Mycol Progress (2017) 16:47–62
DOI 10.1007/s11557-016-1249-x

ORIGINAL ARTICLE

Circumscription of species in the *Hodophilus foetens* complex (Clavariaceae, Agaricales) in Europe

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Received: 22 September 2016 / Revised: 17 November 2016 / Accepted: 22 November 2016 / Published online: 12 December 2016

Abstract Four European *Hodophilus* species with an odour similar to naphthalene, a strong unpleasant odour similar to that of mothballs, are recognized based on sequence and/or morphological data. The traditional concept defines *Ho. foetens* as the only *Hodophilus* species with a naphthalene odour in Europe. This name is now assigned to one of the studied species based on morphological examination of the holotype specimen. A recently collected specimen is proposed as the epitype. The other three species with a naphthalene odour are described here as new: *Ho. pallidus*, *Ho. subfoetens* and *Ho. tenuicystidiatus.* They are distinguishable in the field based on a combination of lamellae number and colour of basidiomata. All four species are grouped in the *Ho. foetens* superclade, one of two superclades, together with the *Ho. micaceus* superclade, in the genus *Hodophilus*. All are different species from North American taxa with a naphthalene-like odour recognised in a previous study. The *Ho. foetens* superclade also includes one species identified as *Ho. atropunctus* that does not have a distinctive odour. The type collection of *Ho. alboflocccipes*, a recently described European species with a naphthalene odour, is placed together with some collections without a distinctive odour in the *Ho. micaceus* superclade.

Section Editor: Zhu-Liang Yang

Electronic supplementary material The online version of this article (doi:10.1007/s11557-016-1249-x) contains supplementary material, which is available to authorized users.

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Keywords Agaricoid · *Camarophyllopsis* · Multi-locus phylogeny · Morphology · Type studies

Introduction

Hodophilus foetens (W. Phillips) Birkebak and Adamčík is a gilled member of the family *Clavariaceae* Chevall. (Birkebak et al. 2016). It had been previously included within the genera *Hygrophorus* Fr. (Dennis 1953; Singer 1959; Hesler and Smith 1963) and *Camarophyllopsis* Herink (Boertmann 2012; Kovalenko et al. 2012). The species is the type of the genus *Hodophilus* R. Heim ex R. Heim that is characterized by a hymeniderm pileipellis composed of globose, obpyriform to sphaeropedunculate terminal elements and absence of clamp connections (Birkebak et al. 2016). It is traditionally recognised as the sole European species with an unpleasant strong odour (Boertmann 2012) variously interpreted as similar to that of *Tricholoma sulphureum* (Bull.) P. Kumm. or *Thelephora palmata* (Scop.) Fr. (e.g. Phillips 1878; Heim 1969; Moser 1978): strong, fetid, gas-like (Boertmann 2012) or naphthalene-like (Courtecuisse and Duhem 1994). This odour is the main distinguishing character for the species in Europe. For the odour terminology we follow Ghyselinck (2003) and Adamčík et al. (2016) who analysed odour descriptions of *Ho. foetens* by various authors and concluded that the best fitting term to describe it is naphthalene-like (similar to the odour of mothballs). Recently, Kovalenko et al. (2012) recognised an additional European species with a naphthalene odour, *Camarophyllopsis alboflocipes* A.E. Kovalenko, E.F. Malysheva and O.V. Morozova, based on material from Russia.

In contrast to the situation in Europe, four *Hodophilus* taxa (treated in the genus *Hygrophorus*) with strong odours are recognised from North America (Hesler and Smith 1963), including their interpretation of the European type species. Our recent study using a multi-locus phylogeny combined with new morphological data (Adamčík et al. 2016) recognised five North American *Hodophilus* taxa with a naphthalene odour, two described as new. European collections with this odour are clustered in four different well-supported clades, probably representing different phylogenetic species.

In this study, we focus on European members of *Hodophilus* with a naphthalene odour. We aim to recognise how many phylogenetic species occur in the studied European sampling, their morphological distinguishing characters and which of the species clades correspond to the original concept of *Ho. foetens*.

Materials and methods

Taxon sampling

For the backbone of our study, we used sampling and sequence data published in Adamčík et al. (2016). The sequence dataset of that study comprises, altogether, 34 *Hodophilus* collections with a naphthalene odour: 14 North American and 20 European. We supplemented this with an additional 12 European collections of *Hodophilus* with a naphthalene odour, including the type of *C. alboflocipes*, two *Hodophilus* collections without such odour and one collection identified as *C. atrovelutina* (Romagn.) Argaud. All samples used in this study are listed in Supplementary Table 1. The concept of *Ho. foetens* (sensu stricto) is based only on morphological observations because attempted PCR amplifications of DNA extracts from the type collection were unsuccessful (Adamčík et al. 2016).

DNA extraction, PCR, and sequencing

Three gene regions (nrLSU, nrITS and *rpb2*) were amplified, sequenced and analysed. Protocols of Birkebak et al. (2013) were followed for DNA extraction, PCR, and sequencing. Primer pairs ITS1F-ITS4 (Gardes and Bruns 1993; White et al. 1990) were used to amplify the ITS region. Combinations of LR0R-LR7, LR0R-LR5, or LR0R-LR16 (http://sites.biology.duke.edu/fungi/mycolab/primers.htm) were used to amplify and sequence the nLSU region. The primer pair b6F and b7.1R (Matheny 2005) was used to amplify and sequence the most variable region of the *rpb2* gene between conserved domains 6 and 7. Sequencing was performed at the University of Tennessee Genomics Core facility (Knoxville, Tennessee, USA) and at the SEQme sequencing company (Dobříš, Czech Republic).

Phylogenetic analyses

Alignments for individual regions were created in CLUSTAL X (Larkin et al. 2007) and manually adjusted by eye in AliView (Larsson 2014). Individual alignments were concatenated in SeaView version 4 (Gouy et al. 2010). PartitionFinder (Lanfear et al. 2014) was used to identify the best partition scheme and molecular models under the AICc criterion. Maximum likelihood (ML) phylogenetic reconstruction was performed with RAxML version 7.4.2 (Stamatakis et al. 2008) implemented in RAxML GUI (Silvestro and Michalak 2012) with 1000 bootstrap replicates. Bayesian inference (BI) was performed in MrBayes v3.2.2 (Ronquist et al. 2011) running ten million generations and sampling parameter states and trees every ten thousand generations. In order to ensure convergence had been reached, the average standard deviation of split frequencies was monitored to

ensure it fell below 0.01, and trace files of the parameters were examined to ensure proper mixing. A 25% burn-in was used. We consider bootstrap values >70% and posterior probabilities >0.95 as strong support for clades. Bootstrap values between 50 and 70% and posterior probabilities between 0.80 and 0.95 can be considered as moderate support for clades. States and provinces for the United States and Canada are abbreviated and country abbreviations follow the three-letter ISO code (International Organization for Standardization, Geneva, Switzerland). All sequences are deposited in GenBank. The concatenated final alignment has been deposited at TreeBASE (19902).

Morphological analyses

Macromorphological descriptions were prepared from fresh material shortly after collection from the field. However, in some cases when such data were limited (because older collections were all identified directly as *C. foetens* without field descriptions), we also used photographs to supplement the descriptions or to verify some macromorphological characters. The number of full length lamellae was counted (i.e. those spanning the whole gill region) and is treated in the species descriptions as "L". The number of short lamellulae between each pair of full length lamellae is labelled as "l" (Bas et al. 1988). Lamellae of dry specimens were also observed under a stereo microscope (Zeiss model 437166). Colour nomenclature standards follow Kornerup and Wanscher (1967).

Microscopical structures were examined on desiccated herbarium specimens in Congo red solution with ammonia after a short treatment in aqueous 10% KOH. Features were observed under an Olympus CX-41 light microscope with an oil-immersion lens at a magnification of 1000×. All drawings of microscopic structures, with the exception of basidiospores, were made with a camera lucida using an Olympus U-DA drawing attachment at a projection scale of 2000×. Basidiospores were scanned with an Artray Artcam 300MI camera and measured by Quick Micro Photo (version 2.1) software. Enlarged scanned pictures of spores were used for measuring with an accuracy of 0.1 μm and for making line drawings. Q-value is the length/width ratio of basidiospores. Statistics of microscopic dimensions are based on 30 measurements and given as a mean value plus/minus standard deviation; values in parentheses give measured minimum or maximum values. Basidiospores were tested in Melzer's reagent for amyloid or dextrinoid reactions (Moser 1978).

Older or insufficiently preserved specimens of *Hodophilus* specimens display collapsed hyphal structures in the pileipellis. Hyphal terminations often form compact conglomerates that do not dissolve in the KOH solution. This makes it especially difficult to trace septa and can cause a bias in length values and length/width ratio values of the terminal cells. For this reason, such insufficiently conserved specimens were eliminated from our morphological analyses, with exception of the *Ho. foetens* type. In our analysis of micromorphological characters, we included all characters used in our previous study on North American *Hodophilus* species with a naphthalene odour (Adamčík et al. 2016). In addition, dimensions of subterminal cells of hyphae in the pileipellis are used because we observed that they are frequently inflated, sphaeropedunculate or clavate in the *Ho. foetens* type. Pileipellis elements near the pileus margin and the pileus centre were observed and evaluated separately.

Results

Phylogenetic analyses

All nodes recovered from the ML inference were also recovered by the BI analysis. The tree topology and grouping of individual collections (Fig. 1) are nearly identical with results of our previous study on North American *Hodophilus* species with a naphthalene odour (Adamčík et al. 2016). The majority of European collections form four well supported clades that do not merge with any North American collections, and all but two (discussed below) belong to the *Ho. foetens* superclade. Based on morphology (explained below) one clade is assigned to *Ho. foetens*, and three clades correspond to new species described in this study: *Ho. pallidus* Adamčík, Jančovičová & Looney, *Ho. subfoetens* Adamčík, Jančovičová & Looney and *Ho. tenuicystidiatus* Jančovičová, Adamčík & Looney. One difference from the previous study is a newly added collection K(M)175255 that represents a singleton sample in the tree. Our phylogenetic reconstruction clearly suggests that it is an autonomous species, but it is not described and recognised morphologically here because sufficient sampling and macromorphological data are not available. The other ten new samples of *Hodophilus* with a naphthalene odour are clustered in *Ho. foetens* (six new collections, 13 in total), *Ho. tenuicystidiatus* (three new collections, ten in total) and *Ho. subfoetens* (one new collection, five in total). Collections identified as *Ho. atropunctus* based on dark punctuations on the surface of the stipe and an indistinct odour are partly placed in a strongly supported clade within the *Ho. foetens* superclade (four collections), but two such collections are placed in the *Ho. micaceus* superclade and are clustered in one group (*H. micaceus* group 2) together with collections without dark punctuations.

