Diversity within the *Hygrophorus agathosmus* group (Basidiomycota, Agaricales) in Northern Europe

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Abstract

The North European species of the *Hygrophorus agathosmus* group in subsection *Tephroleuci* were studied. Three new species are identified based on morphology, ecology and sequence data. Two species are associated with *Pinus* spp. One of these is described here as *H. suaveolens*, while the other one is only known from one locality in the Nordic countries and seems to have a more South European distribution range. A closely related sister species to *H. agathosmus* is identified based on ITS sequence data, *H. cf. agathosmus*. It is confirmed to have an intercontinental distribution range and to be associated with *Picea* spp. probably on more acidic to neutral soil, whereas *H. agathosmus* s.s. has a more limited North-East European distribution range and occurs in older and rich *Picea abies* forests. A neotype for *H. agathosmus* is here selected from South Sweden. *Hygrophorus agathosmus* f. *albus* and *H. agathosmus* f. *aureofloccosus* are confirmed as forms. No genetic differences in the ITS region between specimens with grey cap colour and the two forms were observed. A key to the species in Northern Europe is provided.

Keywords Waxcap fungi · Host preference · Hygrophoraceae · Molecular systematics · Taxonomy

Introduction

The genus *Hygrophorus* Fr.: Fr includes species that form ectomycorrhizal associations with roots of trees and are mainly distributed in the temperate zones of the Northern Hemisphere (Tedersoo et al. 2010). Many species show strong host preferences, a character that has proved to be useful for separation of morphologically similar species (Larsson and Jacobsson 2004; Jacobsson and Larsson 2007). The genus is considered rather well-known with about 50 accepted species in Europe (e.g. Candusso 1997) and about 40 species in the Nordic countries (Kovalenko 2012; Larsson et al. 2011).

Lodge et al. (2014) revised the family *Hygrophoraceae* Lotsy and proposed a DNA-based classification of *Hygrophorus*. In this new classification, the subgenus *Colorati* (Bataille) E. Larss. was divided into three sections: *Olivaceoumbrini* (Bataille) Konrad & Maubl., *Pudorini* (Bataille) Konrad & Maubl. and *Aurei* (Bataille) E. Larss. Section *Olivaceoumbrini* is further divided into subsections *Olivaceoumbrini* (Bataille) Singer and *Tephroleuci* (Bataille) Singer.

The species in the *H. agathosmus* group belong to subsection *Tephroleuci* and are all united by having a sweetish smell reminiscent of bitter almonds, hyacinths, or bunch-flowered daffodil (*Narcissus tazetta*). The smell can be more or less pronounced depending on species. Traditionally, two species with a sweetish smell have been recognised in the Nordic countries: *H. agathosmus* (Fr.) Fr. which is common in moist, nutrient-rich and old forest stands of *Picea abies* and *H. hyacinthinus* Quél. (Fig. 1a), which is associated with *Picea abies* in herb-rich forests on calcareous soils (Kovalenko 2012). *Hygrophorus agathosmus* is wide-spread and often produces large amounts of basidiomata, even fairy rings in suitable habitats, while *H. hyacinthinus* is rare and in most Nordic countries a redlisted species, classified as endangered (EN) in Norway (Henriksen and Hilmo 2015) and Sweden (Gärdenfors 2010), and as vulnerable (VU) in Finland (Rassi et al. 2010).

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Fig. 1 Photos of species in *Hygrophorus* subsection *Tephroleuci*. **a** *H. hyacinthinus* (EL326-10). **b** *H. exiguus* (EL190-14). **c** *Hygrophorus* sp. (EL289-11). **d** *H. cf. agathosmus* (EL298-13). **e** *H. suaveolens* (Kleine14112501). **f** *H. pustulatus* (EL223-08)

A rather recently described species in subsection *Tephroleuci*, *H. exiguus* E. Larss., E. Campo & M. Carbone (Fig. 1b, Larsson et al. 2014), occurs in old growth *Picea abies* forests often in close association with *Tricholoma inamoenum* (Fr.) Gillet. The species is small, with a pileus rarely exceeding 3 cm in diameter and with a long stipe often deeply buried in the moss. In Northern Europe, it was probably overlooked because of the small basidiomata, growing in the same type of forests and having a similar smell of bitter almonds as *H. agathosmus*. The species was encountered and reported from Southern Europe under the name *H. odoratus* A. H. Sm. & Hesler (Bon 1990; Candusso 1997; Bidaud 2007), but the molecular data clearly shows that the two are separate species (Larsson et al. 2014).

Thorough analyses of sequence data of specimens from a wide, intercontinental geographic distribution Moreau et al. (2018) demonstrated an unexpectedly high genetic diversity within the yellow waxcap *H. hypothejus* Fr.: Fr. (section *Aurei*). The diversity could be correlated to geographic origin, ecology and host preferences. This suggests that the diversity and number of species within *Hygrophorus* may be higher than current estimations.

In this study, well-documented specimens from the *H. agathosmus* group from Northern Europe were sequenced

with the aim of further exploring the genetic diversity, host preferences and geographic distribution of species. In addition, specimens of the white form *H. agathosmus* f. *albus* Candusso and the form with yellow floccules at stipe apex and cap margin *H. agathosmus* f. *aureofloccosus* Bres. were sampled and their taxonomic status was evaluated.

Material and methods

Morphological data

The majority of the sequenced specimens in this study were collected by the authors. Additional specimens were received as loan from the herbaria UPS, TU, AMNH and MA. Permission to extract DNA and sequence the ITS region was granted. Abbreviation of herbaria follows Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>).

