (3C2), greyish beige (4C2), olive (3D3–4), ivory (4B3), brownish grey to greyish brown (7–8D2–3), usually darker in the center, somewhat paler towards margin and becoming darker again in the area of the marginal striations, occasionally entirely off-white, in some collections with iridescent or metallic shine; pileal margin striate, striations deep 1/4 to 1/3, sometimes up to 1/2 of pileal radius; velar remnants often (in over 50 % of basidiomata) present on pileal surface in the form of single, adpressed, irregularly shaped patches or sometimes as numerous fragments, initially whitish, quickly becoming ochraceous. *Stipe* up to 17 cm long, 1.5 cm wide at the apex and 3.5 cm at the base, up to twice as long as the pileal diameter, more or less cylindrical, slightly widened towards the base, whitish floccose to smooth, in young basidiomata sometimes with a distinct cottony rim where the volva begins; *volva* robust, splitting into 2 to 4 lobes, up to 5 cm tall from stipe base to the upper lobe, saccate (type IV) rarely vaginate (type III), not or only slightly constricted at the base, membranous, up to 3 mm thick, in mature basidiomata sometimes receding, usually entirely whitish, sometimes with small ochraceous spots on the outer face, rarely entirely yellowish ochraceous coloured, whitish on the interior face, outer surface sometimes rugulose; limbus internus present. *Lamellae* adnexed, truncate, up to 10 mm broad, white or whitish, sometimes salmon upon drying, margin serrate, flocculose, concolorous with the sides; 0–2 tiers lamellulae. *Spore print* white. *Odour* indistinct or distinct, unpleasant, resembling *A. strobiliformis* to some extent. *Taste* not recorded. *Macrochemical* reactions: 10 % phenol on stipe, lamellae and context produced a purple colour; 5 % KOH was pale yellowish on the stipe surface and negative on the pileus, lamellae and stipe trama; 10 % NH<sub>4</sub>OH was negative on all tissues; tincture of guaiac was negative on all tissues.



**FIGURE 3.** Macromorphological features and variability of *Amanita amplivelata*. a. SOMF30801 (holotype), b–l. Paratypes: b–c SOMF30810, d SOMF30802, e SOMF30806, f SOMF30803, g FBozok1085, h FBozok1097, i SOMF30808, j–k PRM958042, l SOMF30804. In a, b, c, e, g and i note the prominent volva and in f and i–l the ample remnants of the general veil, which often turn ochraceous tinted. Photos: a–f, i, l B. Assyov, g–h F. Bozok, j–k J. Borovička.

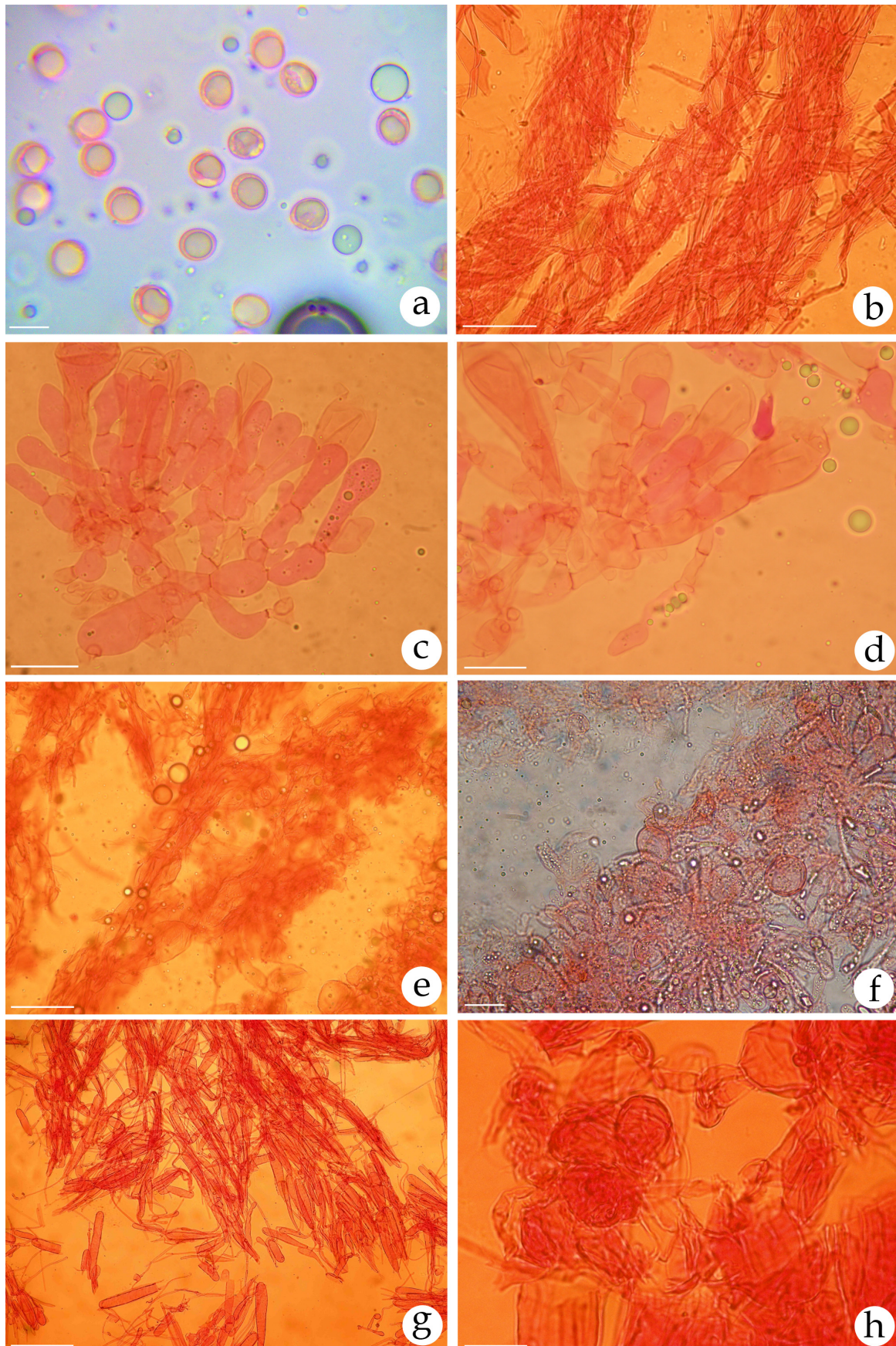
*Pileipellis* an ixocutis about 100–150  $\mu\text{m}$  thick, covered in some areas with a thin gelatinous layer containing hyphae 2–3  $\mu\text{m}$  broad; the main layer is a homogeneous stratum consisting of hyphae 3  $\mu\text{m}$  broad, helically arranged and forming a rope-like entangled, resistant bundle; presence of a few hyphae of thromboplerous type, strongly cyanophilous, 5–7  $\mu\text{m}$  broad; hyphae of the pileipellis hyaline, but in 10 % KOH form a faintly yellow mass, seen in all collections examined (presumably residual shade of vacuolar pigment, colouring the hyphae in fresh state). *Context of pileus* consisting mainly of elongated physaloid elements of very variable size, for example,  $190 \times 35 \mu\text{m}$ ,  $70 \times 20 \mu\text{m}$  or  $45 \times 22 \mu\text{m}$ ; the shortest sometimes catenulate, held together by a network of hyphae 5–7  $\mu\text{m}$  broad; the overall structure with matted aspect, without entanglement, very fragile. *Basidia* narrowly clavate to elongate clavate,  $33\text{--}82 \times 12\text{--}22 \mu\text{m}$ , mostly tetrasporic but with a significant proportion of bisporic basidia; sterigmata moderately to very thin, 2.5–6.5  $\mu\text{m}$  long. *Subhymenium* mostly of inflated-ramose (type 2 of Bas 1969) to sometimes subcellular elements,