The type of *C. alboflocipes* is placed in the genus *Hodophilus*, and although it is described as having an odour identical to *Ho. foetens*, it is placed in the *H. micaceus* superclade in a terminal group labelled as *Ho. micaceus* clade 3. This strongly supported group contains another four collections, but at least three of them lack any distinctive odour. One collection from Kew [K(M)161018], originally identified as

Ho. (*Camarophyllopsis*) *foetens*, is placed in the *Ho. micaceus* superclade within the group *Ho. micaceus* group 1, but we were not able to ascertain whether this was identified based on the presence of a naphthalene odour.

Morphological delimitation of genetically defined groups

Only a single *Hodophilus* species with a naphthalene odour had been recognised (*Ho. foetens*) prior to the discovery of *Ho. alboflocipes* by Kovalenko et al. (2012), and thus the morphological observations presented here are based mainly on notes describing samples collected after 2013. The only older, fully described collection is SAV F-3488 belonging to *Ho. subfoetens*, represented only by older collections (2002–2005). *Hodophilus pallidus* is represented by two collections that were documented by photos in the field, but have no description of macromorphological characters. The macromorphological description of *Ho. tenuicystidiatus* was prepared based on two recent collections (SLO725 and SLO772) and of *Ho. foetens* (sensu stricto) is based on five collections (SAV F-4447, SAV F-4448, SLO673, SLO769 and SLO770). The differences in field aspect are summarised and compared in Table 1.

Based on Kovalenko et al. (2012), it seems that the recently described *C. alboflocipes* is different from all other *Hodophilus species* with a naphthalene odour. It is described as having a yellow coloured pileus and stipe surface, with the latter bearing fine, white granules or scales on the stipe surface. However, the species is probably variable in colour, because in our phylogeny, it is grouped with four other collections and at least two of them (PAM06091103, SAV F-3032) had no distinctive yellow colour or white granulations. Based on our morphological investigation of the type, micromorphological characters offer a more decisive delimitation of the species from other European species with a naphthalene odour. *Hodophilus alboflocipes* (type) has very numerous small (length and width up to 5 μm) subterminal and subsequent cells in the pileipellis, the character that defines the whole *Ho. micaceus* superclade (Adamčík et al. 2016). In addition, we confirm the presence of the very specific caulocystidia observed by Kovalenko et al. (2012). The caulocystidia are not only nodulose, but often very twisted and lobate.

The dark brown colour of basidiomata described and illustrated in the protologue of *Ho. foetens* (Phillips 1878, as *Hygrophorus foetens*) clearly corresponds to our observations of basidiomata that turn partly black during maturation and drying (Table 1). In agreement with this are micromorphological characters (Table 2, Fig. 2): caulocystidia are the widest among all observed European species, and the subterminal cells of hyphae in the pileipellis are more frequently inflated (especially near the pileus margin). This species was described from Wales, and accordingly, it is the most frequent among studied material from the UK (Fig. 1). The other three species are briefly distinguished here as: *Ho. tenuicystidiatus* by closer lamellae and very narrow caulocystidia, *Ho. subfoetens* and *Ho. pallidus* both with more distant lamellae and differing from each other by shorter terminal cells in the pileipellis near the pileus centre of the latter (Tables 1, and 2).

Taxonomy

Dichotomous key to European *Hodophilus* species with a napthalene odour

1 Pileus and stipe surface usually with conspicuous yellow tints; subterminal cells in pileipellis frequently small (shorter than 5 μm); caulocystidia often irregularly inflated, nodulose, lobate and twisted

Hodophilus alboflocipes

1* Basidiomata without or with only dull yellow-brownish colours; subterminal cells in pileipellis rarely small; caulocystidia rarely lobate or twisted

2 Lamellae moderately close (L = 18–30)

3 Basidiomata becoming dark brown to black, especially near the pileus margin upon maturation or drying; caulocystidia on average wider than 7.5 μm

Hodophilus foetens

3* Mature or dry basidiomata not becoming darker; caulocystidia on average up to 7 μm wide

Hodophilus tenuicystidiatus

2* Lamellae distant [L = 10–18(–20)]

4 Pileus orange grey to greyish orange when fresh, drying pale orange; terminal cells of hyphae near the pileus centre with ratio of length/width mainly <2.5

Hodophilus pallidus

4* Pileus brown, grey brown, brownish grey, or when dry dark brown; terminal cells of hyphae near the pileus centre with ratio of length/width mainly >2.5

Hodophilus subfoetens

Hodophilus alboflocipes (A.E. Kovalenko, E.F. Malysheva & O.V. Morozova) Looney & Adamčík, comb. nov.

Fig. 1 Maximum Likelihood phylogeny inferred from three loci (ITS, LSU, and *rpb2*) with species-level clades highlighted as well as the two known superclades composing the genus *Hodophilus*. The species clade names in green are North American and in black European. Collection labels are updated with appropriate taxon labels except where collector identifications disagree. In blue are new samples added in this study. Also included are collection labels, country (and in some cases state/province), and whether this represents a type collection. Bootstrap values followed by Bayesian posterior probabilities are indicated at nodes

