



ORIGINAL ARTICLE

Phylogenetic and morphological studies reveal large diversity and three new species in *Amanita* sect. *Vaginatae* (*Agaricales*, *Basidiomycota*) from Europe

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Abstract

European members of the species-rich sect. *Vaginatae* of the genus *Amanita* are studied focusing on Central (Austria, Hungary, N Italy and Romania), Western (France) and North European (Norway) collections. The combination of a 4-locus (nrDNA ITS, nrDNA LSU, *RPBI* and *TEF1- α*) molecular phylogenetic analysis and a morphological approach resulted in the discovery of three new species: *Amanita deflexa* and *A. griseofulva* from stirps *Fulva* and *A. opaca* from stirps *Coryli*. Furthermore, the albinotic white forms of *A. griseofulva* (f. *albida*) and *A. opaca* (f. *cettoi*) are formally named. As a result of the comprehensive taxonomic revision of *Amanita* sect. *Vaginatae*, 370 newly generated sequences are deposited to GenBank, and 17 species new to Hungary are reported. This study provides another step towards understanding the taxonomy and diversity of *Amanita* section *Vaginatae* in Europe.

Keywords *Amanitaceae* · Ectomycorrhizal fungi · Multi-locus analysis · Revision · Taxonomy

Introduction

The globally distributed genus *Amanita* Pers. is one of the iconic groups of basidiomycetous macrofungi in *Agaricales*. The genus includes economically important edible species as well as lethally poisonous ones. A supposedly strictly saprotrophic basal lineage of *Amanita* with squarrose universal veil was isolated in a separate genus by Vizzini et al. (2012) as *Aspidella*, E. J. Gilbert (nom. illegit.) and then by Redhead et al. (2016), as *Saproamanita* Redhead, Vizzini, Drehmel & Contu. The splitting of *Amanita* into two genera along the lines of trophic status did not receive broad acceptance in

the scientific community (Tulloss et al. 2016). Apart from *Saproamanita* species, the genus *Amanita* primarily includes a majority of ectomycorrhizal (EcM) species, representing functionally important elements in most terrestrial ecosystems, from xerophilic tropical forests to arctic-alpine micro-sylvae (Gilbert 1941; Bas 1969; Singer 1986). In some either natural or planted forests, with native as well as introduced trees, some species of *Amanita* may dominate the local EcM communities and possibly address toxicological issues (e.g. Wolfe et al. 2010).

Few studies during the past few decades have explored different aspects of the phylogeny of the genus (Weiß et al. 1998; Drehmel et al. 1999; Oda et al. 1999; Zhang et al. 2004; Redhead et al. 2016; Tulloss et al. 2016; Cui et al. 2018). The systematic proposed by Cui et al. (2018), which divides *Amanita* into three subgenera (*Amanita*, *Amanitina* and *Lepidella*) and eleven sections based on morphological and molecular data, is now the most widely accepted one. The subgenus *Amanita* includes four sections (*Amanita*, *Amarrendiae*, *Caesareae* and *Vaginatae*) whereas the sections *Amidella*, *Arenariae*, *Phalloideae*, *Roanokenses*, *Strobiliformes* and *Validae* are members of the subgenus *Amanitina*. The subgenus *Lepidella* which basically represents the genus *Saproamanita* accepted by some authors (e.g. Redhead et al. 2016) includes the solely section *Lepidella*. The

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number of species of the genus *Amanita* is estimated to be around 1000 (Yang et al. 2018), of which approximately 700 are accepted worldwide (Codjia et al. 2023). In the last two decades, about 220 taxa of the genus *Amanita* have been published as new to science from all over the world. This can be explained both by the examination of samples from previously less studied areas and by the increasing use of molecular methods that contributed to the discovery of a significant number of new taxa, even from existing collections. As a result, a high number of morphologically defined species are now found to be species complexes (Zhang et al. 2015, Thongbai et al. 2018).

The genus has extensively been studied in Europe by means of morphological approaches (e.g. Sartory and Maire 1923, Gilbert 1941, Bas 1969, Romagnesi 1992, Contu 1997, 1999, 2003, Traverso 1998, Neville and Poumarat 2009). Molecular phylogenetic research involving European species of the genus date back to the end of the twentieth century, and the genus has recently received increasing attention (Weiß et al. 1998; Moreno et al. 2008; Redhead et al. 2016, Vizzini et al. 2016; Loizides et al. 2018, Hanss and Moreau 2020, Alvarado et al. 2022).

Amanita sect. *Vaginatae* (Fr.) Quél., so-called ‘ringless *Amanitas*’, is one of the taxonomically most challenging and most diverse groups within the genus with ca. 400 estimated number of species (Ševčíková et al. 2021). Morphologically, the species of this section can be characterised by the striate-sulcate pileus margin, the lack of annulus, the elongate stipe without having a bulb and the presence of more or less well-developed universal veil remnants at the stipe base as well as the clampless basidia (Yang 1997). Recent molecular phylogenetic studies revealed a globally high species diversity of this section (e.g. Kim et al. 2013; Malysheva & Kovalenko 2015; Tang et al. 2015; Vizzini et al. 2016; Liu et al. 2017; Cui et al. 2018; Thongbai et al. 2018; Lambert et al. 2018; Ullah et al. 2019). Hanss and Moreau (2020) published the first comprehensive revision of the European species in *Amanita* sect. *Vaginatae* focusing on the grey-coloured species. They recognised and fixed 28 phylogenetic species based on nrDNA ITS sequences and morphological data. After this fundamental work, further new *Vaginatae* species and records have been published from Europe in various taxonomic papers (Ševčíková et al. 2021; Migliozi and Donato 2022a, b; Illescas and Plaza 2022; Plaza 2022; Hanss and Moreau 2022). During our revision based on phylogenetic and morphological data of the sect. *Vaginatae* in Hungary, we discovered several lineages which were not possible to assign to currently recognized taxa (Varga et al. 2021). Extending our study on a European scale made it possible to compare our data with those of other European regions such as Western and Northern Europe. These comparisons reinforced that those lineages are distinct from known species. As a result, here, we describe three new

species of *Amanita* sect. *Vaginatae* based on phylogenetic evidence of 4-locus (nrDNA ITS, nrDNA LSU, *RPB1* and *TEF1- α*) molecular phylogenetic analysis, macroscopic and microscopic data. Basidiospore size and shape in *Amanita* sect. *Vaginatae* have been known as mainly overemphasised characters in species delimitation in the past; however, in some species it can still be a stable character (Vizzini et al. 2016). A statistical analysis on basidiospore measurements was systematically driven for the species studied here to test whether basidiospore biometrics would be suitable characters to delimit species among the studied species of sect. *Vaginatae*. Our results contribute to further insights of the diversity of ringless *Amanitas* in Europe as well as provide the first comprehensive revision of this group in Hungary.

Materials and methods

Macromorphological studies

A total of 151 specimens of *Amanita* sect. *Vaginatae* and four specimens of other sections of the genus were collected from Hungary, France, Austria, Italy, Norway and Romania. Macroscopic observations were made based on fresh collections. All collections were photographed in situ or in laboratory on plate in order to document the main morphological appearance of the basidiomata. Photos were taken in situ on the field or in laboratory. The shape of the volva and their terminology were adopted from Fraiture (1993) (Fig. 1). Macroscopic descriptions given in this study avoid superfluous details of macroscopic characters that obscure the understanding of the unambiguous features of the species. In the descriptions, we focused on highlighting the particularities of the new species introduced in this study.

Microscopy

The principles and methods used for microscopy as well as terminology used for microscopical structures and spore features follow Bas (1969). The types of subhymenium follow Bas (1969) and were reproduced and numbered from 1 to 5 in Hanss and Moreau (2020). Nikon Eclipse 220 and Carl Zeiss 4013014 light microscopes with magnifications of 100 \times , 400 \times and 1000 \times 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 reinflated in “ramollisseur GDS” and mounted in SDS Congo red (after Clémenton 1999) or alternatively reinflated in 3% KOH and observed in aqueous Congo red or in 3% KOH, or alternatively reinflated and observed in ammoniacal Congo red with phloxin. Photographs were taken by Canon EOS 700D and Nikon Coolpix P5100

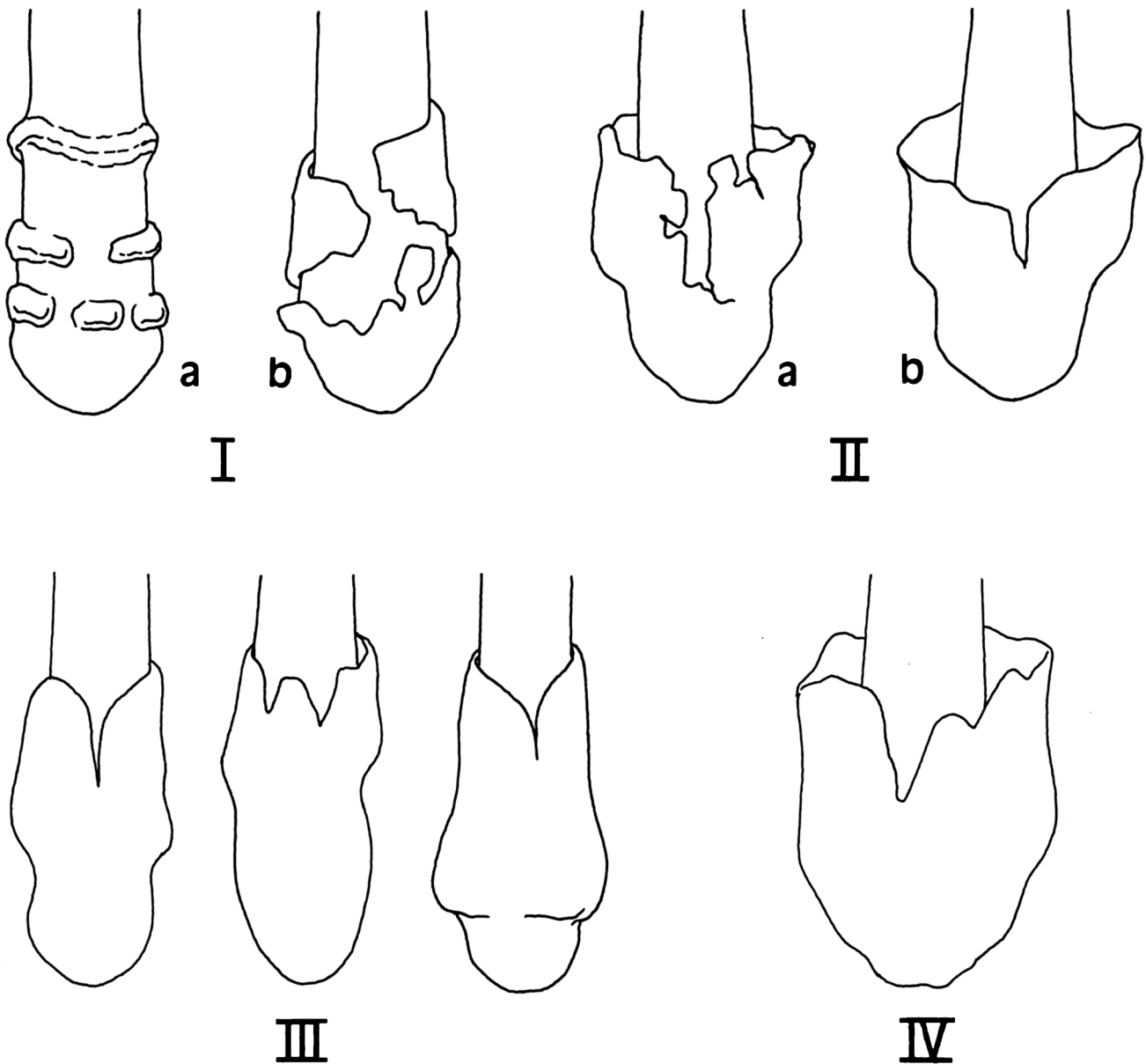


Fig. 1 Types of the shapes of volva in *Amanita* sect. *Vaginatae* based on Fraiture (1993): **I** universal veil friable, either powdery (**a**) or forming a fragmented volva at the base of the stipes (**b**); **II** lower part close to the stipe, upper part well away from the stipe; **III** vaginate

volva; the base may be variable, more or less long attached to the stipe or slightly dilated and **IV** saccate volva, thick to very thick, generally markedly membranous

cameras. Spore length, width and Q -value (length/width ratio of a basidiospore in side-view) were calculated using Piximètre (www.piximetre.fr) or manually determined for 30 spores per specimen. The data were analysed by ANOVA and other tests and post hoc Tukey's pairwise tests were conducted to study differences of spore data of different species using the software PAST4.09 (Hammer et al. 2001). Sections of volva were made on their upper part, where remains of partial veil on their internal face are usually absent.

Molecular analyses

Genomic DNA was extracted from 4–5 mm pieces of dried herbarium specimens using (i) the NucleoSpin Plant II Mini Kit (Macherey-Nagel, Düren, Germany) following the manufacturer's instructions (in ELTE, Budapest, Hungary) or (ii) based on the protocol communicated by the MycoSeq project of the Société Mycologique de France/CEFE Montpellier (see also Hanss and Moreau 2020) using the REDExtract-N-Amp Plant PCR Kit (Sigma-Aldrich, Saint Louis,

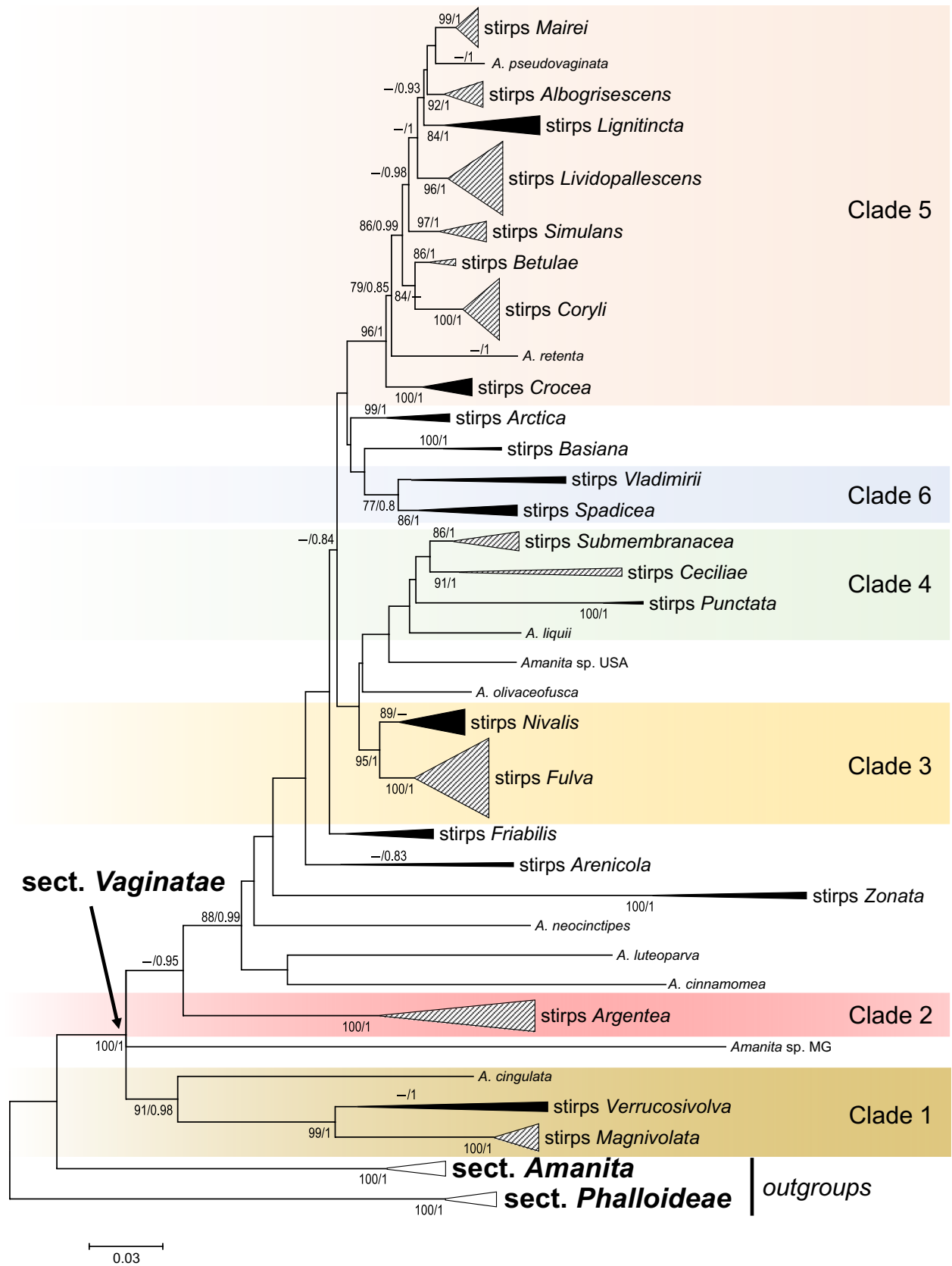


Fig. 2 Phylogenetic tree based on maximum likelihood and Bayesian analyses, derived from 4-locus dataset (ITS, LSU, *RPB1* and *TEF1- α*) showing relationships above species level within *Amanita* sect. *Vaginatae* using sect. *Amanita* and sect. *Phalloideae* as outgroups. Stirp level clades are compressed. Corrugation shows previously recognized stirpes (Hanss and Moreau 2020), while black clades indicate newly named stirpes in this study. ML bootstrap values ($\geq 70\%$) and Bayesian posterior probabilities (≥ 0.8) are reported above branches, on the left and right sides of the slashes, respectively. The scale bar represents 0.03 expected change per site per branch

MO, USA), also following the manufacturer's instructions, or by Alvalab (Spain) employing a modified protocol based on Murray and Thompson (1980).

We targeted four nuclear loci: the nuclear ribosomal internal transcribed spacer regions (nrDNA ITS), nuclear ribosomal large subunit (nrDNA LSU), DNA-dependent RNA polymerase II largest subunit (*RPB1*) and the translation elongation factor 1-alpha (*TEF1- α*) genes.

The ITS region was amplified by PCR with the combinations of primers ITS1F, ITS5, ITS4, ITS4B and, for problematic cases, ITS2 and ITS3 (White et al. 1990; Gardes & Bruns 1993), under the conditions detailed in Richard et al. (2015) or used the following PCR protocol: initial denaturation step for 5 min at 94 °C, followed by 35 cycles of denaturation at 94 °C, for 30 s, annealing at 52 °C for 30 s and extension at 72 °C for 40 s and final extension at 72 °C for 10 min. The primer pairs LR0R/LR7 (Vilgalys and Hester 1990) for LSU, RPB1-Af/RPB1Cr (Matheny et al. 2002) for *RPB1* and EF1-983F/EF1-2218R (Rehner and Buckley 2005) for *TEF1- α* were used for rest of the PCR amplifications which were performed in Tianlong Genesy 96T Thermal Cycler in 25- μ l reaction mixture (also used for most of the ITS PCR) contained the following amounts 14.1 μ l ddH₂O, 2.5 μ l 10 \times Dream Taq Buffer (Thermo Scientific), 2.5 μ l 2mM dNTP (Thermo Scientific), 1.25 μ l of each primer (10 μ M), 0.4 μ l Dream Taq DNA polymerase (Thermo Scientific, 5 U/ μ l) and 3 μ l DNA extract.

Touchdown PCR was used to amplify *RPB1*, which differs from the previous one in 6 preceding repetitive cycles in which the annealing temperature of 52 °C is reached gradually from 58 °C by decreasing 1 °C per cycle. Unlike the program used for ITS, annealing at 59 °C for 30 s and extension at 72 °C for 1 min, settings were used to amplify *TEF1- α* region.

In some cases, ITS amplification was made directly from basidiome samples by the Phire Plant Direct PCR Kit (Thermo Scientific, USA). This 20- μ l-PCR mixture contained 7 μ l ddH₂O, 10 μ l 2 \times Phire Plant Direct PCR Master Mix, 1 μ l of each primer (10 μ l) and 1 μ l template DNA. The reaction included 5 min initial denaturation step at 98 °C, 41 cycles of denaturation at 98 °C, for 5 s, annealing at 55 °C for 5 s and extension at 72 °C for 7 s and final extension at 72 °C for 1 min. PCR products were checked in 1.5%

agarose gel stained with EcoSafe, and illuminated by UV-transilluminator (NuGenius, Syngene).

