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ORIGINAL ARTICLE

European *Hodophilus* (Clavariaceae, Agaricales) species with yellow stipe

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Abstract

Phylogenetic reconstruction of *Hodophilus* species with a yellow colour on the stipe based on nrITS, nrLSU and *rpb2* sequences revealed six European species. All these species correspond to the widely accepted European concept of a single species *Hodophilus micaceus*. Four of these species are described and illustrated. *H. micaceus* and *H. phaeoxanthus* are recognised as two separate species and *H. albofloccipes* as a synonym of the latter. Two species, *H. anatinus* and *H. cambriensis*, are described as new. Possible endemism of *H. micaceus* and *H. cambriensis* to the British Isles is discussed. All analysed North American samples represent different species to those found in Europe. The North American species *Hygrophorus rugulosus* is combined in the genus *Hodophilus*. The preliminary key uses position and development of the yellow colour during maturation as the most important distinguishing character. The presence of the yellow colour is discussed as a possible synapomorphic character.

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

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Introduction

Birkebak et al. (2016) re-installed the genus *Hodophilus* R. Heim ex R. Heim based on polyphyly of agaricoid members of the family Clavariaceae that were formerly all placed in the single agaricoid genus *Camarophyllopsis* Herink. They defined the genus morphologically by a hymeniderm (often pluristratous) type of pileipellis composed of inflated elements. This first multilocus phylogeny of agaricoid Clavariaceae taxa has recently been followed by phylogenetic studies on *Hodophilus* species defined by easily distinguishable morphological characters: foetid species (Adamčík et al. 2016, 2017a) and species with dark dots on the stipe (Adamčík et al. 2017b). The abovementioned studies recognised two major *Hodophilus* clades: *H. foetens* superclade and *H. micaceus* superclade, but these phylogenetically supported groups do not correspond to morphological groups defined in the literature (Boertmann 2012). The *H. foetens* superclade encompasses the majority of the species with a strong naphthalene odour, but *Hygrophorus subfuscescens* var. *odora* A.H. Sm. & Hesler having this odour is outside this superclade, and odourless *H. atropunctus* (Pers.) Birkebak & Adamčík belongs to it. The two recognised species with dark dots on the stipe, *H. atropunctus* and *H. variabilipes* Jančovičová, Adamčík & Looney, are also placed in different superclades (Adamčík et al. 2017b).

Morphological characters traditionally used for species classification were shown to have a polyphyletic origin, but they are still useful for preliminary species grouping, they support morphological identification and allow tracing of phylogenetically defined species in the published literature. In several cases, morphology is the only tool for clarifying concepts of old names when the type is old or missing, when sequencing the type material of *H. foetens* (W. Phillips) Birkebak & Adamčík has failed (Adamčík et al. 2017a) or when no authentic material is cited in the protologue as is the case for *H. atropunctus* (Adamčík et al. 2017b). The traditional European concept recognises four widely accepted *Hodophilus* groups: species with naphthalene odour represented by *H. foetens*, species with dark dots on the stipe represented by *H. atropunctus*, species with distinct yellow colours on the stipe represented by *H. micaceus* (Berk. & Broome) Birkebak & Adamčík and species with a brown stipe and without any yellow colours represented by *H. hymenocephalus* (A.H. Sm. & Hesler) Birkebak & Adamčík (Printz and Læssøe 1986; Horak 2005; Boertmann 2008, 2012; Kovalenko et al. 2012).

This study focuses on *Hodophilus* members with yellow tints on the stipe. The oldest available name is *H. micaceus* (originally described in the genus *Hygrophorus* by Berkeley and Broome 1879). Romagnesi (1971) described another species with a yellow stipe, *Hygrophorus phaeoxanthus* Romagn., but he did not even mention *H. micaceus*. Bon (1977) accepted both species and stated that *H. micaceus* was the species exclusively occurring in the British Isles. Printz and Læssøe (1986) introduced the synonymy between *H. micaceus*, *H. phaeoxanthus* and the North American *H. subfuscescens* (A.H. Sm. & Hesler) Adamčík, Birkebak & Looney, which became widely accepted (Arnolds 1990; Orton 1988; Boertmann 2012; Horak 2005) and *H. micaceus* remained the single accepted *Hodophilus* (*Camarophyllopsis*) species with a yellow stipe by most authors except Bon (1999).

More recently, Kovalenko et al. (2012) recognised *H. albofloccipes* (A.E. Kovalenko, E.F. Malysheva & O.V. Morozova) Looney & Adamčík with a yellow stipe, differing from *H. micaceus* by an unpleasant smell (similar to *H. foetens*) and white pruina or granulations on the stipe surface. Another recently described species with a yellow-brownish stipe, *H. variabilipes* Jančovičová, Adamčík & Looney (Adamčík et al. 2017b), is variable with regard to the presence or absence of dark, or pale dots or granulations on the stipe surface.

Based on our experience with this genus that shows large morphological variability, and the preliminary molecular data (Adamčík et al. 2017a, b), we expected the existence of more than one species with a yellow stipe. The aim of this study is therefore a phylogenetic reconstruction of the *Hodophilus* members with yellow tints on the stipe and morphological characterisation of recognised phylogenetic species, with the emphasis on European species.

Materials and methods

Taxon sampling

Altogether, 36 European *Hodophilus* collections with distinct yellow colours on the stipe were analysed. Type specimens of three species with a yellow stipe were included, viz. *H. albofloccipes*, *H. micaceus* and *H. phaeoxanthus*. For the phylogenetic placement, we used sequences previously published by Adamčík et al. (2017a, b) supported by another five newly sequenced *Hodophilus* samples. The complete dataset used for the phylogenetic analyses is presented in Supplementary Table 1.

DNA extraction, PCR and sequencing

Three gene regions (nrITS, nrLSU and *rpb2*) were amplified, sequenced and analysed. Protocols of Birkebak et al. (2013) were followed for DNA extraction, PCR and sequencing. The primer pair ITS1F-ITS4 (Gardes and Bruns 1993; White et al. 1990) was 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 nrLSU 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 SEQme sequencing Company (Dobříš, Czech Republic).