the subhymenial cell supporting one to many basidia; the branches immediately below the basidia are fixed several on the lower branch. *Lamellar trama* 40–250 µm thick, with a mediostratum made of an undifferentiated material, whose elements are difficult to separate without breaking the most fragile and of which a few small oval physaloid cells, parallel to the axis are visible; hymenopodium indistinct. *Lamellar edge* sterile, covered with a gelatinous layer 30–40 µm thick, containing a few marginal cells; below this layer the basidia are partially mixed with marginal cells of the same shape, globose to subovoid, rarely pyriform 20–55 × 19.5–35 µm, with a pedicel of variable length and 3 µm wide. *Universal veil (volva)* 3-layered (on some individuals, one or the other external strata may be missing up to a certain height); a medium layer, covered by an outer and an inner stratum with a more compact structure; the main layer about 500–1500 µm thick, composed of loosely arranged hyphae, crossed by compact clusters of hyphae 3–5(–8) µm broad, very strongly entangled with each other and very strongly related to oval, medium-sized physaloid elements measuring, e.g., 50 × 20 µm, 60 × 35 µm, or 9 × 30 µm, or more rarely subspherical, e.g., 35 × 30 µm; filamentous hyphae abundant, inflated elements moderately abundant to common; both inner and outer strata, of variable thickness, are of the same composition with entanglement stronger than the main stratum, but a little less strong than clusters, resulting in a thick, moderately supple material; in cases when the volvas are thin, the structure of the middle stratum is tighter, more difficult to interpret and therefore less characteristic. *Stipe trama* essentially composed of vertically disposed, very long, slenderly clavate acrophysalids, 80–320 × 15–35 µm, ensuring the rigidity; these are the terminal members of predominantly vertical, quite short, 3–5 µm broad hyphae; on the inner wall of the usually hollow stipe, acrophysalid-like cells of spherical shape are present, contrasting with the acrophysalids of the context; those acrophysalid-like cells are sometimes agglomerated in a gelatinous in appearance matrix (possible pith precursors). *Basidiospores* mostly broadly ellipsoid or subglobose, usually with a single guttule, rarely pluriguttulate, (8.9–)9.1–13.8 (–16.8) × (7.4–)8.0–11.8(–13.6) µm, Q = (1.0–)1.05–1.36(–1.4), L<sub>av</sub> = 10.3–12.0, W<sub>av</sub> = 8.5–10.4, Q<sub>av</sub> = 1.08–1.3 (n = 505, m = 13, p = 13). *Microchemical reactions*: K–K reaction negative.