Sanger sequencing was performed with primers used in PCR at LGC Genomics (Berlin, Germany) or at Eurofins Genomics (Ebersberg, Germany). PreGap4 and Gap4 of Staden Package (Staden et al. 2000) as well as the Codon-Code Aligner package (CodonCode Corp., Centerville, Massachusetts, USA) were used for sequence assembly and editing. The purified sequences were compared to those downloaded in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) and UNITE (<https://unite.ut.ee/>) databases using BLASTn (Altschul et al. 1990). ITS, LSU, *RPB1* and *TEF1- α* sequences obtained were aligned for each gene separately with MAFFT online v7 (<http://mafft.cbrc.jp/alignment/server>) using E-INS-i strategy for ITS, G-INS-i for LSU, FFT-INS-i for *RPB1* and *TEF1- α* (Katoh and Standley 2013). In the case of ITS, the phylogenetically informative indels were coded using the "simple indel coding" algorithm (Simmons et al. 2001) in FastGap 1.2 (Borchsenius 2009). Nucleotide alignments and the binary character matrix were edited in MEGA 7 software (Kumar et al. 2016) and concatenated in SeaView 5 (Gouy et al. 2021).

For maximum likelihood phylogenetic analysis, raxmlGUI 2.0 (Edler et al. 2021) was employed. The GTR-GAMMA substitution model was applied for the six nucleotide partitions (ITS1, 5.8S, ITS2, LSU, *RPB1* and *TEF1- α*), while the one binary partition (indel characters) was set to default. To determine support value, a 1000-replicant rapid-bootstrap analysis was chosen. MrBayes 3.2.6 (Ronquist et al. 2012) was used to infer Bayesian phylogeny. The alignment was partitioned as describe above. For the six nucleotide partitions the GTR + Γ substitution model was applied, while the two-parameter Markov model was set for the binary characters. Two independent runs of four Markov Chain Monte Carlo (MCMC) were performed each for 10 million generations, sampling every 1000th generation. The first 30% of the trees was discarded as burn-in. For the remaining trees, a 50% majority rule consensus phylogram with posterior probabilities as nodal supports was computed. The best scoring ML tree from Maximum Likelihood analysis was further edited in MEGA 7 and Microsoft PowerPoint.

Results

Phylogeny

The final alignment is composed of 390 nrDNA ITS, 201 LSU, 75 *RPB1* and 93 *TEF1- α* sequences and 5453 characters (ITS: 892, LSU: 1441, *RPB1*: 1367, *TEF1- α* : 1187 and binary characters: 566). The concatenated 4-locus alignment is included in the Supplementary Material. Phylogenetic trees from maximum likelihood and Bayesian inference

analyses showed congruent topologies. The best-scoring ML tree is chosen to depict phylogenetic relationships in *Amanita* sect. *Vaginatae* shown in Figs. 2 and 3. The 370 newly generated sequences (157 ITS, 84 LSU, 74 *RPBI* and 55 *TEF1- α*) were deposited in GenBank (Table 1).

A compressed tree is shown in Fig. 2 presenting six clades and 22 stirps as the main phylogenetic structure within sect. *Vaginatae*. Half of the lineages (stirps *Arctica*, *Arenicola*, *Basiana*, *Crocea*, *Friabilis*, *Lignitincta*, *Nivalis*, *Spadicea*, *Verrucosivolva*, *Vladimirii* and *Zonata*) are newly recognized. Most of the lineages received strong support in both ML and BI analyses, especially those of containing European species. Some non-European species could not be assigned any of these stirps under the current sampling; therefore, they remained singletons. Fig. 3 represents the species level phylogenetic relationships of sect. *Vaginatae*. We recognized 36 species (Figs. 4, 5, 6, 7, 8, 9, 10, 11, 12, 13 and 14) from our studied 151 European specimens which clustered in 17 stirps across the phylogenetic tree (Fig. 3). We could not assign any proper scientific name to four species level lineages, of which in one case we applied the ‘aff.’ prefix (*A. aff. arctica*) using morphological similarity and leaving taxonomic conclusions to later studies. The remaining three distinct species of which two belong to stirps *Fulva* while one is a member of the stirps *Coryli* are described here new to science based on molecular and morphological evidences.

Taxonomy

Amanita deflexa Hanss, Dima & L. Albert, sp. nov., Figs. 4, 5.

Mycobank: MB#846787.

Holotype: France, Haut-Rhin, la Gauchmatt, Soulmatt, in a *Pinus nigra* forest, J-L. Muller, 1 Sept 2014, LIP 0004489 (isotype JMH2019039 in herb. J-M. Hanss); GenBank PP375656 (ITS) and PP273643 (*TEF1- α*).

Etymology: the epithet *deflexus*, participle of *deflecto*, here granted to the feminine with *Amanita*, the verb *deflecto* being taken in the acceptance to turn away, to move away.

Diagnosis: Differs from *Amanita fulva* by the pileus colour that varies with the age of the fungus, by the volva which is strongly coloured inside and on the outer upper rim, by the two-layered volva, as well as by nucleotide composition of ITS marker.

Description: Pileus campanulate to convex plan and then slightly depressed with a small nipple with age, 4-cm diameter, with ridged margin. The colour is very dark at first and then it takes a shade varying from yellow to orange, with the centre much darker. With aging, it becomes dull. Lamellae free, crowded, whitish to cream. Stipes 5–10 cm long, smooth, long white, which can take with age faintly coloured reflections in the tones of the pileus. Volva 2.5–3 cm high,

type II, externally white, tinted with an intense colour varying from red-brown to yellow on the upper part, near the edge and inside. Basidiospores 7–12.5 \times 7–11.7 μ m, globose to subglobose, $Lav = 11.02 \mu$ m, $Wav = 10.35 \mu$ m, $Qav = 1.068$. Mature basidia few, rather long, 60–80 \times 20–25 μ m, sometimes curved at the base, sterigmata 5–6 μ m long. Lamellar trama up to 100- μ m thick formed by a mediostratum of hyphae 3–4- μ m thick mixed with elongated oval physaloid cells forming chains, e.g. 60 \times 20 μ m or 50 \times 14 μ m. Few oval physaloid cells of the same sizes presented sometimes under the subhymenium. The whole forms a compact matrix. Subhymenial cell under the mature basidia ramose, type 1a, enlarged at the top and markedly attenuated at the base, 15–20 \times 6–8 μ m, more rarely cylindrical. Subhymenial cells under young basidia ramose to strongly inflated ramose. The other elements of the subhymenial tree are of various shapes, up to subcellular. Lamellar edge sterile by the presence of numerous marginal cells with largely oval head (30 \times 20 μ m to 40 \times 30 μ m), more rarely subglobose (30 \times 30 μ m), immersed in a gelatinous matrix but occasionally can more or less emerge in places. The peduncle is very variable in length as in all cells of this type. Pileipellis about 200- μ m thick, ixocutis with 25- μ m-wide gelatinous matrix, containing 2- μ m-thick congophobic parallel hyphae, stratum of the parallel hyphae 3–4(–6)- μ m-thick, elongated to cylindrical, ellipsoid acrophysalides, e.g. 70 \times 20 μ m present, but 160 \times 22 μ m becoming more numerous towards the context. Differentiated subpellis lacking. Context mainly composed of elongated acrophysalides, e.g. 150 \times 50 μ m to 200 \times 55 μ m, mixed with hyphae of 5–6 μ m, is oriented in all directions. The whole forms a medium-intricate and weakly resistant tissue. Volva thin, with a thickness of 500–600 μ m comprising a weakly gelified, filamentous, 50- μ m thick outer stratum and a main stratum composed of tangled hyphae mixed with physaloid cells. The outer stratum is weakly gelified on its outer part. It is composed of 3- μ m-thick septate hyphae, parallel to the stipe, with quite rare and clearly elongated physaloid cells. The main stratum consists of 5–7(–10)- μ m-thick hyphae, septate, tangled in all directions, clearly entangled outwards and entangled much looser inwards. The physaloid cells, in average proportion, are equally distributed over thickness, subspherical (e.g. 50 \times 40 μ m or 70 \times 60 μ m), oval and terminal (e.g. 60 \times 35 μ m), cylindrical (e.g. 90 \times 20 μ m), rarely elongated, sometimes with 3 connections (e.g. 90 \times 20 μ m).

Phylogenetic relationship: *Amanita deflexa* is a sister species of the recently typified *A. fulva* (Moreau et al. 2023), from which it differs by 5 substitution and indel positions (99% similarity) in the ITS region and by 8 nucleotides (98% similarity) in the *TEF1- α* region. The *A. fulva* complex is a challenging group with several closely related but well-separated species, distributed globally (Fig. 3).

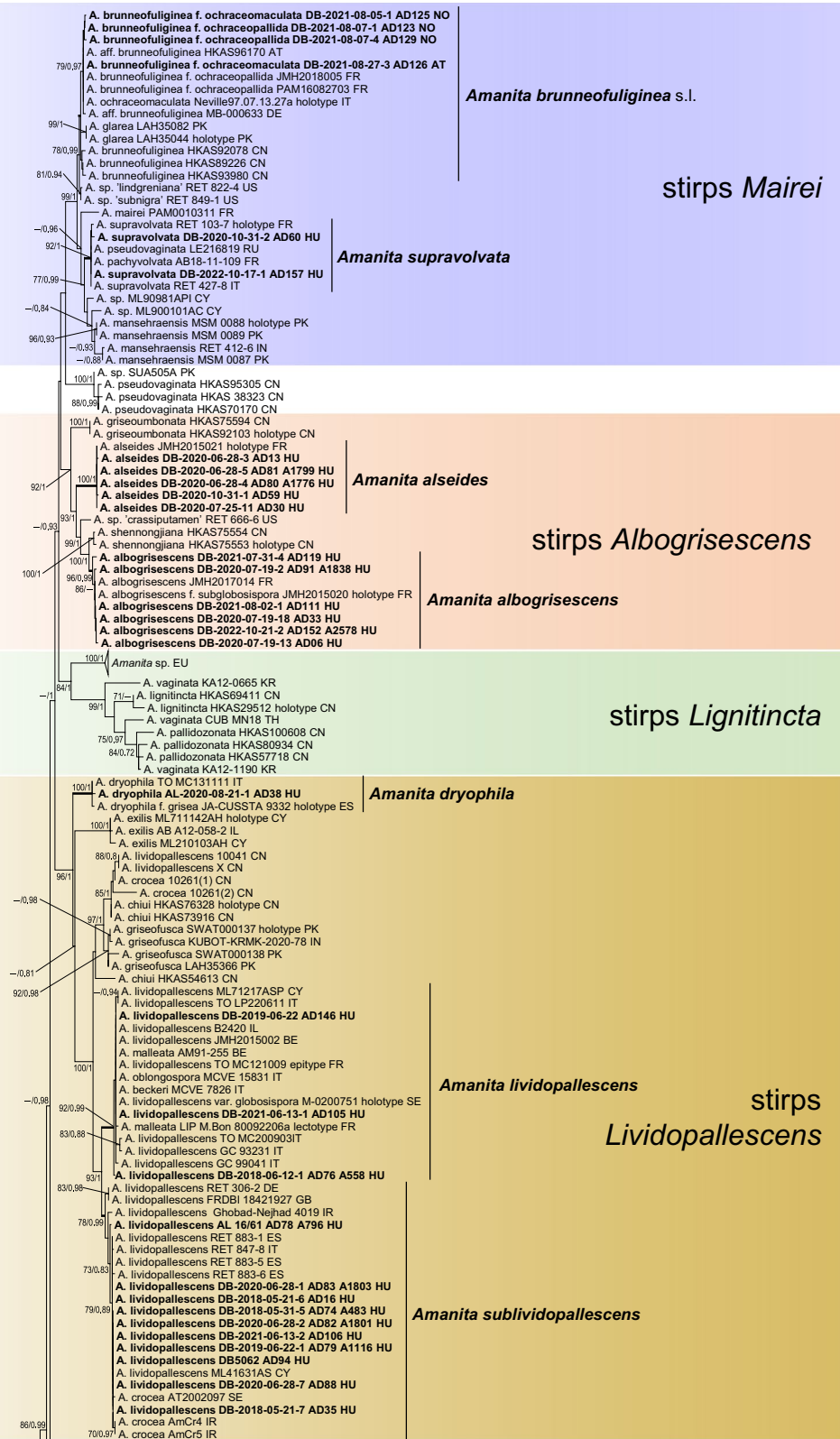


Fig. 3 Phylogenetic tree based on maximum likelihood and Bayesian analyses, derived from 4-locus dataset (ITS, LSU, *RPB1* and *TEF1*- α) of *Amanita* sect. *Vaginatae* specimens and those of reference materials. The sequences newly generated in this study are in bold. ML

bootstrap values ($\geq 70\%$) and Bayesian posterior probabilities (≥ 0.8) are reported above branches, on the left and right sides of the slashes, respectively. The scale bar represents 0.03 expected change per site per branch

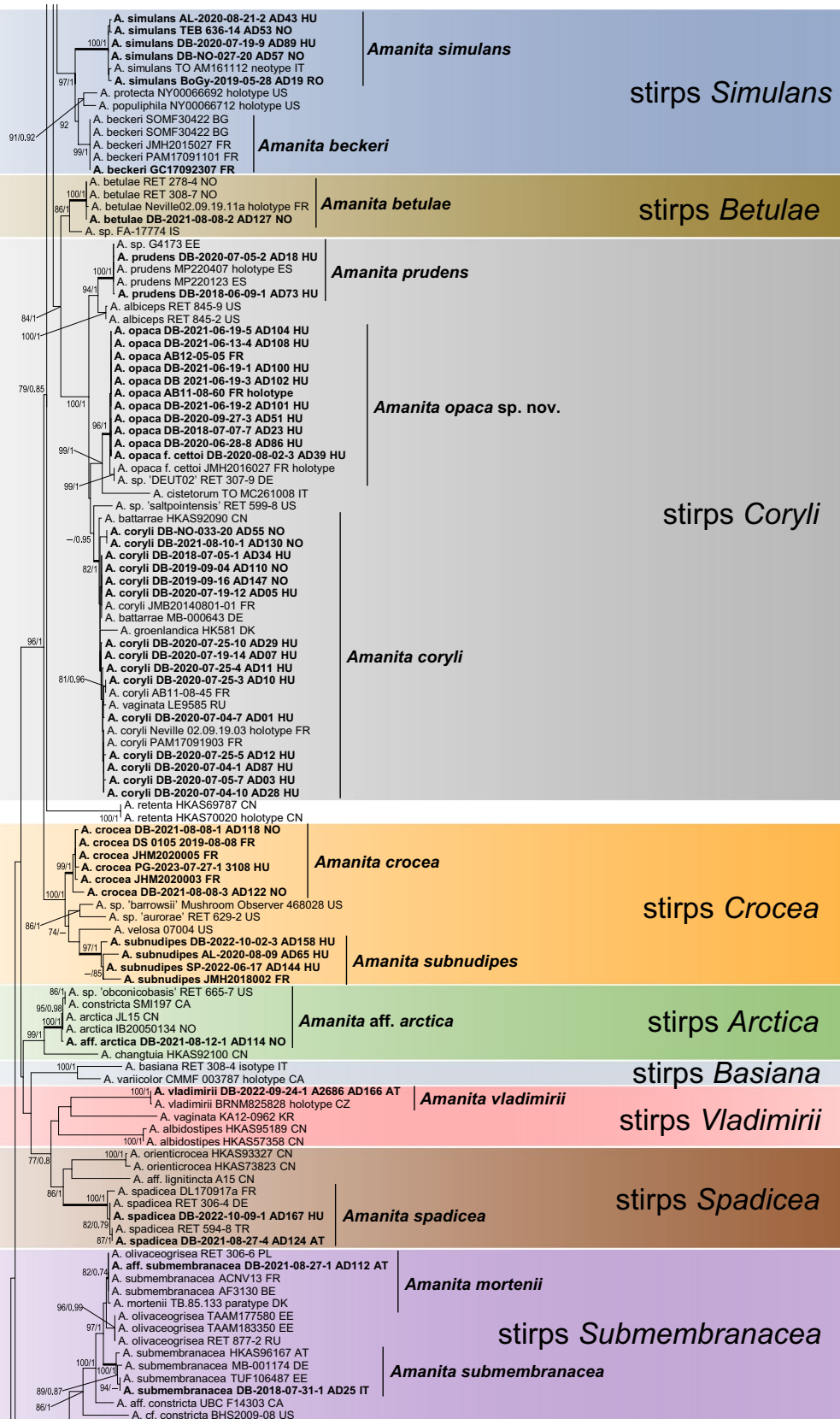


Fig. 3 (continued)

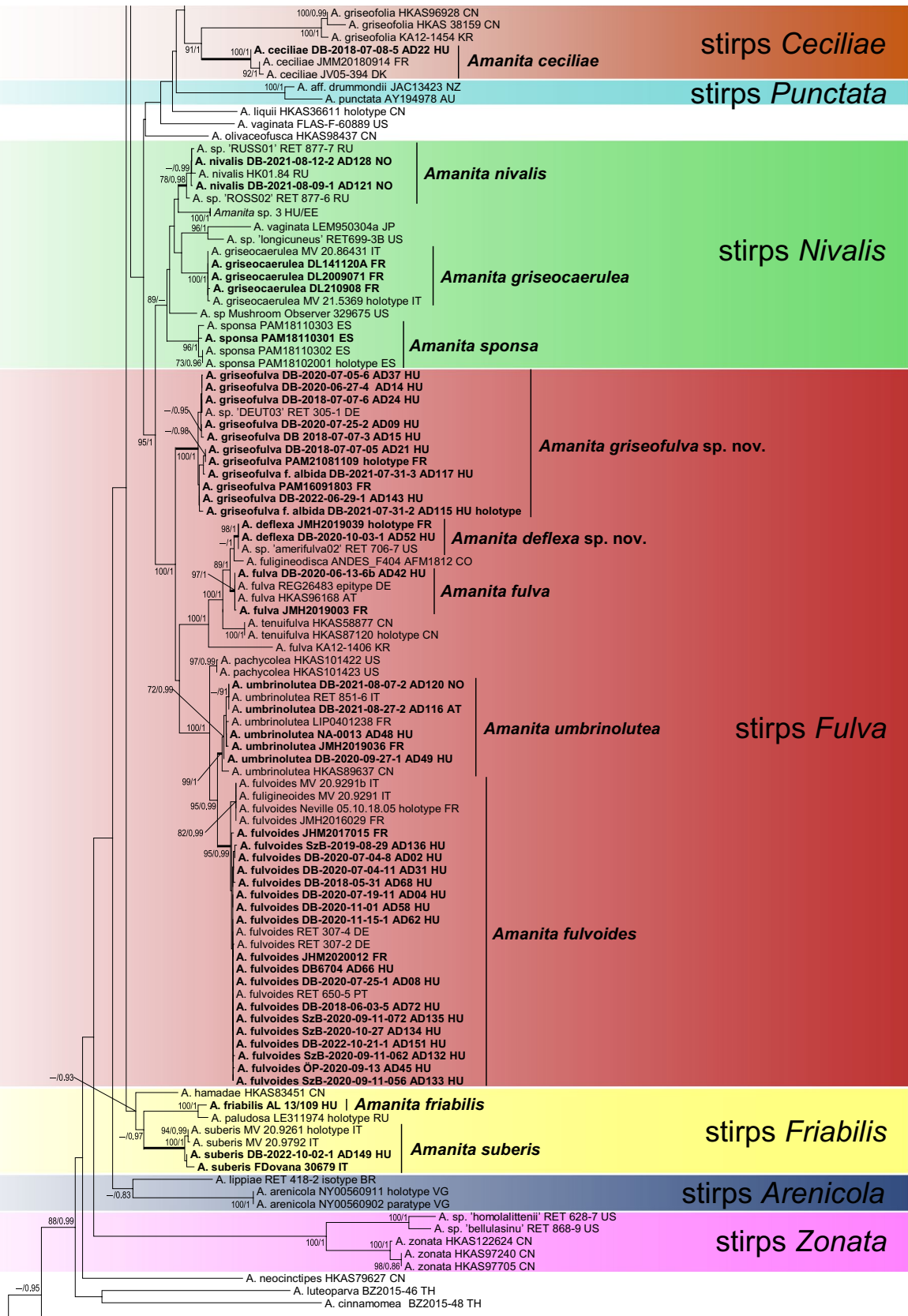


Fig. 3 (continued)