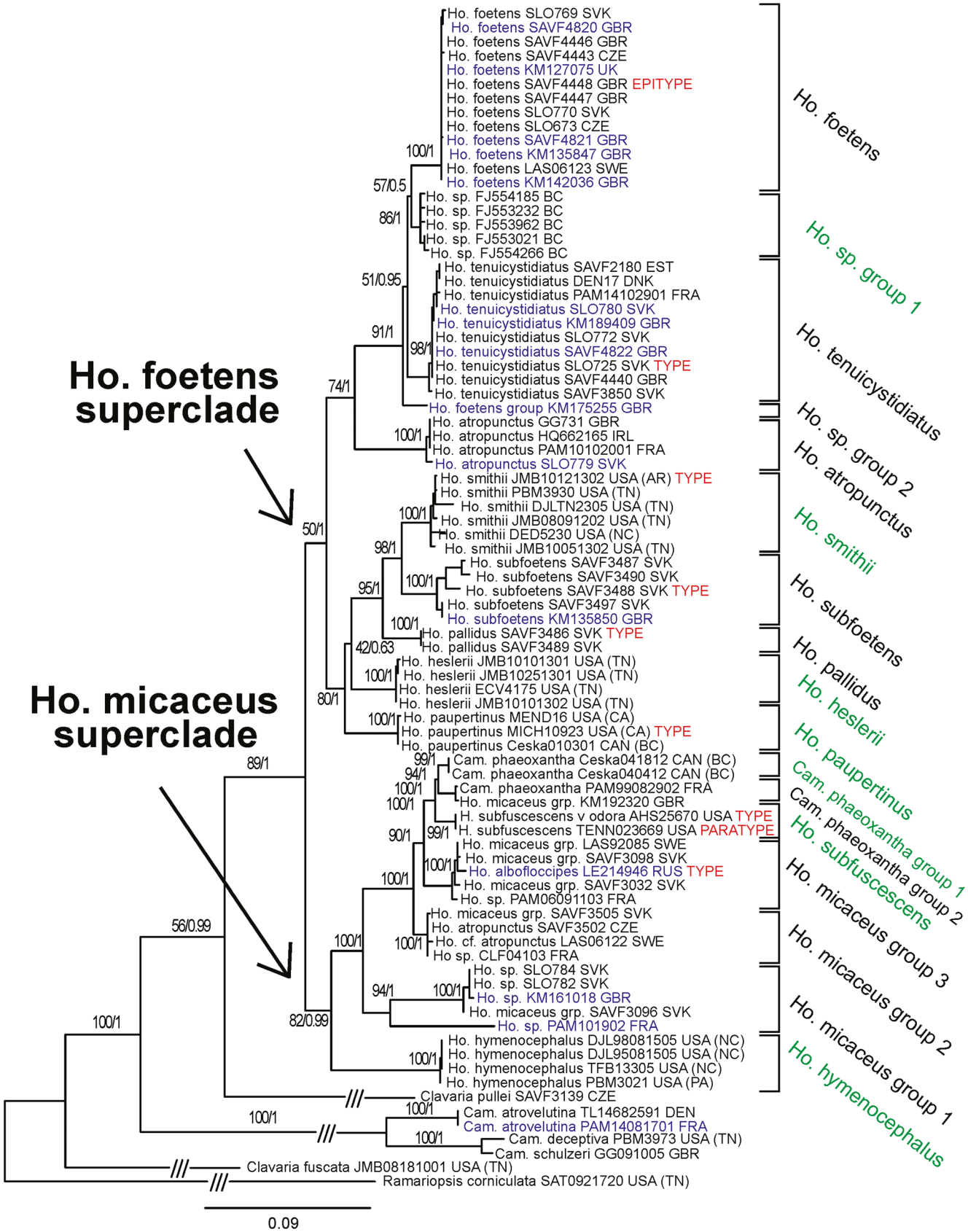

Ho. foetens superclade
Ho. micaceus superclade
Ho. foetens SLO769 SVK
Ho. foetens SAVF4820 GBR
Ho. foetens SAVF4446 GBR
Ho. foetens SAVF4443 CZE
Ho. foetens KM127075 UK
Ho. foetens SAVF4448 GBR EPITYPE
Ho. foetens SAVF4447 GBR
Ho. foetens SLO770 SVK
Ho. foetens SLO673 CZE
Ho. foetens SAVF4821 GBR
Ho. foetens KM135847 GBR
Ho. foetens LAS06123 SWE
Ho. foetens KM142036 GBR
Ho. sp. FJ554185 BC
Ho. sp. FJ553232 BC
Ho. sp. FJ553962 BC
Ho. sp. FJ553021 BC
Ho. sp. FJ554266 BC
Ho. tenuicystidiatus SAVF2180 EST
Ho. tenuicystidiatus DEN17 DNK
Ho. tenuicystidiatus PAM14102901 FRA
Ho. tenuicystidiatus SLO780 SVK
Ho. tenuicystidiatus KM189409 GBR
Ho. tenuicystidiatus SLO772 SVK
Ho. tenuicystidiatus SAVF4822 GBR
Ho. tenuicystidiatus SLO725 SVK TYPE
Ho. tenuicystidiatus SAVF4440 GBR
Ho. tenuicystidiatus SAVF3850 SVK
Ho. foetens group KM175255 GBR
Ho. atropunctus GG731 GBR
Ho. atropunctus HQ662165 IRL
Ho. atropunctus PAM10102001 FRA
Ho. atropunctus SLO779 SVK
Ho. smithii JMB10121302 USA (AR) TYPE
Ho. smithii PBM3930 USA (TN)
Ho. smithii DJLTN2305 USA (TN)
Ho. smithii JMB08091202 USA (TN)
Ho. smithii DED5230 USA (NC)
Ho. smithii JMB10051302 USA (TN)
Ho. subfoetens SAVF3487 SVK
Ho. subfoetens SAVF3490 SVK
Ho. subfoetens SAVF3488 SVK TYPE
Ho. subfoetens SAVF3497 SVK
Ho. subfoetens KM135850 GBR
Ho. pallidus SAVF3486 SVK TYPE
Ho. pallidus SAVF3489 SVK
Ho. heslerii JMB10101301 USA (TN)
Ho. heslerii JMB10251301 USA (TN)
Ho. heslerii ECV4175 USA (TN)
Ho. heslerii JMB10101302 USA (TN)
Ho. paupertinus MEND16 USA (CA)
Ho. paupertinus MICH10923 USA (CA) TYPE
Ho. paupertinus Ceska010301 CAN (BC)
Cam. phaeoxantha Ceska041812 CAN (BC)
Cam. phaeoxantha Ceska040412 CAN (BC)
Cam. phaeoxantha PAM99082902 FRA
Ho. micaceus grp. KM192320 GBR
H. subfuscescens v odora AHS25670 USA TYPE
H. subfuscescens TENN023669 USA PARATYPE
Ho. micaceus grp. LAS92085 SWE
Ho. micaceus grp. SAVF3098 SVK
Ho. albofloccipes LE214946 RUS TYPE
Ho. micaceus grp. SAVF3032 SVK
Ho. sp. PAM06091103 FRA
Ho. micaceus grp. SAVF3505 SVK
Ho. atropunctus SAVF3502 CZE
Ho. cf. atropunctus LAS06122 SWE
Ho sp. CLF04103 FRA
Ho. sp. SLO784 SVK
Ho. sp. SLO782 SVK
Ho. sp. KM161018 GBR
Ho. micaceus grp. SAVF3096 SVK
Ho. sp. PAM101902 FRA
Ho. hymenocephalus DJL98081505 USA (NC)
Ho. hymenocephalus DJL95081505 USA (NC)
Ho. hymenocephalus TFB13305 USA (NC)
Ho. hymenocephalus PBM3021 USA (PA)
Clavaria pullei SAVF3139 CZE
Cam. atrovelutina TL14682591 DEN
Cam. atrovelutina PAM14081701 FRA
Cam. deceptiva PBM3973 USA (TN)
Cam. schulzeri GG091005 GBR
Clavaria fuscata JMB08181001 USA (TN)
Ramariopsis corniculata SAT0921720 USA (TN)
0.09
Ho. foetens
Ho. sp. group 1
Ho. tenuicystidiatus
Ho. sp. group 2
Ho. atropunctus
Ho. smithii
Ho. subfoetens
Ho. pallidus
Ho. heslerii
Ho. paupertinus
Cam. phaeoxantha group 1
Cam. phaeoxantha group 2
Ho. subfuscescens
Ho. micaceus group 3
Ho. micaceus group 2
Ho. micaceus group 1
Ho. hymenocephalus

Table 1 Comparison of field characters observed from European *Hodophilus* taxa with a naphthalene odour according to our observations and for *Hodophilus alboflocipes* according to Kovalenko et al. (2012)

Species epithet	Pileus colour	Lamellar colour	Number of lamellae	Stipe surface
albofloccipes	yellow, ochre-brown, sometimes with olivaceous tints, darker near the centre, paler and almost white near the margin, when dry pale greyish-beige	ochre, yellow-brown, paler near the pileus margin	>20 (counted from the photo in the protologue)	fine white granules or scales on yellow background along the all length
foetens	fresh young basidiomata light brown, yellowish brown or dark brown, towards margin paler, when dry or mature turning at spots or completely brownish black	first beige, when mature dark grey brown	18–26 (30)	shiny, near lamellae usually with darker fibrils or punctuations
tenuicystidiatus	fresh or young basidiomata brown orange or brown and towards the margin pale orange, grey-orange or dull yellow, when dry orange-grey to brown orange	brownish orange, grey brown	20–34	shiny, near lamellae with paler floccules
subfoetens	when wet brownish grey to grey brown, when dry brownish black	grey brown or chocolate brown	15–20	shiny except where slightly pruinose near lamellae
pallidus	when wet orange-grey to greyish orange, when dry pale brownish orange	concolourous with the pileus surface	10–17	smooth and near the lamellae with pale, fine granulations

≡ *Camarophyllopsis albofloccipes* A.E. Kovalenko, E.F. Malysheva & O.V. Morozova, *Mikol. Fitopatol*. 46: 64. 2012 (Basionym).

MycoBank No.: MB 818293

Hodophilus foetens (W. Phillips) Birkebak & Adamčík, *Mycologia* 108(5): 866. 2016

Figs. 2–5, 6–7, 13, 17, 21, 25

≡ *Hygrophorus foetens* W. Phillips, *Grevillea* 7(42): 74. 1878.

≡ *Camarophyllus foetens* (W. Phillips) J.E. Lange, *Dansk. Bot. Ark*. 4(4):18. 1923

≡ *Aeruginospora foetens* (W. Phillips) M.M. Moser, *Röhrlinge-Blätterpilze*, 3rd ed.: 69. 1967

≡ *Hygrocybe foetens* (W. Phillips) P.D. Orton & Watling, *Notes Roy. Bot. Gard. Edinburgh* 29: 134. 1969

≡ *Hygrotrama foetens* (W. Phillips) Singer, Beih. *Sydowia* 7: 3. 1973

≡ *Camarophyllopsis foetens* (W. Phillips) Arnolds, *Mycotaxon* 25(2): 643. 1986

MycoBank No.: MB810136

Holotypus: K(M) 92776.

Epitypus (designated here): SAV F-4448.

Diagnosis: Pileus with brown colours that become darker brownish black when mature or dry, especially near the margin; lamellae moderately close (L = 18–26), stipe near lamellae usually with darker fibrils or punctuations, flesh with a strong naphthalene odour; caulocystidia obtuse, mainly longer than 30 μm and wider than 8 μm (26.5–61 × 6.5–11.5 μm), towards bases usually attenuated or pedunculate and flexuous; pileipellis a hymeniderm, near the pileus margin composed of sphaeropedunculate, obpyriform or clavate terminal cells, subterminal cells of hyphae near the pileus margin often inflated and wider than 8 μm.

Pileus 5–20(40) mm broad, convex to plano-convex, sometimes weakly depressed near the centre, rarely with indistinct low umbo; margin inflexed, later straight, crenate, when wet translucently striated at 1/3 to 2/3; surface matt, smooth, but towards the centre slightly rugulose or veined, when dry cracked into irregular, blackish scales; weakly hygrophanous, fresh young basidiomata light brown (clay 5D5), yellowish brown (bronze 5E5) or dark brown (chocolate brown 6F4), towards the margin greyish orange (5B3) or light brown (bronze 6D5), when dry or mature turning at spots or completely brownish black (5F3). **Stipe** 15–62(70) × 1–4 mm, cylindrical and narrowed towards the base, usually flexuous, sometimes compressed or longitudinally grooved, smooth, shiny, at the apex usually with darker fibrils or punctuations, at the base sometimes white tomentose; often at the apex light brown (blonde 5D4), brown (hair 5E4) to yellowish brown (bronze 5E5), towards the base brown (chestnut 6E7) to dark brown (chocolate 6F4), sometimes uniformly coloured in one of these colours. **Lamellae** 1–3 mm deep, L = 18–26 (30), l = 1–3, short decurrent, at first beige (4C3, ivory 4B3, putty 4B2), when mature dark grey brown (6F3 to 6F2), edges entire, concolourous or paler than the sides. **Flesh** 0.5–2 mm thick, elastic, with a strong naphthalene odour, light coloured (greyish-brownish).

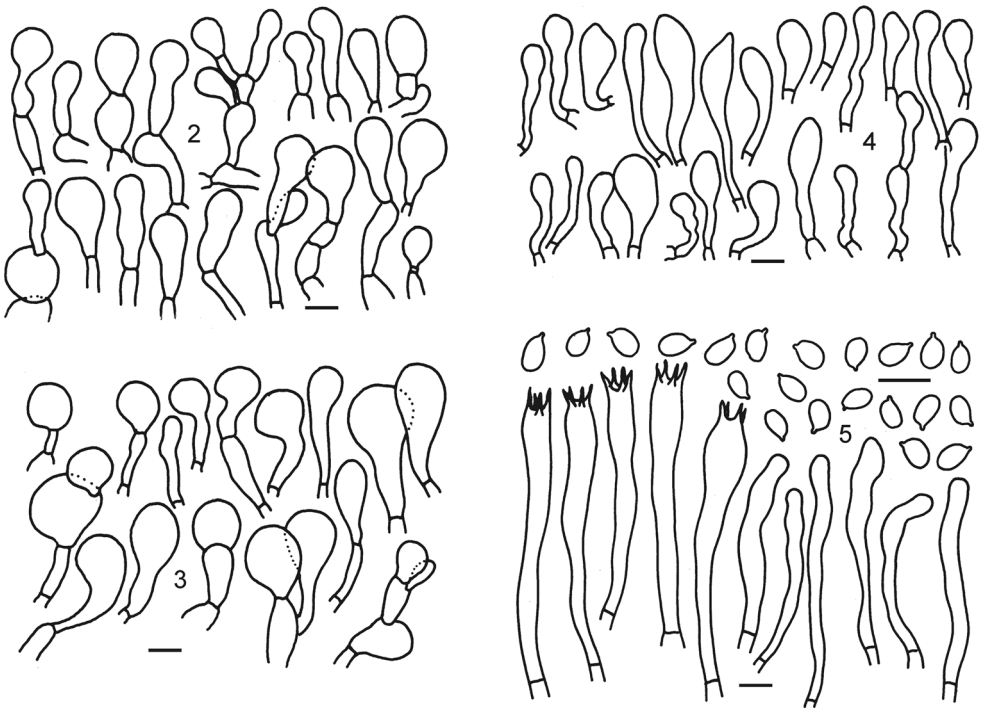
Basidiospores (4.5)5.1–5.9(6.6) × (3.8)4.2–4.7(5.4) μm, av. 5.5 × 4.5 μm, Q (length/width) = (1.02)1.17–1.30(1.47), av. Q = 1.24, broadly ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage 0.5–0.8(1) μm long. **Basidia** 4-spored, (32)38–48(58) × 6–7(–7.5) μm, av. 43.1 × 6.6 μm, hyaline, narrowly clavate, attenuated and flexuous toward base. **Basidioles** cylindrical to narrowly clavate, often flexuous, obtuse, ca. 22–40 × 3–5.5 μm. **Pleurocystidia** absent. **Marginal cells** on the lamellar edges not well differentiated, similar to basidioles on lamellar sides. **Lamellar trama**