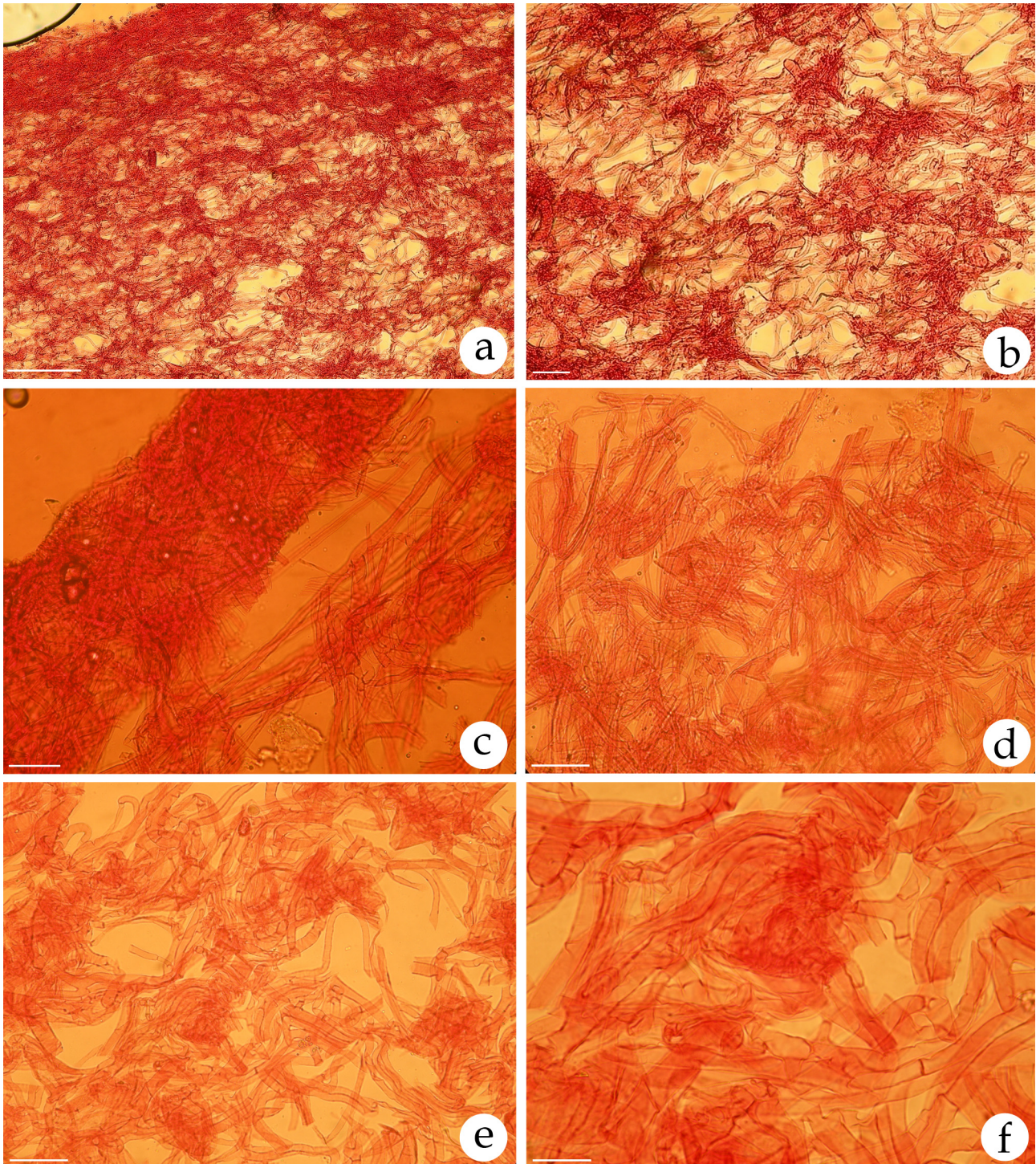
*Habit and habitat*:—Found from June to November in natural forests, plantations and parklands with trees of genus *Populus* Linnaeus (1754: 456).

*Additional specimens examined (paratypes)*:—BULGARIA. Sofia capital province, Sofia city, West Park, a lawn with *Populus × canadensis* and *Pinus wallichiana*, 42°42'10.3"N, 23°15'35.9"E, elev. ca 625 m, 11 June 2020, B. Assyov & I. Penchev (SOMF 30802!, LIP 0004526!, FBozok 1224!; nrITS: OR524134; nrLSU: OR512419; TEF-1α: OR526521); *idem*, 3 November 2020, B. Assyov (SOMF 30803! nrITS: OR524135); *idem*, 8 June 2021, I. Penchev (SOMF 30804!, LIP 0004525!, FBozok 1230!; nrITS OR524136); *idem*, 9 June 2021, Ts. Yordanova (SOMF 30805!; nrITS: OR524137); *idem*, 42°42'2.67"N, 23°15'15.60"E, elev. ca 645 m, mixed scrub, under *P. × canadensis*, 11 June 2020, B. Assyov & I. Penchev (SOMF 30806!; LIP 0004527!, FBozok 1223!; nrITS: OR524138); Sofia province, Novi Han municipality, in the vicinity of Karapoltsi village, 42°37'01.1"N, 23°42'16.8"E, elev. ca 585 m, under *P. × canadensis*, 7 July 2020, D. Dimitrova (SOMF 30807!, FBozok 1225!; nrITS: OR524139; nrLSU: OR524139); *idem*, 42°36'59.5"N, 23°42'15.9"E, elev. ca 585 m, in a grassland close to *P. × canadensis*, 8 June 2021, B. Assyov (SOMF 30808!, LIP 0004528!, FBozok 1228!; nrITS: OR524140); Pernik province, between Trun town and Ezdimirtsitsi village, 42°50'09.1"N, 22°41'28.0"E, elev. ca 800 m, forest of *Populus tremula* and *Carpinus betulus*, 5 September 2020, B. Assyov (SOMF 30809!; LIP 0004523!, FBozok 1227!; nrITS: OR524141); *idem*, 42°50'07.6"N, 22°41'28.2"E, elev. ca 805 m, 28 June 2021, B. Assyov (SOMF 30810!, LIP 0004522!, FBozok 1229!; nrITS: OR524142); CZECH REPUBLIC. Highland, Žďár nad Sázavou, in town, near ŽĎAS company compound, in grassplot and mineral soil under mature *Populus nigra* trees, on acid background but soil could have been influenced by artificial sources of calcium (e.g., mortar), 49°33'21.8"N, 15°55'49.9"E, elev. ca 580 m, 3 July 2010, J. Borovička & J. Kubrová (PRM 958042!, BRNM 829044!; nrITS: OR524132; nrLSU: OR524132); FRANCE. Hautes Pyrénées (65), Castet de Gerde, young recolonisation afforestation natural extension of a forest on calcareous soil with *Betula pendula*, *Corylus avellana*, *Salix caprea* and (a little further on) *Populus tremula*, 43°3'29.51"N, 0°10'2.39"E, elev. ca 630 m, 7 July 2013, G. Corriol (GC13070701, BBF!; nrITS: OR524143); TÜRKIYE. Ankara province, Çubuk province, between Kışlacık and Yıldırım village, 40°25'51.8"N, 32°54'20.5"E, elev. ca 1548 m, plantation of *Populus tremula*, 17 June 2021, F. Bozok, H. Taşkın, M. Yarar (FBozok 1085!, FBozok 1097!; nrITS: OR524144 & OR524145).