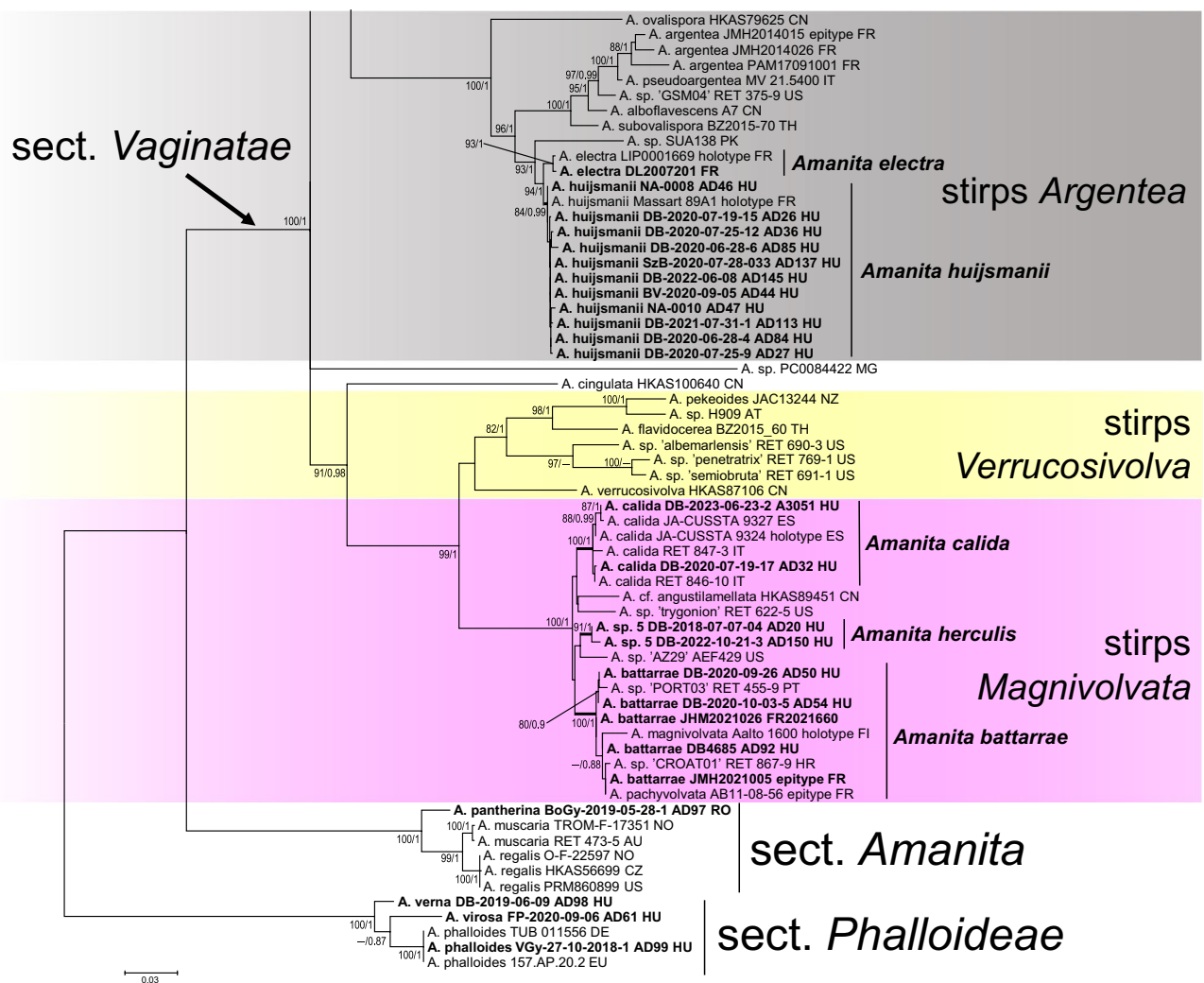


Fig. 3 (continued)

Habitat and distribution: Associated with *Pinus sylvestris* on acidic soil and with *P. nigra* on calcareous soil. Distribution is currently uncertain due to the confusion with *A. fulva*. Currently known from Europe (France and Hungary — own collections and one GenBank entry: MH508370) and USA (Pennsylvania, Indiana, Massachusetts and Virginia according to ITS sequence data from GenBank entries: JX860436, KP284293, MK522007, MK522008, MZ668288, ON392627, ON243897 and OR026696).

Comments: this taxon is recognizable by its reminiscence to the habitus of *Amanita fulva*, by the variable colour of the pileus, by the particular colour of the inner and the upper outer surfaces of the volva. The main characteristic of microscopic differentiation is the presence of an external stratum 50- μ m-thick, partially gelified, occurring parallel to the stipe hyphae. It is the only European taxon of the stirps *Fulva* to have a two-layered volva. The subhymenial cells are of the

same type as those of *Amanita fulva* but with a greater difference in thickness between the top and bottom of the cell in *Amanita deflexa*. Finally, it differs from *Amanita fulva* by its growth under pines. By its two-layered volva and by the change in colour of the pileus during its development, this species deviates not only from *Amanita fulva* but from all other European taxa of the stirps *Fulva*.

Additional collections examined: France, Haut-Rhin, la Gauchmatt, Soulmatt, under *Pinus nigra*, 29 Oct 2019, J.-L. Muller, JMH2019039 (herb. J.-M. Hanss); Vienne, Chavigny, Forêt de Mareuil, 26 Oct 2022, Y. Bellanger, JMH2022008 (herb. J.-M. Hanss). Hungary, Vas County, Órség, Orfalu, “Blueberry Trail”, 3 Oct 2022, L. Albert, B. Dima, DB-2020-10-03-1/AD52 (ELTE).

Amanita griseofulva Hanss, P.-A. Moreau, Dima & D. Varga, sp. nov., Figs. 6, 7.

Mycobank: MB#846788.

Table 1 Sequences used in this study

Name	Strain/voucher	Country	ITS	LSU	<i>RPB1</i>	<i>TEF1-α</i>	References
<i>A. albiceps</i>	RET 845-9	USA	MN963576	in ITS	–	–	Tulloss et al., unpublished
<i>A. albiceps</i>	RET 845-2	USA	MN963577	in ITS	–	–	Tulloss et al., unpublished
<i>A. albidostipes</i>	HKAS57358	China	MH508500	MH486756	–	MH508983	Cui et al. (2018)
<i>A. albidostipes</i>	HKAS95189	China	MH508501	MH486757	–	–	Cui et al. (2018)
<i>A. alboflavescens</i>	A7	China	FJ441037	–	–	–	Zhang et al., unpublished
<i>A. albogriseus</i>	JMH2017014	France	MN490654	–	–	–	Hanss and Moreau (2020)
<i>A. albogriseus</i>	DB-2020-07-19-13 (AD06)	Hungary: Heves, Parádóhuta	–	PP375232	PP358491	PP273658	This study
<i>A. albogriseus</i>	DB-2020-07-19-18 (AD33)	Hungary: Heves, Parádóhuta	PP375697	PP375229	PP358488	PP273656	This study
<i>A. albogriseus</i>	DB-2020-07-19-2 (AD91)	Hungary: Heves, Parádóhuta	PP375701	PP375233	PP358492	PP273659	This study
<i>A. albogriseus</i>	DB-2021-08-02-1 (AD111)	Hungary: Győr-Moson-Sopron, Tényő	PP375700	PP375231	PP358490	–	This study
<i>A. albogriseus</i>	DB-2021-07-31-4 (AD119)	Hungary: Borsod-Abaúj-Zemplén, Újhuta	PP375698	PP375230	PP358489	PP273657	This study
<i>A. albogriseus</i>	DB-2022-10-21-2 (AD152_A2578)	Hungary: Pest, Budapest	PP375699	–	–	–	This study
<i>A. albogriseus</i> f. <i>subglobosipora</i>	JMH2015020	France	MN490648	–	–	–	Hanss and Moreau (2020)
<i>A. alseides</i>	JMH2015021	France	MN490649	–	–	–	Hanss and Moreau (2020)
<i>A. alseides</i>	DB-2020-06-28-3 (AD13_A1771)	Hungary: Somogy, Bószénfa	PP375702	PP375234	PP358493	PP273660	This study
<i>A. alseides</i>	DB-2020-07-25-11 (AD30)	Hungary: Heves, Parádóhuta	PP375703	PP375235	PP358494	PP273661	This study
<i>A. alseides</i>	DB-2020-10-31-1 (AD59)	Hungary: Vas, Szalafő	PP375706	PP375236	PP358495	–	This study
<i>A. alseides</i>	DB-2020-06-28-4 (AD80)	Hungary: Somogy, Bószénfa	PP375704	–	–	–	This study
<i>A. alseides</i>	DB-2020-06-28-5 (AD81)	Hungary: Budai-hegység	PP375705	–	–	–	This study
<i>A. angustilamellata</i> cf.	HKAS89451	China	MH508292	MH486431	–	MH508716	Cui et al. (2018)
<i>A. arctica</i>	IB20050134	Norway	KX834234	–	–	–	Vizzini et al. (2016)
<i>A. arctica</i>	JL15	China	ON059325	–	–	–	Gao, unpublished
<i>A. arctica</i> aff.	DB-2021-08-12-1 (AD114)	Norway: Oppland, Dovre, Fokstua	PP375771	PP375266	PP358525	PP273681	This study
<i>A. arenicola</i>	NY00560911	British Virgin Islands	KU985216	–	–	–	Tulloss et al., unpublished
<i>A. arenicola</i>	NY00560902	British Virgin Islands	KU985210	MK277509	–	–	Tulloss et al., unpublished
<i>A. argentea</i>	JMH2014015	France	MN490675	–	–	–	Hanss and Moreau (2020)
<i>A. argentea</i>	JMH2014026	France	MN490650	–	–	–	Hanss and Moreau (2020)
<i>A. argentea</i>	PAM17091001 (LIP)	France	MN490698	–	–	–	Hanss and Moreau (2020)
<i>A. basiana</i>	RET 308-4 (isotype)	Italy	KP258986	KP258987	–	–	Tulloss et al., unpublished
<i>A. battarrae</i>	HKAS92090	China	MH508266	MH486388	–	MH508689	Cui et al. (2018)
<i>A. battarrae</i>	MB-000643	Germany	MH508267	MH486389	–	MH508690	Cui et al. (2018)
<i>A. battarrae</i>	LIP 0004501 (JMH2021005) (epitype)	France	PP375783	–	–	–	This study
<i>A. battarrae</i>	DB-2020-09-26-3 (AD50)	Hungary: Zala, Nemesnép	PP375779	PP375273	PP358531	PP273688	This study

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPBI</i>	<i>TEFI-α</i>	References
<i>A. battarrae</i>	DB-2020-10-03-5 (AD54)	Hungary: Vas, Felsőszölnök	PP375780	PP375274	PP358532	PP273689	This study
<i>A. battarrae</i>	DB4685 (AD92)	Hungary: Vas, Felsőszölnök	PP375781	MK277548 (as <i>A. sp.</i>)	–	–	This study
<i>A. battarrae</i>	JHM2021026 (FR2021660)	France	PP375782				This study
<i>A. beckeri</i>	PAM17091101 (LIP)	France	MN490691	–	–	–	Hanss and Moreau (2020)
<i>A. beckeri</i>	JMH2015027	France	MN490686	–	–	–	Hanss and Moreau (2020)
<i>A. beckeri</i>	SOMF30422	Bulgaria	ON287053	–	–	–	Ševčíková et al. (2021)
<i>A. beckeri</i>	MCVE 7826	Italy	JF907758	–	–	–	Osmundson et al. (2013)
<i>A. beckeri</i>	SOMF30422	Bulgaria	ON287053	–	–	–	Assyov et al. (2022)
<i>A. beckeri</i>	PAM17091101 (LIP)	France	MN490691	–	–	–	Hanss and Moreau (2020)
<i>A. beckeri</i>	GC17092307 (FR2019644)	France	PP375715	–	–	–	This study
<i>A. betulae</i>	Neville 02.09.19.11a (G)	France	MN490668	–	–	–	Hanss and Moreau (2020)
<i>A. betulae</i>	RET 278-4	Norway	MT229878	–	–	–	Tulloss et al., unpublished
<i>A. betulae</i>	RET 308-7	Norway	MT229849	–	–	–	Tulloss et al., unpublished
<i>A. betulae</i>	DB-2021-08-08-2 (AD127)	Norway: Oppland, Lunner	PP375707	PP375237	PP358496	PP273662	This study
<i>A. brunneofulginea</i>	HKAS93980	China	MH508271	MH486396	–	–	Cui et al. (2018)
<i>A. brunneofulginea</i>	HKAS89226	China: Sichuan	MH508269	MH486393	–	MH508693	Cui et al. (2018)
<i>A. brunneofulginea</i>	HKAS92078	China	MH508270	MH486394	–	MH508694	Cui et al. (2018)
<i>A. brunneofulginea</i> aff.	MB 000633	Germany	MH508252	–	–	–	Cui et al. (2018)
<i>A. brunneofulginea</i> aff.	HKAS96170	Austria	MH508249	MH486361	–	MH508664	Cui et al. (2018)
<i>A. brunneofulginea</i> f. <i>ochraceomaculata</i>	DB-2021-08-05-1 (AD125)	Norway: Oppland, Lunner	PP375711	PP375239	PP358498	PP273664	This study
<i>A. brunneofulginea</i> f. <i>ochraceomaculata</i>	DB-2021-08-27-3 (AD126)	Austria: Steiermark, Eisenerz	PP375710	–	–	–	This study
<i>A. brunneofulginea</i> f. <i>ochraceopallida</i>	PAM16082703	France	MN490688	–	–	–	Hanss and Moreau (2020)
<i>A. brunneofulginea</i> f. <i>ochraceopallida</i>	JMH2018005	France	MN490660	–	–	–	Hanss and Moreau (2020)
<i>A. brunneofulginea</i> f. <i>ochraceopallida</i>	DB-2021-08-07-1 (AD123)	Norway: Oppland, Lunner	PP375713	–	–	–	This study
<i>A. brunneofulginea</i> f. <i>ochraceopallida</i>	DB-2021-08-07-4 (AD129)	Norway: Oppland, Lunner	PP375712	PP375240	PP358499	PP273665	This study
<i>A. calida</i>	JA-CUSSTA 9324 (holotype)	Spain	OK316924	–	–	–	Illescas and Plaza (2022)
<i>A. calida</i>	JA-CUSSTA 9327	Spain	OK316925	–	–	–	Illescas and Plaza (2022)
<i>A. calida</i>	RET 846-10	Italy	MW013162	in ITS	–	–	Tulloss et al., unpublished
<i>A. calida</i>	RET 847-3	Italy	MT073007	in ITS	–	–	Tulloss et al., unpublished
<i>A. calida</i>	DB-2020-07-19-17 (AD32)	Hungary: Heves, Parádhuta	PP375778	PP375272	PP358530	PP273687	This study
<i>A. calida</i>	DB-2023-06-23-2 (A3051)	Hungary: Borsod-Abaúj-Zemplén, Fónagyság	PP375714	–	–	–	This study
<i>A. ceciliae</i>	JMM20180914	France	MN490692	–	–	–	Hanss and Moreau (2020)
<i>A. ceciliae</i>	JV05-394	Denmark	UDB002315	–	–	–	Unpublished

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPBI</i>	<i>TEFI-α</i>	References
<i>A. ceciliae</i>	DB-2018-07-08-5 (AD22)	Hungary: Borsod-Abaúj-Zemplén, Zubogy	PP375773	PP375268	PP358526	PP273683	This study
<i>A. changtuia</i>	HKAS92100	China	MH508299	MH486442	–	MH508724	Cui et al. (2018)
<i>A. chiui</i>	HKAS54613	China	MH508301	MH486444	–	MH508726	Cui et al. (2018)
<i>A. chiui</i>	HKAS76328	China	MH508303	–	–	–	Cui et al. (2018)
<i>A. chiui</i>	HKAS73916	China	MH508302	–	–	–	Cui et al. (2018)
<i>A. cingulata</i>	HKAS100640	China	MH508309	MH486454	–	–	Cui et al. (2018)
<i>A. cinnamomea</i>	BZ2015_48	Thailand	MF461576	MF461557	–	–	Thongbai et al. (2018)
<i>A. cistetorum</i>	MC261008 (TO)	Italy	KX834236	–	–	–	Vizzini et al. (2016)
<i>A. constricta</i>	SMI197	Canada	HQ650724	–	–	–	Kranabetter et al. (2009)
<i>A. constricta</i> aff.	UBC-F14303	Canada	AY228351	–	–	–	Nguyen et al., unpublished
<i>A. constricta</i> cf.	BHS2009-08	USA	GU220373	–	–	–	Hibbett et al., unpublished
<i>A. coryli</i>	AB11-08-45	France	MN490656	–	–	–	Hanss and Moreau (2020)
<i>A. coryli</i>	JMB20140801-01	France	MN490699	–	–	–	Hanss and Moreau (2020)
<i>A. coryli</i>	PAM17091903 (LIP)	France	MN490690	–	–	–	Hanss and Moreau (2020)
<i>A. coryli</i>	Neville 02.09.19.03 (G)	France	MN490667	–	–	–	Hanss and Moreau (2020)
<i>A. coryli</i>	DB-2020-07-04-7 (AD01)	Hungary: Heves, Paráóhuta	PP375734	PP375252	PP358511	PP273669	This study
<i>A. coryli</i>	DB-2020-07-05-7 (AD03)	Hungary: Heves, Paráóhuta	PP375736	PP375254	PP358512	–	This study
<i>A. coryli</i>	DB-2020-07-19-12 (AD05)	Hungary: Heves, Paráóhuta	PP375728	–	–	–	This study
<i>A. coryli</i>	DB-2020-07-19-14 (AD07)	Hungary: Heves, Paráóhuta	PP375725	PP375248	PP358507	PP273667	This study
<i>A. coryli</i>	DB-2020-07-25-3 (AD10)	Hungary: Heves, Paráóhuta	PP375722	–	–	–	This study
<i>A. coryli</i>	DB-2020-07-25-4 (AD11)	Hungary: Heves, Paráóhuta	PP375723	PP375246	PP358505	–	This study
<i>A. coryli</i>	DB-2020-07-25-5 (AD12)	Hungary: Heves, Paráóhuta	PP375733	–	–	–	This study
<i>A. coryli</i>	DB-2020-07-04-10 (AD28)	Hungary: Heves, Paráóhuta	PP375724	PP375247	PP358506	–	This study
<i>A. coryli</i>	DB-2020-07-25-10 (AD29)	Hungary: Heves, Paráóhuta	PP375727	PP375249	PP358508	–	This study
<i>A. coryli</i>	DB-2018-07-05-1 (AD34)	Hungary: Borsod-Abaúj-Zemplén	PP375729	PP375250	PP358509	–	This study
<i>A. coryli</i>	DB-NO-033-20 (AD55)	Norway: Bærum, Daelivann	PP375735	PP375253	–	–	This study
<i>A. coryli</i>	DB-2020-07-04-1 (AD87)	Hungary: Heves, Paráóhuta	PP375726	–	–	–	This study
<i>A. coryli</i>	DB-2019-09-04 (AD110)	Norway	PP375730	–	–	–	This study
<i>A. coryli</i>	DB-2021-08-10-1 (AD130)	Norway	PP375732	PP375251	PP358510	PP273668	This study
<i>A. coryli</i>	DB-2019-09-16 (AD147)	Norway	PP375731	–	–	–	This study
<i>A. crocea</i>	PG-2023-07-27-1	Hungary: Borsod-Abaúj-Zemplén	PP375716	–	–	–	This study
<i>A. crocea</i>	10261(1)	China	MG367250	–	–	–	Tian, H., unpublished
<i>A. crocea</i>	AT2002097	Sweden	JQ912665	in ITS	–	–	Ihrmark et al. (2012)
<i>A. crocea</i>	AmCr4	Iran	MF278767	–	–	–	Yousefshahi et al., unpublished
<i>A. crocea</i>	AmCr5	Iran	MF278768	–	–	–	Yousefshahi et al., unpublished