Phylogenetic analyses

Sequences of individual gene regions were assembled using ClustalX (Larkin et al. 2007) and manually adjusted and concatenated in SeaView 4 (Gouy et al. 2010). The concatenated dataset was subjected to maximum likelihood (ML) and Bayesian inference (BI) phylogenetic analyses, which were performed in raxmlGUI (Silvestro and Michalak 2012) and MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003), respectively. ML analysis was done using 1000 rapid ML bootstrap searches. Three partitions (ITS, LSU, *rpb2*) were set and the GTRGAMMA nucleotide substitution model was selected for each partition. BI was performed with the GTR + Γ + I model of evolution. The same partition scheme was used as for the ML analysis (see above). The BI settings were: four Markov chain Monte Carlo (MCMC) over 10 million generations, sampling every 1000th generation, two independent runs and burn-in of 30% (the first 3000 trees were discarded). Post burn-in trees were used to compute a 50% majority rule consensus phylogram. *Ramariopsis corniculata* was chosen as the outgroup.

Phylogenetic trees from both ML and BI analyses resulted in largely congruent topologies (Fig. 1). ML bootstrap values (BS) > 70% and Bayesian posterior probabilities (PP) > 0.95 were considered evidence for statistical branch support. All sequences are deposited in GenBank. The concatenated final alignment has been deposited in TreeBASE (TB2:S22666).

Morphological analyses

Macromorphological descriptions were prepared from fresh material shortly after collection from the field. The number of full-length lamellae is treated in the species descriptions as "L." The number of short lamellulae between each pair of full-length lamellae is labelled as "l" (Vellinga 1988). Colour nomenclature standards follow Kornerup and Wanscher (1967).

Microscopic structures were examined on herbarium specimens in Congo red solution with ammonia after a short treatment in aqueous 10% KOH. The same micromorphological characters were observed as those in our previous study on European *Hodophilus* species with a naphthalene odour (Adamčík et al. 2017a). Pileipellis elements near the pileus margin and the pileus centre were observed and evaluated separately. Features were observed under an Olympus CX-41 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. All other elements are measured with accuracy of 0.5 μm. *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)—all tests were negative, and data are omitted from the descriptions.

Results

Phylogenetic analyses

This study is based on 73 newly generated sequences (34 ITS, 22 LSU and 17 *rpb2*) corresponding to 35 samples. The final dataset consists of 131 samples represented by 128 ITS, 101 LSU and 77 *rpb2* sequences. Types of *H. albofloccipes* and *H. phaeoxanthus* were successfully sequenced, but the DNA extraction of the *H. micaceus* holotype failed. The *Hodophilus micaceus* superclade, encompassing mainly collections without a strong smell, received strong support. All collections with a yellow colour on the stipe are grouped in a strongly supported clade together with *H. variabilipes*, a species with yellow-brown stipe. Within this clade, the yellow-stiped collections form a weakly supported (MLBS = 50, BPP = 0.5, support values not indicated in Fig. 1) monophyletic group, except for a single sample without a yellow tint on the stipe represented by the type of *Hygrophorus rugulosus* that is nested within this clade. European yellow-stiped collections are clustered in six species clades that received full or strong support. The types of *H. albofloccipes* and *H. phaeoxanthus* are grouped in one of these clades together with 12 other samples. The remaining five species clades do not contain a type sequence. Based on morphological arguments given below, we identified one of the species clades as *H. micaceus*. Two other species clades are described here as new species and two remain undescribed due to lack of field observations. North American samples form two independent species clades and one single-specimen clade, all nested within the clade containing European yellow-stiped samples. Our phylogeny clearly demonstrated that two type collections of North American species previously classified in the genus *Hygrophorus* are placed in the *H. micaceus* superclade, and we formally combine one of them in the genus *Hodophilus* below. The combination *H. subfuscescens* was already made in Adamčík et al. (2016).


H. phaeoxanthus 14233-C10 DEU
H. phaeoxanthus SAV F-3098 SVK
H. phaeoxanthus O-F-21064 NOR
H. phaeoxanthus SAV F-4442 FRA
H. phaeoxanthus SLO781 SVK
H. albofloccipes LE 214946 RUS HOLOTYPE
H. phaeoxanthus PC0139813 FRA HOLOTYPE
H. phaeoxanthus 14229-C14 DEU
H. phaeoxanthus GB0060390 SWE
H. phaeoxanthus H07 AT H8 DEU
H. phaeoxanthus O-F-21057 NOR
H. phaeoxanthus DMS-679291 DEN
H. phaeoxanthus SAV F-3032 SVK
H. phaeoxanthus CL/F04.874 FRA
H. phaeoxanthus
99/1
82/-
H. subfuscescens TENN 023669 USA PARATYPE
H. subfuscescens v odora MICH10953 USA TYPE
99/1
H. subfuscescens
H. cf phaeoxanthus EU AG8 DEU
H. cf phaeoxanthus EU 14119-C6 DEU
100/1
H. cf. phaeoxanthus EU
97/1
H. cf phaeoxanthus UBC 28222 CAN
H. cf phaeoxanthus UBC 28418 CAN
95/1
H. cf. phaeoxanthus CAN
H. anatinus O-F-245610 NOR
H. anatinus O-F-245595 NOR
H. anatinus DB6109 SWE HOLOTYPE
H. anatinus PAM99082902 FRA
H. anatinus SAV F-20084 GBR
H. anatinus K(M)192320 GBR
H. anatinus SAV F-20083 GBR
-/0.96
92/1
H. anatinus
H. rugulosus AHS37565 USA ISOTYPE
H. rugulosus
H. cf. micaceus G07 AT H7 DEU
H. cf. micaceus 14232-C11 DEU
H. cf. micaceus DMS-696878 DEN
97/1
H. cf. micaceus
H. cambriensis SAV F-20082 GBR
H. cambriensis K(M)160555 GBR
H. cambriensis SAV F-4839 GBR
H. cambriensis SAV F-4831 GBR HOLOTYPE
100/1
H. cambriensis
H. micaceus K(M)187335 GBR
H. micaceus K(M)146133 GBR
H. micaceus SAV F-20086 GBR
H. micaceus SAV F-4840 GBR EPITYPE
H. micaceus K(M)159737 GBR
H. micaceus K(M)190819 GBR
100/1
93/-
H. micaceus
100/1
H. variabilipes
93/1
100/1
Hodophilus sp. SLO782 SVK
Hodophilus sp. SLO784 SVK
Hodophilus sp. SAV F-3097 SVK
100/1
Hodophilus sp.
-/0.98
100/1
H. hymenocephalus
99/1
100/1
H. smithii
100/1
H. subfoetens
99/1
100/1
H. pallidus
100/1
H. paupertinus
93/1
H. cf. foetens group 3
100/1
H. hesleri
74/0.99
100/1
H. atropunctus
86/1
H. cf. foetens group 2
96/1
99/1
H. tenuicystidiatus
89/0.99
H. cf. foetens group 1
99/1
H. foetens
91/0.99
100/1
Camarophyllopsis
99/1
Clavaria pullei
Clavaria fuscata
Lamelloclavaria petersenii
Ramariopsis corniculata
0.02