Macro-morphological characters and ecology were observed in the field, and fresh basidiomata photographed. Colour codes refer to Kornerup and Wanscher (1962). Micro-morphological characters were measured from dried material mounted in Congo red NH₃ solution at × 1000 magnification. Photos of micro-morphological characters were

made using Axioskop 2 (Zeiss, Oberkochen, Germany) light microscope and the AxioVision software (<http://www.zeiss.com/microscopy/int/home.html>). For each specimen, the length and width of a minimum of 30 spores were measured and the ratio calculated ($Q = \text{length/width}$). In addition, 10 basidia and sterigmata, as well as hyphae of trama, pilei- and stipitipellis, were measured.

Molecular data

Forty specimens from Northern Europe, Germany, Spain and Canada were targeted for sequencing. In addition, ITS and LSU sequence data of specimens from subsection *Tephroleuci* were included from previous studies (Larsson et al. 2014; Lodge et al. 2014). ITS sequences type was also blasted in GenBank (Clark et al. 2016) and the UNITE database (Köljalg et al. 2013) to search for additional data generated from curated specimens or from environmental samples as soil and ectomycorrhizae. In total, 12 sequences were found and added to the data set. Sequence data of *H. pustulatus* (Pers.) Fr. (Fig. 1f) was selected as out-group for rooting of trees. The species belongs in subsection *Tephroleuci* characterised by the greyish-brown colour of the cap and the non-viscid stipe but is odourless, lacking the characteristic sweetish smell of the *H. agathosmus* group (Kovalenko 2012).

Sequences from the complete internal transcribed spacer (ITS) region and about 900 base pairs (bp) of the 5' end of the large subunit (LSU) of the nuclear ribosomal DNA were generated. Protocols for DNA extraction, PCR and primers follow Larsson et al. (2018). The type specimens were extracted using a modified CTAB method and PCR and sequencing followed protocols described in Larsson and Jacobsson (2004).

Sequences were edited and assembled using Sequencher 5.1 (Gene Codes, Ann Arbor, Michigan). Alignment was performed using the L-INS-i strategy as implemented in MAFFT v. 7.017 (Kato and Standley 2013). The alignment was adjusted using Aliview 1.17.1 (Larsson 2014). Sequences generated for this study have been deposited in GenBank with accession numbers MH656439–MH656479. Specimens sequenced for this study are indicated with an asterisk (*) in the list of studied material and the GenBank number is specified.

For inferring phylogenetic relationships among species, heuristic searches were performed using the maximum parsimony method in PAUP* (Swofford 2003). All transformations were considered unordered and equally weighted. Variable regions with ambiguous alignment were excluded and gaps were treated as missing data. Heuristic searches with 1000 random-addition sequence replicates and TBR branch swapping were performed, saving at most 25 trees in each replicate. Relative robustness of clades was assessed by the

bootstrap method using 1000 heuristic search replicates with 10 random taxon addition sequence replicates and TBR branch swapping, the latter saving at most 100 trees in each replicate.

Bayesian analysis was carried out in MrBayes 3.2.6 (Ronquist and Huelsenbeck 2012), with a best-fit model of nucleotide evolution supplied by MrModeltest 2.2 (Nylander 2004). Eight default-setting Metropolis-Coupled Markov Chain Monte Carlo (MCMCMC) chains were run for 10 million generations with trees sampled every 5000 generations and an initial burn-in of 1000 trees. A 50% majority-rule consensus phylogram was computed from the remaining trees.

Results

The aligned complete dataset consisted of 65 sequences and 1521 characters. After exclusion of ambiguous regions, mainly from the beginning and the end of the data set 1474 characters remained for the analyses. Of these, 1338 were constant, 14 were variable but parsimony uninformative and 122 (8.3%) were parsimony informative. The maximum parsimony analysis yielded 9610 equally most parsimonious trees (length = 195 steps, CI = 0.8051 and RI = 0.9604). One of the trees is presented as a phylogram (Fig. 2).

The bootstrap analysis recovered seven terminal clades with low to strong bootstrap support and three single branches. The clades correspond to *H. agathosmus* (74%), *H. cf. agathosmus* (64%), *Hygrophorus* sp. (100%), *H. hyacinthinus* (100%), *H. suaveolens* (97%), *H. exiguus* (100%) and *H. odoratus* (86%). The single branch with sequence data from a mycorrhizal study on *Arbutus menziesii* originating from North America is recovered close to *H. agathosmus*. The sequence named *H. morrisii* Pk. and the sequence data originating from a soil sample of *Pinus* from Mexico both were recovered close to *H. odoratus* with strong support (Fig. 2).

As suggested by MrModeltest, the nucleotide evolution model HKY + G was used for the ITS1 spacer, K80 was used for the 5.8S gene and GTR + I was used for the ITS2 spacer and LSU region in the Bayesian analysis. The MCMC analysis converged well in advance of the burn-in threshold and chain mixing was found to be satisfactory, as assessed by using Tracer v1.5 (Drummond et al. 2012). In the Bayesian analysis, the same terminal clades were recovered as monophyletic with support as in the bootstrap analysis, except that the clade *H. cf. agathosmus* collapsed within the major clade of *H. agathosmus* s. l. The Bayesian tree topology is similar to the MP bootstrap tree. BPP values are indicated on corresponding branches (Fig. 2).