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPBI</i>	<i>TEF1-α</i>	References
<i>A. crocea</i>	DB-2021-08-08-1 (AD118)	Norway: Oppland, Lunner, Roa, S. Oppdalen	PP375762	–	PP358523	PP273679	This study
<i>A. crocea</i>	DB-2021-08-08-3 (AD122)	Norway: Oppland, Lunner, Roa, S. Oppdalen	PP375763	PP375265	PP358524	PP273680	This study
<i>A. crocea</i>	DS 0105 2019-08-08	France	PP375766	–	–	–	This study
<i>A. crocea</i>	JHM2020005 (ALV25753)	France	PP375764	–	–	–	This study
<i>A. crocea</i>	JHM2020003 (ALV25752)	France	PP375765	–	–	–	This study
<i>A. deflexa</i>	DB-2020-10-03-1 (AD52)	Hungary: Vas, Orfalu	PP375655	PP375202	PP358468	PP273642	This study
<i>A. deflexa</i>	LIP 0004489 (JMH2019039) (holotype)	France	PP375656	–	–	PP273643	This study
<i>A. deflexa</i> (as <i>A.</i> 'sp. amerifulva02')	RET 706-7	USA	MK522008	MK536606	–	–	Tulloss et al., unpublished
<i>A. drummondii</i> aff.	JAC13423	New Zealand	MT863764	MT862272	–	MT977111	Cooper, unpublished
<i>A. dryophila</i>	TO MC131111	Italy	KX834238	–	–	–	Vizzini et al. (2016)
<i>A. dryophila</i>	AL-2020-08-21-1 (AD38)	Hungary: Heves, Parádsóhuta	PP375748	PP375261	PP358519	PP273673	This study
<i>A. dryophila</i> f. <i>grisea</i>	JA-CUSSTA 9332	Spain	ON888675	–	–	–	Illescas, unpublished
<i>A. electra</i>	DL140901a (LIP0001669)	France	MN490646	–	–	–	Hanss & Moreau (2020)
<i>A. electra</i>	DL2007201	France	PP375795	–	–	–	This study
<i>A. exilis</i>	ML711142AH	Cyprus	MH603610	MZ508450	–	–	Loizides et al. (2018)
<i>A. exilis</i>	AB-A12-058-2	Israel	MZ508449	–	–	–	Loizides et al., unpublished
<i>A. exilis</i>	ML210103AH	Cyprus	MH603597	–	–	–	Loizides et al. (2018)
<i>A. flavidocerea</i>	BZ2015 60	Thailand	MF461578	MF461560	–	–	Thongbai et al. (2018)
<i>A. friabilis</i>	AL 13/109	Hungary: Heves, Parádsasvár	PP375800	–	–	–	This study
<i>A. fulgineodisca</i>	ANDES_F404 AFM1812	Colombia	FJ890027	FJ890039	–	–	Vargas et al. (2011)
<i>A. fulgineoides</i>	MV 20.9291	Italy	ON922886	–	–	–	Migliozzi and Donato (2022a, b)
<i>A. fulva</i>	KA12-1406	South Korea	KF017933	KF021672	–	–	Kim et al. (2013)
<i>A. fulva</i>	HKAS96168	Austria	MH508371	MH486555	–	MH508826	Cui et al. (2018)
<i>A. fulva</i>	DB-2020-06-13-6b (AD42)	Hungary: Somogy, Barcs	PP375654	PP375200	PP358467	PP273640	This study
<i>A. fulva</i>	JMH2019003	France	PP375801	PP375201	–	PP273641	This study
<i>A. fulva</i> (epitype)	REG26483	Germany	OP663322	OP647100	–	–	Moreau et al. (2023)
<i>A. fulvooides</i>	RET 650-5	Portugal	MK569749	–	–	–	Tulloss et al., unpublished
<i>A. fulvooides</i>	MV 20.9291b	Italy	OP082403	–	–	–	Migliozzi & Donato (2022a, b)
<i>A. fulvooides</i>	Neville 05.10.18.05 (G)	France	MN490672	–	–	–	Hanss and Moreau (2020)
<i>A. fulvooides</i>	JMH2016029	France	MN490680	–	–	–	Hanss and Moreau (2020)
<i>A. fulvooides</i>	RET 307-4	Germany	MT980917	in ITS	–	–	Tulloss et al., unpublished
<i>A. fulvooides</i>	RET 307-2	Germany	MT980916	in ITS	–	–	Tulloss et al., unpublished
<i>A. fulvooides</i>	DB-2020-07-04-8 (AD02)	Hungary: Heves, Parádsóhuta	PP375661	PP375207	PP358471	–	This study
<i>A. fulvooides</i>	DB-2020-07-19-11 (AD04)	Hungary: Heves, Parádsóhuta	PP375662	PP375208	PP358472	–	This study
<i>A. fulvooides</i>	DB-2020-07-25-1 (AD08)	Hungary: Heves, Parádsóhuta	PP375663	–	–	–	This study

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPB1</i>	<i>TEF1-α</i>	References
<i>A. fulvoides</i>	DB-2020-07-04-11 (AD31)	Hungary: Heves, Parádóhuta	PP375664	PP375209	PP358473	–	This study
<i>A. fulvoides</i>	ÖP-2020-09-13 (AD45)	Hungary: Heves, Várászó	PP375665	PP375210	PP358474	–	This study
<i>A. fulvoides</i>	DB-2020-11-01 (AD58)	Hungary: Vas, Szalafő	PP375666	PP375211	PP358475	–	This study
<i>A. fulvoides</i>	DB-2020-11-15-1 (AD62)	Hungary: Komárom-Esztergom, Héreg	PP375667	PP375212	PP358476	PP273646	This study
<i>A. fulvoides</i>	DB6704 (AD66)	Hungary: Pest, Budapest	PP375674	PP375213	–	–	This study
<i>A. fulvoides</i>	DB-2018-05-31 (AD68)	Hungary: Pest, Budakeszi	PP375675	PP375214	PP358477	–	This study
<i>A. fulvoides</i>	DB-2018-06-03-5 (AD72)	Hungary: Heves, Reesk	PP375668	–	–	–	This study
<i>A. fulvoides</i>	SzB-2020-09-11-062 (AD132)	Hungary: Borsod-Abaúj-Zemplén, Miskolc	PP375673	–	–	–	This study
<i>A. fulvoides</i>	SzB-2020-09-11-056 (AD133)	Hungary: Borsod-Abaúj-Zemplén, Miskolc	PP375672	–	–	–	This study
<i>A. fulvoides</i>	SzB-2020-10-27 (AD134)	Hungary: Borsod-Abaúj-Zemplén, Miskolc	PP375669	–	–	–	This study
<i>A. fulvoides</i>	SzB-2020-09-11-072 (AD135)	Hungary: Borsod-Abaúj-Zemplén, Miskolc	PP375670	–	–	–	This study
<i>A. fulvoides</i>	SzB-2019-08-29 (AD136)	Hungary: Borsod-Abaúj-Zemplén, Miskolc	PP375676	–	–	–	This study
<i>A. fulvoides</i>	DB-2022-10-21-1 (AD151_A2573)	Hungary: Pest, Budapest	PP375671	–	–	–	This study
<i>A. fulvoides</i>	JHM2017015	France	–	PP375216	–	PP273647	This study
<i>A. fulvoides</i>	JHM2020012	France	–	PP375215	–	–	This study
<i>A. glareae</i> (holotype)	LAH35044	Pakistan	KY781174	KY781175	–	–	Jabeen et al. (2017)
<i>A. glareae</i>	LAH35082	Pakistan	KY788652	–	–	–	Jabeen et al. (2017)
<i>A. griseocaerulea</i>	MV 20.86431	Italy	ON994667	–	–	–	Migliozi and Donato (2022a, b)
<i>A. griseocaerulea</i>	DL141120A	France	PP375691	PP375228	–	PP273655	This study
<i>A. griseocaerulea</i>	DL2009071	France	PP375692	–	–	–	This study
<i>A. griseocaerulea</i>	DL210908	France	PP375693	–	–	–	This study
<i>A. griseocaerulea</i>	MV 21.5369 (holotype)	Italy	ON818545	–	–	–	Migliozi and Donato (2022a, b)
<i>A. griseofolia</i>	HKAS38159	China	AY436448	AY436488	–	–	Zhang et al. (2004)
<i>A. griseofolia</i>	KA12-1454	South Korea	KF017936	–	–	–	Kim et al. (2013)
<i>A. griseofolia</i>	HKAS96928	China	MH508379	MH486567	–	MH508837	Cui et al. (2018)
<i>A. griseofulva</i>	DB-2020-07-25-2 (AD09)	Hungary: Heves, Parádóhuta	PP375677	PP375217	PP358478	PP273648	This study
<i>A. griseofulva</i>	DB-2020-06-27-4 (AD14_A1779)	Hungary: Baranya, Pécs	PP375679	PP375219	PP358480	–	This study
<i>A. griseofulva</i>	DB-2018-07-07-3 (AD15)	Hungary: Borsod-Abaúj-Zemplén, Zubogy	PP375678	PP375218	PP358479	–	This study
<i>A. griseofulva</i>	DB-2018-07-07-05 (AD21)	Hungary: Borsod-Abaúj-Zemplén, Zubogy	PP375685	PP375223	–	–	This study
<i>A. griseofulva</i>	DB-2018-07-07-6 (AD24)	Hungary: Borsod-Abaúj-Zemplén, Zubogy	PP375680	PP375220	PP358481	–	This study
<i>A. griseofulva</i>	DB-2020-07-05-6 (AD37)	Hungary: Heves, Parádóhuta	PP375681	PP375221	PP358482	PP273649	This study
<i>A. griseofulva</i>	DB-2022-06-29-1 (AD143)	Hungary: Vas, Bajánsenye	PP375684	–	–	–	This study

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPB1</i>	<i>TEF1-α</i>	References
<i>A. griseofulva</i>	LIP 0404490 (PAM21081109) (holotype)	France, Mayenne, forêt d'Ombrée-d'Anjou-Combrée	PP375686	–	–	PP273651	This study
<i>A. griseofulva</i>	PAM16091803	France, Nord, Saint-Amand-les-Eaux	PP375687	PP375224	–	PP273652	This study
<i>A. griseofulva</i> f. <i>albida</i>	DB-2021-07-31-2 (holotype) (AD115)	Hungary: Borsod-Abaúj-Zemplén, Újhuta	PP375682	PP375222	PP358483	PP273650	This study
<i>A. griseofulva</i> f. <i>albida</i>	DB-2021-07-31-3 (AD117)	Hungary: Borsod-Abaúj-Zemplén, Újhuta	PP375683	–	PP358484	–	This study
<i>A. griseofusca</i>	SWAT000138	Pakistan	MH241059	–	–	–	Kiran et al. (2018)
<i>A. griseofusca</i>	SWAT000137	Pakistan	MH241057	–	–	–	Kiran et al. (2018)
<i>A. griseofusca</i>	KUBOT-KRMK-2020-78	India	MZ452030	–	–	–	Kantharaja and Krishnappa, unpublished
<i>A. griseofusca</i>	LAH35366	Pakistan	MH241055	–	–	–	Kiran et al. (2018)
<i>A. griseoumbonata</i>	HKAS92103 (holotype)	China	MH508389	MH486578	–	MH508847	Cui et al. (2018)
<i>A. griseoumbonata</i>	HKAS75594	China	MH508388	MH486577	–	–	Cui et al. (2018)
<i>A. groenlandica</i>	HK581	Greenland	UDB002328	–	–	–	Unpublished
<i>A. hamadae</i>	HKAS83451	China	MH508395	MH486586	–	MH508853	Cui et al. (2018)
<i>A. herculis</i>	DB-2022-10-21-3 (AD150)	Hungary: Pest, Budapest	PP375777	–	–	–	This study
<i>A. herculis</i>	DB-2018-07-07-4 (AD20)	Hungary: Borsod-Abaúj-Zemplén, Zubogy	PP375776	PP375271	PP358529	PP273686	This study
<i>A. huijsmanii</i>	Massart 89A1 (LIP)	France	MN490684	–	–	–	Hanss and Moreau (2020)
<i>A. huijsmanii</i>	DB-2020-07-19-15 (AD26)	Hungary: Heves, Parádhuta	PP375787	PP375276	PP358534	–	This study
<i>A. huijsmanii</i>	DB-2020-07-25-9 (AD27)	Hungary: Heves, Parádhuta	PP375785	PP375275	PP358533	PP273690	This study
<i>A. huijsmanii</i>	DB-2020-07-25-12 (AD36)	Hungary: Heves, Parádhuta	PP375792	PP375278	PP358537	–	This study
<i>A. huijsmanii</i>	BV-2020-09-05 (AD44)	Hungary: Zala, Lenti	PP375784	–	–	–	This study
<i>A. huijsmanii</i>	NA-0008 (AD46)	Hungary: Zala, Lenti	PP375788	PP375277	PP358535	PP273691	This study
<i>A. huijsmanii</i>	NA-0010 (AD47)	Hungary: Zala, Lenti	PP375793	PP375279	PP358538	–	This study
<i>A. huijsmanii</i>	DB-2020-06-28-4 (AD84)	Hungary: Budai-hegység	PP375786	–	–	–	This study
<i>A. huijsmanii</i>	DB-2020-06-28-5 (AD85)	Hungary: Budai-hegység	PP375794	PP375280	PP358539	–	This study
<i>A. huijsmanii</i>	DB-2021-07-31-1 (AD113)	Hungary: Borsod-Abaúj-Zemplén, Újhuta	PP375791	PP375282	PP358536	PP273692	This study
<i>A. huijsmanii</i>	SzB-2020-07-28-033 (AD137)	Hungary: Borsod-Abaúj-Zemplén, Miskolc	PP375789	–	–	–	This study
<i>A. huijsmanii</i>	DB-2022-06-08-1 (AD145)	Hungary: Győr-Moson-Sopron	PP375790	–	–	–	This study
<i>A. lignitincta</i>	HKAS69411	China	MH508424	MH486625	–	MH508883	Cui et al. (2018)
<i>A. lignitincta</i>	HKAS29512	China	–	AF024461	–	–	Weiß et al. 1998
<i>A. lignitincta</i> aff.	A15	China	FJ441045	–	–	–	Cao et al., unpublished
<i>A. lippiae</i>	RET 418-2	Brazil	KP258991	KP258992	–	–	Tulloss et al., unpublished
<i>A. liquii</i>	HKAS36611 (holotype)	China	AY436462	AY436493	–	–	Zhang et al. (2004)
<i>A. lividopallescens</i>	TO MC121009	France	KX834245	–	–	–	Vizzini et al. (2016)
<i>A. lividopallescens</i>	10041	China	MG367252	–	–	–	Tian, H., unpublished
<i>A. lividopallescens</i>	X	China	MW488314	–	–	–	Zhou, H., unpublished

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPBI</i>	<i>TEF1-α</i>	References
<i>A. lividopallescens</i>	ML71217ASP	Cyprus	MH603608	–	–	–	Loizides et al. (2018)
<i>A. lividopallescens</i>	LP220611 (TO)	Italy	KX834244	–	–	–	Vizzini et al. (2016)
<i>A. lividopallescens</i>	B2420	Israel	MZ576431	in ITS	–	–	Loizides et al., unpublished
<i>A. lividopallescens</i>	JMH2015002	Belgium	MN490679	–	–	–	Hanss and Moreau (2020)
<i>A. lividopallescens</i>	Ludwig 3735 (M-0200751)	Sweden	KX834247	–	–	–	Vizzini et al. (2016)
<i>A. lividopallescens</i>	MC200903 (TO)	Italy	KX834246	–	–	–	Vizzini et al. (2016)
<i>A. lividopallescens</i>	GC93231	Italy	KX834242	–	–	–	Vizzini et al. (2016)
<i>A. lividopallescens</i>	GC99041	Italy	KX834243	–	–	–	Vizzini et al. (2016)
<i>A. lividopallescens</i>	RET 306-2	Germany	MW013159	–	–	–	Tulloss et al., unpublished
<i>A. lividopallescens</i>	FRDBI 18421927	UK	MW487964	–	–	–	Janke et al., unpublished
<i>A. lividopallescens</i>	Ghobad-Nejhad 4019	Iran	MT535691	–	–	–	Ghobad-Nejhad et al., unpublished
<i>A. lividopallescens</i>	RET 883-1	Spain	OP019475	in ITS	–	–	Tulloss et al., unpublished
<i>A. lividopallescens</i>	RET 847-8	Italy	MT073008	in ITS	–	–	Tulloss et al., unpublished
<i>A. lividopallescens</i>	RET 883-5	Spain	OP019476	in ITS	–	–	Tulloss et al., unpublished
<i>A. lividopallescens</i>	RET 883-6	Spain	OP019477	in ITS	–	–	Tulloss et al., unpublished
<i>A. lividopallescens</i>	ML41631AS	Cyprus	MH603609	–	–	–	Loizides et al. (2018)
<i>A. lividopallescens</i>	DB-2018-06-12-1 (AD76)	Hungary: Pest, Budakeszi	PP375759	–	–	PP273677	This study
<i>A. lividopallescens</i>	DB-2021-06-13-1 (AD105)	Hungary: Komárom-Esztergom, Tardos	PP375760	–	–	–	This study
<i>A. lividopallescens</i>	DB-2019-06-22 (AD146)	Hungary: Baranya, Kárász	PP375761	PP375283	–	PP273678	This study
<i>A. luteoparva</i>	BZ2015_46	Thailand	MF461575	MF461556	–	–	Thongbai et al. (2018)
<i>A. magnivolva</i>	M. Aalto 1600 (H, holotype)	Finland	MN490645	–	–	–	Hanss and Moreau (2020)
<i>A. mairei</i>	PAM0010311 (LIP)	France	MN490695	–	–	–	Hanss and Moreau (2020)
<i>A. malleata</i>	AM91-255	Belgium	MF461572	–	–	–	Thongbai et al. (2018)
<i>A. malleata</i>	M.Bon 80092206a (LIP)	France	MN545697	–	–	–	Hanss and Moreau (2020)
<i>A. mansehraensis</i>	MSM 0088 (holotype)	Pakistan	MG195980	MG195982	–	MH495970	Saba et al. (2019)
<i>A. mansehraensis</i>	MSM 0089	Pakistan	MG195981	MG195983	–	–	Saba et al. (2019)
<i>A. mansehraensis</i>	RET 412-6	India	MT445430	–	–	–	Tulloss et al., unpublished
<i>A. mansehraensis</i>	MSM 0087	Pakistan	MG195979	MG195984	–	–	Saba et al. (2019)
<i>A. mortenii</i>	TB.85.133 (paratype)	Greenland	UDB002335	–	–	–	Unpublished
<i>A. mortenii</i>	DB-2021-08-27-1 (AD112)	Austria: Steiermark, Eisenerz	PP375775	PP375270	PP358528	PP273685	This study
<i>A. muscaria</i>	O-F-22597	Norway	UDB037204	–	–	–	Unpublished
<i>A. muscaria</i>	TROM-F-17351	Norway	UDB037483	–	–	–	Unpublished
<i>A. muscaria</i>	RET 473-5	Australia	KP866167	KP866168	–	–	Tulloss et al., unpublished
<i>A. neocinctipes</i>	HKAS79627	China	–	MH486653	–	MH508910	Cui et al. (2018)
<i>A. nivalis</i>	HK01.84	Russia	UDB002338	–	–	–	unpublished
<i>A. nivalis</i>	DB-2021-08-09-1 (AD121)	Norway: Oppland, Dovre	PP375689	PP375226	PP358486	PP273653	This study
<i>A. nivalis</i>	DB-2021-08-12-2 (AD128)	Norway: Oppland, Dovre	PP375690	PP375227	PP358487	PP273654	This study
<i>A. oblongospora</i>	MCVE 15831	Italy	JF907762	–	–	–	Osmundson et al. (2013)
<i>A. ochraceomaculata</i>	Neville 97.07.13.27a (G, holotype)	Italy	MN490673	–	–	–	Hanss and Moreau (2020)