◀ **Fig. 1** Maximum likelihood phylogeny inferred from three loci (nrITS, nrLSU, *rpb2*) with species-level clades containing European collections with yellow stipe highlighted. Names of taxa are followed by collection labels, country, and whether this represents a type collection. Bootstrap values followed by Bayesian posterior probabilities are indicated at nodes. Clades not being focused in this paper are compressed

Morphological delimitation of genetically defined species

Our morphological study focuses on four species recognised in the phylogenetic study for which we have sufficient morphological observations on fresh basidiomata. Among the available valid species names, we assigned (based on the position of the type sequence) the name *H. phaeoxanthus* to one species clade, with *H. albofloccipes* as its synonym. The second name, *H. micaceus*, is identified based on its morphology and origin. This species was described (Berkeley and Broome 1879) and illustrated (Cooke 1888) as having an initially yellow, then greyish pileus and a consistently yellow stipe, both colorations perfectly fitting our collection SAV F-4840 that is proposed here as an epitype of the species. *Hodophilus micaceus* was described from North Wales and we studied the type collection together with other collections deposited in the Kew Herbarium (K). Three of the four studied collections originate from North Wales or the adjacent region of England (K(M)146133, K(M)187335, K(M)159737). This species is the most common among the studied collections of *Hodophilus* without a strong odour from the UK. The poor condition of the type specimen does not allow confirmation of a match of the microscopic structures with the epitype, but at least the cellular structure of the pileipellis confirms its classification in the genus *Hodophilus*. Two other well-represented species clades are recognised and described as new species in this study.

All four species described below display a yellow colour on the surface of the stipe and also on the very young pileus. However, the position of the yellow colour and its development during the maturation seem to have crucial importance for species delimitation (Table 1). *Hodophilus micaceus* is the only species where the young basidiomata are completely yellow, the stipe persistently vivid yellow also in mature stages and the pileus changing first to yellow brown or brown and then to grey buff to pale beige. In the other three species, the pileus of young basidiomata is yellowish brown to brown and the stipe colour changes soon to become partly to almost completely brown with age. The difference among species is how the colour changes over time. One of the new species, *H. anatinus*, starts to develop a brown colour on the stipe near the apex and this darkens and expands towards the base with age. The remaining two species, *H. phaeoxanthus* and *H. cambriensis*, usually show brown or darker colours near the base of the stipe. They differ from each other in colour development during maturation. In the first species, the stipe remains two-coloured of warm brown and yellow tints, but in the second one, it quickly changes to dark grey brown to almost black. *Hodophilus variabilipes* usually has dark dots on the stipe surface, but if not, it can be recognised by its

Table 1 Comparison of selected field characters observed on European *Hodophilus* taxa with yellow colour on the stipe

Species names	Pileus colour	Stipe colour and surface
H. anatinus	When moist and fresh greyish brown, when dry orange grey to grey brown	Very young light yellow, soon near the apex greyish yellow to brown, when mature the brown colour gradually expanding towards the base and when old almost completely dark brown; surface near the apex finely pruinous, towards the base smooth, shiny
H. cambriensis	When moist and fresh brownish grey, near the centre slightly paler and also with a yellow tint, drying from the centre, when dry uniformly pale orange grey	First greyish yellow to yellowish brown, later darkening from the base to light brown and dark grey brown, when old almost black; surface very finely pruinous, later smooth
H. micaceus	Young and fresh uniformly bright vivid yellow, later becoming yellow brown to brown, soon drying from the centre to yellowish grey, pale grey-buff or pale beige	Persistently and uniformly vivid yellow (lemony to egg), reminiscent of *Clavulinopsis helvola*; surface smooth, shiny
H. phaeoxanthus	When moist and fresh uniformly yellowish brown to brown, when dry near the margin yellowish brown, greyish brown, orange grey to brownish orange, near the centre paler, orange grey, brownish grey, pale orange to greyish brown	Usually 2-coloured (yellow and brown)—yellow, golden yellow, brownish orange, light brown, yellowish brown, greyish brown, brown—the position and intensity of yellow tints is variable but the base is usually brown; surface near the apex almost along entire length slightly pruinous or sometimes distinctly white farinose, towards the base smooth and shiny
H. variabilipes	Fresh and young brown, dark brown to greyish brown, when dry discolouring first at the centre to yellowish brown, greyish brown, orange grey to olive brown	Evenly coloured over the whole length, greyish yellow, brownish orange, yellowish brown or dark brown; surface usually with very distinct dark brown floccules or granules and towards the base fibrils, some collections with completely smooth and shiny stipe surface, rarely with fine white granulations along entire length

uniform colour along the entire length: at first greyish or brownish yellow but with age the yellow tint may disappear completely.

Despite our considerable efforts to find some additional micro-morphological characters, we have not found any specific one for an individual species (Table 2). It seems that the spores of *H. cambriensis* are often narrower with *Q* up to 1.2 compared with the other species, but the difference is small and requires multiple measurements. *Hodophilus micaceus* usually has shorter (and often also smaller) subterminal cells of the hyphae in pileipellis near the pileus margin. It seems that *H. anatinus* has narrower terminal cells of the hyphae in pileipellis near the pileus centre and may be distinguished from *H. micaceus* and *H. cambriensis* using this character. The caulocystidia of *H. phaeoxanthus* are often flexuous, twisted, nodulose or lobate, but this was not consistently observed in all collections of the species, and it was also observed in other species. The presence of marginal cells on the lamella edges is interesting, but again, this character is present in multiple species, and not in all specimens of a species.