**FIGURE 4.** Micromorphological features of *Amanita amplivelata*. a. Basidiospores; b. Pileipellis weakly dissociated; c. Subhymenium; d. Subhymenium with subglobose subhymenial cell; e. Lamellar trama; f. Lamellar edge with the loose gelatinous layer seen detached at the top of the photo; g. Stipe acrophysalids and hyphae; h. Stipe cells fixed on the inner wall. Photos by: a B. Assyov, c–h J.-M. Hanss. Scale bars: a = 10  $\mu\text{m}$ ; b–d = 20  $\mu\text{m}$ ; f, h = 50  $\mu\text{m}$ ; e, g = 100  $\mu\text{m}$ .



**FIGURE 5.** Micromorphology of the volva of *Amanita amplivelata*. a, b. General view; c, d. External stratum detail; e, f. Main stratum detail (clusters). Photos by J.-M. Hanss. Scale bars: a = 100  $\mu\text{m}$ ; b–e = 50  $\mu\text{m}$ ; f = 20  $\mu\text{m}$ .

## Discussion

The species status of *A. amplivelata* is unequivocally supported by the analysis of the nrITS sequences and the multilocus phylogeny of nrITS, nrLSU, and TEF-1 $\alpha$  DNA regions. Moreover, the complete identity of the nrITS region of the 14 sequenced collections from a vast geographic range may imply that the species is well-established and isolated, as well as highly conservative at least as far as this DNA region is concerned. The species is also morphologically and ecologically well-characterised, featuring a robust, squat basidiomata and an ample, saccate volva sometimes stained yellow ochraceous or ochraceous grey, and occurring apparently associated with trees of the family Salicaceae, mostly

the genus *Populus*. The pileal colours show a high chromatic variability, ranging from off-white through different tints of grey (sometimes with a metallic shine) to shades of buff. The buff colours are especially common in rainy periods and such basidiomata are present in the same localities where fruitbodies with a greyish-tinted pileus appear in drier weather, and thus one may assume that those colour changes are related to humidity seeing as sequences from collections with buff-tinted pilei are identical to grey ones. Some collections are entirely buff brown from the start and others are somewhat olive-tinted. This variability is not unusual as high chromatic plasticity is already well-known in a few other European *Vaginatae* (Vizzini *et al.* 2016, Hanss & Moreau 2020, Assyov *et al.* 2021) but it is particularly notable in *A. amplivelata*. Another characteristic trend of the new species is the tendency of the veil remnants to develop yellowish buff colouration. It is usually more pronounced on veil patches on the pileus when present and less so on the volva. Among the microscopic features of *A. amplivelata*, the volva with the “crocea”-type structure is notable (*i. e.*, with a main stratum of loosely arranged hyphae, surrounding compact clusters of hyphae strongly entangled around physaloid elements) as well as the inflated-ramose to subcellular subhymenium and predominantly broadly ellipsoid basidiospores. The micro-architecture of the volva seems a particularly useful character in the ringless species of *Amanita*. It is however very important that it is studied following a well-established protocol. The internal, lower parts of the volva may contain inner stratum, believed by some authors to represent a partial veil, which is rich in inflated elements. A study of sections from the upper part, before the appearance of those tissues, is thus preferable in order to establish the true microstructure. The microscopy of the lamellar trama also has certain peculiarities, particularly when studied on dried material. In such cases the result is more compressed tissue, that is to say more parallel to the axis than in fresh material. If parallel physaloid cells are observed, they may possibly have had a more bilateral arrangement when fresh.

Two species may be considered macroscopically quite close to *A. amplivelata*, with the same habit, a saccate, but persistently white volva and also microscopically with the same structure of the main stratum of the volva. The first of these is *A. crocea* (Quél. in Bourdot 1898: 52) Singer (1951: 386). This species is distinguished from *A. amplivelata* by the daffodil yellow to orange pileus, more conspicuous stipe floccosity, at first white then becoming orange, as well as subglobose spores. The volva has a thin outer stratum and this species occurs under *Betula*, *Quercus*, *Picea*, and *Abies*, on acidic soil. The second species with a similar microstructure of the volva is *A. dryophila* Consiglio & Contu (1999: 287). It is separated from *A. amplivelata* by the combination of an initially yellow pileus, sometimes turning intense brown with age, thick but relatively fragile volva, broadly ellipsoidal spores and occurrence under *Quercus spp.* *Amanita crocea* is the central species of the stirp *Crocea* and *A. dryophila* is phylogenetically close to *A. lividopallescens* (Gillet 1888: tab. 23) Bigeard & Guillemin (1913: 752).

Another species that features a similar microscopic structure of the central stratum of the volva as in *A. amplivelata* is *A. spadicea* Persoon (1797: 66) *sensu* Hanss & Moreau (2020), and recently resolved by Moreau *et al.* (2023). This species however, is phylogenetically distant from *Amanita amplivelata*, representing a sister lineage to Clade 3 in Hanss & Moreau (2020) and placed in the newly defined Clade 6 in Ševčíková *et al.* (2021). Furthermore, it differs in its intense dark brown, umbonate pileus and a characteristic stipe cover formed by fine, dark brown squamules although it also features a thick vaginate or sometimes type II volva and subglobose spores. It occurs under various deciduous and coniferous trees, from the lowlands to the mountains, but it has never been reported with *Populus spp.* as a potential mycorrhizal host so far.