Table 2 Average values of 30 measurements of selected micromorphological characters observed on studied *Hodophilus* taxa with an unpleasant odour

species epithet	herbarium no.	spores			caulocystidia		TC margin			STC margin		TC centre			STC centre	
		L	W	Q	L	W	L	W	Q	L	W	L	W	Q	L	W
foetens	K(M) 0009276 *	5.9	4.3	1.39	**31.6**	**8.7**	27.2	14.3	2.1	17.6	**8.9**	23.4	11.4	2.03	16.9	8.4
	K(M) 0135847	5.3	4.5	1.17	**35**	**9.1**	30.1	16.5	1.89	24.9	**9.4**	33.9	16.2	2.16	25.3	6.7
	LAS06123	5.9	4.4	1.29	**63.4**	**10.5**	37.9	17.3	2.28	30.9	**9**	31.3	11	2.88	24.1	6.2
	SAV F-4443	5.7	4.6	1.23	**50.3**	**7.9**	32.2	12.7	2.65	26	**9.6**	27.5	12.1	2.4	27.1	8.9
	SAV F-4446	5.8	4.5	1.3	**37.8**	**8.4**	36.1	13.2	2.93	31.3	**8.4**	31.4	11.2	3.01	31.4	8.2
	SAV F-4447	5.6	4.6	1.24	**36.1**	**8.7**	54.8	15.5	3.81	51.1	**11.7**	37.8	14.5	2.67	34.1	8.2
	SAV F-4448	5.3	4.4	1.2	**39.1**	**8.6**	35.5	12.6	3.17	36.4	**7.3**	45.9	10.4	4.5	36.9	6.3
	SAV F-4820	5.9	4.8	1.24	**53.4**	**9.6**	36.1	14.3	2.67	37.6	**10.4**	28.3	8.9	3.3	23.5	6
	SLO673	5.4	4.4	1.24	**34.7**	**9.6**	32.1	19.4	1.83	19.3	**7.3**	32.6	14.8	2.31	28.4	8.4
	SLO769	5.3	4.3	1.23	**42.6**	**7.5**	37.5	19.8	1.95	30.2	**11.4**	31	13.3	2.49	24.8	9.8
	SLO770	5.2	4.3	1.23	**32.9**	**8.9**	35.8	16.5	2.29	23.1	**7.2**	35	16	2.23	25.1	5.8
tenuicystidiatus	K(M) 189409	5.4	4.5	1.21	24	**4.6**	29	9.4	3.2	20	5.6	35	8.1	4.5	23	4.7
	LIP (PAM14102901)	5	4	1.24	34	**5.2**	28	13	2.7	20	6.3	24	9.9	2.4	18	5.2
	SAV F-2180	5.2	4	1.31	43	**6.2**	22	6.9	3.3	32	4.4	23	7.2	3.4	22	5.2
	SAV F-3850	5.7	4.1	1.41	35	**5.5**	26	13	2.1	24	6.8	31	12	2.7	21	6.3
	SAV F-4440	4.8	3.9	1.21	38	**6.7**	41	20	2.3	31	8.7	49	20	2.7	34	8.1
	SAV F-4822	5.4	4.5	1.21	23	**4.5**	24	13	1.9	14	5.8	21	12	1.9	11	4.1
	SLO725 *	5.6	4.4	1.26	27	**5.8**	24	9.7	2.5	17	6.3	23	12	2.4	21	6.3
	SLO772	5.2	4	1.3	28	**5.8**	29	12	2.6	14	5.7	22	7.9	3	22	6.2
	SLO780	5.6	4.5	1.25	28	**5.4**	24	10	2.5	22	7.7	26	9.9	2.6	16	4.7
subfoetens	K(M) 0135850	5.3	4.4	1.19	**24**	7.5	31	15	2.1	29	8.9	49	19	**2.7**	20	6.9
	SAV F-3487	5.5	4.3	1.29	**27**	6.6	32	16	2.1	25	6.7	37	12	**3.2**	28	5.8
	SAV F-3488 *	5.2	3.9	1.32	**31**	6.9	37	13	3	23	5.8	30	10	**3.3**	19	4.7
	SAV F-3490	5.4	4.2	1.28	**26**	7.5	31	12	2.8	25	6.5	30	8.6	**3.6**	28	5.6
	SAV F-3497	5.2	4	1.3	**23**	7.5	34	11	3.8	19	5.5	34	11	**3.3**	20	5.4
pallidus	SAV F-3486 *	5.5	4.1	1.34	**27**	7.5	29	18	1.7	22	5.6	31	17	**1.9**	27	6.4
	SAV F-3489	5.3	4.5	1.19	**27**	9.1	30	13	2.5	25	7.8	29	12	**2.5**	19	5.5

* type specimens, TC and STC margin/centre – terminal and subterminal cells in pileipellis near the pileus margin/centre, L – length, W – width, Q – length/width ratio. The values in bold indicate important differences

strongly intricate, subparallel to irregularly oriented, scarcely branched and irregularly inflated, hyphae 3–10(15) μm wide, composed of 20–100 μm long, fusiform or irregularly ventricose cells. **Subhymenium** pseudoparenchymatic, 15–25 μm deep, composed of branched, dense, 2–5 μm wide hyphae. **Pileipellis** near the pileus margin a hymeniderm, composed of cells arranged in one rank; terminal cells sphaeropedunculate, obpyriform or clavate, occasionally irregularly lobate, usually thin-walled, measuring (12)22–51(110) × (6)10–21.5(40) μm, av. 36.8 × 15.8 μm, Q = (0.98)1.32–3.71(8.5), av. Q = 2.5; subterminal cells usually cylindrical or fusiform and distinctly narrower but often also inflated, short and small cells (shorter than 10 μm) occasional, often bearing incrusted dark pigments, occasionally nodulose or with lateral projections, few branched, measuring (5)14.5–47(103) × (2.5)5–13.5(22) μm, av. 30.9 × 9.3 μm; terminal cells of hyphae in pileipellis near the pileus centre usually narrower, mainly clavate, often pedicellate and flexuous, measuring (11)20.5–46(83) × (5.5)7–16.5(28) μm, av. 33.4 × 12.8 μm, Q = (1)1.55–4.01(9.43), av. Q = 2.78; subterminal cells less frequently inflated and nodulose, often branched and flexuous, measuring (4)15–40(85) × (2)4–11(18) μm, av. 27.6 × 7.5 μm; pileus trama interwoven, 5–15 μm wide, subparallel, irregularly inflated and often branched, composed of up to 100 μm long cells, but often shorter than 20 μm. **Caulocystidia** fascicled, thin- or occasionally slightly thick-walled, repent or ascending, with terminal cells clavate, subcapitate or obpyriform, obtuse, often pedicellate and flexuous towards septum, measuring (12)26.5–61(149) × (4)6.5–11.5(19) μm, av. 42.8 × 8.9 μm; stipe trama of 5–12(15) μm wide, parallel hyphae, composed of 15–90(150) μm long cells. **Clamp connections** absent in all tissues.



Figs. 2–5 *Hodophilus foetens* (holotypus). 2. Hyphal terminations in pileipellis near the pileus margin. 3. Hyphal terminations in pileipellis near the pileus centre. 4. Caulocystidia. 5. Spores, basidia and basidiola. *Scale bar* = 10 μm, spores are 50% more magnified

Material examined: **Czech Republic**. Protected landscape area Blanský les, Chvalšiny, 9 September 2009, Z Egertová (SAV F-4443); Bílé Karpaty Mts., SE of the Vyškovec village, near the Ve Vlčí Nature Reserve (eastern edge), 24 October 2014, J Matouš (SLO673); **Slovakia**. Podunajská nížina lowland, SE of the Banka village, near the Koliba pod Ahojom, 24 September 2014, S Jančovičová (SLO770); *ibid*. 26 September 2014, S Jančovičová (SLO769); **Sweden**. Västra Götaland, Uddevalla, Ramseröd Nature Reserve, 7 October 2006, L and A Stridvall *LAS06/123* (GB0060378); **United Kingdom**. England. Oxfordshire, Cothill Fen NNR, 26 October 2012, JA Webb (SAV F-4820); *ibid*. 27 October 2012, JA Webb (SAV F-4821); N Ireland. Tyrone, Omagh, Mountjoy Presbyterian Church, 5 November 2014, SE Evans [K(M)127075)]; Wales. Breconshire, Powys, Clydach, 5 November 2005, BM Spooner [K(M)135847]; Carmarthenshire, Brecon Beacons National Park, Brest CWM Llwyd, 22 October 2006, SE Evans [K(M)142036]; Breconshire, Mynydd Epynt, 2 October 2014, SE Evans (SAV F-4448); *ibid*. 24 October 2014, PJ Roberts (SAV F-4446); *ibid*. 5 November 2014, PJ Roberts (SAV F-4447).