The specimens identified in the field as *H. agathosmus* f. *albus* clustered in both the *H. agathosmus* and *H. cf.*

◀ **Fig. 2** Phylogram showing the phylogenetic relationships among the species in *Hygrophorus* subsection *Tephroleuci*, based on ITS and LSU sequence data. Bootstrap values and Bayesian Posterior Probabilities are indicated on branches. Clades discussed in the text are indicated with bars and species epithets. Sequences originating from type specimens are marked

agathosmus clades and also the specimens of *H. agathosmus* f. *aureofloccosus* clustered in the *H. agathosmus* clade (Fig. 2) suggesting they are just colour forms.

Taxonomy

Hygrophorus agathosmus (Fr.) Fr., *Epicr. syst. mycol.*: 325 (1838) Figs. 4a–c

- ≡ *Agaricus agathosmus* Fr., *Observ. mycol.* 1: 16 (1815)
- ≡ *Hygrophous agathosmus* (Fr.) Fr., *Epicr. syst. mycol.*: 325 (1838) f. *agathosmus*
- ≡ *Hygrophous agathosmus* (Fr.) Fr., *Epicr. syst. mycol.*: 325 (1838) var. *agathosmus*
- ≡ *Limaceum pustulatum* var. *agathosmum* (Fr.) P. Kumm. Führ Pilzk.:119 (1871)
- ≡ *Limaceum agathosmum* (Fr.) Wünsche, *Die Pilze*: 116 (1877)
- = *Agaricus cerasinus* Berk., *Engl. Fl. Fungi* 5(2): 12 (1836)
- = *Hygrophorus cerasinus* (Berk.) Berk., *Outl. Brit. Fung.*: 197 (1860)
- = *Hygrophous agathosmus* f. *aureofloccosus* Bres., *Iconogr. Mycol.* 7:tab. 320 (1928)
- = *Hygrophous agathosmus* var. *aureofloccosus* (Bres.) A. Pearson & Dennis, *Trans. Br. mycol. Soc.*, 31(3–4): 163 (1948)
- = *Hygrophous agathosmus* f. *albus* Candusso, *Fungi europ.* 6:104 (1997)

Original diagnosis 1815:

Agaricus agathosmus, pileo convexiusculo carnosio papilloso suaveolenti, cinereo, lamellis albis decurrentibus, stipite folido albo. In silvis abietinis densis, una cum Ag. inamoeno, sed rarior. Septembr. Octobr.

Descr. Stipes solidus 2 uncialis crassit. pennae anserinae aequalis glaber basi albido pubescens laevis albus rectus, raro curvatus, elasticus, demum cavus. Variat sursum subattenuatus et squamuloso-pubescens. Pileus carnosus convexus demum planiusculus 1–1½ unc., interdum subviscosus, papillis minutissimis dilutioribus obsitus. Lamellae albae 2-natae decurrentes distinctae latiusculae. Odor gratissimus.

Diu pro varietate Agar. pustulati P. habui, a quo caractere aegre distinguitur, sed odore gratissimo, colore et magnitudine satis differre videtur. Ceterum nullo modo Ag. eburneo affinis, ut de fungo hoc attulerunt observatores diligentissimi de Albertini et de Schweiniz. - Noster Ag. fragranti potius affinis et hinc summa differentia apparet!

When Fries described *Agaricus agathosmus* (Fries 1815), he did not refer to any painting, drawing or authentic material and he regarded *A. agathosmus* as a rather rare species. Later (Fries 1838, as *Hygrophorus*), he emended the description to partly include *H. pustulatus*, but still characterised the species as having a pleasant smell of aniseed. In Fries herbarium (UPS), two collections of *H. agathosmus* are preserved: one from the Presovsky area (Slovakia) collected by Kalchbrenner but not dated, and the other from Tammela, Finland, collected by Karsten and dated 2 October 1869. Obviously, none of them were at hand when Fries described the species. In the Uppsala, herbarium there is also a painting of *H. agathosmus*, signed by Fries (No. 737) and dated 21 September 1856 (Strid 1994). This painting is certainly representative for the species (Fig. 3). Since no material suitable for lectotypification is known, we have to select a neotype. For this, we then prefer recently collected material with a photo of fresh basidiomata from which we have been able to generate genetic information.

Emended description:

Neotype (designated here): *MykoBank* no.: MBT383487

SWEDEN: Öland, Böda, Trollskogen NR, herb-rich, mixed coniferous forest, 5 Oct 2017, E. Larsson 398-17 (GB-0159607!), isoneotype UPS, GenBank Acc. No. MH656445)

Pileus 30–50 (– 80) mm wide, campanulate, obtusely conical with involute margin when young, soon becoming plano-convex, applanate, with a broad umbo or slightly depressed with age, grey to greyish-brown, usually slightly paler towards the margin, margin whitish or yellowish, finely fibrillose, pale or completely white pileus forms common, glabrous, minutely fibrillose at centre, when moist viscid. *Lamellae* arcuate, subdecurrent to short-decurrent, *L* = 35–60, distant to subdistant, thick, waxy, with lamellulae, intervenose, white, sometimes with a pale greyish or pinkish tint. *Stipe* up to 5–8 × 0.5–1.5 cm, cylindrical, slightly clavate, tapering towards the base, whitish with floccules especially in the upper half, with age pale greyish, at apex with white or sometimes yellow floccules. Context whitish, taste mild, smell strong, sweetish like bitter almonds. Spore deposit white.