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPBI</i>	<i>TEFI-α</i>	References
<i>A. olivaceofusca</i>	HKAS98437	China: Yunnan	MH508459	MH486693	–	–	Cui et al. (2018)
<i>A. olivaceogrisea</i>	RET 306-6	Poland	MT073014	–	–	–	Tulloss et al., unpublished
<i>A. olivaceogrisea</i>	RET 877-2	Russia	MW526936	in ITS	–	–	Tulloss et al., unpublished
<i>A. olivaceogrisea</i>	TAAM183350	Estonia	MN490664	–	–	–	Hanss and Moreau (2020)
<i>A. olivaceogrisea</i>	TAAM177580	Estonia	MN490663	–	–	–	Hanss and Moreau (2020)
<i>A. opaca</i>	DB-2018-07-07-7 (AD23)	Hungary: Borsod-Abaúj-Zemplén, Zubogy	PP375739	PP375257	PP358515	–	This study
<i>A. opaca</i>	DB-2020-09-27-3 (AD51)	Hungary: Vas, Szalafő	PP375741	PP375259	PP358517	PP273672	This study
<i>A. opaca</i>	DB-2020-06-28-3 (AD86)	Hungary: Budai-hegység	PP375742	PP375260	PP358518	–	This study
<i>A. opaca</i>	DB-2021-06-19-1 (AD100)	Hungary: Veszprém, Úrkút	PP375743	–	–	–	This study
<i>A. opaca</i>	DB-2021-06-19-2 (AD101)	Hungary: Veszprém, Úrkút	PP375744	–	–	–	This study
<i>A. opaca</i>	DB-2021-06-19-3 (AD102)	Hungary: Veszprém, Úrkút	PP375745	–	–	–	This study
<i>A. opaca</i>	DB-2021-06-19-5 (AD104)	Hungary: Veszprém, Úrkút	PP375746	–	–	–	This study
<i>A. opaca</i>	LIP 0004500 (AB11-08-60) (holotype)	France	PP375802	–	–	–	This study
<i>A. opaca</i>	DB-2021-06-13-4 (AD108)	Hungary: Komárom-Esztergom, Tardos	PP375747	–	–	–	This study
<i>A. opaca</i>	AB12-05-05	France	PP375803	–	–	–	This study
<i>A. opaca</i> f. <i>cettoi</i>	JMH2016027 (holotype)	France	MN493559	–	–	–	Hanss and Moreau (2020)
<i>A. opaca</i> f. <i>cettoi</i>	DB-2020-08-02-3 (AD39)	Hungary: Nógrád, Mátraalmás	PP375740	PP375258	PP358516	–	This study
<i>A. orienticrocea</i>	HKAS73823	China	MH508463	MH486698	–	MH508941	Cui et al. (2018)
<i>A. orienticrocea</i>	HKAS93327	China	MH508466	MH486702	–	MH508943	Cui et al. (2018)
<i>A. ovalispora</i>	HKAS79625	China	MH508479	MH486722	–	MH508957	Cui et al. (2018)
<i>A. pachycolea</i>	HKAS101423	USA	MH508481	MH486725	–	MH508959	Cui et al. (2018)
<i>A. pachycolea</i>	HKAS101422	USA	MH508480	MH486724	–	MH508958	Cui et al. (2018)
<i>A. pachyvolvata</i>	AB18-11-109	France	MN490701	–	–	–	Hanss and Moreau (2020)
<i>A. pachyvolvata</i>	AB11-08-56 (epitype)	France	MN490652	–	–	–	Hanss and Moreau (2020)
<i>A. pallidozonata</i>	HKAS100608	China	MH508486	MH486739	–	–	Cui et al. (2018)
<i>A. pallidozonata</i>	HKAS80934	China	–	MH486741	–	–	Cui et al. (2018)
<i>A. pallidozonata</i>	HKAS57718	China	–	MH486740	–	–	Cui et al. (2018)
<i>A. paludosa</i>	LE311974	Russia	MH100735	MH100732	–	–	Morozova, unpublished
<i>A. pantherina</i>	BoGy-2019-05-28-1 (AD97)	Romania: Harghita, Odorheiu Secuiesc	PP375796	–	–	–	This study
<i>A. pekeoides</i>	JAC13244	New Zealand	MT863761	MT862269	–	MT977108	Cooper, unpublished
<i>A. phalloides</i>	157.AP.20.2	Europe	MG516220	in ITS	–	–	Jansson et al. (2018)
<i>A. phalloides</i>	TUB 011556	Germany	–	DQ071810	DQ067953	–	Garnica et al. (2007)
<i>A. phalloides</i>	VGy-2018-10-27-1 (AD99)	Hungary: Vértes	PP375798	–	–	–	This study
<i>A. populiphila</i>	NY00066712	USA	KX834250	KP224342	–	–	Vizzini et al. (2016)
<i>A. protecta</i>	NY00066692 (holotype)	USA	KP224324	–	–	–	Tulloss et al., unpublished
<i>A. prudens</i>	MP220407	Spain	OP279587	–	–	–	Plaza, unpublished
<i>A. prudens</i>	MP220123	Spain	OP279588	–	–	–	Plaza, unpublished
<i>A. prudens</i>	DB-2020-07-05-2 (AD18_A1829)	Hungary: Heves, Parádhóhuta	PP375737	PP375255	PP358513	PP273670	This study

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPB1</i>	<i>TEF1-α</i>	References
<i>A. prudens</i>	DB-2018-06-09-1 (AD73)	Hungary: Heves, Gyöngyösoroszi	PP375738	PP375256	PP358514	PP273671	This study
<i>A. pseudoargentea</i>	MV 21.5400	Italy	ON922911	–	–	–	Migliozzi & Donato (2022a, b)
<i>A. pseudovaginata</i>	HKAS70170	China	MH508532	MH486792	–	MH509018	Cui et al. (2018)
<i>A. pseudovaginata</i>	HKAS 38323	China	AY436470	–	–	–	Zhang et al. (2004)
<i>A. pseudovaginata</i>	LE216819	Russia	KM658285	–	–	–	Malysheva and Kovalenko (2015)
<i>A. pseudovaginata</i>	HKAS95305	China	MH508534	MH486794	–	MH509020	Cui et al. (2018)
<i>A. punctata</i>	-	Australia	AY194978	–	–	–	Sawyer et al., unpublished
<i>A. regalis</i>	HKAS56699	Czech Republic	MH508537	MH486797	–	–	Cui et al. (2018)
<i>A. regalis</i>	PRM 860899	USA	LT594941	in ITS	–	–	Kubrova et al., unpublished
<i>A. retenta</i>	HKAS69787	China	MH508542	MH486801	–	MH509027	Cui et al. (2018)
<i>A. retenta</i>	HKAS70020	China	MH508543	MH486802	–	–	Cui et al. (2018)
<i>A. shennongjiana</i>	HKAS75553 (holotype)	China	MH508590	MH486862	–	MH509085	Cui et al. (2018)
<i>A. shennongjiana</i>	HKAS75554	China	MH508591	MH486863	–	MH509086	Cui et al. (2018)
<i>A. simulans</i>	AM161112 (TO, neotype)	Italy	KX834255	–	–	–	Vizzini et al. (2016)
<i>A. simulans</i>	BoGy-2019-05-28_1 (AD19_A1049)	Romania: Harghita, Odorheiu Secuiesc	PP375717	PP375241	PP358500	–	This study
<i>A. simulans</i>	AL-2020-08-21-2 (AD43)	Hungary: Heves, Parádóhuta	PP375718	PP375242	PP358501	PP273666	This study
<i>A. simulans</i>	TEB 636-14 (AD53)	Norway: Oppland	PP375721	PP375245	PP358504	–	This study
<i>A. simulans</i>	DB-NO-027-20 (AD57)	Norway: Porsgrunn, Vestskogen	PP375719	PP375243	PP358502	–	This study
<i>A. simulans</i>	DB-2020-07-19-9 (AD89)	Hungary: Heves, Parádóhuta	PP375720	PP375244	PP358503	–	This study
<i>Amanita</i> sp.	G4748	Estonia	UDB0374610	–	–	–	Unpublished
<i>Amanita</i> sp.	Mushroom Observer 329675	USA	MT357079	–	–	–	Clements, unpublished
<i>Amanita</i> sp.	G4173	Estonia	UDB0462350	–	–	–	Tedersoo et al., unpublished
<i>Amanita</i> sp.	SUA138	Pakistan	MF489722	MF491875	–	–	Sadiquillah et al., unpublished
<i>Amanita</i> sp.	H909	Australia	GQ925403	–	–	–	Justo et al. (2010)
<i>Amanita</i> sp.	PC-0084422	Madagascar	JQ512097	JQ512088	–	–	Tang et al. (2015)
<i>Amanita</i> sp.	ML90981API	Cyprus	MH603606	–	–	–	Loizides et al. (2018)
<i>Amanita</i> sp.	ML900101AC	Cyprus	MH603607	–	–	–	Loizides et al. (2018)
<i>Amanita</i> sp.	SUA505A	Pakistan	MW425338	–	–	–	Ullah et al., unpublished
<i>Amanita</i> sp.	FA-17774	Iceland	UDB000929	–	–	–	unpublished
<i>Amanita</i> sp. 'albemarlensis'	RET 690-3	USA	MK085521	MK085520	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'aurorae'	RET 629-2	USA	MK569760	–	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'barrowsii'	Mushroom Observer 468028	USA	OK491620	–	–	–	Clements, unpublished
<i>Amanita</i> sp. 'bel-lulasinu'	RET 868-9	USA	MT013997	in ITS	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'crassiputamen'	RET 666-6	USA	MN820546	in ITS	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'homolalittinii'	RET 628-7	USA	KU248100	–	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'lindgreniana'	RET 822-4	USA	MN820550	in ITS	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'longicuneus'	RET 699-3B	USA	KY580766	KY580764	–	–	Tulloss et al., unpublished

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPBI</i>	<i>TEFI-α</i>	References
<i>Amanita</i> sp. 'obconicobasis'	RET 665-7	USA	OK076901	in ITS	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'penetratrix'	RET 769-1	USA	MH836563	MH836552	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'saltpointensis'	RET 599-8	USA	OK316958	in ITS	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'semio-bruta'	RET 691-1	USA	KY435402	KY435401	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'sp-AZ29'	AEF429	USA	KY614232	–	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'sp-CROAT01'	RET 867-9	Croatia	MT036492	in ITS	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'sp-DEUT02'	RET 307-9	Germany	MW526941	–	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'sp-DEUT03'	RET 305-1	Germany	MW526943	in ITS	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'sp-GSM04'	RET 375-9	USA	KX018794	KX018802	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'sp-PORT03'	RET 455-9	Portugal	MN336274	MN336273	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'sp-ROSS02'	RET 877-6	Russia	MW526934	in ITS	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'sp-RUSS01'	RET 877-7	Russia	MW526933	–	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'subnigra'	RET 849-1	USA	MT073017	in ITS	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 'trygonion'	RET 622-5	USA	KU186809	KU186810	–	–	Tulloss et al., unpublished
<i>Amanita</i> sp. 3	DB-2018-07-08-4 (AD17)	Hungary: Borsod-Abaúj-Zemplén, Zubogy	PP375688	PP375225	PP358485	–	This study
<i>A. spadicea</i>	RET 306-4	Germany	MT036490	–	–	–	Tulloss et al., unpublished
<i>A. spadicea</i>	RET 594-8	Turkey	MW426549	–	–	–	Tulloss et al., unpublished
<i>A. spadicea</i>	DL170917a	France	MN490685	–	–	–	Hanss and Moreau (2020)
<i>A. spadicea</i>	DB-2021-08-27-4 (AD124)	Austria: Steiermark, Eisenerz	PP375772	PP375267	–	PP273682	This study
<i>A. spadicea</i>	DB-2022-10-09-1 (AD167)	Hungary: Vas, Orfalu	PP375804	–	–	–	This study
<i>A. sponsa</i>	PAM18110303	Spain	OQ357629	–	–	–	Hanss and Moreau (2022)
<i>A. sponsa</i>	PAM18110302	Spain	OQ357631	–	–	–	Hanss and Moreau (2022)
<i>A. sponsa</i>	PAM18102001 (holotype)	Spain	OQ357630	–	–	–	Hanss and Moreau (2022)
<i>A. sponsa</i>	PAM18110301	Spain	PP375694	–	–	–	This study
<i>A. suberis</i>	MV 20.9261	Italy	OP297211	–	–	–	Migliozzi V and Donato G, unpublished
<i>A. suberis</i>	MV 20.9792	Italy	OP297212	–	–	–	Migliozzi and Donato, unpublished
<i>A. suberis</i>	DB-2022-10-02-1 (AD149)	Hungary: Komárom-Esztergom, Várgesztes	PP375695	–	–	–	This study
<i>A. suberis</i>	FDovana 30679	Italy	PP375696	–	–	–	This study
<i>A. sublividopallescens</i>	DB-2018-05-21-6 (AD16)	Hungary: Pest, Budakeszi	PP375749	PP375262	PP358520	PP273674	This study
<i>A. sublividopallescens</i>	DB-2018-05-21-7 (AD35)	Hungary: Pest, Budakeszi	PP375750	PP375263	PP358521	PP273675	This study
<i>A. sublividopallescens</i>	DB-2018-05-31-5 (AD74)	Hungary: Pest, Budakeszi	PP375751	–	–	–	This study

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPBI</i>	<i>TEFI-α</i>	References
<i>A. sublividopallescens</i>	AL 16/61 (AD78)	Hungary: Pest	PP375758	–	–	PP273676	This study
<i>A. sublividopallescens</i>	DB-2019-06-22 (AD79)	Hungary: Baranya, Kárász	PP375756	–	–	–	This study
<i>A. sublividopallescens</i>	DB-2020-06-28-2 (AD82)	Hungary: Budai-hegység	PP375752	–	–	–	This study
<i>A. sublividopallescens</i>	DB-2020-06-28-1 (AD83)	Hungary: Budai-hegység	PP375755	PP375264	PP358522	–	This study
<i>A. sublividopallescens</i>	DB-2020-06-28-7 (AD88)	Hungary: Pest, Budakeszi	PP375757	–	–	–	This study
<i>A. sublividopallescens</i>	DB5062 (AD94)	Hungary: Pest, Budakeszi	PP375753	MK277543 (as <i>A. cf. beckeri</i>)	–	–	This study
<i>A. sublividopallescens</i>	DB-2021-06-13-2 (AD106)	Hungary: Komárom-Esztergom, Tardos	PP375754	–	–	–	This study
<i>A. submembranacea</i>	TUF106487	Estonia	UDB011777	–	–	–	Liiv, unpublished
<i>A. submembranacea</i>	MB-001174	Germany	MH508626	MH486916	–	MH509135	Cui et al. (2018)
<i>A. submembranacea</i>	AF3130	Belgium	MF461571	–	–	–	Thongbai et al. (2018)
<i>A. submembranacea</i>	ACNV13	France	MW589093	–	–	–	Piarroux et al. (2021)
<i>A. submembranacea</i>	HKAS96167	Austria	MH508625	MH486915	–	MH509134	Cui et al. (2018)
<i>A. submembranacea</i>	DB-2018-07-31-1 (AD25)	Italy: South Tyrol, Trafoi	PP375774	PP375269	PP358527	PP273684	This study
<i>A. subnudipes</i>	AL-2020-08-09 (AD65)	Hungary: Somogy	PP375767	–	–	–	This study
<i>A. subnudipes</i>	SP-2022-06-17 (AD144, A2528)	Hungary: Pest, Pusztavacs	PP375768	–	–	–	This study
<i>A. subnudipes</i>	DB-2022-10-02-3 (AD158)	Hungary: Komárom-Esztergom, Várgesztes	PP375769	–	–	–	This study
<i>A. subnudipes</i>	JMH2018002 (ALV17093)	France	PP375770	–	–	–	This study
<i>A. subovalispora</i>	BZ2015_70	Thailand	MF461580	MF461562	–	–	Thongbai et al. (2018)
<i>A. supravolvata</i>	RET 427-8	Italy	MN336277	in ITS	–	–	Tulloss et al., unpublished
<i>A. supravolvata</i>	RET 103-7 (isotype)	France	KP258995	–	–	–	Tulloss et al., unpublished
<i>A. supravolvata</i>	DB-2020-10-31-2 (AD60)	Hungary: Vas, Szalafő	PP375708	PP375238	PP358497	PP273663	This study
<i>A. supravolvata</i>	DB-2022-10-17-1 (AD157)	Hungary: Veszprém, Fenyőfő	PP375709	–	–	–	This study
<i>A. tenuifulva</i>	HKAS58877	China: Yunnan	MH508635	MH486928	–	MH509145	Cui et al. (2018)
<i>A. tenuifulva</i>	HKAS87120 (holotype)	China: Yunnan	–	MH486929	–	MH509146	Cui et al. (2018)
<i>A. umbrinolutea</i>	LIP 0401238	France	MN490658	–	–	–	Hanss and Moreau (2020)
<i>A. umbrinolutea</i>	RET 851-6	Italy	MT980922	in ITS	–	–	Tulloss et al., unpublished
<i>A. umbrinolutea</i>	HKAS89637	China	MH508638	MH486934	–	MH509151	Cui et al. (2018)
<i>A. umbrinolutea</i>	NA-0013 (AD48)	Hungary: Vas, Bajánsénye	PP375657	PP375204	PP358469	PP273644	This study
<i>A. umbrinolutea</i>	DB-2020-09-27-1 (AD49)	Hungary: Vas, Szalafő	PP375658	PP375205	PP358470	–	This study
<i>A. umbrinolutea</i>	DB-2021-08-27-2 (AD116)	Austria: Steiermark, Eisenerz	PP375660	–	–	–	This study
<i>A. umbrinolutea</i>	DB-2021-08-07-2 (AD120)	Norway: Oppland, Lunner, Roa, S. Oppdalen	PP375659	–	–	–	This study
<i>A. umbrinolutea</i>	JMH2019036	France	–	PP375206	–	PP273645	This study
<i>A. vaginata</i>	LEM950304a	Japan	AB015691	–	–	–	Oda et al. (1999)
<i>A. vaginata</i>	LE9585	Russia	KM658298	–	–	–	Malysheva and Kovalenko (2015)
<i>A. vaginata</i>	MN18 (CUB)	Thailand	AB458889	–	–	–	Disyatat et al. (2016)
<i>A. vaginata</i>	KA12-1190	South Korea	KF017949	KF021688	–	–	Kim et al. (2013)

Table 1 (continued)

Name	Strain/voucher	Country	ITS	LSU	<i>RPB1</i>	<i>TEF1-α</i>	References
<i>A. vaginata</i>	KA12-0665	South Korea	KF017948	KF021687	–	–	Kim et al. (2013)
<i>A. vaginata</i>	KA12-0962	South Korea	KF017950	KF021689	–	–	Kim et al. (2013)
<i>A. vaginata</i>	FLAS-F-60889	USA	MH016871	–	–	–	Kaminsky et al., unpublished
<i>A. variicolor</i>	CMMF 003787	Canada	MG734656	–	–	–	Lambert et al. (2018)
<i>A. velosa</i>	07004	USA	GQ250409	GQ250424	–	–	Harper and Davis, unpublished
<i>A. verna</i>	DB-2019-06-09 (AD98)	Hungary: Pest, Pusztavacs	PP375799	–	–	–	This study
<i>A. verrucosivolva</i>	HKAS87106	China	–	–	–	MH509157	Cui et al. (2018)
<i>A. virosa</i>	FP-2020-09-06 (AD61)	Hungary: Vas, Orfalu	PP375797	PP375281	PP358540	–	This study
<i>A. vladimirii</i>	DB-2022-09-24-1 (AD166)	Austria: Burgenland, Rohonc	PP375805	–	–	–	This study
<i>A. vladimirii</i>	BRNM825828 (holotype)	Czech Republic	MW208927	MW208923	–	MW208627	Ševčíková et al. (2021)
<i>A. zonata</i>	HKAS97240	China	–	MH486959	–	MH509179	Cui et al. (2018)
<i>A. zonata</i>	HKAS122624	China	ON794400	–	–	–	Wang et al. (2022)
<i>A. zonata</i>	HKAS97705	China	MH508657	MH486961	–	–	Cui et al. (2018)

Newly generated sequences are marked in boldface

Holotype: France, Mayenne, forêt d'Ombrée-d'Anjou-Combrée, under *Betula pendula* and *Quercus petraea* on oligotrophic soil with *Pteridium aquilinum*, A. Gasch & P-A. Moreau, 21 Aug 2021, LIP 0404490 (ex PAM21081109); GenBank PP375686 (ITS) and PP273651 (*TEF1- α*).

Etymology: the epithet *griseofulva* refers to the similarity of the species with *Amanita fulva*, with a distinct, greyish coloured pileus.

Diagnosis: Reminiscent of *Amanita fulva* by the slender habitus, but it differs by growing strictly under deciduous trees on all types of soil, by a vaginate, semi-friable to friable volva often broken into small patches, by a quickly plane-convex pileus, not fawn but grey, grey-beige, yellow-grey and sometimes also dark grey-brown to bronze-green, by a partial veil forming small white aggregates that are clearly visible on young basidiomata, by a subhymenial tree with isodiametric cells under almost all basidia and by a unique phylogenetic position.