Hodophilus tenuicystidiatus Jančovičová, Adamčík & Looney, sp. nov.

Figs. 8–9, 14, 18, 22, 26

MycoBank No.: MB818291

Etymology: the epithet refers to the narrow caulocystidia

Holotypus: SLO725

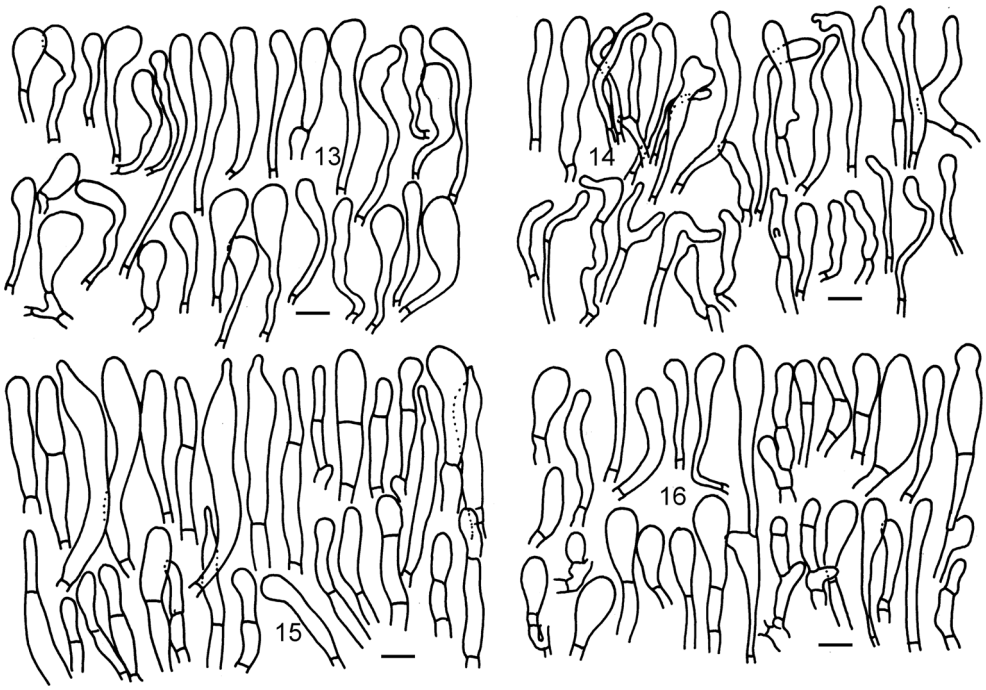
Diagnosis: Pileus fresh or when wet pale brown with a paler margin, becoming pale orange-grey to brown orange when dry, often rugose especially towards the centre; lamellae moderately close (L = 20–34); stipe apex with pale floccules, flesh with a strong naphthalene odour; caulocystidia crowded in large patches, mainly less than 7 μm wide (20.5–43 × 4–7 μm), flexuous, often with lateral nodules or projections; pileipellis a hymeniderm, terminal cells near the pileus margin sphaeropedunculate, subglobous, obpyriform or broadly clavate, subterminal cells of hyphae near the pileus margin rarely inflated and wider than 8 μm.

Pileus 8–16 mm broad, hemispherical, convex to planoconvex, usually depressed near the centre; margin inflexed to straight, crenate, when wet translucently striated halfway to the disc; surface matt, at first smooth but soon becoming rugose or veined especially towards the centre, hygrophanous; fresh or young basidiomata brown orange (blonde 5C4) or brown (hair 5E4) and towards the margin pale orange (5A3), grey-orange (5B3) or dull yellow (3B3), when dry orange-grey (5B2) to brown orange (5C3). **Stipe** 20–40 × 2–4 mm, usually flexuous, cylindrical and narrowed towards the base, sometimes compressed or longitudinally grooved, occasionally gnarled, smooth, shiny, apex with pale floccules, at the base white tomentose at times, near lamellae usually grey-orange (5B3) to brown (6D3), near the base light brown (blonde 5D4), yellowish brown (bronze 5E5), dark brown (chocolate 6F4) or dark grey-brown (6F3), sometimes uniformly coloured in one of these colours. **Lamellae** 1–3 mm deep, moderately close, L = 20–34, l = 1, sometimes anastomosed, short to deeply decurrent, brownish orange (5C3), grey brown (nougat 5D3), edges entire, concoloured. **Flesh** 0.5–1 mm thick in half radius of the pileus, elastic, with a strong

Figs. 6–12 Basidiomata field aspect of 6. *Hodophilus foetens* (SAV F-4443) photo by Z. Egertová. 7. *Hodophilus foetens* (SLO770) photo by S Jančovičová. 8. *Hodophilus tenuicystidiatus* (SLO725, holotypus) photo by S Jančovičová. 9. *Hodophilus tenuicystidiatus* (PAM14102901) photo by P.-A. Moreau. 10. *Hodophilus subfoetens* (SAV F-3497) photo by P Marstad. 11. *Hodophilus pallidus* (SAV F-3486, holotypus) photo by S Jančovičová. 12. *Hodophilus pallidus* (SAV F-3489) photo by S Jančovičová. *Scale bar* = 1 cm

naphthalene odour but also with unpleasant mercaptan components, orange grey (5B2).

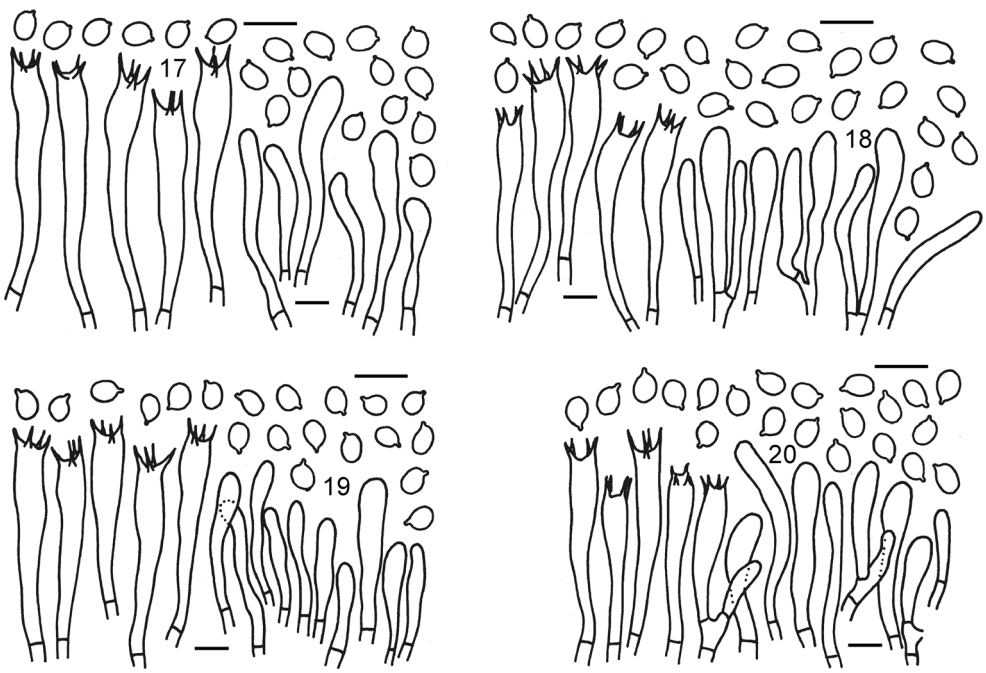
Basidiospores (4.3)4.9–5.7(6.5) × (3.5)3.8–4.5(5) μm, av. 5.3 × 4.2 μm, Q = (1.04)1.19–1.36(1.54), av. Q = 1.28, broadly ellipsoid to ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage up to 0.6-0.8 μm long. **Basidia** 4-spored, (29)33.5–39(42) × (5)5.5–6.5 μm, av. 36.3 × 6.2 μm, hyaline, narrowly clavate, attenuated and flexuous toward the base. **Basidioles** cylindrical to narrowly clavate, obtuse, often flexuous, ca. 2.5–5.5 μm wide. **Pleurocystidia** absent. **Marginal cells** on the lamellar edges not well differentiated, similar to basidiola (sterile immature basidia in hymenium) on lamellar sides. **Lamellar trama** composed of sub-parallel hyphae of mainly ventricose-fusiform cells, 4–15(20) μm wide, septa usually less distant than 100 μm (often <50 μm). **Subhymenium** pseudoparenchymatic, 15–25 μm deep, composed of branched, dense, 2–5 μm wide hyphae, gradually passing to underlying hyphae of the trama. **Pileipellis** near the pileus margin a hymeniderm, composed of cells arranged in one or two ranks; terminal cells sphaeropedunculate, subglobous, obpyriform or broadly clavate, measuring (9.5)18–38(63) × (4.5)6.5–17.5(34) μm, av. 28.1 × 12 μm, Q = (1.06)1.51–3.72(7.83), av. Q = 2.61; subterminal cells mainly narrow and cylindrical, occasionally also laterally inflated or nodulous, occasionally branched, measuring (2.5)10–33(65) × (2)3.5–10(20) μm, av. 21.5 × 6.6 μm. Hyphal terminations in pileipellis near the pileus centre occasionally with yellowish brown intracellular pigments, occasionally also with thick-walled elements, with terminal cells sphaeropedunculate or clavate, less frequently obpyriform, often lobate or undulate, occasionally with lateral projections, measuring (6)16–41.5(76) × (5)6–15.5(33) μm, av. 28.8 × 10.8 μm, Q = (0.71)1.51–4.3(9.67), av. Q = 2.9; subterminal cells more frequently flexuous, nodulous or with lateral projections, some with darker incrusted pigments, usually not branched, measuring