Spores [*n* = 159] elliptical, oblong to ovoid, with a distinct obtuse hilar appendage, smooth, hyaline, inamyloid, (8.6–) 9.4–9.6–9.8 (– 11.0) × (4.9–) 5.6–5.7–5.9 (– 6.4) μm, average *Q* = 1.64–1.69–1.73. *Basidia* mainly 4-spored, narrowly clavate, 40–55 × 7–9 μm, sterigmata 6–7.5 μm long. *Hymenophoral trama* bilateral to slightly divergent composed of interwoven cylindrical hyphae 5–8 μm wide and thin-walled inflated hyphae with terminal cells up to 20 μm wide.

Pileipellis an ixotrichoderm up to 400 μm thick; made up of loosely arranged interwoven, branched hyphae 3.5–7 μm wide, in matrix smooth, intracellularly pigmented. *Subpellis* composed of densely arranged, interwoven hyphae up to 15 μm broad.

Fig. 3 Fries painting no. 737 of *Hygrophorus agathosmus*, signed 21/9, 1856, deposited in Herbarium UPS. (Photo: Jan Nilsson)

Stipitipellis a cutis, up to 60 μm thick, made up of 3–5 μm wide loosely interwoven branched hyphae with scattered free ends, smooth, hyaline. *Stipititrama* composed of hyaline more or less parallel hyphae 8–14 μm wide. *Floccules* at apex made up of compact erect branched hyphae, 3.5–6.0 μm wide, loosely scattered free ends cylindrical or slightly enlarged, up to 8 μm wide.

Clamp connections present in all tissues.

Ecology and distribution Associated with *Picea abies* usually on nutrient-rich soil in moist herb-rich forests. Confirmed sequence specimens were all collected from old-growth forests, most of them situated on more or less calcareous soils. Other species found on the same localities are *H. piceae*, *H. discoideus*, *Tricholoma inamoenum*, *Sarcodon imbricatus* and *Lactarius scrobiculatus*. The sequenced specimens originate from Estonia, Finland, Norway, Russia and Sweden (Fig. 4).

Material studied *Hygrophorus agathosmus* ESTONIA: Saare, Kärla, Sauvere, mixed forest on calcareous soil, 3 Sep 2007, leg. V. Liiv, det. E. Larsson (*TU106100, MH656442); Saare, Lümada, Audaku, Viidumäa NR, spruce forest, 4 Sep 2007, leg. V. Liiv, det. V. Liiv (*TU106085, MH656443).

FINLAND: Etälä-Hämä, Lammi, rich, mixed coniferous forest with *Picea abies* and *Corylus avellana*, 2 Sep 2000, leg. E. Larsson 1-00, det. E. Larsson (GB-0150351). NORWAY: Telemark, Bamble, Røsskleiva, mixed coniferous forest on calcareous soil dominated by *Picea abies*, *Corylus avellana*, *Pinus sylvestris*, 10 Oct 2015, leg. E. Larsson, M. Jeppson, det. E. Larsson (*EL191-15, MH656454). SWEDEN: Bohuslän, Tossene, Anneröd Hogsäm NR, in grass under *Picea abies*, 19 Oct 2013, leg. E. Larsson, det. E. Larsson (*EL429-13, MH656455); Dalsland, Skållerud, Häverud, Östebo Ö, herb-rich coniferous forest with *Picea abies* and *Corylus avellana*, 17 Sep 2011, leg. E. Larsson, A. Stridvall, S. Jacobsson, det. E. Larsson (*EL249-11, MH656452); Gotland, Ardre, Ollajvs NR, moist *Picea abies* forest on calcareous soil with *Quercus robur*, *Betula pendula* and *Corylus avellana*, 27 Sep 2010, leg. E. Larsson, A. Stridvall, S. Jacobsson, det. E. Larsson (EL327-10, KJ720195); Ibidem, (*EL345-10, MH656446); Gotland, Dalhem, Malmskogen, moist coniferous forest on calcareous soil, 30 Sep 2011, leg. E. Larsson, det. E. Larsson (*EL331-11, MH656453); Medelpad, Sättna, 2–3 km V. Västmansjö, old-growth forest with *Picea abies*, 27 Sep 2003, leg. S. Muskos 03-10, det. S. Muskos (GB-0076510, KJ720194); Närke, Axberg, Kvinnerstatorp, *Picea abies* dominated mixed forest on

calcareous ground with *Populus tremula* and *Betula pendula*, 10 Sep 2008, leg. E. Larsson, det. E. Larsson (*EL110-08, MH656450); Västergötland, Medelplana, Eriksberg, moist *Picea abies* forest, 19 Sep 2012, leg. E. Larsson, det. E. Larsson (*EL229-12, MH656456); Västergötland, Skepplanda, Slereboåns dalgång NR, 16 Sep 2012, leg. E. Larsson, det. E. Larsson (*EL194A-12, MH656447); Öland, Böda, Trollskogen NR, herbrich mixed coniferous forest on sand, 5 Oct 2017, leg. E. Larsson, det. E. Larsson (*EL398-17, MH656445).