Below, we provide a preliminary key to *Hodophilus* species with yellow colour on the stipe, but this should be revised in the future with the addition of at least two other species recognised in our phylogeny but not investigated morphologically in this study.

Taxonomy

Preliminary key to *Hodophilus* species with yellow colour on the stipe

1 stipe with distinct dark dots or without dots (rarely pale or absent) coloured uniformly greyish yellow, yellowish brown,

Table 2 Average values of 30 measurements of selected micromorphological characters observed on the four *Hodopilus* species with yellow colour on the stipe

Species epithet	Herbarium No.	Spores			Caulocystidia		TC margin			STC margin		TC centre			STC centre		Marginal cells	
		L	W	*Q*	L	W	L	W	*Q*	L	W	L	W	*Q*	L	W	L	W
H. anatinus	DB6109	4.8	3.8	1.25	48.7	9.6	32.6	22.6	1.48	14.9	5.4	32.8	19.9	1.75[a]	15.0	6.1	–	–
	SAV F-20083	5.4	4.2	1.28	43.4	10.0	33.4	20.2	1.76	26.6	9.6	–	–	–	–	–	31.4	7.8
	SAV F-20084	5.2	4.1	1.26	39.9	8.7	40.7	27.8	1.48	28.1	13.7	29.4	14.8	2.12[a]	28.6	10.0	–	–
	K(M)192320	5.2	4.2	1.25	45.9	8.1	–	–	–	–	–	–	–	–	–	–	–	–
	NOBAS301216	5.2	4.2	1.23	32.0	8.3	31.2	17.9	1.83	22.2	9.7	30.3	17.6	1.85[a]	20.4	9.7	27.0	6.9
H. cambriensis	SAV F-4831	5.2	4.4	1.17[a]	49.0	9.4	38.3	28.4	1.37	20.5	11.9	38.0	23.9	1.64	17.8	9.8	–	–
	K(M)160555	4.8	4.0	1.18[a]	49.5	8.6	–	–	–	–	–	27.7	16.1	1.81[a]	24.0	8.2	–	–
	SAV F-20082	5.2	4.5	1.15[a]	43.9	8.6	37.0	25.4	1.47	19.0	9.6	36.7	24.0	1.54	20.5	9.4	30.6	9.5
	SAV F-4839	5.0	4.2	1.20	42.0	8.7	29.6	19.3	1.54	16.2	7.0	30.2	20.7	1.47	17.9	7.3	–	–
H. atropunctus	SAV F-4840	4.9	3.9	1.28	36.9	7.0	36.3	22.5	1.73	14.2[a]	6.9	35.4	24.4	1.53	15.2	7.7	31.7	6.5
	K(M)190819	4.7	3.7	1.26	48.9	9.7	39.4	29.5	1.39	9.9[a]	5.4	39.7	28.1	1.55	11.1	5.3	22.6	8.3
	K(M)146133	–	–	–	41.2	9.0	31.9	23.9	1.35	11.3[a]	6.0	35.0	26.0	1.38	12.8	6.2	–	–
	K(M)187335	4.9	4.0	1.25	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	K(M)159737	5.4	4.3	1.25	43.9	10.5	32.0	25.9	1.24	12.9	7.4	38.6	28.8	1.38	10.0	7.3	27.5	10.5
	SAV F-20086	5.1	4.1	1.24	36.3	8.7	33.8	21.4	1.60	11.4	6.0	35.4	22.7	1.58	9.5	4.4	32.9	7.6
H. phaeoxanthus	PC139813 (type)	4.8	3.9	1.23	35.2	7.1	30.4	22.8	1.37	24.9	11.0	27.1	20.8	1.31	24.1	10.7	26.0	7.8
	LE 214946	5.4	4.3	1.28	22.9	7.0	26.2	14.8	2.00	12.3	6.4	24.7	17.0	1.48	14.9	7.6	–	–
	SLO781	5.1	4.3	1.17	36.8	7.9	26.6	17.8	1.54	14.1	7.7	34.3	23.1	1.49	19.5	9.7	29.8	7.5
	SAV F-3032	5.4	4.4	1.23	28.6	6.5	45.5	28.6	1.65	23.4	9.4	45.8	30.2	1.54	18.3	6.8	32.2	9.2
	SAV F-3098	5.2	4.3	1.23	40.5	8.1	37.6	28.3	1.34	16.5	6.0	37.1	28.2	1.31	16.9	6.3	28.4	6.6
	SAV F-4442	4.7	3.9	1.20	39.7	8.6	40.9	27.1	1.57	19.2	7.5	41.0	28.1	1.53	20.0	7.4	–	–
	C (DMS-679291)	4.9	4.0	1.23	49.4	10.1	39.1	27.7	1.43	21.6	6.5	44.8	29.9	1.57	21.2	6.9	37.0	9.1
	SLO771	4.8	3.9	1.23	35.2	7.1	30.4	22.8	1.37	24.9	11.0	27.1	20.8	1.31	24.1	10.7	26.0	7.8

En dash indicates missing values due to absence of a structure or insufficient conditions of the studied herbarium specimen

TC and STC margin/centre, terminal and subterminal cells in pileipellis near the pileus margin/centre; L, length in micrometres; W, width in micrometres, Q, length/width ratio

[a] Important differences (with no or little overlap between at least one species pair)

brownish orange to dark brown but without any pure yellow colour . . . . *H. variabilipes*

1* Stipe never with dark dots, at least partly, esp. when young, with pure yellow tints, often with different colours near the apex or near the base 2

2 Young basidiomata completely yellow, stipe persistently vivid yellow, remaining so when mature . . . . . *H. micaceus*

2* Young basidiomata with a yellowish brown pileus, with the stipe colour changing soon and becoming partly to almost completely brown with age 3

3 Stipe of young basidiomata near the apex usually yellow brown to grey brown and darker than below; terminal elements in pileipellis near pileus centre relatively narrow, with length/width ratio > 1.6 . . . . *H. anatinus*

3* Stipe of young basidiomata near the apex usually not darker than in the middle or near the base; terminal elements in pileipellis near pileus centre usually with length/width ratio < 1.6 4

4 Stipe at first yellow to brownish yellow, with age gradually changing to dark grey brown to almost black near base; spores in average with $Q \leq 1.2$ . . . . *H. cambriensis*

4* Stipe usually two-coloured with pale yellow, golden yellow, brownish orange near the apex and light brown, yellowish brown or greyish brown near the base, not becoming distinctly darker with age; spores usually in average with $Q >$ 1.2. . . . . *H. phaeoxanthus*

Hodophilus rugulosus (A.H. Sm. & Hesler) Adamčík & Jančovičová, comb. nov.