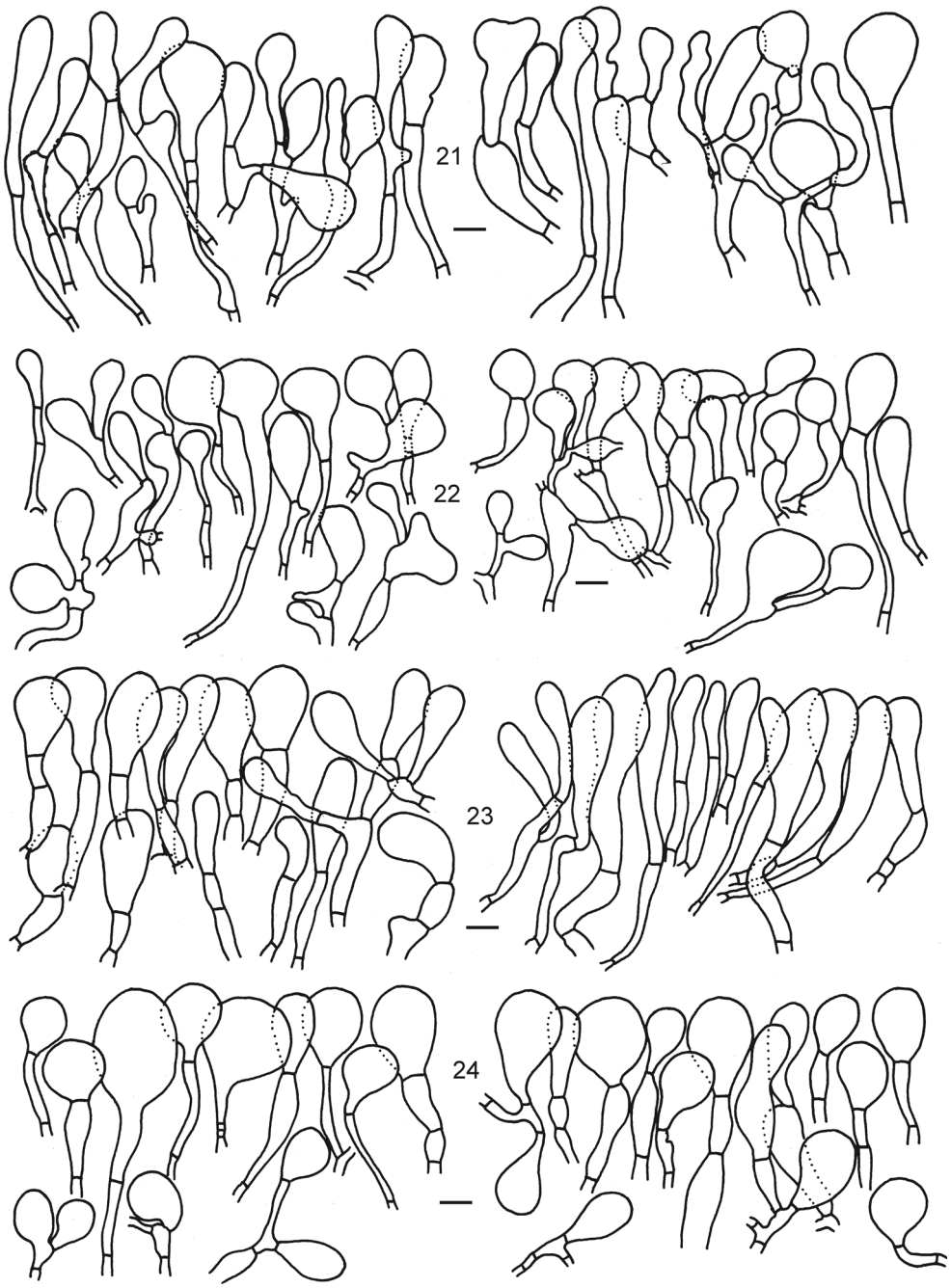
Figs. 13–16 Caulocystidia of 13. *Hodophilus foetens* (SAV F-4448, epitypus). 14. *Hodophilus tenuicystidiatus* (SAV F-3850). 15. *Hodophilus subfoetens* (SAV F-3488, holotypus). 16. *Hodophilus pallidus* (SAV F-3486, holotypus). *Scale bar* = 10 μm

(2)9.5–34(80) × (2)3–8.5(24) μm, av. 21.9 × 5.8 μm. Pileus trama of interwoven, 5–20 μm wide, subparallel, irregularly inflated and often branched hyphae, also with few narrow (3–5 μm) and pigmented hyphae, composed of up to 100 μm long cells, but often some shorter than 50 μm. **Caulocystidia** crowded in large patches, intricate, very variable in shape, mainly narrow subcylindrical or narrowly clavate, some wider, broadly clavate, usually thin-walled, often very flexuous, occasionally nodulous or with projections, usually with darker or sometimes very dark intracellular or parietal pigments, measuring (14)20.5–43(74) × (2)4–7(13) μm, av. 31.8 × 5.5 μm. Stipe trama of 3–12(18) μm wide, parallel hyphae, composed of 20–100 μm long cells (few >100 μm). **Clamp connections** absent in all tissues.

Material examined: **Denmark**. NW Jutland, Skive, Marienlyst Strand, 2 September 2007, D. Boertmann *DEN-17* (CFMR7071); **Estonia**. Saaremaa, Viieristi protected area,



Figs. 17–20 Spores, basidia and basidiola of 17. *Hodophilus foetens* (SAV F-4448, epitypus). 18. *Hodophilus tenuicystidiatus* (SAV F-3850). 19. *Hodophilus subfoetens* (SAV F-3488, holotypus). 20. *Hodophilus pallidus* (SAV F-3486, holotypus). *Scale bar* = 10 μm, spores are 50% more magnified



Figs. 21–24 Hyphal terminations in pileipellis near the pileus margin of 21. *Hodophilus foetens* (SAV F-4448, epitypus). 22. *Hodophilus tenuicystidiatus* (SAV F-3850). 23. *Hodophilus subfoetens* (SAV F-3488, holotypus). 24. *Hodophilus pallidus* (SAV F-3486, holotypus). *Scale bar* = 10 μm

20 September 2008, S Adamčík (SAV F-2180); **France**. Oise: Sacy-le-Grand, marais de Sacy, 29 October 2014, P Clowez *PAM14102901* (LIP); **Slovakia.** Oravské Beskydy Mts., Oravská Polhora village, Slaná voda, 9 October 2012, N Rybáriková (SAV F-3850); Podunajská nížina lowland, SE of the Banka village, near the Koliba pod Ahojom, 26 September 2014, S Jančovičová (SLO772, SLO780); Malé Karpaty Mts., NNW of the Plavecké Podhradie village, 9 October 2014, S Jančovičová (SLO725); **United Kingdom**. England. Oxfordshire, Hinksey Heights Fen, 26 September 2010, JA Webb (SAV F-4822); Northamptonshire, King's Cliffe, Ring Haw, 23 October 2013, J Blincow [K(M)189409]; Wales. Pembrokeshire, Somerton farm, 14 November 2010, D Harries (SAV F-4440).

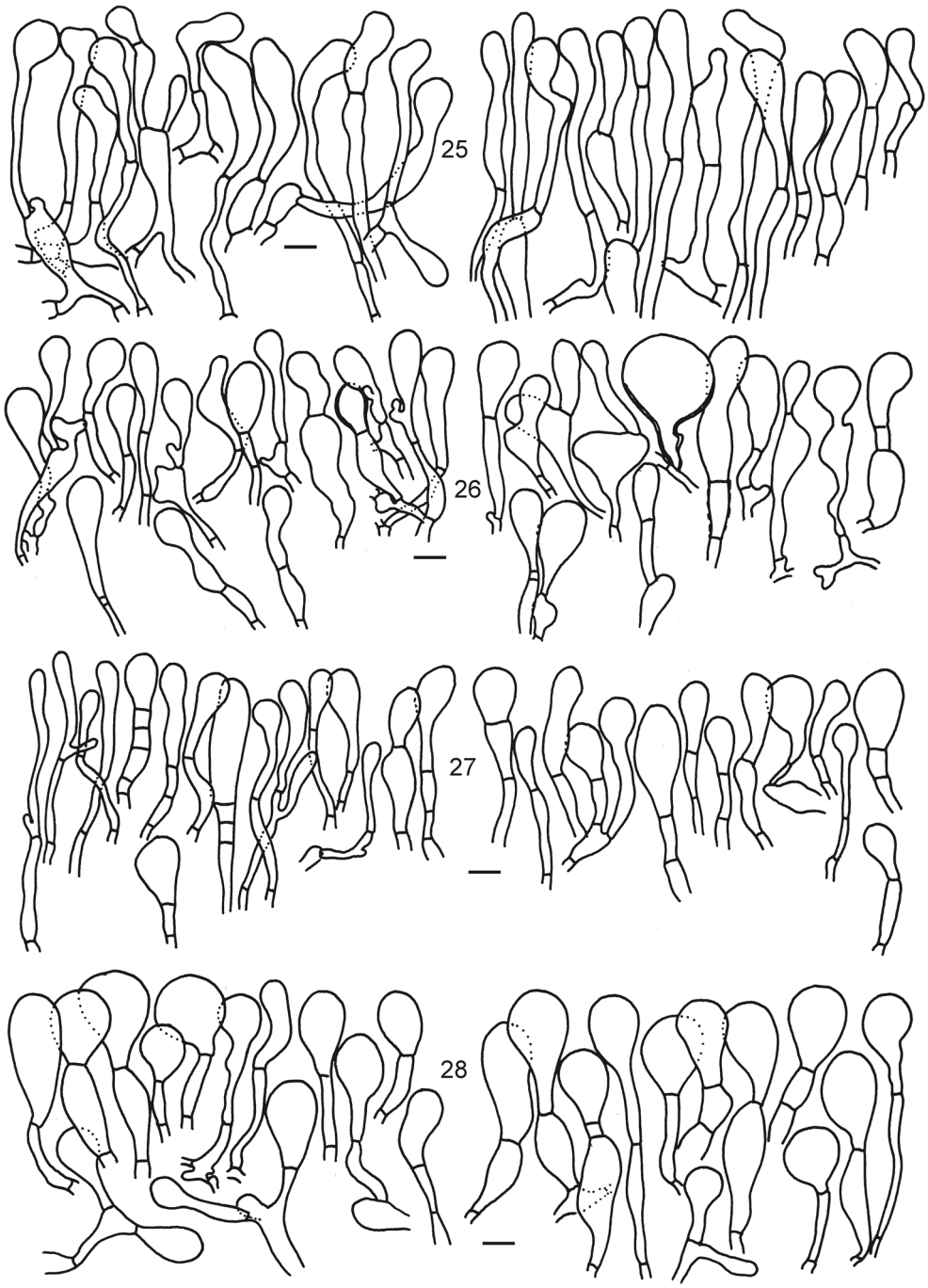
Hodophilus subfoetens Adamčík, Jančovičová & Looney, sp. nov. Figs. 10, 15, 19, 23, 27

MycoBank No.: MB 818292

Etymology: the species is named based on pileus colour resembling *Ho. foetens*

Holotypus: SAV F-3488

Diagnosis: Pileus with brown colours that become darker brownish black when mature or dry, lamellae relatively distant (L = 15–20); stipe only slightly pruinose near lamellae, flesh



Figs. 25–28 Hyphal terminations in pileipellis near the pileus centre of 25. *Hodophilus foetens* (SAV F-4448, epitypus). 26. *Hodophilus tenuicystidiatus* (SAV F-3850). 27. *Hodophilus subfoetens* (SAV F-3488, holotypus). 28. *Hodophilus pallidus* (SAV F-3486, holotypus). *Scale bar* = 10 μm

with strong naphthalene odour; caulocystidia obtuse or apically constricted, usually not flexuous, clavate or subcylindrical, mainly shorter than 30 μm and moderately wide (15.5–36.5 × 5–9.5 μm); pileipellis a hymeniderm, terminal cells near the pileus margin clavate or obpyriform, subterminal cells of hyphae near the pileus margin rarely inflated and wider than 8 μm, terminal cells of hyphae near the pileus centre relatively narrow (length/width ration >2.5).