Hygrophorus agathosmus f. *albus* FINLAND: Etelä-Häme, Lammi, rich, mixed coniferous forest with *Picea abies* and *Corylus avellana*, 2 Sep 2000, leg. E. Larsson, det. E. Larsson (*EL2-00, GB-0150352, MH656440). NORWAY: Akershus, Nesodden, Torvet, Sörby S, rich, mixed coniferous forest with *Picea abies* and *Corylus avellana*, 11 Sep 2010, leg. E. Larsson, det. E. Larsson (*EL304–10, MH656439). SWEDEN: Bohuslän, Tossene, Anneröd Hogsäm NR, in grass under *Picea abies*, 19 Oct 2013, leg. E. Larsson, det. E. Larsson (*EL430-13, MH656449); Gotland, Viklau, Tjaukle, grazed, mixed *Picea abies* forest, 30 Sep 2011, leg. G. Gyða Eyjólfssdóttir, det. E. Larsson (*GB-0107410, MH656448); Västergötland, Husaby, coniferous forest on calcareous soil, 13 Sep 1980, leg. L. & A. Stridvall, LAS80-409, det. L. Stridvall (*GB-0063990, MH656441).

Hygrophorus agathosmus f. *aureofloccosus* NORWAY: Buskerud, Drammen, between Landfallstjern and Myrdammen, spruce forest, 19 Sep 2017, leg. G. Gulden, det. G. Gulden, E. Larsson (*GG6-17, MH656444). SWEDEN: Gotland, Tofta, Smågårde, mixed coniferous forest on sand, under *Picea abies*, 28 Sep 2010, leg. E. Larsson, A. Stridvall, S. Jacobsson, det. E. Larsson (*EL368-10, MH656451).

***Hygrophorus suaveolens* Kleine & E. Larss. sp. nov.**
Figs. 1e and 5a–f

Mycobank No.: MB827920

Holotype: Sweden, Uppland, Heliga trefaldighet, Malma Bergsvägen 26, managed meadow area with *Picea abies* and *Pinus sylvestris*, 16 Nov 2017, leg. M. Iwarsson & M. Krikorev, det. M. Krikorev & E. Larsson 448B-17 (GB-0159606), isotype UPS, GenBank Acc. No. MH939180).

Etymology: Refers to the sweetish smell of bitter almonds.

Diagnosis: Small- to medium-sized species fruiting from October to December, in the central to northern parts of Europe. Resembles *H. agathosmus* but differs by the smaller basidiomata, a darker olive-brown disc zone on the pileus, and by being associated with *Pinus* spp. on acid to neutral soils.

Pileus 20–35 (–50) mm broad, campanulate, obtusely conical with involute margin when young, soon becoming applanate, with a broad umbo or slightly depressed,

sometimes becoming crenulate at margin, grey-brownish (5:3E, 5:4D) to somewhat olive-brownish (4:4F, 4:5F) in the centre, distinctly paler towards the margin, becoming more uniformly grey when drying, when moist viscid. **Lamellae** arcuate, subdecurrent to decurrent, $L = 18–44$, distant to subdistant, thick, waxy, with lamellulae, white, sometimes with a pale incarnate tint in young basidiomata. **Stipe** up to $5–8 \times 0.5–1$ cm, cylindrical, slightly clavate or tapering towards the base, fragile, glutinous when young, remaining distinctly viscid when old, first whitish with floccules especially at the top, later pale greyish brown to brownish and less pronounced flocculose. **Context** whitish, taste mild, smell sweetish reminding of bitter almonds, similar to *H. agathosmus*. Spore deposit white.

Spores [$n = 190$] elliptical to ovoid, sometimes with a suprahilar depression, more rarely subamygdaliform, with a distinct obtuse hilar appendage, smooth, hyaline, inamyloid, $(8.4–) 9.6–9.9–10.1 (–11.2) \times (4.9–) 5.8–5.9–6.0 (–6.4) \mu\text{m}$, average $Q = 1.61–1.68–1.73$. **Basidia** mainly 4-spored, narrowly clavate, $45–60 \times 8–10 \mu\text{m}$, sterigmata $6–8 \mu\text{m}$ long. **Hymenophoral trama** bilateral to slightly divergent, composed of interwoven cylindrical hyphae $4–8 \mu\text{m}$ wide and thin-walled inflated hyphae with terminal end cells up to $20 \mu\text{m}$ wide.

Pileipellis an ixotrichoderm up to $300 \mu\text{m}$ thick; made up of loosely arranged interwoven, branched hyphae $1.5–5 \mu\text{m}$ wide, in matrix smooth, hyaline or intracellular pigmented, upper layer with incrustated pigmented hyphae. In water and carbol fuchsin with visible small droplets on hyphae. **Subpellis** composed of densely arranged, sub-parallel interwoven hyphae up to $17 \mu\text{m}$ broad.

Stipitipellis a cutis, up to $50 \mu\text{m}$ thick, made up of $5–8 \mu\text{m}$ wide interwoven branched hyphae, with scattered free ends, smooth, hyaline, or with intracellular pigments. **Stipititrampa** of hyaline more or less parallel interwoven hyphae $6–12 \mu\text{m}$ wide. **Floccules** at apex made up of compact erect branched hyphae, $3.5–5 \mu\text{m}$ wide, loosely scattered free ends, cylindrical or slightly enlarged up to $7 \mu\text{m}$ wide. In water and carbol fuchsin, with small visible droplets on hyphae.

Clamp connections present in all tissues.

Ecology and distribution Growing solitary or in groups under *Pinus sylvestris* and *Pinus nigra*. Fruiting late in the season from October to December. So far confirmed from Germany and Sweden. However, sequence data from environmental soil samples originating from Canada suggest that the species also occurs in North America (Fig. 5).