A thick, saccate volva like that of *A. amplivelata* is also found (usually very thick) in *A. battarrae* (Boudier 1902: 272) Bon (1985:16), recently typified by Hanss & Moreau (2023), *A. magnivolvata* Aalto (1974: 93), *A. pachyvolvata* (Bon 1978: 36) Krieglsteiner (1984: 191) and *A. calida* Plaza & Illescas (in Illescas & Plaza Canales 2022: 45). All of these species belong to stirp *Magnivolvata* or Clade 1 as defined in Hanss & Moreau (2020), included in the most basal lineage in the phylogeny of *Vaginatae* (series *Penetratrices nom. prov. in* Tulloss & Yang 2023). All the European species known to us are recognizable by their rather stocky habit and by the large, three-layered, generally rusty brown spotted volva. They also display a middle layer of volva consisting of bundles of flexuous hyphae, a unique character within the European *Vaginatae*, and distinctive from *A. amplivelata* and other thick-veiled species of “Clade 5”. The ramose subhymenial arborescence includes at least one element (usually the hypobasidial one) with a bulge of variable shape and position, also unique among the European *Vaginatae*. Finally, the partial veil is absent to very scattered on the stipe, and the pileus is either uniformly brown to grey or slightly darker at centre, or sharply zonate.

*Amanita vladimirii* Ševčíková, Hanss & Moreau (in Ševčíková *et al.* 2021: 164) is another large, grey *Amanita*, with a smooth stipe and a saccate volva, which is white at the beginning but may stain ochraceous brownish (not rusty brown) where bruised. Microscopically the volva is 3-layered, the middle layer consisting of hyphae parallel to the stipe, distinct from the volval architecture seen in *A. amplivelata*. Furthermore, *A. vladimirii* displays distinctly smaller (8–11.5 × 6.7–10.5 µm), globose to subglobose basidiospores and occurs in deciduous forests under Fagaceae (Ševčíková *et al.* 2021).

To complete the list of European *Amanita* species with saccate volva, but in another clade (Clade 2 or “stirps *Argentea*”; Hanss & Moreau 2020), *A. argentea* Huijsman (1959: 14) has a tall, membranous volva with a clear internal limb of type “*argentea*”, a whitely floccose stipe, a grey pileus becoming silvery upon drying, hemispherical in shape that becomes depressed with expansion (Hanss & Moreau 2020). The 1-layered volva in *A. argentea* consists of hyphae parallel to the stipe hyphae, almost without physaloid articles. In *Amanita electra* Hanss (in Hanss & Moreau 2000), most parts of the volva consist of acrophysalids parallel to the stipe. The peculiar micro-architecture of volva in those two species distinguishes them from *A. amplivelata*.

The rusty brown spots on the outer surface of the universal veil are a character of high systematic value that characterises stirps *Fulva* and *Magnivolvata* (Hanss & Moreau 2020). The yellow or ochraceous spots of the universal veil seen in *A. amplivelata* may exist in several species, especially in *A. brunneofuliginea* Yang (1997: 96), *A. coryli* Neville & Poumarat (2009: 34), *A. supravolvata* Lanne (1979: 24), *A. simulans*, and *A. albogrisescens* (also consult Vizzini *et al.* 2016, Hanss & Moreau 2020). The occurrence of the spots varies between different collections of a single species but when they are present, they may help in identification.

*Amanita amplivelata* and *A. brunneofuliginea* have a close nrITS identity (95.77 % for MH508270 *A. brunneofuliginea* sequence). *Amanita brunneofuliginea* is a common boreo-continental species occurring in *Abies* and *Picea* forests, preferentially on calcareous soils, with a characteristic narrowly papillate pileus, whitish to ash grey with a more or less pronounced ochraceous tinge, up to light beige or yellowish beige, sometimes sub-zonate. The most certain characteristic for distinguishing this species from *A. amplivelata* is the ramose subhymenium with lateral projections (type 1b). Additionally, unlike in *A. amplivelata*, the pileus of *A. brunneofuliginea* is usually lacking remnants of a universal veil and the stipe is devoid of any remains of a partial veil. The volva of *A. brunneofuliginea* is vaginate, rather than saccate and microscopically it is of the “common” type, *i. e.*, one stratum of mixed structure with regularly tangled elements. Its polymorphism has led to the distinction of several forms: f. *ochraceomaculata* (Neville, Poumarat & Fraiture 2000:261) P.-A. Moreau (in Hanss & Moreau 2020: 119) is characterised by numerous yellow spots of more or less polygonal shape, regularly distributed over the entire primary veil; f. *ochraceopallida* (Contu 1997: 137) Hanss (in Hanss & Moreau 2020: 119) has a white volva, with or without spots, rarely entirely ochraceous.

*Amanita supravolvata* and *A. mairei* Foley (1949: 117) could be confused with *A. amplivelata*. They are sister species of *A. brunneofuliginea* (Hanss & Moreau 2020 and Fig. 2) and both have a grey pileus, sometimes with a brownish note and become silvery upon drying. Velar remnants on the pileus are sometimes faintly stained with ochre. However, the volva is of type II, without a limbus internus of type “*argentea*”, and 1-layered. Other differences with *A. amplivelata* are a subhymenium of type Ib, branched with a lateral projection, and the apparently strict association with pines (*Pinus spp.*) preferentially on sandy soils (Hanss & Moreau 2020).

*Amanita coryli* Neville & Poumarat (2009: 34) may resemble to some degree *A. amplivelata* by the ochraceous or greyish coloured pilei and its volva, which could be spotted yellow or yellowish ochraceous. It is often associated with the Betulaceae, essentially *Corylus spp.* but also *Betula spp.* It could be also found in other associations (Hanss & Moreau 2020; Bozok *et al.* 2023), with Fagaceae (*Castanea*, *Quercus*) and with alpine *Salix* and *Dryas* in subalpine grasslands. It is generally a small, slender species, medium-sized in alpine grasslands and tall and vigorous when it grows under *Betula* reminiscent of *A. lividopallescens*. The volva of *A. coryli* is always vaginate (type III) contrasting with the saccate volva in *A. amplivelata*, and microscopically of the mixed type with elements oriented in all directions, with a thin external layer (Neville & Poumarat 2009). The subglobose to globose basidiospores in *A. coryli* (Neville & Poumarat 2009) may in some cases also help to separate it from *A. amplivelata*, although some collections of the latter species may produce subglobose spores too.