Pileus 6–18 mm broad, convex, weakly depressed near the centre when old, margin striated at 2/3 when wet, sometimes slightly crenulated, surface smooth, near the centre rugulose, matt, hygrophanous, colour when wet brownish grey to grey brown (5E3, hair brown 5E4, drab 6D2), when dry brownish black (nutria brown 6D2). **Stipe** 20–30 × 1–1.5 mm, cylindrical and usually narrowed near the base, smooth and shiny except where slightly pruinose near lamellae, concolourous with the pileus. **Lamellae** 1–2 mm wide, L = 15–20, l = 0–1, short decurrent, grey brown (bronze 5E5) or chocolate brown (6F4). **Flesh** elastic, with a naphthalene odour.

Basidiospores (4.6)5–5.7(6.4) × (3.3)3.9–4.5(5) μm, av. 5.3 × 4.2 μm, Q = (1.08)1.20–1.36(1.53), av. Q = 1.28, broadly ellipsoid to ellipsoid, hyaline, smooth, inamyloid, not

dextrinoid, thin-walled, hilar appendage 0.5–0.9 μm long. **Basidia** 4-spored, (28)32.5–39(41) × (5)5.5–6.5 μm, av. 35.6 × 5.9 μm, hyaline, narrowly clavate, attenuated and slightly flexuous toward base. **Basidioles** cylindrical to narrowly clavate, often flexuous, obtuse, 3–5.5 μm wide. **Pleurocystidia** absent. **Marginal cells** on the lamellar edges not well differentiated. **Lamellar trama** of intricate, subparallel or irregularly oriented, often narrowed near septa, composed of fusiform or irregularly ventricose cells, mixed with a few narrow and cylindrical, 5–10 (25) μm wide and up to 100 μm long. **Subhymenium** pseudoparenchymatic, 15–25 μm deep, composed of branched, dense, 2–5 μm wide hyphae. **Pileipellis** near the pileus margin a hymeniderm, composed of cells arranged in one rank; terminal cells clavate or obpyriform, thin-walled, measuring (16)22.5–43(64) × (6)9–17.5(38) μm, av. 32.9 × 13.3 μm, Q = (0.9)1.45–4.09(12), av. Q = 2.77; subterminal cells usually narrow, cylindrical, not branched, not flexuous, measuring (3.5)13.5–35(47) × (2)3.5–10(22) μm, av. 24.3 × 6.7 μm. Pileipellis elements near the pileus centre similar to those near the margin, terminal cells of hyphae often narrower and/or longer, measuring (15)23–47.5(73) × (5.5)7.5–16(25) μm, av. 35.4 × 11.8 μm, Q = (1.07)1.91–4.5(10), av. Q = 3.21; subterminal cells similar to those near the pileus margin, measuring (4)11.5–37.5(66) × (2)3–8.5(22) μm, av. 24.6 × 5.7 μm. Pileus trama of interwoven, 3–20 μm wide, subparallel to irregularly oriented hyphae, composed of fusiform, ventricose or some dispersed sub-cylindrical, up to 100 μm long (frequently even shorter than 20 μm) cells. **Caulocystidia** dispersed or in relatively small fascicles, repent or with ascending tips, thin-walled, clavate or subcylindrical, usually not flexuous, obtuse or apically constricted, measuring (11)15.5–36.5(75) × (3)5–9.5(14) μm, av. 26 × 7.2 μm. Stipe trama of 3–10 μm wide, parallel, cylindrical, entire hyphae, with septa usually not more than 100 μm distant. **Clamp connections** absent in all tissues.

Material examined: **Slovakia**. Záhorská nížina lowland, Abrod National Natural Reserve, 30 September 2002, S Adamčík (SAV F-3488); Biele Karpaty Mts., Krivoklátske lúky Nature Monument, 31 July 2005, S Adamčík (SAV F-3497); Biele Karpaty Mts., Blažejová Nature Monument, 27 September 2005, S Jančovičová, (SAV F-3490); Laborecká vrchovina Mts., Jaruchy, 12 October 2005, J Terray (SAV F-3487); **United Kingdom**. Wales. Monmouthshire, Abergavenny, The Blorenge, 5 November 2005, R Shotbolt [K(M)135850].

Hodophilus pallidus Adamčík, Jančovičová & Looney, sp. nov. Figs. 11–12, 16, 20, 24, 28

MycoBank No.: MB 818294

Etymology: the epithet refers to pale colour of basidiomata

Holotypus: SAV F-3486

Brief diagnosis: Pileus orange-grey to greyish orange, when dry pale brownish orange; lamellae distant (L = 10–17); stipe near lamellae with pale, fine granulations, flesh with strong naphthalene odour; caulocystidia obtuse, fascicled or isolated, clavate or subcylindrical, occasionally also with short ellipsoid terminal cells, mainly shorter than 30 μm and wider than 7 μm (14.5–39.5 × 5.5–11 μm); pileipellis a hymeniderm, terminal cells near the pileus margin subglobous or obpyriform, subterminal cells of hyphae near the pileus margin rarely inflated and wider than 8 μm, terminal cells of hyphae near the pileus centre usually broad and often subglobous (length/width ration mainly <2.5).

Pileus 6–18 mm broad, convex, margin slightly translucently striate when wet, slightly crenulated, inflexed and only straight when old, surface smooth, but wrinkled near the margin when old, matt, hygrophanous, when wet orange-grey (6B2 to 6B3) to greyish orange (5B2 to 5B3), when dry pale brownish orange (5A2). **Stipe** 25–40 × 1–2 mm, cylindrical and usually flexuous, smooth and near the lamellae with fine pale granulations, near the lamellae greyish orange (5B3) to orange grey (6B3), towards the base sometimes darker brownish orange (5C3), orange-brown to grey-brown (7C3-7E3). **Lamellae** 1–2 mm wide, distant, L = 10–17, l = (0)1, short decurrent, concolourous with the pileus surface, edges entire. **Flesh** elastic, with strong naphthalene odour.

Basidiospores (4.7)5.1–5.7(6.1) × (3.5)3.9–4.6(5) μm, av. 5.4 × 4.3 μm, Q = (1.02)1.17–1.36(1.49), av. Q = 1.27, broadly ellipsoid to ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage 0.6–1.1 μm long. **Basidia** 4-spored, (27)30.5–38(45) × 5–6(6.5) μm, av. 34.3 × 5.6 μm, hyaline, narrowly clavate, attenuated and slightly flexuous toward base. **Basidioles** cylindrical to narrowly clavate, often flexuous, obtuse, 3–5.5 μm wide. **Pleurocystidia** absent. **Marginal cells** on the lamellar edges not well differentiated, but in average shorter than basidioles on lamellar sides. **Lamellar trama** of intricate, subparallel or irregularly oriented, near septa often narrowed, composed of fusiform or irregularly ventricose cells, mixed with a few narrow and cylindrical, 5–10(25) μm wide and up to 100 μm long. **Subhymenium** pseudoparenchymatic, 15–25 μm deep, composed of branched, dense, 2–5 μm wide hyphae. **Pileipellis** near the pileus margin a hymeniderm, composed of cells arranged in one rank; terminal cells subglobous or obpyriform, occasionally thick-walled, measuring (15)19.5–39(62) × (8)10.5–20(29.5) μm, av. 29.4 × 15.3 μm, Q = (0.95)1.21–2.95(5.3), av. Q = 2.09, usually regularly rounded and not pedicellate; subterminal cells usually narrow, cylindrical or narrowly fusiform, occasionally branched, rarely inflated, not flexuous or nodulous, measuring (2)12–35(55) × (2.5)3–10.5(18) μm, av. 24.3 × 6.7 μm. Pileipellis elements near the pileus centre similar to those near the margin, terminal cells of hyphae more frequently pedicellate but otherwise similar to those near the pileus margin, measuring (17)22.5–37(49) × (8.5)10.5–18(24) μm, av. 29.8 × 14.2 μm, Q = (1.02)1.5–2.93(4), av. Q = 2.22; subterminal cells similar

to those near the pileus margin but more frequently inflated, measuring (5)13–32.5(47) × (2)3.5–8.5(12.5) μm, av. 22.8 × 5.9 μm. Pileus trama of interwoven, 3–20 μm wide, subparallel to irregularly oriented hyphae, composed of fusiform, ventricose or some dispersed sub-cylindrical, up to 100 μm long (frequently even shorter than 20 μm) cells. **Caulocystidia** fascicled, but some dispersed and isolated, mixed with dispersed basidia, repent or with ascending tips, thin-walled, clavate or subcylindrical, but occasionally also with short ellipsoid terminal cells, usually not flexuous, obtuse, terminal cells measuring (6)14.5–39.5(60) × (3.5)5.5–11(18) μm, av. 27 × 8.3 μm. Stipe trama of 3–10 μm wide, parallel, cylindrical, entire hyphae, with septa usually not more than 100 μm distant. **Clamp connections** absent in all tissues.