Material studied GERMANY: Sachsen, Markkleeberg, Neue Harth Süd, reforestation area with *Pinus nigra*, 20 Nov 2007, leg. J. Kleine 07112001, det. J. Kleine and E. Larsson (*GB-0159604, MH656475); Ibidem, 27 Nov 2014, leg. J. Kleine 14112,01, det. J. Kleine and E. Larsson (*GB-0159602,

MH656477); Ibidem Markkleberger See, reforestation area with *Pinus nigra* and *P. sylvestris*, 25 Nov 2014, leg. J. Kleine 1411201, det. J. Kleine and E. Larsson (*GB-0159603, MH656476). SWEDEN: Uppland, Heliga trefaldighet, Malma Bergsväg 26, managed meadow garden with *Picea abies* and *Pinus sylvestris*, 2 Dec 2014, leg. M. Iwarsson, det. E. Larsson (*GB-0159605, MH656478); Öland, Persnäs, Jordhamn, under *Pinus sylvestris* on sandy soil, 8 Dec 2017, leg. Jan Olsson, det. E. Larsson (*GB-0159600, MH656473); Ibidem, Algutsrum, S. om Törnbotens stugby, in grass under *Pinus sylvestris*, 31 Oct 2015, leg. M. Jeppson (MJ10154) and A. Molia, det. E. Larsson (GB-0159601); Västergötland, Göteborg, Högsbatorp, under *Pinus sylvestris*, 18 Nov 2016, leg. Anders Aronsson, det. E. Larsson 390-16, (*GB-0159609, MH656474).

Additional material studied *Hygophorus* aff. *agathosmus*. CANADA: Quebec, L'Islet Co., St. Aubert, 20 Sep 1963, leg. J.W. Groves, det. J.W. Groves (UPS F-528300, MH656464); Newfoundland, mixed coniferous forest, 28 Sep 2012, leg. J. Graham, det. J. Graham (*MH656463). NORWAY: Trøndelag, Steinkjer, Skratåsén, mixed forest with *Picea abies*, 5 Sep 2009, leg. E. Larsson, M. Jeppson, det. E. Larsson, M. Jeppson (*EL179-09, MH656458); Troms, Storfjord, Lulledalen, close to Mullejokka, mixed coniferous forest on calcareous soil, under *Picea abies*, 30 Aug 2013, leg. E. Larsson, K. Bendiksen, J. Vauras, det. E. Larsson (*EL294-13, MH656460). SWEDEN: Lule Lappmark, Jokkmokk, Kassavare, moist mixed coniferous forest with *Picea abies*, *Betula pendula*, *Pinus sylvestris*, 1 Sep 2011, leg. E. Larsson, det. E. Larsson (*EL175-11, MH656462); Ibidem, Sitoättno, mixed *Picea abies* dominated forest, 31 Aug 2011, leg. E. Larsson, A. Dahlberg, S. Lund, det. E. Larsson (*EL160-11, MH656459); Lycksele Lappmark, Tärna, Voitatjaure, mixed coniferous forest, 21 Aug 2015, leg. Nico Dam, det. E. Larsson (*EL141-15, MH656467); Öland, Böda, Kesnäsudden, grazed meadow area with *Pinus sylvestris* and *Picea abies*, 5 Oct 2017, leg. E. Larsson, det. E. Larsson (*EL384-17, MH656457).

Hygophorus aff. *agathosmus* f. *albus*. ICELAND: Vaglaskógur Fnóadal, Arnpórslunur, under *Picea* and *Betula*, 13 Sep 2009, leg. G.G. Eyjólfsdóttir, det. G.G. Eyjólfsdóttir (*AMNH-185145, MH656461). DENMARK: Lolland, Fuglsang Storskov, under *Picea abies*, 3 Oct 2007, leg. E. Larsson, det. E. Larsson (*EL134-07, MH656465); Sjælland, Store Dyrehave S of Hillerød, under *Picea abies*, 10 Nov 1999, leg. B.T. Olsen, det. B.T. Olsen (*C-F41536, MH656466).

Hygophorus sp. SPAIN: Madrid, Zarzalejo, Puerto de la Cruz Verde, en humus de *Pinus sylvestris* y *P. pinaster*, leg. F. Prieto, A. González & et al., det. F. Prieto (*MA-F74970, MH656469). SWEDEN: Gotland, Gammelgarn, Danbo, Sjausrå, sandy heathland with *Pinus sylvestris*, 27 Sep 2011,

leg. E. Larsson, A. Stridvall, S. Jacobsson, det. E. Larsson (*EL289-11, MH656468).

Hygophorus hyacinthinus. SLOVAKIA: Banskobystrický Kraj, Muránska Planina NP, Murán, Velka Lúka, Sedo Javorinko, rich mixed *Picea* forest, 10 Oct 2008, leg. E. Larsson, I. Kautmanova, M. Jeppson, det. E. Larsson (EL259-08, KJ720191). SWEDEN: Gotland, Ardre, Ollajvs NR, moist *Picea abies* forest on calcareous soil with scattered *Quercus robur*, *Betula pendula* and *Corylus avellanea*, 27 Sep 2010, leg. E. Larsson, A. Stridvall, S. Jacobsson, det. E. Larsson (*EL326-10, MH656470); Medelpad, Matfors, rich forest with *Picea abies* on calcareous ground, 30 Aug 1995, leg. S. Muskos, det. S. Muskos (GB-0124675, HM143012).