MycoBank No.: MB 825020.

≡ *Hygrophorus rugulosus* A.H. Sm. & Hesler, Sydowia 8: 330. 1954 (Basionym).

≡ *Hygrotrama rugulosa* (A.H. Sm. & Hesler) Singer, Beihefte zur Sydowia 7: 4. 1973.

≡ *Camarophyllopsis rugulosa* (A.H. Sm. & Hesler) Arnolds, Mycotaxon 25(2): 643. 1986.

Hodophilus anatinus Dima, Adamčík & Jančovičová, sp. nov. (Figs. 2–3 and 12–17)

MycoBank No.: MB 825021.

Etymology: The colour change of basidiomata during maturation resembles that of mallard (*Anas platyrhynchos*): ducklings are yellow on their lower parts and with age they become almost entirely brown.

Holotypus: Sweden. Jämtland, Trång, Jale, 27 August 2016, on ground in a calcareous pasture grazed by cattle, B. Dima *DB6109* (BP106947).

Diagnosis: Pileus greyish brown, when dry orange grey and grey brown; stipe at first yellow, soon becoming greyish yellow to brown near the apex, the brown colour expanding downwards with age and finally the stipe become almost completely brown; flesh without a strong odour; spores in average 5.2 × 4.1 µm, av. $Q = 1.25$; pileipellis mainly a hymeniderm, terminal cells of the hyphae near the pileus centre mainly subglobose, obpyriform, with average length/width ratio < 1.6.

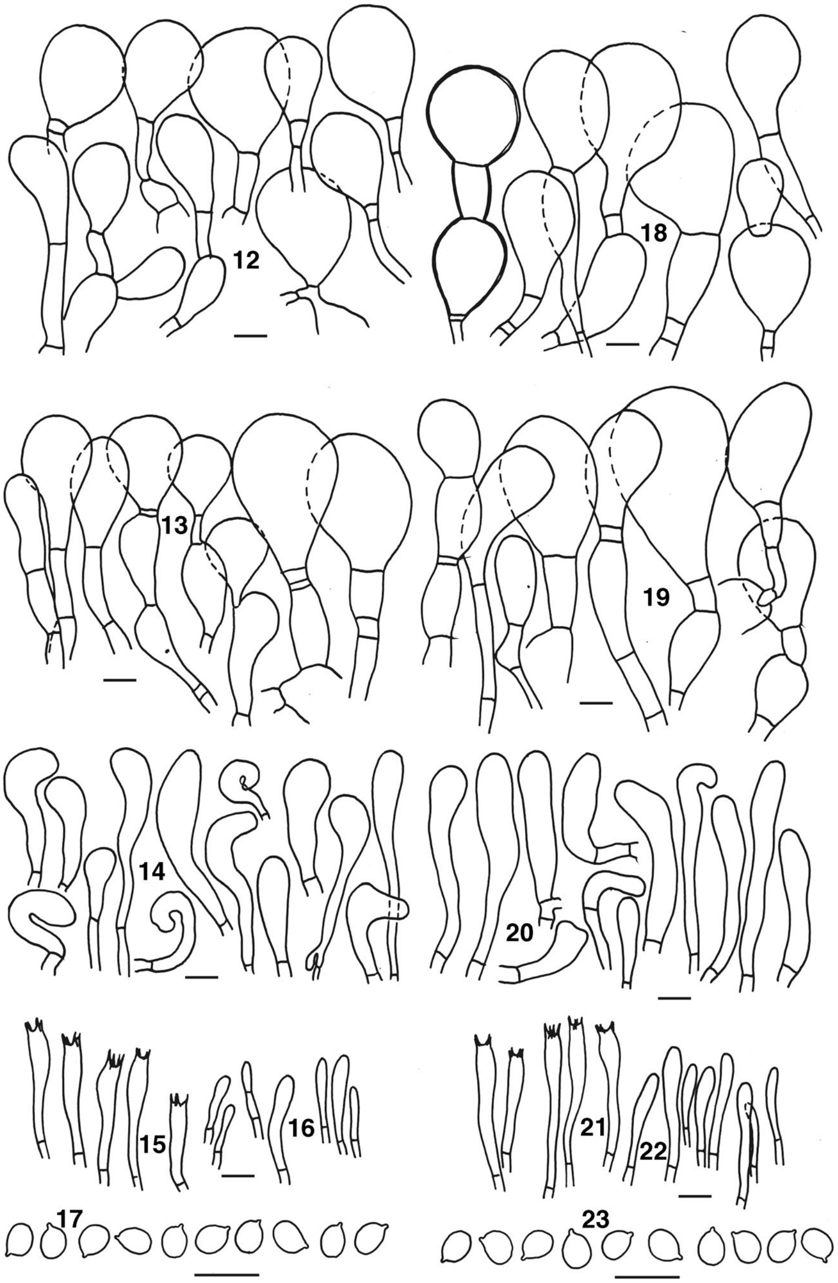
Pileus (Figs. 2–3) 8–20 mm broad, convex to plano-convex, truncate or weakly depressed near the centre; margin first slightly inflexed, soon straight, slightly crenate, when moist weakly translucently striate up to half the diameter; surface matt, smooth, sometimes rugulose, hygrophanous, when moist and fresh greyish brown (milk coffee 6D3), when dry orange grey (5B2) to grey brown (7C2–7D3). *Stipe* 20–35 × 2–3 mm, cylindrical, sometimes flexuous, usually narrowed towards the base, often compressed, grooved; near the lamellae finely pruinose, towards the base smooth, shiny, at the base with white tomentum; very young light yellow (pastel yellow 3A4), soon near the lamellae greyish yellow (champagne 4B4) to brown (fawn 7E4), with age the brown colour gradually expands towards the base, when old almost completely dark brown (7F4). *Lamellae* $L = 16–24$, $l = 0–1$, shortly or deeply decurrent, concolorous with the pileus, first orange grey (5B2), mature grey brown (7D3); edges entire, paler than the sides. *Flesh* elastic; odour indistinct, with a weak unpleasant component.