Description: Pileus 2–8 cm in diameter, quickly plane-convex, and then slightly depressed with a small persistent umbo, grey, grey-beige, yellow-grey and sometimes also dark grey-brown to bronze-green, shortly striate at the margin in some specimens. Lamellae white, only slightly greying with age; edge with grey edge on mature specimens. Stipes 4.5–10-cm high, often quite thin but sometimes more solid which can give an aspect of *Amanita fulvoides*, most often white, with tiny clusters of white partial veil remains visible on young mushrooms. Dark coloured collections may have a coloured stipe with age. Volva 1.2–2-cm high, vaginate, fragile, thin, whole (type III) or fragmented (type I), white, stained with brown spots. Basidiospores 8.8–13

× 8–12 μm , globose to subglobose, $L_{av} = 9.76 \mu\text{m}$, $W_{av} = 9.32 \mu\text{m}$, $Q_{av} = 1.03$. Basidia of stocky appearance because of the small length/width ratio, clearly capitated then rather abruptly tapered down, 55–70 × 14–20 μm , mostly 4-spored but 2-spored basidia are relatively frequent. Sterigmata 5–6 μm long. Lamellar trama about 100 μm broad, reduced to a mediostrium whose elements show an essentially parallel arrangement. It is composed of 4–6- μm thick hyphae, either septate with short elements to 40 μm in length or with very long elements. Many physaloid cells mostly elongated, the largest around 8 × 20 μm or more rarely spherical, 25 × 25 μm . The whole forms a solid matrix that is difficult to decompose. Subhymenium under ripe basidia isodiametric, type 4 or 5, subhymenial cell 15 × 15 μm or 20 × 20 μm , more rarely ramoso and fixed on an isodiametric cell. Under the immature basidia, the subhymenium is always cellular. Lamellar edge wrapped in a gelatinous matrix from which sometimes a few subspherical marginal cells emerge, 30–20 × 25–18 μm , pedunculated, grouped in bundles or irregularly distributed on the edge (in some places of the lamella edge marginal cells lacking). Pileipellis 150–180 μm broad, forms an ixocutis with a thin gelatinous layer, comprising some thin hyphae 1–3 μm broad, covering a cutis of 3–5 μm broad hyphae, almost parallel, arranged in twist (spiral) ensuring mechanical coherence, with some very elongated acrophysalids, e.g. 80 × 10 μm . Transition zone with context non-observable. Context of pileus mostly composed of elongated physaloid cells, e.g. 140 × 30 μm , 100 × 40 μm , 45 × 17 μm and sometimes forming chains and hyphae up to 4–5- μm thick. The whole is weakly entangled. Volva ca. 600 μm broad with a high density of quite massive, largely ellipsoid,



Fig. 4 Representative specimens of *Amanita deflexa*: **a, b** JMH2019039 (LIP 0004489, holotype, France); **c, d** DB-2020-10-03-1 (AD52, Hungary). Photos: **a, b** J-L. Muller; **c, d** B. Dima

physaloid cells, e.g. $80 \times 60 \mu\text{m}$, $50 \times 30 \mu\text{m}$, more rarely almost spherical, $35 \times 30 \mu\text{m}$, maintained by 4–5- μm thick hyphae, strongly septate, with short, 50–60- μm long segments. Acrophysalides sometimes present, e.g. $30 \times 9 \mu\text{m}$, $45 \times 40 \mu\text{m}$. The entanglement is a little stronger outward.

Phylogenetic relationship: *Amanita griseofulva* is rather isolated, representing the most basal clade in stirps *Fulva*, differing by at least 16 substitution and indel positions (95% similarity) from the closest species (*A. pachycolea*) in the ITS region. Intraspecific genetic variability is very low,

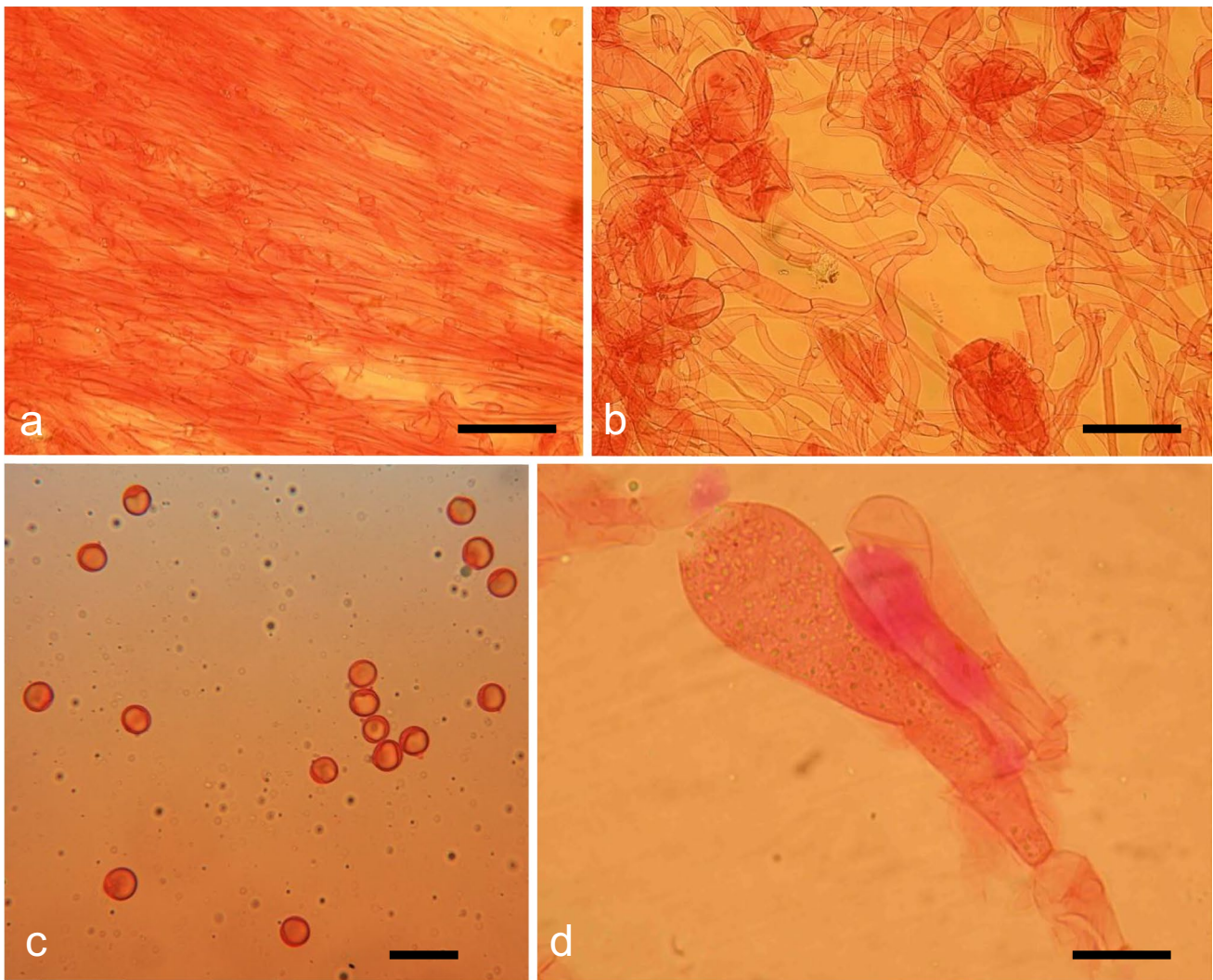


Fig. 5 Important microstructures of the newly described *Amanita deflexa*: **a** external layer of the volva (JMH2019029), **b** main layer of the volva (JMH2019029); **c** basidiospores (DB-2020-10-03-1), **d** sub-

hymenial cell (JMH2019029). Photos: **a–b, d** J.-M. Hanss, **c** D. Varga. Scale bars: *a* = 20 μ m, *b* = 75 μ m, *c* = 20 μ m, *d* = 20 μ m

most sequences are identical, and few have 1–2 nucleotide differences.

Habitat and distribution: in mixed deciduous forests under *Quercus*, *Carpinus* and *Fagus* on all types of soils, from calcareous to oligotrophic soils. Presumably not unfrequent in Western and Central Europe, but verified data are scattered to date with known occurrences from France, Germany, UK (soil sample – GenBank: KM374392) and Hungary where it seems widespread from the westernmost to the easternmost areas. Fruiting in summer.

Comments: Macroscopically, *A. griseofulva* forms small- to medium-sized basidiomata, characterised by a lowly umbonate pileus which can display a variety of colours but most often rather pale, a rather slender stipe, most often white, covered with a slight partial veil forming white to light grey punctuations of a unique appearance among the

taxa within the stirps *Fulva*, and a fragile, rust-stained, vaginate volva, mainly entire but also dissociated pieces on pileus or around base. The only medium entanglement of the volva does not always seem to be able to ensure mechanical strength of a tissue in which physaloid cells dominate. The subhymenium is cellular, a relatively rare property in the sect. *Vaginatae* and therefore remarkable. This species has many microscopic similarities to *A. fulvoides*. In case of doubt, the structure of the pileipellis will make it possible to distinguish them.

Additional collections examined: France, Nord, Saint-Amand-les-Eaux, Forêt domaniale de Raismes-Saint-Amand-Wallers, Drève des Prés Charniers, parcel 309, under *Quercus petraea* and *Carpinus betulus* on clay-limestone, soil stirred up by wild boars, P.-A. Moreau, 18 Sept 2016, PAM16091803 (LIP0401182); Beuvry-la-Forêt, forêt

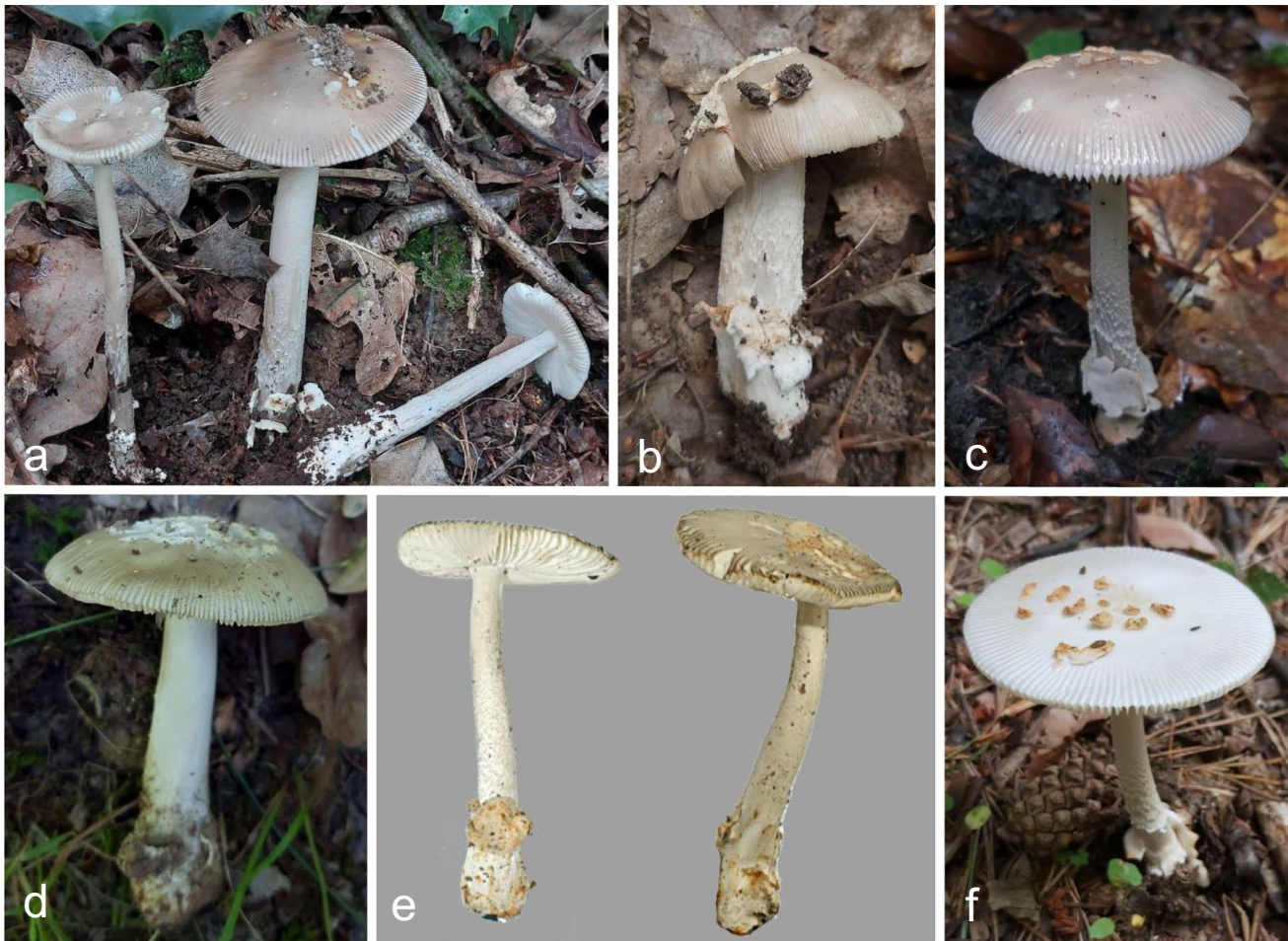


Fig. 6 Representative specimens of *Amanita griseofulva*: **a** PAM21081109 (LIP 0404490, holotype, France), **b** DB-2020-07-05-6 (AD37, Hungary), **c** DB-2020-07-25-2 (AD09, Hungary), **d**

DB-2020-06-27-4 (AD14, Hungary), **e** (PAM16091803, France); and *Amanita griseofulva* f. *albida*: **f** DB-2021-07-31-2 (AD115, holotype, Hungary). Photos: **a, e** P-A. Moreau; **b, c, d** B. Dima; **f** A. Nagy

domaniale de Marchiennes, parcel 15, under *Quercus petraea* and *Betula pendula* on oligotrophic soil, P-A. Moreau, 12 Sept 2019, PAM19091201 (PAM19091201). Hungary, Heves County, Mátra Mts, Parádfürdő, under *Quercus cerris* and *Q. petraea*, A. Nagy, B. Dima, 5 July 2020, DB-2020-07-05-6/AD37 (ELTE); Mátra Mts, Parádsasvár, under *Fagus sylvatica* and *Quercus petraea*, A. Nagy, B. Dima, 25 July 2020, DB-2020-07-25-2/AD09 (ELTE); Baranya County, Mecsek Mts, Pécs, Éger-tető, under *Quercus cerris* and *Q. petraea*, B. Szűcs, B. Dima, 27 Jun 2020, DB-2020-06-27-4 AD14/(ELTE); Borsod-Abaúj-Zemplén County, Rudabánya Mts, Zubogy, under *Quercus petraea* and *Carpinus betulus*, I. Fedor, 7 July 2018, DB-2018-07-07-6/AD24 (ELTE); Rudabánya Mts, Zubogy, under *Quercus petraea* and *Carpinus betulus*, M. Németh, 7 July 2018, DB-2018-07-07-3/AD15 (ELTE); Rudabánya Mts, Zubogy, under *Quercus petraea* and *Carpinus betulus*, B. Bognár, 7 July 2018, DB-2018-07-07-05/AD21 (ELTE); Vas County, Órség, Bajánsenye, under *Quercus petraea*,

Carpinus betulus, *Fagus sylvatica* and *Pinus sylvestris*, B. Dima, D. Varga, 29 Jun 2022, DB-2022-06-29-1 AD143/ (ELTE).

Amanita griseofulva f. *albida* Hanss & Dima, f. nov., Fig. 6f.

Mycobank: MB#850078.

Holotype: Hungary, Borsod-Abaúj-Zemplén County, Zemplén Mts, Újhuta, under *Quercus petraea*, *Pinus sylvestris*, *Carpinus betulus* and *Betula pendula*, A. Nagy, B. Szűcs, B. Dima, 31 July 2021, DB-2021-07-31-2/AD115 (BP); GenBank PP375682 (ITS), PP375222 (LSU), PP358483 (*RPB1*) and PP273650 (*TEF1- α*).

Etymology: the epithet *albida* refers to the white basidiomata of this form.

Diagnosis: Differs from typical *Amanita griseofulva* by an entirely white pileus.

Comments: Genetically this apigmented form of *A. griseofulva* shows no difference from the sequences of the

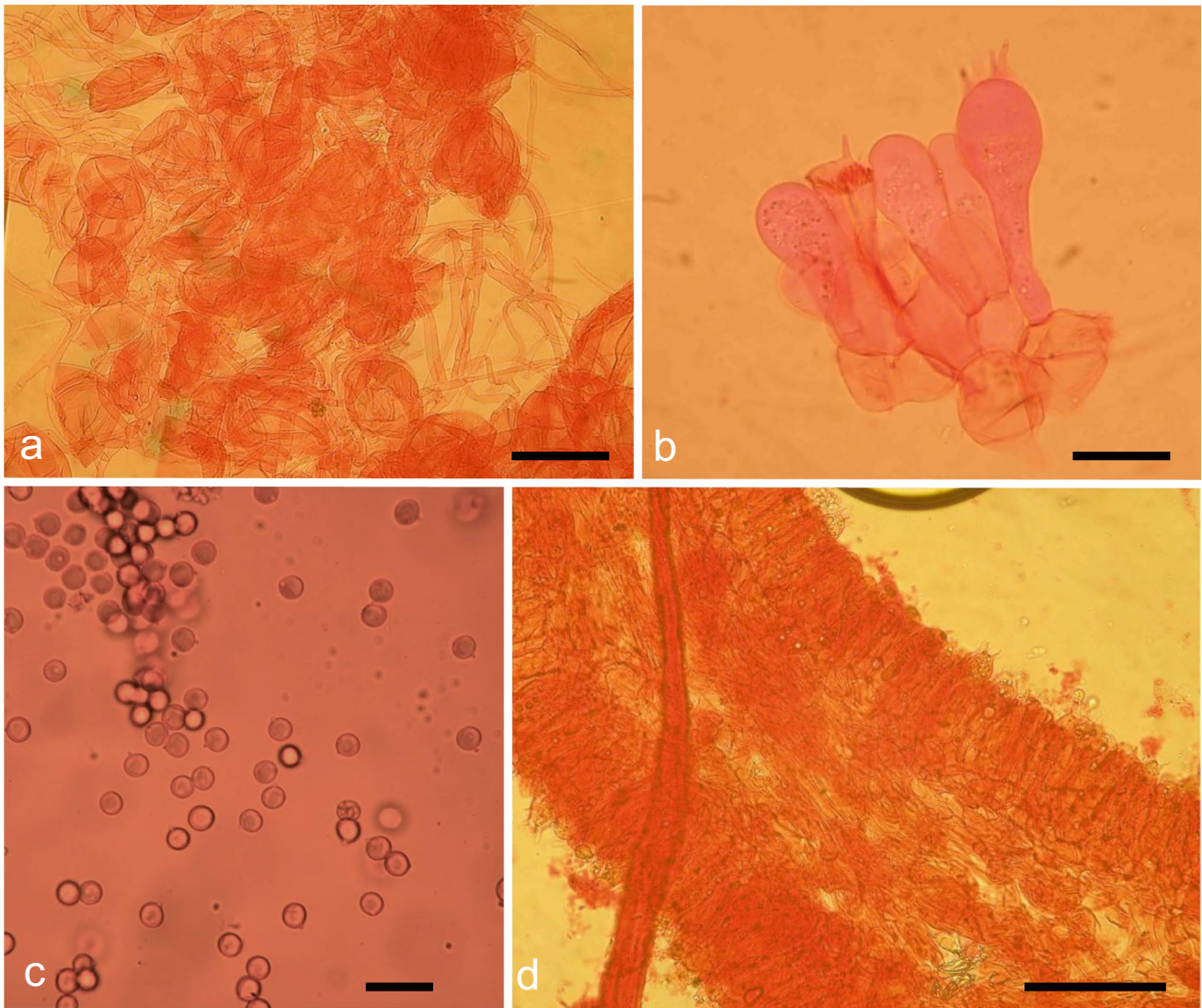


Fig. 7 Important microstructures of the newly described *Amanita griseofulva*: **a** structure of the volva (PAM20181109), **b** subhymenium (PAM20181109), **c** basidiospores (DB-2020-07-05-6), **d** lamel-

lar trama (PAM20181109). Photos: **a–b, d** J.-M. Hanss, **c** D. Varga. Scale bars: *a* = 65 μ m, *b* = 15 μ m, *c* = 20 μ m, *d* = 100 μ m

typical form and the two collections studied are nested within the *A. griseofulva* clade.

Additional collection examined: Borsod-Abaúj-Zemplén County, Zemplén Mts, Újhuta, in mixed forest, K. Gábor Békésné, 31 July 2021, DB-2021-07-31-3/AD117 (ELTE).

Amanita opaca Hanss, Dima, Bidaud & D. Varga, sp. nov., Figs. 8, 9.

Mycobank: MB#846789.

Holotype: France, Ain, Marchamp, locality “le Moyeux”, alt. 800 m, under *Quercus pubescens* and *Carpinus betulus* on calcareous soil, A. Bidaud, 12 Aug. 2011, LIP 0004500 (isotype AB11-08-60 in herb. A. Bidaud); GenBank PP375802 (ITS).

Etymology: Latin epithet *opacus*, understood in the sense dull, refers to the peculiar aspect of pileic surface on all studied collections.

Diagnosis: differs from the closely related *Amanita coryli* by a slightly more robust habitus, by a dull pileus with two or more colours, and by larger spores. The rather fragile, white, sometimes yellow-spotted volva has a particular microscopic structure, mainly composed of oval, physaloid cells wrapped in tendrils of helical hyphae, arranged in parallel to the stipe, and as long as the height of the volva.