*Amanita albogrisescens* Contu (2000: 8), a highly polymorphic species apparently strictly associated with Fagaceae, may have an ochraceous-spotted universal veil (sometimes turning brown to grey with age, especially the pileal remnants). The pileus declines three basic colours, namely grey, brown and ochraceous yellow (Hanss & Moreau 2020). Those characters overlap to a certain degree with those of *A. amplivelata*. The most striking characteristic of *A. albogrisescens* is the distinctly two-layered pileipellis, *i. e.*, a gelatinised layer without hyphae, 200 µm thick, covering a 50 µm-thick suprapellis of parallel hyphae 3 µm wide, and a subpellis made of distinctly intertwined hyphae 6 µm wide (Hanss & Moreau 2020). In *A. amplivelata* the pileipellis is composed of an upper stratum of strongly gelatinized hyphae and a lower stratum of rope-like entangled bundles of hyphae. The spores in *A. albogrisescens* range from subglobose (f. *subglobispora* Hanss in Hanss & Moreau 2020:107) to ellipsoid in f. *albogrisescens*, and in f. *separata* Contu (1999:162) ex Hanss (in Hanss & Moreau 2000: 106), f. *pseudolactea* (Contu 2001: 24) Hanss (in Hanss & Moreau 2020: 106) and f. *cinereifolia* (Contu 2007: 6) Hanss (in Hanss & Moreau 2020: 107). *Amanita amplivelata* has predominantly broadly ellipsoid basidiospores.

*Amanita simulans* Contu (2001: 11) is the species most easily confused with *A. amplivelata* in the field as its most usual mycorrhizal hosts are *Populus spp.* (Fraiture & De Beuckeleer 2014, Vizzini *et al.* 2016), like *A. amplivelata*. *Amanita simulans* usually has a grey pileus, but it can be brown or white (Fraiture & De Beuckeleer 2014, Vizzini *et al.* 2016). Microscopically, the white volva of types II or III is unique and distinct from that of *A. amplivelata*, being formed by a majority of spherocysts connected by a network of entangled slender hyphae (the most entangled structure amongst European *Vaginatae*), with an outer stratum of layered spherocysts (Ševčíková *et al.* 2021). Finally, the basidiospores in *A. simulans* are globose to subglobose (Fraiture & De Beuckeleer 2014, Vizzini *et al.* 2016) whilst broadly ellipsoid in *A. amplivelata*.

*Amanita lividopallescens*, is another large sometimes grey ringless *Amanita* similar in colouring to *A. amplivelata*. However, the pileus is more often grey with yellow or beige grey tints and rarely pure grey (see Vizzini *et al.* 2016). However, it has remarkably variable spores, with the  $Q_{av}$  ranging from 1 to 1.5 (Vizzini *et al.* 2016). Furthermore, the volva is composed of two strata with a main stratum of hyphae parallel to the stipe, which is distinct from that of *A. amplivelata*. The association with Fagaceae is another difference.

*Amanita cistetorum* is reminiscent of *A. amplivelata* on account of the squat stature, the grey pileus (except albinotic specimens) and the subglobose basidiospores with the average  $Q$  of about 1.16 (Contu & Pacioni 1998). However, its white volva is not saccate and does not show ochre spots, and its ecology seems to be restricted to the Mediterranean Cistaceae shrublands (Contu & Pacioni 1998). Furthermore phylogenetic analyses place this species in stirp *Coryli* (Hanss & Moreau 2020; Fig. 2).

Finally, our analysis of the nrITS locus suggests *Amanita retenta* Y.Y. Cui, Q. Cai & Zhu L. Yang (in Cui *et al.* 2018) is closely related to the new species. It is an Asian species, which may macroscopically resemble *A. amplivelata* on account of the colour of pilei, the saccate volva, and the pileal remnants, which often persist on the pileal surface, as well as microscopically by the overlapping size of the basidiospores (Cui *et al.* 2018). *Amanita retenta* however can be easily distinguished by its two-layered volva, the outer layer of which is composed of abundant inflated cells and longitudinally arranged filamentous hyphae, and the inner layer composed of longitudinally arranged filamentous hyphae and scarce to scattered inflated elements (Cui *et al.* 2018). In addition, *A. retenta* is said to occur in pine or mixed forests with Fagaceae and Pinaceae (Cui *et al.* 2018), a habitat rather different to the *Populus spp.* dominated habitat of *A. amplivelata*.

Our field observations suggest that *A. amplivelata* is associated with trees of the genus *Populus*, even though some of the collections came from mixed stands with species of *Pinus* Linnaeus (1754: 434), like *P. wallichiana* Jackson (1938: 85) in one Bulgarian locality (planted), and *P. sylvestris* Linnaeus (1753: 1000) in the place where one of the Turkish collections was found, or *Carpinus betulus* Linnaeus (1753: 998) in the holotype locality. However, at least part of the examined specimens could be unequivocally linked to poplars, *P. × canadensis* Moench (1785: 81), *P. nigra*, and *P. tremula* Linnaeus (1753: 1034) in particular, being the only trees present in some of the studied localities. No characteristic soil pattern could be implied so far and the species seems to occur on both non-calcareous and calcareous, generally nutrient rich, loamy soils. The variety of habitats in which the new species was found, as well as the wide geographic range of its presumed hosts of the genus *Populus*, leave little doubt that further studies will reveal that it shows certain ecological plasticity as it seems to establish itself well in artificial poplar plantations and other man-made habitats such as parklands, purportedly acting as a pioneer species. In addition, *A. amplivelata* may fruit both in shaded situations deep in forests, as well as next to solitary *Populus spp.* in mown grasslands with dense grass tussocks.