Basidiospores (Fig. 17) (4.6)4.8–5.5(6.1) × (3.7)3.8–4.4(4.8) µm, av. 5.2 × 4.1 µm, $Q = (1.14)1.19–1.31(1.44)$, av. $Q = 1.25$, broadly ellipsoid, hyaline, smooth, thin-walled; hilar appendage up to 0.4–0.8 µm long. *Basidia* (Fig. 15) 4-spored, narrowly clavate, (27)31–38.5(42) × (5)6–7(8) µm, av. 34.7 × 6.5 µm. *Basidiola* (Fig. 16) cylindrical to narrowly clavate, obtuse, ca. 10–30 × 2.5–5.5 µm. *Pleurocystidia* absent. *Marginal cells* on the lamellar edges, well differentiated in the collections SAV F-20083 and NOBAS 301216, narrowly or broadly clavate, obtuse, (15)22–36.5(53) × (5)6–8.5(11) µm, av. 29.2 × 7.3 µm. *Pileipellis* (Fig. 12) a hymeniderm, rarely a transition to epithelium; terminal cells near the pileus margin obpyriform, subglobose or broadly clavate, often with thickened walls (up to 1 µm), (11)24.5–42(58) × (11)14.5–27.5(37) µm, av. 33.3 × 21 µm, $Q = (0.85)1.12–2.21(3.36)$, av. $Q = 1.67$; subterminal cells usually distinctly narrower, cylindrical, rarely inflated and branched, (3.5)10–33.5(53) × (3)4–13.5(24) µm, av. 21.8 × 8.7 µm; small cells (shorter than 5 µm) rare or occasional. Terminal cells near the pileus centre (Fig. 13) smaller and narrower than those near the pileus margin, (14)22.5–39.5(59) × (7)12–24(35) µm, av. 31.1 × 18 µm, $Q = (1)1.21–2.51(4)$, av. $Q = 1.86$; subterminal cells similar to those near the pileus margin, (2)8–32(74) × 3.5–13(25) µm, av. 19.8 × 8.3 µm. *Caulocystidia* (Fig. 14) without dark pigments, thin-walled, ascending or repent, usually clustered in patches; terminal cells mostly narrowly clavate to clavate, rarely ventricose, often pedunculate, frequently flexuous, occasionally curved to twisted, mostly obtuse, occasionally apically narrowed, (13)27–57.5(100) × (5)7–11.5(13) µm, av. 42.3 × 9.1 µm. Clamp connections absent in all parts.

Additional material examined: *France.* Haute-Savoie, La Clusaz, L'Etale, in alpine vegetation with *Salix herbacea*,

Figs. 2–11 Basidiomata field aspect of *Hodophilus* species with yellow stipe. 2. Young basidiomata of *H. anatinus* (O-F-245595), photo by T. Læssøe. 3. Mature basidiomata of *H. anatinus* (BP (DB6109), holotype), photo by B. Dima. 4. Nearly mature basidiomata of *H. cambriensis* in a short grass vegetation (K(M)160555), photo by D. Harries. 5. Young basidiomata of *H. cambriensis* (SAV F-4839), photo by M. Adamčík. 6. Mature basidiomata of *H. cambriensis* in dry conditions (SAV F-4831, holotype), photo by M. Adamčík. 7. Basidiomata of *H. micaceus* (SAV F-20086), photo by D. Harries. 8. Basidiomata of *H. micaceus* (SAV F-4840, epitype), photo by M. Adamčík. 9. Mature basidiomata of *H. phaeoxanthus* (SLO781), photo by S. Jančovičová. 10. Mature basidiomata of *H. phaeoxanthus* (SAV F-3032), photo by A. Ronikier. 11. Basidiomata of *H. phaeoxanthus* (SAV F-4442) photo by Z. Egertová. Scale bar = 1 cm

together with *H. atropuncta* and *H.* cf. *foetens*, 29 August 1999, P-A Moreau *PAM99082902* (LIP). *Norway.* Vestfold, Larvik, Løvallåsen S, in grass turf on calcareous rocks, 31 August 2012, T Læssøe & A Molia (O-F-245595); ibid., 16 October 2012, T Læssøe & A Molia (O-F-245610). *UK: England.* Dove Dale, Lin Dale, calcareous pasture, in moss and grass, 21



Figs. 12–23 Microscopic structure of *Hodophilus anatinus* (left, BP (DB6109), holotype) and *H. cambriensis* (right, SAV F-4831, holotype). 12. Hyphal terminations in pileipellis near the pileus margin. 13. Hyphal terminations in pileipellis near the pileus centre. 14. Caulocystidia. 15. Basidia. 16. Basidioles. 17. Spores. 18. Hyphal terminations in pileipellis near the pileus margin. 19. Hyphal terminations in pileipellis near the pileus centre. 20. Caulocystidia. 21. Basidia. 22. Basidioles. 23. Spores. Drawings by S. Jančovičová. Scale bar = 10 μm

October 2016, R Foster (SAV F-20084); Wales. Caernarvonshire, Mariandyrys (near), in short turf (limestone pavement), 31 October 2013, C E Aron (K(M)192320); England, Beresford, Wolfscole Dale, calcareous pasture, in moss and grass, 20 October 2016, R Foster (SAV F-20083).