Material examined: **Slovakia**. Biele Karpaty Mts., Krivoklátske lúky Nature Reserve, 26 September 2005, S Adamčík (SAV F-3486); Biele karpaty Mts., Grúň Nature Monument, 26 September 2005, S Adamčík (SAV F-3489).

Discussion

Placement, delimitation and nomenclature of *Ho. alboffloccipes*

The phylogenetic placement and naphthalene odour of *Ho. alboffloccipes* constitute a similar pattern as in the North American species *Ho. subfuscescens* **(**A.H. Sm. & Hesler**)** Adamčík, Birkebak & Looney (Adamčík et al. 2016). They are both placed in the *H. micaceus* superclade apart from all other species with a naphthalene odour, which are grouped in the *Ho. foetens* superclade (Fig. 1). Species clades that include the types of those two species also contain both collections with and without a naphthalene or unpleasant odour. Both of these species bear olive and yellow-brown tints and both have frequent small subterminal cells in the pileipellis. One collection originally identified as *C. foetens* included in this study [K(M)161018] placed in another species clade (*Ho. micaceus* group 1) was probably identified based on the naphthalene odour. This suggests that sometimes this odour may also appear in various members of *Ho. micaceus* superclade, although probably not with a strong intensity and not persisting in the dry specimens. *Hodophilus alboffloccipes*, despite its odour, is morphologically and genetically distinguished from other species in the *Ho. foetens* superclade. More challenging is the nomenclature of this species, because the species clade with the type of *Ho. alboffloccipes* contains specimens without distinctive odour and any older name used for European *Hodophilus* species might be a synonym and the correct one. We think that the delimitation of *Ho. alboffloccipes* requires observation and type studies of other taxa of the *Ho. micaceus* superclade, and for this reason we did not provide a description and other notes on our collection of this species.

Morphological delimitation and variability of species within *Ho. foetens* superclade

Our previous study (Adamčík et al. 2016) showed the significance of micromorphological characters for species delimitation, contrary to similar habit (field appearance) of North American taxa, that do not allow their identification in the field. This has been demonstrated in particular for *Ho. heslerii* Adamčík, Birkebak & Looney and *Ho. smithii* Adamčík, Birkebak & Looney. All North American taxa included in that study have been defined by a unique combination of micromorphological characters that allow the preparation of a key without using macromorphological characters. The morphological analysis of European *Hodophilus* members, however, does not show decisive differences among all species under the microscope. The most conspicuous and useful microscopic element seems to be morphology of caulocystidia. *Hodophilus tenuicystidiatus* has a maximum average value of caulocystidia width of 6.7 μm that only partly overlaps with *Ho. subfoetens* (minimum average width 6.6 μm) and does not overlap with the other two species at all (Table 2). In addition, the caulocystidia of *Ho. tenuicystidiatus* are flexuous and occasionally also nodulous or with lateral projections, while in *Ho. subfoetens* they are more regularly shaped. The shape and length of caulocystidia are also useful for differentiating *Ho. foetens* from *Ho. subfoetens* and *Ho. pallidus*. All three species have a similar width of caulocystidia (but they are usually narrower and on average up to 7.5 μm in *Ho. subfoetens*). *Hodophilus subfoetens* and *Ho. pallidus* differ from *Ho. foetens* especially by usually not having flexuous caulocystidia that often have short terminal cells with average lengths up to 31 μm, in contrast to a minimum of 31.6 μm for *Ho. foetens*. *Hodophilus subfoetens* and *Ho. pallidus*, however, do not show any conspicuous differences under the microscope. The caulocystidia of *Ho. subfoetens* are often apically constricted (Fig. 15), while in *Ho. pallidus* they are always obtuse-rounded (Fig. 16). This character, however, was not conspicuous and consistent in all studied collections. The distinct difference we observed in the shape of terminal cells of hyphae near the pileus centre that are narrower and with length/width ratio always above 2.7 in the first but up to 2.5 in the second species. However, we think that the reliability of this character should be checked on a larger sampling (only two collections of *Ho. pallidus* studied).

Field characters delimit pairs of the studied European species. *Hodophilus foetens* and *Ho. tenuicystidiatus* have usually more than 20 lamellae and the other two species, *Ho. subfoetens* and *Ho. pallidus*, have a maximum 20 lamellae (not including short lamellulae). Lamellae number or spacing has not been used for species delimitation within the genus *Hodophilus*, but is used in various groups of small agarics (e.g. Adamčík and Jančovičová 2011). A useful character is also pileus colour that becomes dark brown to black brown with age or drying in *Ho. foetens* and *Ho. subfoetens*, while it remains pale brown or becomes even paler brownish in the other two species. Dark brownish-black spots or areas on the surface of basidiomata of *Ho. foetens* are particularly conspicuous and typical. The number of lamellae was also observed on each individually studied basidiomata in dried material (under a stereo microscope) and, in our opinion, our data are statistically sufficient to recognise the species pairs. The pileus colour of *Ho. subfoetens* and *Ho. pallidus*, however, is described based on a limited number of observations and we recommend combining this character with micromorphological features discussed above.

Ecology and distribution

This study confirms the conclusion of Adamčík et al. (2016) that, contrary to North American *Hodophilus* taxa reported mainly from forest habitats, European samples reported prior to or during this study were collected mainly in grasslands or bushy forest margins. The core of our European collections of *Hodophilus* with a naphthalene odour have been sampled from Slovakia and the United Kingdom. Both these countries have representatives of all four species clades except *Ho. pallidus*, which was collected only in Slovakia. Moreover, *Ho. foetens* and *Ho. tenuicystidiatus* samplings also contain Scandinavian collections, and these two species are probably well distributed in temperate and boreal areas of Europe. It is not possible to conclude much about the distribution of *Ho. subfoetens* and *Ho. pallidus* based on available data. Slovakian data show that all four species may co-occur in one relatively small area. Even at a single site, more than one species may be present: *Ho. foetens* (SLO769, SLO770) and *Ho. tenuicystidiatus* (SLO772, SLO780) were collected during one day (26 September 2016) at a single site near the Banka village, and *Ho. subfoetens* (SAV F-3497) and *Ho. pallidus* (SAV F-3486) were both collected at Krivoklátske lúky Nature Manument (Supplementary Table 1).

Hodophilus with a naphthalene odour in European literature

The morphological descriptions of *Ho. foetens* in the current European literature used to be limited to spore dimensions and some brief information about pileipellis or other micromorphological characters. Such data on the microscopy of *Ho. foetens* are not reliable to compare with species differences described here, and we must rely only on macromorphological characters when trying to understand a concept of the species.

A major part of European authors followed the species concept of *Ho. foetens* presented in the original diagnosis (Phillips 1878) and described the pileus colour as dark brown (Lange 1940; Moser 1967; Printz and Silvertsen 1992; Horak 2005). Other authors are less specific in the interpretation of the brown colour of the pileus and their descriptions may encompass all four species described here (Bresadola 1928; Heim 1969; Bon 1977). The darker blackish colour that develops during maturation of basidiomata are mentioned only by Boertmann (2012) in the key to Nordic species of the genus *Camarophyllopsis*. Although almost all European mycologists (except for Kovalenko et al. 2012) follow the wide concept of *Ho. foetens* as a single species with a naphthalene odour, their descriptions are sometimes probably based on material of one species in a narrow-concept only. Ghyselinck (2003) published a photo of *Ho. foetens* that shows dark spots on the pileus and moderately close gills typical for *Ho. foetens*. Arnolds (1990) described this species as having a brown pileus becoming paler when dry and 12–22 lamellae, which corresponds to our description of *Ho. pallidus*. Kovalenko et al. (2012) described the pileus of *Ho. foetens* as having tobacco brown, yellow-brown and grey-brown colours becoming paler when dry and relatively wide caulocystidia, which may correspond to *Ho. pallidus*. In conclusion, European data about the distribution of *Ho. foetens* needs urgent revision and most probably contains information about more than one species.

Notes on *Hodophilus* species without a naphthalene odour

Based on our knowledge and unpublished type studies, five species of the genus *Hodophilus* without a strong naphthalene odour are widely accepted in the European literature (treated in the genus *Camarophyllopsis*). European keys to identification of *Camarophyllopsis* accept three (e.g. Arnolds 1990; Boertmann 2012) to five (Bon 1977) *Hodophilus* species without this odour. *Hodophilus atropunctus* is the only species accepted in every general European publication of the genus, a species identified by its darker scales or granulations on the stipe. Collections with such a stipe surface are placed in our phylogeny in two different clades within both *Hodophilus* superclades (one clade labelled as *Ho. micaceus* group 2 in Fig. 1 because it also contains collections without darker scales or granulations), but we do not have enough information to judge which one corresponds to the typical *Ho. atropunctus*. The remaining species without a naphthalene odour are recognised based on the colour of the stipe and lamellae. Some authors (Bon 1977; Horak 2005; Boertmann

2012) also reported North American species *Ho. hymenocephalus* from Europe, but our tree (Fig. 1) shows no European collection in the *Ho. hymenocephalus* clade and suggests this species does not occur in Europe. Three remaining species names, *Ho. micaceus*, *C. phaeoxantha* (Romagn.) Arnolds and *C. phaeophylla* (Romagn.) Arnolds (the latter two not combined yet in the genus *Hodophilus*), might correspond to any of the remaining European clades of *Hodophilus* without a naphthalene odour (labelled as *Ho. micaceus* group 1-3 and *C. phaeoxantha* group 2 in Fig. 1).

Acknowledgments The authors would like to thank David Harries, Peter Roberts, Shelley Evans, Judy Webb, Zuzana Egertová, Miroslav Caboň and Per Marstad for their contribution of specimens, photographs and/or assistance with field work. We also thank the staff and curators of the herbaria at K and LE for providing loans. Specifically, we would like to thank Kew Fungarium staff, A. Martyn Ainsworth, Angela Bond and Lee Davies (Royal Botanic Gardens, Kew, UK) for selection of British representative collections of the *Ho. foetens* complex used in this study. The research of SA, KA and SJ was granted by the national grant Vega 02/0075/14 and a grant from Slovak-American Foundation to SA.

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