So far *A. amplivelata* is known from its type collections from Bulgaria, the Czech Republic, France and Türkiye, a range effectively spanning about 2500 km by air, from the Near East almost to the Atlantic coast of Europe. This suggests it could be much more widespread on this continent and maybe even in western Asia, but unrecognised so far. *Amanita simulans*, as already mentioned above, is the only other European species, proven to occur with hosts of genus *Populus* (Vizzini *et al.* 2016). It is not unlikely that the two species may co-occur in certain localities and this is a matter worth pursuing further, and it cannot be excluded that, like the previous, *A. amplivelata* may occasionally associate with alternative hosts.

**TABLE 1.** Taxa of *Amanita*, included in the molecular phylogenetic analyses.

Species	Identifier	Sequences			Reference
		nrITS	nrLSU	TEF-1 $\alpha$	
<i>A. albogrisescens</i>	GC02017	KX834249			Vizzini <i>et al.</i> (2016)
<i>A. albogrisescens</i>	JMH2017014	MN490654			Hanss & Moreau (2020)
<i>A. albidostipes</i>	HKAS95189	MH508501	MH486757	MH508984	Cui <i>et al.</i> (2018)
<i>A. albidostipes*</i>	HKAS57358	NR159585	NG064586	MH508983	Cui <i>et al.</i> (2018)
<i>A. alseides*</i>	JMH2015021	MN490649			Hanss & Moreau (2020)
<i>A. alseides</i>	GC02017	KX834249			Vizzini <i>et al.</i> (2016)
<i>A. amplivelata*</i>	<b>SOMF 30801!/LIP 0004524!/FBozok 1226</b>	<b>OR524133</b>	<b>OR512418</b>	<b>OR526520</b>	this study
<i>A. amplivelata</i>	<b>SOMF 30806!/LIP 0004527!/FBozok 1223!</b>	<b>OR524138</b>			this study
<i>A. amplivelata</i>	<b>SOMF 30802!/LIP 0004526!/FBozok 1224!</b>	<b>OR524134</b>	<b>OR512419</b>	<b>OR526521</b>	this study
<i>A. amplivelata</i>	<b>SOMF 30807!, FBozok 1225</b>	<b>OR524139</b>	<b>OR524139</b>		this study
<i>A. amplivelata</i>	<b>SOMF 30809!/LIP 0004523!</b>	<b>OR524141</b>			this study
<i>A. amplivelata</i>	<b>SOMF 30803</b>	<b>OR524135</b>			this study
<i>A. amplivelata</i>	<b>SOMF 30808!/LIP 0004528!/FBozok 1228!</b>	<b>OR524140</b>			this study
<i>A. amplivelata</i>	<b>SOMF 30810/LIP 0004522!</b>	<b>OR524142</b>			this study
<i>A. amplivelata</i>	<b>SOMF 30805</b>	<b>OR524137</b>			this study
<i>A. amplivelata</i>	<b>SOMF 30804!/LIP 0004525!/FBozok 1230!</b>	<b>OR524136</b>			this study
<i>A. amplivelata</i>	<b>PRM 958042</b>	<b>OR524132</b>	<b>OR524132</b>		this study
<i>A. amplivelata</i>	<b>BBF GC13070701</b>	<b>OR524143</b>			this study
<i>A. amplivelata</i>	<b>FBozok 1085</b>	<b>OR524144</b>			this study
<i>A. amplivelata</i>	<b>FBozok 1097</b>	<b>OR524145</b>			this study
<i>A. beckeri</i>	JMH2015027	MN490686			Hanss & Moreau (2020)
<i>A. beckeri</i>	LIP:PAM17091101	MN490691			Hanss & Moreau (2020)
<i>A. betulae</i>	G:P. Neville 02091911a	MN490668			Hanss & Moreau (2020)
<i>A. betulae</i>	DB2021-08-08-2	OQ860071	OQ860073	OQ974180	B. Dima, unpubl.
<i>A. brunneofuliginea</i> f. <i>ochraceomaculata</i>	P. Neville 97071327a	MN490673			Hanss & Moreau (2020)
<i>A. brunneofuliginea</i> f. <i>ochraceopallida</i>	JMH2018005	MN490660			Hanss & Moreau (2020)
<i>A. chiui*</i>	HKAS76328	MH508303	NG064563	MH508727	Cui <i>et al.</i> (2018)
<i>A. chiui</i>	HKAS73916	MH508302			Cui <i>et al.</i> (2018)
<i>A. cistetorum</i>	TO MC261008	KX834236			Vizzini <i>et al.</i> (2016)
<i>A. cistetorum</i>	TO MC141208	KX834235			Vizzini <i>et al.</i> (2016)
<i>A. coryli*</i>	G:P. Neville 02091903	MN490667			Hanss & Moreau (2020)
<i>A. coryli</i>	AB11-08-45	MN490656			Hanss & Moreau (2020)
<i>A. coryli</i>	DB2020-07.04-7	OQ860070	OQ860072	OQ974179	B. Dima, unpubl.
<i>A. crocea</i>	<b>DS 0105 2019 08 08</b>	<b>OR524147</b>			this study
<i>A. crocea</i>	<b>JHM202000</b>	<b>OR524148</b>			this study
<i>A. dryophila</i>	TO MC131111	KX834238			Vizzini <i>et al.</i> (2016)
<i>A. dryophila</i>	<b>DL2008301</b>	<b>OR524146</b>			this study
<i>A. glarea*</i>	LAH35044	NR151657	NG058601		Jabeen <i>et al.</i> (2017)
<i>A. glarea</i>	K16	KY788649	KY788653		Jabeen <i>et al.</i> (2017)
<i>A. glarea</i>	SUA712 LAH35217	KY817312			Sadiquillah, unpubl.
<i>A. griseofusca*</i>	SWAT00137	NR159567	NG064533		Kiran <i>et al.</i> (2018)
<i>A. griseofusca</i>	LAH35366	MH241055	MH241056	MH282854	Kiran <i>et al.</i> (2018)
<i>A. griseoumbonata*</i>	HKAS92103	NR159579	NG064573	MH508847	Cui <i>et al.</i> (2018)
<i>A. griseoumbonata</i>	HKAS75594	MH508388	MH486577	MH508846	Cui <i>et al.</i> (2018)
<i>A. griseoumbonata</i>	HKAS69588	MH508387	MH486576	MH508845	Cui <i>et al.</i> (2018)
<i>A. lividopallescens*</i>	TO MC121009	KX834245			Vizzini <i>et al.</i> (2016)