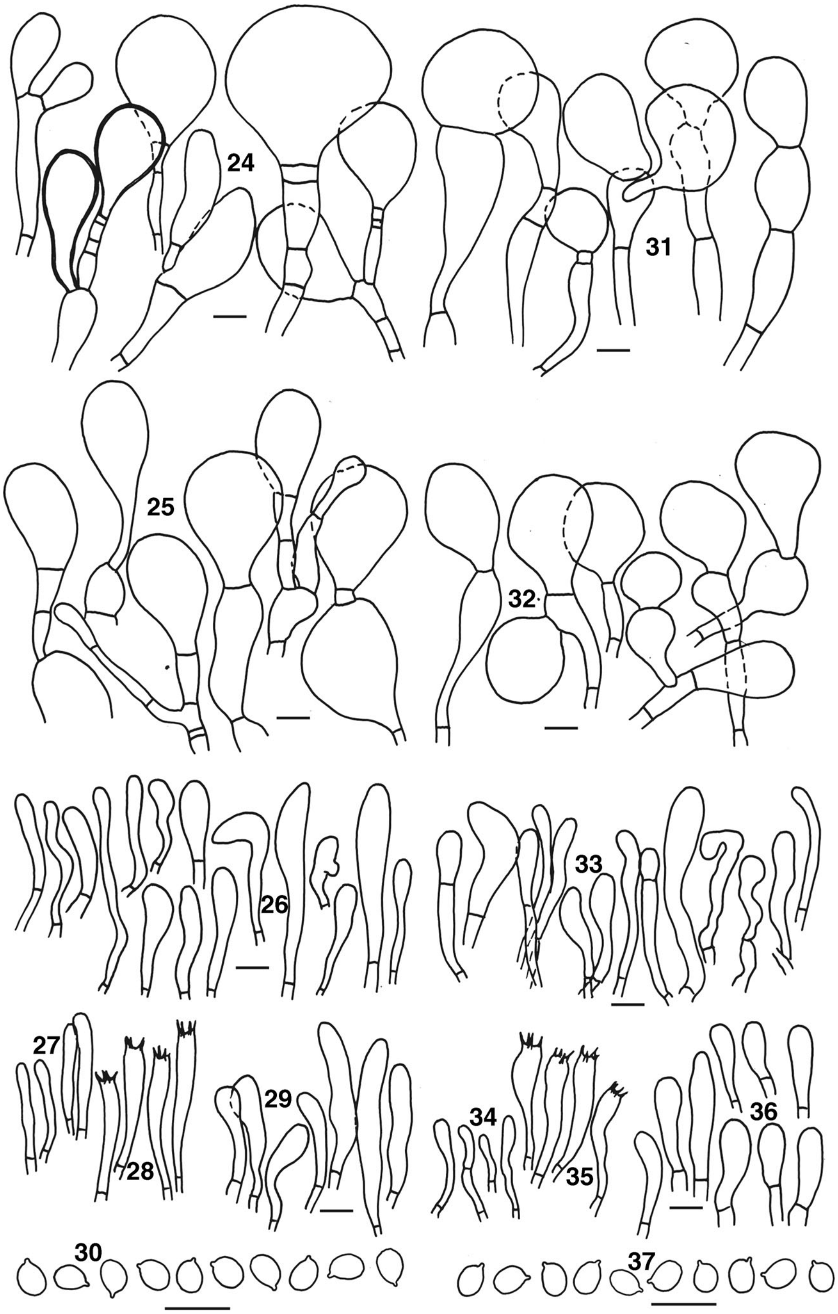
Hodophilus cambriensis Adamčík & Harries, sp. nov. (Figs. 4–6 and 18–23)

MycoBank No.: MB 825022.

Etymology: Cambria is the Latin name of Wales, the country of origin of all studied collections.

Holotypus: UK. Wales, Pembrokeshire, Orielton Wood, Orielton Field Study Centre, coord. 51° 39′ 24.19″ N, 4° 57′ 3.48″ W, on ground at woodland edge associated with *Fraxinus*, *Acer*, *Quercus*, *Coryllus*, *Hedera helix*, *Rubus*, 8 October 2016, S Adamčík (SAV F-4831).

Diagnosis: Pileus brownish grey and paler near the centre, when dry uniformly pale orange grey; stipe first greyish yellow to yellowish brown, later darkening from the base, light brown to dark grey brown, when old almost black; flesh without a strong odour; spores in average 5.1 × 4.3 μm, av. $Q = 1.18$; pileipellis mainly a hymeniderm, terminal cells of hyphae near the pileus centre mainly subglobose, obpyriform, with average $Q \leq 1.2$.



Figs. 24–37 Microscopic structure of *Hodophilus micaceus* (left, SAV F-4840, epitype) and *H. phaeoxanthus* (right, PC0139813, holotype). 24. Hyphal terminations in pileipellis near the pileus margin. 25. Hyphal terminations in pileipellis near the pileus centre. 26. Caulocystidia. 27. Basidioles. 28. Basidia. 29. Marginal cells on the lamellar edges. 30. Spores. 31. Hyphal terminations in pileipellis near the pileus margin. 32. Hyphal terminations in pileipellis near the pileus centre. 33. Caulocystidia. 34. Basidioles. 35. Basidia. 36. Marginal cells on the lamellar edges. 37. Spores. Drawings by S. Jančovičová. Scale bar = 10 μm

Pileus (Figs. 4–6) (5)10–20 mm broad, semiglobose, soon convex to applanate, margin inflexed, slightly and irregularly crenulate, often also lobate, not striate; surface matt, smooth, sometimes slightly rough, when old rugulose, hygrophanous, when moist and fresh brownish grey (5C2 to 6D3), near the centre slightly paler and also with a yellow tint, drying from the centre, when dry uniformly pale orange grey (alabaster 5B2). Stipe 18–28 × 1.5–2(5) mm, cylindrical, flexuous, sometimes narrowed towards the base; very finely pruinose, later smooth; at first greyish yellow (champagne 4B4 to sand 4B3) to yellowish brown (hair brown 5E4), later darkening from the base to light brown (7D6) and dark grey brown (7E3), when old almost black. Lamellae up to 4 mm deep, $L = 13–21$, $l = 0–1$, usually shortly decurrent when young, mature deeply decurrent; pale orange grey (alabaster 5B2), later brown beige (6E3); edges concolourous, entire. *Flesh* in pileus relatively fragile; odour weakly unpleasant.