Hygophorus exiguus. FINLAND: Koillismaa, Kuusamo, Oulanka NP, Ampumavaara, in moist *Picea abies* dominated mixed forest, 18 Aug 2009, leg. F. Calleda, E. pini, G. Boerio, M. Carbone, det. E. Campo, M. Carbone, E. Larsson (TUR-A190791!, KJ720198). ITALY: Lombardia, Bergamo, Schilpario, in mossy mixed *Picea abies* and *Abies alba* forest, 6 Aug 2011, leg. Mantovani, Calleda (GB-0179914, KJ720200). SWEDEN: Västerbotten, Degerfors, Klubbrännan, in old-growth forest with *Picea abies*, 26 Aug 2011, leg. N. Dam, det. N. Dam, E. Larsson (GB-0179915, KJ720199); Medelpad, Borgsjö, Gammelbodarna, mixed grazed forest with *Picea abies*, 25 Aug 2010, leg. E. Larsson, A. Stridvall, S. Jacobsson, leg. E. Larsson (*EL187-10, MH656472); Västergötland, Skepplanda, Slereboåns dalgång NR, moist old-growth forest with *Picea abies*, 21 Sep 2014, leg. E. Larsson, K-H Larsson, det. E. Larsson (*EL189-14, MH656471).

Hygophorus occidentalis. USA: Michigan, Ann Arbor, Saginaw Forest, Ann, 8 April 1936, leg. Smith, det. Smith (*TENN10197!, MH656479).

Hygophorus odoratus. USA: Oregon, Paradise Park, Mt. Hood, Clackamas Co., 20 Oct 1947, leg. A.H. Smith 28387 (MICH54605!, KJ720193); Mile Bridge, Mt. Hood Nat. Forest, 26 Oct 1947, leg. A.H. Smith 28300 (MICH28300, KJ720192).

Hygophorus pustulatus. DENMARK: Lolland, Guldborgsund, Fuglsang, 3 Oct 2007, leg. E. Larsson, det. E. Larsson (EL130-07_KJ720196). SLOVAKIA: Banskobystrický Kraj, Veporské vrchy Mts, Cierny Balog, Dobrocsky prales Nature Reserve, 7 Oct 2008, leg. E. Larsson, det. E. Larsson (EL223-08, KJ720197).

Key to the North European species in subsection *Tephroleuci*

Cap colour white, grey to greyish-brown. Veil absent or fragmentary. Stipe not viscid or at most slightly viscid, usually mat when dry.

- 1. Smell distinctly sweetish 2
- Smell indistinct *H. pustulatus*

Fig. 4 *Hygrophorus agathosmus*. **a** Basidiomata of the neotype (EL398-17, GB-0159607). **b** Basidiomata of a white form *H. agathosmus* f. *albus* (EL430-13). **c** Yellow floccules at stipe apex of *H. agathosmus* f. *aureofloccosus* (GG6-17, photo: Gro Gulden)

- 2. Smell of *Hyacinthus* or *Narcissus tazetta*; with *Picea* on calcareous soils; rare *H. hyacinthinus*
- Smell of bitter almonds 3
- 3. Pileus rarely exceeding 2.5–3 cm in diameter; with *Picea*; usually deep in moss/needle mat; often close to *Tricholoma inamoenum* *H. exiguus*
- Pileus on average larger to much larger than 2.5–3 cm in diameter 4
- 4. Pileus white *H. agathosmus* f. *albus* or *H. cf. agathosmus* (white form)
- Pileus grey to greyish brown 5
- 5. With *Pinus* 6
- With *Picea* 7
- 6. On calcareous soil; pileus colour uniformly greyish brown *Hygrophorus* sp.
- On more acid to neutral soil; pileus with distinct darker disc *H. suaveolens*
- 7. Usually in rich old-growth forest 8
- Usually on more acid to neutral soils *H. cf. agathosmus*

- 8. Floccules at stipe apex white *H. agathosmus*
- Floccules at stipe apex yellow *H. agathosmus* f. *aureofloccosus*

Discussion

Despite forming mycorrhiza, *Hygrophorus* sequences are surprisingly rare in metabarcoding studies of forest soils and therefore to a large extent missing from public database repositories. Compared to many other groups of ectomycorrhizal fungi information on genetic variation, distribution range and occurrence of *Hygrophorus* species are scanty. With increased sequencing of herbarium collections, new information on species diversity, ecology and distribution will become available (Moreau et al. 2018).

We identified seven clades within subsection *Tephroleuci*, all representing species having the characteristic sweetish smell. Three other sequences downloaded from public

databases seem to represent additional taxa. One sequence identified as *H. morrisii* and originating from North America and another sequence generated from ectomycorrhiza of *Pinus* from Mexico are sister taxa to *H. odoratus*. The third sequence was generated from ectomycorrhizae of *Arbutus menziesii* originating from North America and is recovered as a sister taxon to *H. agathosmus* (Fig. 2). This suggests that at least ten species are present within the group. Six clades represent species that occur in Northern Europe, *H. agathosmus* (Fig. 4a), *H. cf. agathosmus* (Fig. 1d), *Hygrophorus* sp. (Fig. 1c), *H. hyacinthinus* (Fig. 1a), *H. suaveolens* (Figs. 1e, 5a) and *H. exiguus* (Fig. 1b). So far, *H. odoratus* is not

confirmed from Europe. The three identified new species, here named *H. cf. agathosmus*, *H. suaveolens* and *Hygrophorus* sp. all have the same sweetish smell of bitter almonds and the name *H. agathosmus* has probably been applied to all of them.