.....continued on the next page

TABLE 1 (Continued)

Species	Identifier	Sequences			Reference
		nrITS	nrLSU	TEF-1 $\alpha$	
<i>A. lividopallescens</i> var. <i>globispora</i> *	M-0200751 Herb. E Ludwig 3735	KX834247			Vizzini <i>et al.</i> (2016)
<i>A. lividopallescens</i> f. <i>malleata</i>	Bon80092206a	MN545697			Hanss & Moreau (2020)
<i>A. mairei</i>	LIP:PAM0010311	MN490695			Hanss & Moreau (2020)
<i>A. mairei</i>	GC13291	MN490682			Hanss & Moreau (2020)
<i>A. mansehraensis</i> *	MSM0088	MG195980	MG195982	MH495970	Saba <i>et al.</i> (2019)
<i>A. mansehraensis</i>	MSM0087	MG195979	MG195984		Saba <i>et al.</i> (2019)
<i>A. mansehraensis</i>	MSM0089	MG195981	MG195983		Saba <i>et al.</i> (2019)
<i>A. orienticrocea</i>	HKAS73823	MH508463	MH486698	MH508941	Cui <i>et al.</i> (2018)
<i>A. pallidozonata</i> *	HKAS100608&57718	MH508486	NG064583	MH508486	Cui <i>et al.</i> (2018)
<i>A. populiphila</i>	RET103-4	NR154689	NG057058		Tulloss <i>et al.</i> , unpubl.
<i>A. populiphila</i>	RET423-6	KU985228			Tulloss <i>et al.</i> , unpubl.
<i>A. protecta</i> *	RET086-6	NR154690			Tulloss <i>et al.</i> , unpubl.
<i>A. protecta</i>	RET821-1	MW592832	MW592833		Tulloss <i>et al.</i> , unpubl.
<i>A. protecta</i>	RET473-6	KP224328			Tulloss <i>et al.</i> , unpubl.
<i>A. pseudovaginata</i>	HKAS38323	AY436470			Zhang <i>et al.</i> (2004)
<i>A. retenta</i> *	HKAS70020	NR159591	NG064592	MH509028	Cui <i>et al.</i> (2018)
<i>A. retenta</i>	HKAS70024	MH508544	MH486803	MH509029	Cui <i>et al.</i> (2018)
<i>A. retenta</i>	HKAS68379	MH508541	MH486800	MH509026	Cui <i>et al.</i> (2018)
<i>A. retenta</i>	HKAS54672	MH508540	MH486799	MH509025	Cui <i>et al.</i> (2018)
<i>A. simulans</i> *	TO AM161112	NR173159			Vizzini <i>et al.</i> (2016)
<i>A. simulans</i>	TO:JMM101012	KX834258			Vizzini <i>et al.</i> (2016)
<i>A. sp.</i>	SUA505A	MW425338			Ullah <i>et al.</i> , unpubl.
<i>A. sp.</i> ‘ <i>albiceps</i> ’	RET521-10	KP224316			Lamoureux <i>et al.</i> , unpubl.
<i>A. sp.</i> ‘ <i>aurorae</i> ’	RET637-3	MZ545415	MZ545413		Tulloss <i>et al.</i> , unpubl.
<i>A. sp.</i> ‘ <i>aurorae</i> ’	RET 629-2	MK569760			Tulloss <i>et al.</i> , unpubl.
<i>A. sp. barrowsii</i>	Mushroom Observer 481483	ON359835			Clements, unpubl.
<i>A. sp.</i> ‘ <i>chiricahuana</i> ’	CMP1341	KX219634			Tulloss <i>et al.</i> , unpubl.
<i>A. sp.</i> ‘ <i>chiricahuana</i> ’	CMP1835	KX219637			Tulloss <i>et al.</i> , unpubl.
<i>A. sp.</i> ‘ <i>kryorhodon</i> ’	RET578-3	KX270312			Tulloss <i>et al.</i> , unpubl.
<i>A. sp.</i> ‘ <i>kryorhodon</i> ’	RET139-4	KX270308			Tulloss <i>et al.</i> , unpubl.
<i>A. sp.</i> ‘ <i>pahasapaensis</i> ’	RET271-10	KP313578			Tulloss <i>et al.</i> , unpubl.
<i>A. sp.</i> ‘ <i>saltpointensis</i> ’	RET599-8	OK316958			Tulloss <i>et al.</i> , unpubl.
<i>A. spadicea</i>	DL170917a	MN490685			Hanss & Moreau (2020)
<i>A. subnudipes</i>	<b>JMH2018002</b>	<b>OR524149</b>			this study
<i>A. supravolvata</i> *	RET 103-7	NR154693			Tulloss <i>et al.</i> , unpubl.
<i>A. supravolvata</i>	LP20121106	MN490651			Hanss & Moreau (2020)
<i>A. vaginata</i>	KA12-0665	KF017948			Kim <i>et al.</i> (2013)
<i>A. vaginata</i>	CUB:MN18	AB458889			Yomyart <i>et al.</i> , unpubl.
<i>A. velosa</i>	07004	GQ250409	GQ250424		Harper & Davis, unpubl.
<i>A. velosa</i>	10009864	MH018884			Tighe <i>et al.</i> , unpubl.
<i>A. velosa</i>	MUOB364310	MZ997396			Schwartz <i>et al.</i> , unpubl.

Asterisk entries denote the sequences derived from type materials, except for *A. amplivelata*, where only the holotype collection is marked. The column “Identifier” includes fungarium numbers, collectors’ codes or other identifiers as provided in GenBank. The newly generated sequences are marked in bold.

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