Description: Pileus 2–10 cm in diameter, first conical to parabolic, then plane-convex, gradually becoming flat; surface smooth or with small to wide patches of universal veil, with a dull appearance, always composed of two main colours one of which being grey, intimately mixed in certain



Fig. 8 Representative specimens of *Amanita opaca*: **a** AB11-08-60 (LIP 0004500, holotype, France), **b** AB12-05-05 (France), **c** JMH2020007 (France), **d** DB-2020-06-28-8 (AD86, Hungary), **e, f** DB-2021-06-19-5 (AD104, Hungary), **g** DB-2021-06-19-3 (AD102,

Hungary); and *A. opaca* f. *chettoi*: **h** JMH2016027 (LIP 0004499, holotype, France), **i** DB-2020-08-02-3 (AD39, Hungary). Photos: **a, b** A. Bidaud; **c, h** J.-M. Hanss; **d, e, f, g, i** B. Dima

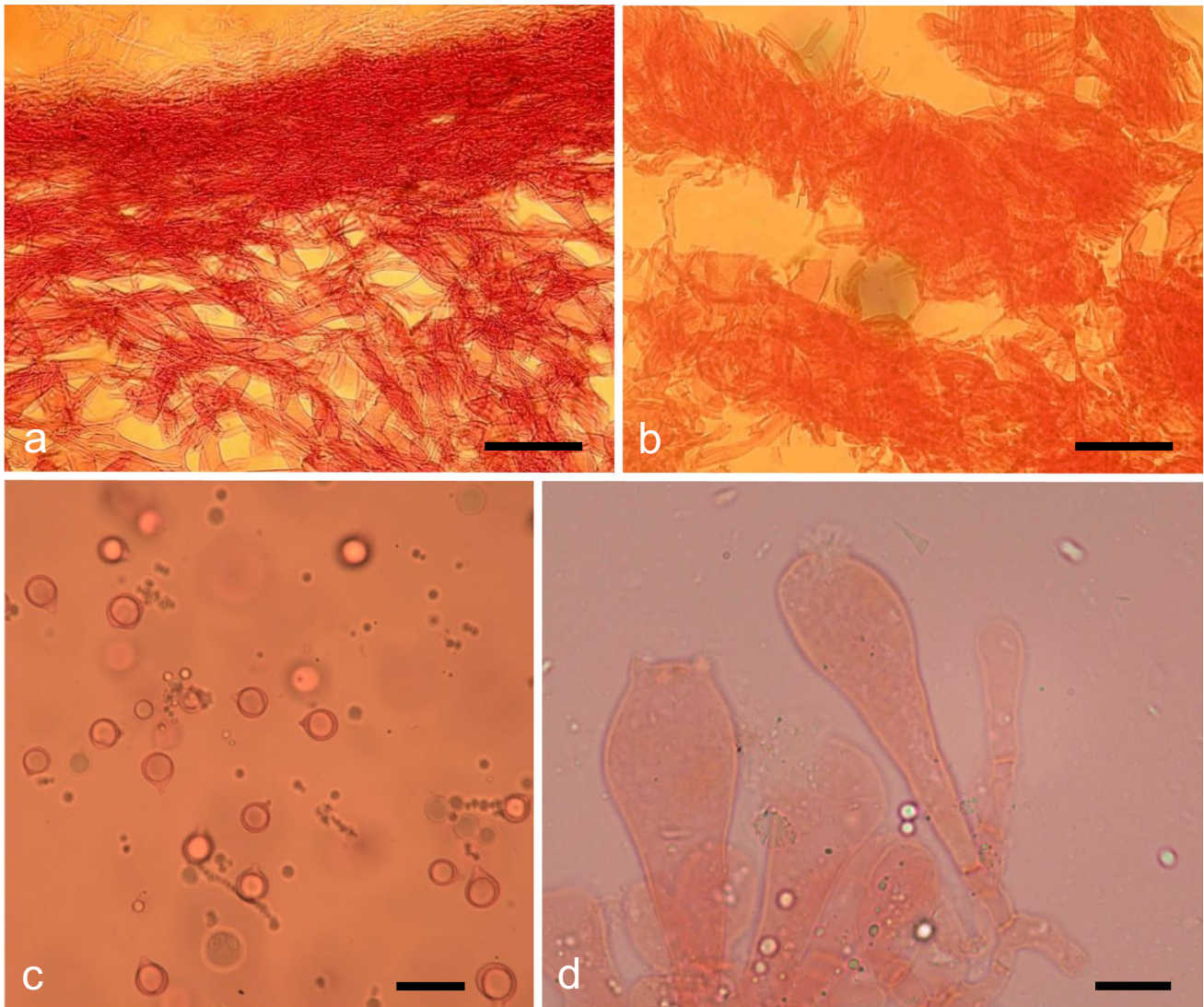


Fig. 9 Important microstructures of the newly described *Amanita opaca*: **a** pileipellis and context (JMH2020007), **b** twisted hyphae of volva enveloping physaloid cells (JMH2020007), **c** basidiospores

(DB-2021-06-19-2), **d** subhymenial cell (JMH2020007). Photos: **a–b**, **d** J.-M. Hanss, **c** D. Varga. Scale bars: $a = 120 \mu\text{m}$, $b = 80 \mu\text{m}$, $c = 20 \mu\text{m}$, $d = 10 \mu\text{m}$

areas where they form a rich palette of gradations, darker in the centre and on the striate margin. Lamellae free, crowded, whitish. Stipes 3–12-cm high, rather thin but sometimes more solid, entirely white, smooth to finely floccose. Volva 1–3-cm high, of a particular type II, long vaginated on the bottom then opening into a short collar, fragile, thin, sometimes fragmented (type I), white and sometimes stained with rusty spots. Basidiospores $10.6\text{--}13.5 \times 10\text{--}12.6 \mu\text{m}$, globose to subglobose, $L_{av} = 12.04 \mu\text{m}$, $W_{av} = 11.20 \mu\text{m}$, $Q_{av} = 1.07$. Basidia generally quite long with an elongated and slender base, $70\text{--}90 \times 20\text{--}25 \mu\text{m}$, rarely more squat, $60\text{--}70 \times 20\text{--}22 \mu\text{m}$. Lamellar trama from about 280- μm thickness at the base to 90 μm towards the tip, little differentiated where we can distinguish a thick mediostratum of about a half of the thickness, relatively parallel to the axis

with few physaloid cells, oval $28 \times 40 \mu\text{m}$ or $37 \times 45 \mu\text{m}$ to clearly elongated ($40 \times 55 \mu\text{m}$) and hyphae of 2–4(5)- μm thick. The hymenophorus has same components of the same measurements. Its physaloid cells are more and more numerous as we approach the subhymenium, with an angle of orientation varying from parallel to almost perpendicular to the axis. The subhymenial stratum appears to be cellular due to a large number of spherocysts, but the subhymenial tree is relatively short with branching elements measuring about $5 \times 10 \mu\text{m}$. Sometimes the subhymenial tree is reduced to a single cell, connected to long, parallel to the edge of the lamella, hyphae. Lamellar edge gelified or not is according to the examined samples. The 60–70- μm gelified layer does not contain hyphae or marginal cells. Below, the basidia are mixed with marginal cells of various forms,



Fig. 10 Representative species of *Amanita* sect. *Vaginatae* in Europe. Stirps *Mairei*: **a** *A. brunneofuliginea* f. *ochraceopallida* DB-2021-08-07-4 (AD129, Norway), **b** *A. supravolvata* DB-2022-10-17-1 (AD157, Hungary); stirps *Albogrisescens*: **c** *A. alseides* DB-2020-06-28-3 (AD13, Hungary), **d** *A. albogrisescens* DB-2022-10-21-2

(AD152, Hungary); stirps *Simulans*: **e** *A. simulans* BoGy-2019-05-28 (AD19, Romania), **f** *A. beckeri* JMH2015027 (France), **g** *A. beckeri* GC17092307 (France). Photos: **a**, **b**, **d** B. Dima; **c** A. Nagy; **e** Gy. Bodó; **f** J.-M. Hanss; **g** G. Corriol



Fig. 11 Representative species of *Amanita* sect. *Vaginate* in Europe. Stirps *Lividopallescens*: **a** *A. dryophila* AL-2020-08-21-1 (AD38, Hungary), **b** *A. lividopallescens* DB-2018-06-12-1 (AD76, Hungary), **c** *A. sublividopallescens* DB5062 (AD94, Hungary); stirps *Betulae*: **d** *A. betulae* DB-2021-08-08-2 (AD127, Norway); stirps *Coryli*: **e** *A.*

prudens DB-2020-07-05-2 (AD18, Hungary), **f** *A. prudens* AB10-08-100 (France), **g** *A. coryli* DB-2020-07-05-7 (AD03, Hungary); stirps *Vladimirii*: **h** *A. vladimirii* DB-2022-09-24-1 (AD166, Austria). Photos: **a** L. Albert; **b** I. Fedor; **c, d, e, g, h** B. Dima; **f** A. Bidaud



Fig. 12 Representative species of *Amanita* sect. *Vaginatae* in Europe. Stirps *Crocea*: **a** *A. crocea* DB-2021-08-08-3 (AD122, Norway), **b** *A. crocea* PG-2023-07-27-1 (A3108, Hungary), **c** *A. subnudipes* DB-2022-10-02-3 (AD158, Hungary), **d** *A. subnudipes* DB-2023-06-10-5 (A3024, Hungary – sequenced, but not included in the analyses); stirps *Submembranacea*: **e** *A. submembranacea* DB-2018-07-31-1 (AD25, Italy), **f** *A. mortenii* DB-2021-08-27-1 (AD112,

Austria); stirps *Arctica*: **g** *A. aff. arctica* DB-2021-08-12-1 (AD114, Norway); stirps *Friabilis*: **h** *A. friabilis* AL13/109 (A3093, Hungary – sequenced, but not included in the analyses), **i** *A. suberis* DB-2022-10-02-1 (AD149, Hungary); stirps *Ceciliae*: **j** *A. ceciliae* DB-2018-07-08-5 (AD22); Photos: **a, d** A. Nagy; **b, c, e, g, i, j** B. Dima; **f, h** L. Albert



Fig. 13 Representative species of *Amanita* sect. *Vaginatae* in Europe. Stirps *Fulva*: **a** *A. fulva* DB-2020-06-13 (AD42, Hungary), **b** *A. fulva* JMH2019003 (France), **c** *A. fulvoides* DB6704 (AD66, Hungary), **d** *A. fulvoides* DB-2018-05-31-2 (AD68, Hungary), **e** *A. umbrinolutea* DB-2021-08-27-2 (AD116, Austria); stirps *Argentea*: **f** *A. huijsma-*

nii NA-0010 (AD47, Hungary), **g** *A. electra* DL140901 (holotype, France); stirps *Spadicea*: **h** *A. spadicea* DB-2022-10-09-1 (AD167, Hungary). Photos: **a** A. Nagy; **b** J.-M. Hanss; **c**, **d**, **e**, **h** B. Dima; **f** A. Nagy; **g** D. Lucas



Fig. 14 Representative species of *Amanita* sect. *Vaginatae* in Europe. stirps *Nivalis*: **a** *A. sponso* PAM18102001 (holotype, France), **b** *A. sponso* (PAM18110303, France), **c** *A. griseocaerulea* (DL141120A, France) **d** *A. griseocaerulea* DL2009071 (France), **e** *A. nivalis* DB-2021-08-12-2 (AD128, Norway); stirps *Magnivolvata*: **f** *A. calida*

DB-2023-06-23-2 (A3051, Hungary — sequenced, but not included in the analyses), **g** *A. calida* DB-2020-07-19-17 (AD32, Hungary), **h** *A. herculis* DB-2022-10-21-3 (AD150, Hungary), **i** *A. battarrae* DB4685 (AD92, Hungary). Photos: **a**, **b** P.-A. Moreau; **c**, **d** D. Lucas, **e**, **g**, **h**, **i** B. Dima; **f** K. Császárné-Erdélyi

ampuliform, sometimes large ($25 \times 45 \mu\text{m}$), subglobular or oval, $20\text{--}30\text{-}\mu\text{m}$ high with a short or long pedicel, and then septate, formed by several small cylindrical cells (e.g. $6 \times 6 \mu\text{m}$). Pileipellis about $200\text{-}\mu\text{m}$ thick, an ixocutis composed of a gelatinized outer matrix, up to $100\text{-}\mu\text{m}$ thick with a few floating hyphae $2\text{--}3\text{-}\mu\text{m}$ thick and a cutis $80\text{--}100\text{-}\mu\text{m}$ thick composed of hyphae $3\text{--}5\text{-}\mu\text{m}$ thick, weakly twisted in a spiral, mixed with a few elongated physaloid elements, e.g. $70 \times 20 \mu\text{m}$, $100 \times 20 \mu\text{m}$ or $160 \times 40 \mu\text{m}$. In the inner part, the physaloid elements become more numerous. Absence of differentiated subpellis. Context of pileus consists mainly of acrophysalids of remarkably broad size, elongated (e.g. $280 \times 60 \mu\text{m}$), sometimes more ovoid (e.g. $320 \times 100 \mu\text{m}$ or $160 \times 60 \mu\text{m}$), sometimes forming chains of some elements, weakly connected by slender hyphae $6\text{--}12\text{-}\mu\text{m}$ wide and globally faintly resistant. Volva thick $600\text{--}700 \mu\text{m}$, formed of a densely entangled tissue of mixed elements, apparently without orientation. A very thin section and a slight dislocation allows to observe that it contains a large number of physaloid cells generally oval of $15\text{--}45 \times 20\text{--}70 \mu\text{m}$ with a Q of $1.2\text{--}1.8$, more rarely spherical (for example $50 \times 50 \mu\text{m}$ or $30 \times 30 \mu\text{m}$) or very long (e.g. $140 \times 12 \mu\text{m}$ or $150 \times 45 \mu\text{m}$ for the internal ones) wrapped by $3\text{--}7\text{-}\mu\text{m}$ -thick hyphae forming tight tendrils, mostly longitudinally oriented.

Externally and internally about $100 \mu\text{m}$ broad, the tissue is even denser but without this changing its structure.

Phylogenetic relationship: *Amanita opaca* belongs to the stirps *Coryli*, differing by 7–8 nucleotide and indel positions (98% similarity) from *A. cistetorum*, 12 changes (97% similarity) from *Amanita* sp. ('saltpointensis') from USA, and at least 17 changes (96% changes) from *A. coryli* from Europe. In our multigene analysis, *A. opaca* forms the sister clade of *A. cistetorum* with strong support. Intraspecific genetic variability is low, most sequences are identical, and only in few cases, 4–5 indel differences have been detected (Fig. 3).

Habitat and distribution: Mixed thermophilous deciduous forests under *Quercus* spp. and *Carpinus betulus* but possibly also with *Betula pendula*. One sequence-verified record is originated under *Pinus nigra* as host tree (GenBank: OQ327043). Known from France, Germany, Greenland (UNITE: UDB002307), Hungary, and the UK (Andy Overall, pers. comm.), but with several records, thus it can potentially be more widespread in Europe.

Comments: *Amanita opaca* is one of the many rather anonymous greyish, greyish-brown 'vaginata' species occurring in thermophilous woodlands of Europe. Currently, morphological differentiation towards other similar species is often difficult. The closely related *A. coryli* has whitish volva, less

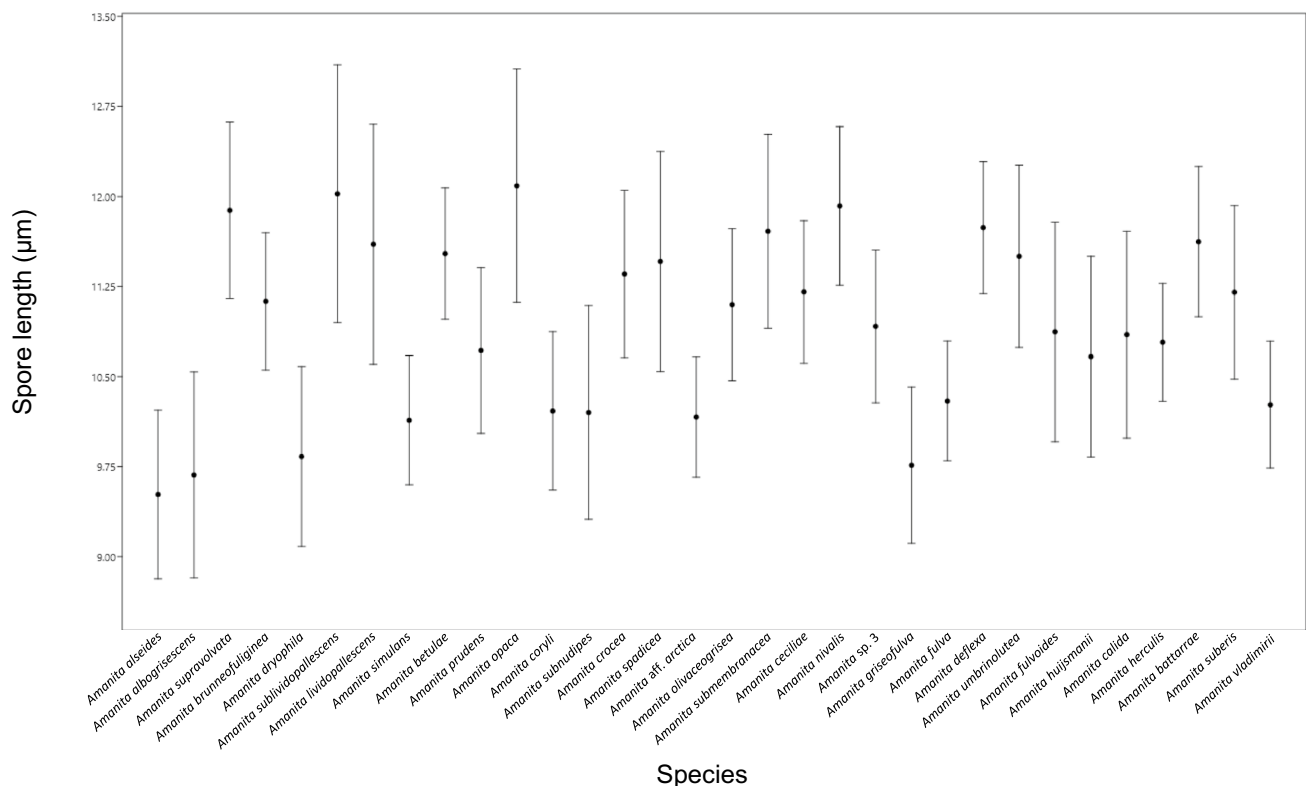


Fig. 15 Comparison of basidiospore length data. Graph showing the mean and standard deviation of spore lengths of 32 species of *Amanita* sect. *Vaginatae*. Following the ANOVA analysis, Tukey's post hoc test was used for pairwise comparisons at $p < 0.05$ significance level

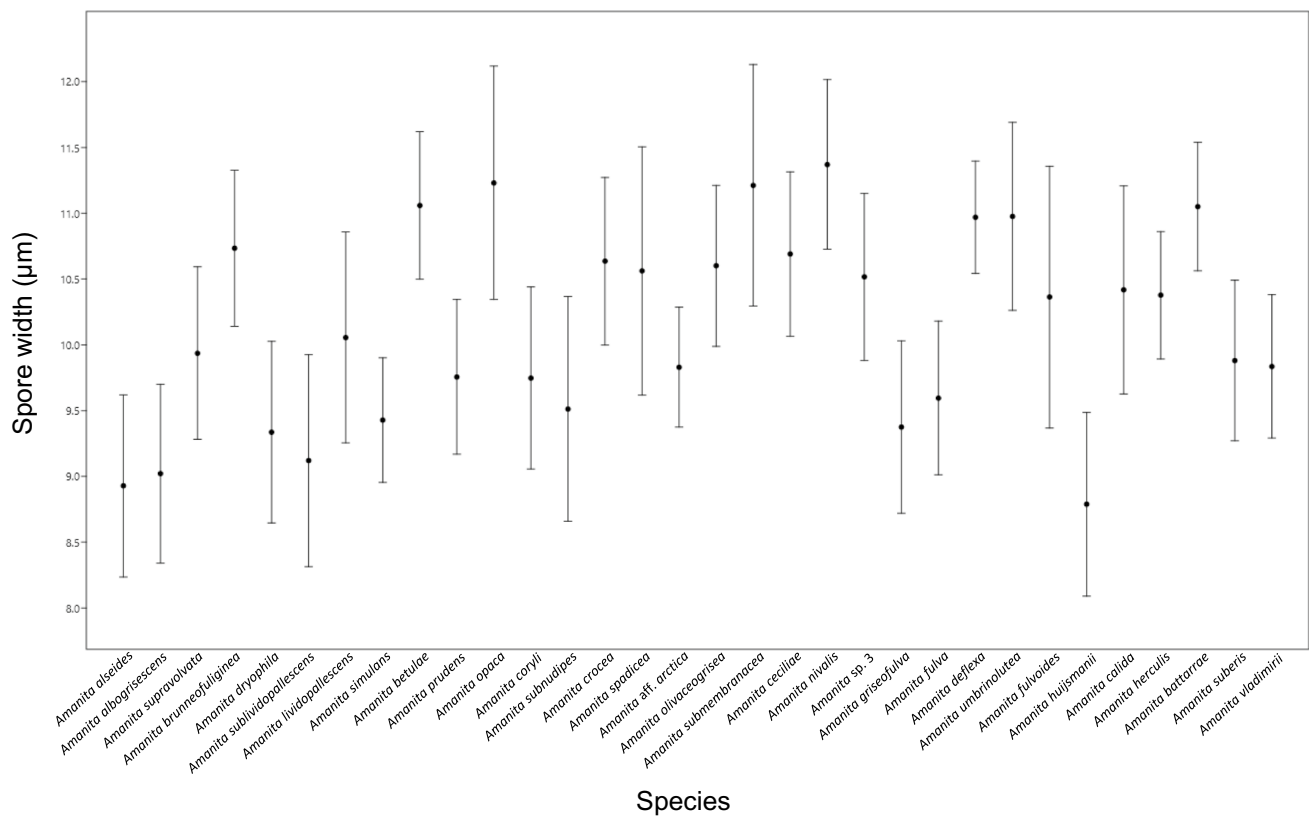


Fig. 16 Comparison of basidiospore width data. Graph showing the mean and standard deviation of spore width of 32 species of *Amanita* sect. *Vaginatae*. Following the ANOVA analysis, Tukey's post hoc test was used for pairwise comparisons at $p < 0.05$ significance level

robust habit, an always strictly vaginate volva and smaller basidiospores (Figs. 15, 16 and 17). The recently described *A. prudens* (Plaza 2022) has a first hemispherical pileus with a moiré aspect, somewhat more or less iridescent. In the beginning of the maturity phase this feature is matched with a shiny to silky character and then the pileus flattens, gradually becomes duller and then of more banal appearance. It is also belonging to stirps *Coryli*, can be distinguished from *A. opaca* based on macromorphology when young basidiomata are studied, in addition it also forms smaller basidiospores than *A. opaca* (Figs. 15, 16 and 17). Tight tendrils enveloping groups of physaloid cells (and forming cylinders) also exist in *A. coryli* and *A. prudens*. But it is in *A. opaca* that they are the tightest and most typical. For this reason, we propose to call this original volva structure “opaca type”.