Sequences of *H. agathosmus* specimens associated with *Picea* spp. are in the maximum parsimony tree split into two supported sister clades, while in the Bayesian tree the branch to the cf. agathosmus clade collapses (Fig. 2). This is surprising since the clades differ by one substitution and three 1–4 bp insertion/deletion events in the ITS1 region and one substitution and two 3 bp insertion/deletion events in the ITS2 region.

Fig. 5 *Hygrophorus suaveolens*. **a** Basidiomata of the holotype (EL448B-17, GB-0159606). **b** Basidia and spores from the lamellae edge. **c** Floccules at stipe apex, with spores among the scattered terminal hyphae. **d** Pilpeipellis hyphae with droplets, stained with carbol fuchsin. **e** Spores close to hymenium. **f** Inflated hyphae in the lamella trama

The status of this taxon will be further studied, but in this paper we provisionally treat it at species level. *Hygrophorus agathosmus* s.s. is here neotypified with a collection from South Sweden, thus defining the name in accordance with the description by Fries. This genotype seems to be restricted to Europe, with its main distribution in the north-eastern parts, and is confirmed from Fennoscandia, Estonia and Russia, always associated with *Picea abies* in nutrient-rich old-growth forests on moist and often also calcareous ground.

Hygrophorus cf. *agathosmus* (Fig. 5d) is in morphology very similar to *H. agathosmus* s.s. but seems to have a much wider distribution range and is present in both Europe and North America. In Europe, it is here confirmed from Denmark, Estonia, Norway and Sweden. In Northern Europe, it seems to have its main distribution in the northern and western parts and was even collected from a *Picea abies* plantation on Iceland. The sequenced Canadian specimens misidentified as *H. occidentalis* A.H. Sm. & Hesler are nested within this clade. We studied the isotype of *H. occidentalis* (TENN) and generated an ITS2 sequence. Although the species has a greyish cap like *H. cf. agathosmus*, it differs in micromorphology e.g. by smaller spores (7.2–) 8.0 (– 8.8) × (3.8–) 4.5 (– 5.0) μm, average $Q = 1.78$. Smith and Hesler (1939) placed the species in subsection *Fuliginei* and said it was associated with oak-pine woods and lacking a specific smell. The sequence data suggest an affinity to *H. eburneus* (Bull.) Fr. An older name to consider for this clade is *H. cerasinus* (Berk.) Berk. which has been synonymized with *H. agathosmus* (e.g. Hesler and Smith 1963). The species is described as having an odour exactly like the leaves of *Prunus laurocerasus*, a pleasant smell of bitter almonds. However, *H. cerasinus* was collected in a fir plantation, suggesting it may also be a name to consider for *Hygrophorus* sp.

Two specimens from the limestone islands in the Baltic Sea (Gotland, Sweden and Saaremaa, Estonia) generated sequences that cluster with a sequence from a Spanish specimen determined to *H. agathosmus*. All three specimens were associated with *Pinus* spp., and the clade is here named *Hygrophorus* sp. (Fig. 2). The species is clearly distinct in both sequence data and morphology, with a darker and more even greyish brown pileus (Fig. 5c). This so far unnamed species may have a predominantly South European distribution and will be dealt with in a separate paper.

Hygrophorus suaveolens was first identified from a reforestation area of a former strip-mining pit in North Western Saxony, Germany, replanted with *Pinus nigra*. It is characterised by the rather small basidiomata, with a pileus that is greyish brown with a darker central disc and often becomes crenulate at margin (Fig. 5a). Moreover, parts of the pileipellis and stipitipellis hyphae are densely covered with conspicuous droplets, which are easily observed in water and can be stained with carbol fuchsin (Fig. 5d), but completely disappear in Congo red NH₃ KOH or SDS solutions. Nevertheless, similar droplets, but considerably

smaller and less conspicuous, can also be observed in *H. agathosmus*. More recently, *H. suaveolens* was also observed in several localities in Sweden, always under *Pinus sylvestris*, very late in the season and often affected by frost. It is seemingly rare but might have been overlooked because of the late-season fruiting and because it is reminiscent of *H. agathosmus*. Three sequences from a soil environmental study of *Picea mariana* in Alaska were retrieved from GenBank. These sequences are nested within the *H. suaveolens* clade with strong support (Fig. 2), suggesting that *H. suaveolens* or a closely related species occurs in North America. The two genotypes differ by four to five insertion/deletion events throughout the ITS region. No collections were available for morphological comparisons.

Different forms and varieties of *H. agathosmus* have been described and here we can confirm that white forms of both *H. agathosmus* (Fig. 4b) and *H. cf. agathosmus* are rather common (Fig. 2), and that no sequence variation within the ITS region has been observed in comparison with grey forms. White and grey forms often fruit in the same forest, but probably develop from different mycelia. Intermediate forms, having basidiomata with pale grey pileus, are also frequently observed. The white form of *H. agathosmus* can easily be mistaken for *H. piceae* Kühner, and probably many such collections are deposited under the wrong name in our herbaria. By checking the presence of the sweetish bitter almond smell in fresh basidiomata such mistakes can easily be avoided.

The occurrence of bright yellow floccules on pileus margin and at stipe apex (Fig. 4c) is confirmed in *H. agathosmus* (Fig. 2). However, no specimen of *H. cf. agathosmus* with yellow floccules was included in this study and, thus, the occurrence of such colour form in the latter taxon could not be confirmed. One specimen included in this study was completely white and with yellow scales (GG6-17) and was thus macro-morphologically reminiscent of *H. chrysodon* (Batsch) Fr. However, the sweetish smell of bitter almonds is always present, making it rather easy to separate it from *H. chrysodon*.

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