Additional collections examined: France, Isère, Vézère-Curtin, les Rochettes, alt. 240 m, A. Bidaud, 3 May 2012, AB12-05-05 (LIP 0004498); Haute-Saône, Lure, water sport centre, in partly planted grove with *Carpinus betulus*, *Betula pendula*, *Acer pseudoplatanus*, *Quercus robur*, *Salix* sp. and *Picea abies*, alt. 300 m, J-M. Hanss, 12 Jun 2020, JMH2020007 (in herb. J-M. Hanss). Hungary, Veszprém County, Bakony Mts, Úrkút, Kab-hegy, under *Quercus* sp. and *Carpinus betulus*, L. Vajda, I.

Sárközi, G. Mokánszki, 19 Jun 2021, DB-2021-06-19-5/AD104 (ELTE), DB-2021-06-19-1/AD100 (ELTE), DB-2021-06-19-3/AD102 (ELTE), DB-2021-06-19-2/AD101 (ELTE); Komárom-Esztergom County, Vértes Mts, Tatabánya, under *Quercus* sp., Gy. Vidra, 13 Jun 2021, DB-2021-06-13-4/AD108 (ELTE); Vas County, Órség, Velemér, under *Carpinus betulus*, A. Nagy, B. Dima, 27 Sept 2020, DB-2020-09-27-3/AD51 (ELTE); Borsod-Abaúj-Zemplén County, Rudabánya Mts, Zubogy, under *Quercus petraea* and *Carpinus betulus*, I. Fedor, 7 July 2018, DB-2018-07-07-7/AD23 (ELTE); Pest County, Buda Mts, Budakeszi, Hidegvölgy, under *Quercus cerris* and *Q. petraea*, A. Nagy, B. Dima, 28 Jun 2020, DB-2020-06-28-8/AD86 (ELTE); Heves County, Mátra Mts, Szuha, under *Betula pendula*, *Populus tremula* and *Carpinus betulus*, A. Nagy, B. Dima, 2 Aug 2020, DB-2020-08-02-3/AD39 (ELTE).

Amanita opaca* f. *cettoi Hanss & Dima, f. nov., Fig. 8h–i. MycoBank: MB#846790.

Holotype: France, Doubs, Laviron, in a mixed forest on calcareous soil, S. Rousset, 5 Oct 2016, LIP 0004499 (isotype JMH2016027 in herb. J-M. Hanss); GenBank MN493559 (ITS, as ‘*A. supravolvata*’).

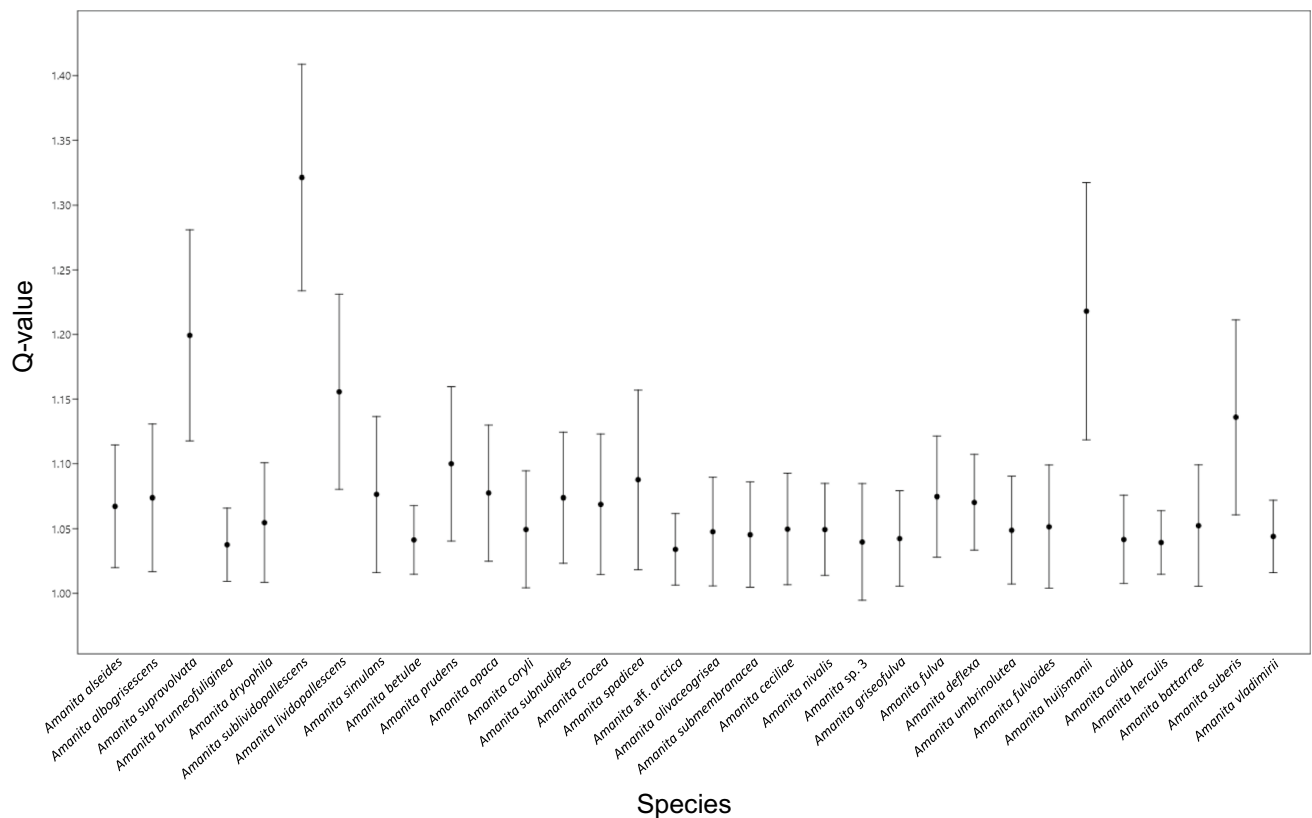


Fig. 17 Comparison of Q -value of spores. Graph showing the mean and standard deviation of basidiospore Q -value of 32 species of *Amanita* sect. *Vaginatae*. Following the ANOVA analysis, Tukey's post hoc test was used for pairwise comparisons at $p < 0.05$ significance level

Etymology: attributed to the Italian mycologist Bruno Cetto, who illustrated this species under the erroneous name “*Amanitopsis alba* Gillet” in volume 3 of the series “I funghi dal Verò”.

Diagnosis: differs from *Amanita opaca* by a uniform white colour of the basidiomata, the volva may be stained yellow like that of the main form.

Comments: Phylogenetically this apigmented form of *A. opaca* shows no difference from the sequences of the main form and are nested within the clade of *A. opaca*.

Discussion

Our study provides a new framework for the phylogenetic relationships of *Amanita* sect. *Vaginatae* in Europe, especially focusing on Central European data. The original aim of the study was to revise the *Vaginatae* species in Hungary; however, the project had soon become international including specimens and sequence data from several other countries (i.e. Austria, France, Italy, Norway and Romania). Based on multigene analyses of nrDNA ITS, nrDNA LSU, *RPB1* and *TEF1- α* sequences, we provide new phylogenetic data of 36 European species from 151 studied material.

We, furthermore, recognized six larger clades including 22 stirps (12 of them are newly identified), which help us to classify species into more natural groups within the section. Comparing to Hanss and Moreau (2020) who recognized five clades and 11 stirps, all of those were recovered in our analyses too, and we followed their classification. Our 36 species were clustered into the stirps *Albogriseascens*, *Arctica*, *Argentea*, *Betulae*, *Ceciliae*, *Coryli*, *Crocea*, *Friabilis*, *Fulva*, *Lividopallescens*, *Magnivolvata*, *Mairei*, *Nivalis*, *Simulans*, *Spadicea*, *Submembranacea* and *Vladimirii*. In stirps *Fulva* and *Coryli*, we describe three new species to science (*A. deflexa*, *A. griseofulva* and *A. opaca*) and apigmented forms of the two last (*A. griseofulva* f. *albida* and *A. opaca* f. *chettoi*). All new species seem to be widespread in Europe but mostly overlooked due to their similarity with related species. *Amanita deflexa* has likely been often confused with *A. fulva* from which it mainly differs by ecology, colour of inner surface of volva, microscopy of volva and ITS sequence. The two other species (*A. griseofulva* and *A. opaca*) described here, due to their greyish pileus colours might have so far been overlooked and were hidden under the collective name *Amanita vaginata* s. lat. The revision and typification of this name will be the object of a separate project.

Additions to microscopical observations

The microscopy applied in this study is the one taught by C. Bas and adopted by current amanitologists. Thin sections reveal an astonishing variability of the histological aspects of certain tissues which, combined with the observation of the spores, of the subhymenium, of the edge of the lamellae, as well as of macroscopic particularities make possible the conception of identification keys to the European *Vaginatae*. Such a key, focused on silvery-capped species, may be found in Hanss and Moreau (2020).

Most often, detailed microscopy can alone bring light to species identification in *Amanita* sect. *Vaginatae*, but doing this properly, requires a good knowledge of the morphology of *Amanita*, precise work as well as precise cutting equipment. Experience is acquired fairly quickly through practice. During the study of very numerous species, we observed that the angle of divergence of the physaloid elements of the lamellar trama becomes smaller to zero during drying. At rehydration, it does not return to its initial value and may, in some cases, remain at zero. The vacuolar pigments of the rehydrated hyphae in *Amanita* are hyaline. When grouped into large packets, they may have a yellowish shade. A brown intracellular necropigment may be present in some sphaerocysts of volva (e.g. in species of Clade 4). The volva of *Amanita* is an organ with highly variable microscopic structure. The volva is an important part of the universal veil protecting during the early development of the fungus. During the growth of the amanitas of the section *Vaginatae*, the ring does not develop, and the partial veil is distributed on the surface of the stipe and on the inner surface of the lower volva. This partial veil is a foreign element to the universal veil and because of that it disrupts the understanding of the structure of the universal veil. Because of this reason, we study the structure of the volva in its upper part. At the bottom of the volva, there is the limbus internus whose study can sometimes be of interest. Our method is to obtain the following information by a fine cut (and not crushing): the composition of the volva from whole elements, the arrangement of the elements in relation to each other, their orientation and their degree of entanglement. This is infinitely richer in information than those with crushing which gives a slurry in which we no longer recognize the structure.

Basidiospore size and shape as diagnostic character in *Amanita* sect. *Vaginatae*

Albeit macromorphologically distinct and phylogenetically unrelated, the three new species described in this study display very similar basidiospore shape (globose to subglobose, with a mean Q value between 1.03 and 1.07), and sizes (ranges from $7\text{--}13.5 \times 7\text{--}12.5 \mu\text{m}$). Nevertheless, there are some differences of the features: the spore length and width of *A. deflexa* is significantly different than those of other species in stirps *Fulva*, except *A. umbrinolutea*, while in

Q value, there is no difference towards the closely related species in this stirps. *Amanita griseofulva* also differs in its spore length and width from all species in the stirps *Fulva*, except *A. fulva*, but we found no difference in Q -value from other species in this stirps. In the case of *A. opaca*, when comparing basidiospores within the stirps *Coryli* which the species belongs to, we found significant differences in spore length and width, but no differences in Q values of *A. opaca*, *A. coryli* and *A. prudens*. However, with its greyish brown pileus colour, *A. opaca* can be very similar to other, more distantly related *Vaginatae* species, where basidiospores are also very similar (Figs. 15, 16 and 17). Albeit overlapping, there were significant differences of the basidiospore length, width and Q value of 32 *Vaginatae* species studied here revealed by the statistical analyses (Table S1). There are differences among all those values analysed; nevertheless, when significant pairwise differences are considered, there is no species which differs from all or similar to all other species studied here (Figs. 15, 16 and 17). The significant pairwise differences and similarities of species studied do not correspond with the main clades/stirps.

In conclusion, based on our statistical analysis, we found that basidiospore length and width data as well as Q values as diagnostic characters in the identification of the studied species cannot be considered as unambiguous overall taxonomic feature in *Amanita* sect. *Vaginatae*, and this observation is in line with the previous study of *A. lividopallescens* complex (Vizzini et al. 2016), where the authors stated that the spore-shape and presence/absence of lamellar sterile elements as specific distinguishing characters within section *Vaginatae* was overemphasized in the past (e.g. Romagnesi 1992; Tulloss 1994; Contu 2000, 2003; Neville and Poumarat 2009).

Amanita sect. *Vaginatae* in Hungary and the benefit of national data to improve diversity knowledge

Despite their taxonomically challenging nature and their widespread occurrence in Hungary, little local data of species within the section *Vaginatae* were available, and no study on their taxonomy and phylogenetics was carried out before our work. These species are found in many habitats throughout the country, especially in hilly and mountainous forests dominated by tree species belong to the genera *Fagus*, *Quercus*, *Carpinus*, *Betula*, *Pinus* and *Picea*. Based on morphological identification, 15 taxa were documented from Hungary: *Amanita argentea*, *A. battarrae*, *A. umbrinolutea*, *A. beckeri*, *A. ceciliae*, *A. crocea*, *A. dryophila*, *A. friabilis*, *A. fulva*, *A. lividopallescens*, *A. lividopallescens* var. *tigrina*, *A. mairei*, *A. pachyvolvata*, *A. vaginata* and *A. vaginata* f. *alba* (Babos 1989; Rimóczi 1994; Pál-Fám 2002; Pál-Fám and Lukács 2002; Benedek and Pál-Fám 2006; Vasas and Locsmándi 2009; Lukács 2010; Albert 2011; Dima et al. 2013; Folcz et al. 2013), but so far these identifications have not been verified by molecular taxonomic methods.

Our comprehensive study revealed that Hungary hosts at least 25 species of *Amanita* section *Vaginatae* of which only eight taxa, *A. ceciliae* (partly as *A. inaurata*), *A. crocea*, *A. dryophila*, *A. friabilis*, *A. fulva*, *A. lividopallescens*, *A. battarrae* (as *A. pachyvolvata*) and *A. umbrinolutea* have previously been reported based on morphological species concept. As a result, we documented 17 species new to Hungary: *Amanita albogrisescens*, *A. alseides*, *A. calida*, *A. coryli*, *A. deflexa*, *A. fulvoides*, *A. griseofulva*, *A. herculis*, *A. huijsmanii*, *A. opaca*, *A. prudens*, *A. simulans*, *A. spadicea*, *A. suberis*, *A. sublividopallescens*, *A. subnudipes* and *A. supravolvata*.

The presence of *A. argentea*, *A. beckeri* and *A. mairei* based on the currently revised species concepts has not yet been confirmed from Hungary. The names *A. argentea* and *A. mairei* in earlier Hungarian publications most likely harbour a number of greyish *Vaginatae* species, but based on DNA sequence data, none of the two species occurs in Hungary to date. The hardwood-associated *A. argentea* and *A. huijsmanii* have commonly been confused until the epitypification of *A. argentea* in Hanss and Moreau (2020). Similarly, the *Pinus*-associated *A. mairei* and *A. supravolvata* have often been misinterpreted until the study of Hanss and Moreau (2020). In the literature, we can find two other cases of confusion: (i) between silvery species and grey species that are never silvery (e.g. *A. argentea* and *A. coryli*) and (ii) between silvery species and coloured species that are occasionally silvery (e.g. *A. argentea* and *A. albogrisescens*). Our study also confirmed that all Hungarian records of *A. beckeri* (Babos 1989) represent *A. fulvoides*. A fleshy species with orange pileus and whitish stipe is often recorded on calcareous soils under *Quercus* in Hungary under the name *Amanita crocea*, but originally this species is associated mainly with *Picea* or *Betula* in acidophilous habitats and has usually orange hues on stipe. Based on our sequence data, all Hungarian records identified as *A. crocea* from *Quercus* forests likely represents *A. subnudipes* (with a whitish stipe), a species described from deciduous woodlands from France (Romagnesi 1982, Tulloss 2000). The occurrence of *A. crocea* s. str. was confirmed based on one collection from the northern mountains under *Betula* and *Picea* (Figs. 3, 12b).

The wide morphological concept of *Amanita vaginata* is currently not fixed. This classical binomial appears in several distantly related lineages within sect. *Vaginatae* across the phylogenetic tree (Fig. 3). Our own records of white forms of *Vaginatae* species (often referred to *A. vaginata* f. *alba* or *A. alba*) represented multiple species belonging to *A. huijsmanii*, *A. griseofulva*, *A. opaca*, *A. coryli*, *A. magnivolvata* and *A. simulans*.

All previous records of *A. battarrae* turned out to be *A. umbrinolutea*, while the specimens of *A. pachyvolvata* represented more species including *A. battarrae* (syn.: *A. magnivolvata*), *A. spadicea* and *A. supravolvata*. Based

on the recent epitypification of *Amanitopsis vaginata* var. *battarrae* and *Amanitopsis pachyvolvata* by Hanss and Moreau (2022), and the type sequence of *A. magnivolvata* in Hanss and Moreau (2020), the three names are here established as synonyms. *Amanita battarrae* is associated with deciduous trees, while the other taxa are associated with conifers. Because Riel (1907) raised *Amanitopsis battarrae* to species rank, the legitimate name to be applied to this taxon is *Amanita battarrae* (Boud.) Bon. Finally, *Amanita lividopallescens* var. *tigrina* were synonymized with *A. lividopallescens* in Vizzini et al. (2016), we, however, recognized two distinct lineages where specimens with ‘lividopallescens’ morphology clustered (Fig. 3). *Amanita lividopallescens* was epitypified in Vizzini et al. (2016) with an ITS sequence. From the 13 Hungarian collections studied here, only three clustered in the clade where the epitype sequence occurred, and ten sequences clustered to another, sister clade which was recently described as *A. sublividopallescens* (Fig. 3) by Migliozi and Di Palma (2024). National records like in this study can help to improve larger-scale taxonomic and biodiversity knowledge when the data are included to an international collaboration.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11557-024-01974-0>.

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Data availability The datasets generated during and/or analysed during the current study are available in GenBank (<https://www.ncbi.nlm.nih.gov/>) and from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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