Basidiospores (Fig. 23) (4.4)4.7–5.4(6) × (3.1)4–4.6(5) μm, av. 5.1 × 4.3 μm, $Q = (1.06)1.12–1.23(1.58)$, av. $Q = 1.18$, subglobose to broadly ellipsoid, hyaline, smooth, thin-walled; hilar appendage up to 0.5–1 μm long. *Basidia* (Fig. 21) 4-spored, hyaline, narrowly clavate, (22)31–44.5(49) × (5)5.5–6(6.5) μm, av. 37.9 × 5.6 μm. *Basidiola* (Fig. 22) cylindrical to narrowly clavate, obtuse, ca. 17–

38 × 2.5–5.5 μm. *Pleurocystidia* absent. *Marginal cells* on the lamellar edges well differentiated only in the collection SAV F-20082, narrowly or broadly clavate, obtuse, (13)21.5–40(53) × (6.5)7–12(15) μm, av. 30.6 × 9.5 μm. *Pileipellis* (Fig. 18) a transition between hymeniderm and epithelium; often composed of inflated cells connected by strongly narrowed, small, cylindrical elements; terminal cells near the pileus margin subglobose, obpyriform, or obovoid, rarely sphaeropedunculate or broadly clavate, often with thickened walls (up to 1 μm), (18)26–43.5(55) × (13)18.5–30(40) μm, av. 34.7 × 24 μm, *Q* = (1)1.17–1.76(2.24), av. *Q* = 1.47; subterminal cells usually distinctly narrower, mostly cylindrical, some inflated and broadly clavate or ventricose, rarely branched, (4)7.5–29(55) × (3)3.5–15(35) μm, av. 18.4 × 9.3 μm; small cells (shorter than 5 μm) rare or occasional. Terminal cells near the pileus centre (Fig. 19) similar in size to those near the pileus margin but usually somewhat narrower, (17)24.5–42.5(61) × (8)15.5–27.5(40) μm, av. 33.6 × 21.6 μm, *Q* = (1.06)1.22–1.98(3), av. *Q* = 1.6; subterminal cells similar to those near the pileus margin, (4)8–31.5(58) × (4)4.5–13(39) μm, av. 19.8 × 8.7 μm. *Caulocystidia* (Fig. 20) without dark pigments, thin-walled, ascending or repent; terminal cells mostly narrowly to broadly clavate, frequently flexuous, occasionally curved, obtuse, (13)31.5–61(103) × (5)6.5–11(14.5) μm, av. 46.1 × 8.8 μm. *Clamp connections* absent in all parts.

Additional material examined: UK: Wales, Pembrokeshire, Somerton farm, shaded earth bank along a stream edge, in moss, associated with *Clavulinopsis luteoalba*, 21 September 2008, D Harries (K(M)160555); ibid., on bare soil on shaded stream-side bank, 20 October 2015, D Harries (SAV F-20082); on the same place as the type collection, 8 October 2016, S Adamčík (SAV F-4839).

Hodophilus micaceus (Berk. & Broome) Birkebak & Adamčík, Mycologia 108: 867. 2016 (Figs. 7–8 and 24–30)

≡ *Hygrophorus micaceus* Berk. & Broome, The Annals and magazine of natural history 3: 207. 1879 (Basionym).

≡ *Hygrocybe micacea* (Berk. & Broome) P.D. Orton & Watling, Notes from the Royal Botanical Garden, Edinburgh 29: 134. 1969.

≡ *Hygrotrama micacea* (Berk. & Broome) Bon, Documents Mycologiques 7(27–28): 46. 1977.

≡ *Camarophyllopsis micacea* (Berk. & Broome) Arnolds, Persoonia 13(3): 386. 1987.

MycoBank No.: MB 810139.

Holotypus: UK: Wales, Denbighshire, Abergele, Dolven, Coed Coch, on clayey soil, October 1878, Miss Ruth Berkeley [K(M)92,783].

Epitypus (designated here): UK: Wales, Pembrokeshire, Kennel Wood, Orielton Field Study Centre, 51° 39′ 27.79″ N, 4° 57′ 14.41″ W, on ground at woodland edge associated with *Fraxinus*, *Acer*, *Quercus*, *Hedera helix*, *Rubus*, 8 October 2016, S Adamčík (SAV F-4840).

Pileus (Figs. 7–8) 7–17 mm broad, semiglobose, convex to plano-convex, rarely depressed near the centre; margin inflexed, when old denticulate, not striate; surface matt, smooth, when old slightly rugulose, hygrophanous, when young and fresh uniformly bright vivid yellow (2A8–3A8), later becoming yellow brown to brown (6E4), soon drying from the centre to yellowish grey, pale grey-buff or pale beige. *Stipe* 20–30 × 1.5–3(−5) mm, cylindrical, flexuous, occasionally narrowed towards the base (especially when old); smooth, shiny; the colour persistently and uniformly vivid yellow (lemony to egg), reminiscent of *Clavulinopsis helvola* (Pers.) Corner. *Lamellae* ca. 2.5 mm deep when mature, L = 17–24, l = (0)1(−3), usually shortly decurrent, mature sometimes long decurrent; first pale yellowish, later pale brownish grey (6C2–6C3); edges concolourous, entire. *Flesh* elastic; without a specific odour.

Basidiospores (Fig. 30) (3.5)4.6–5.4(6) × (3.1)3.7–4.3(4.7) μm, av. 5 × 4 μm, *Q* (length/width) = (1.03)1.19–1.32(1.58), av. *Q* = 1.26, broadly ellipsoid to ellipsoid, hyaline, smooth, thin-walled; hilar appendage 0.5–0.7 μm long. *Basidia* (Fig. 28) 4-spored, hyaline, narrowly clavate and slightly flexuous towards the base, (29)34.5–43.5(51) × (5)5.5–7(7.5) μm, av. 38.7 × 6.3 μm. *Basidiola* (Fig. 27) cylindrical to narrowly clavate, often flexuous, obtuse, (17)20.5–34.5(43) × (2)3.5–6(7) μm, av. 27.4 × 4.8 μm. *Pleurocystidia* absent. *Marginal cells* (Fig. 29) on the lamellar edges often well differentiated, narrowly clavate to clavate, sometimes flexuous and occasionally nodulose or ventricose, obtuse, (14)20.5–37.5(59) × (4.5)6–10(15) μm, av. 28.7 × 8 μm. *Pileipellis* a transition between hymeniderm and epithelium; terminal cells near the pileus margin (Fig. 24) mostly obpyriform, subglobose or ellipsoid, less frequently broadly clavate, often thick-walled (walls up to 1 μm), (17)24–45.5(84) × (10.5)16.5–33(62) μm, av. 34.7 × 24.6 μm, *Q* = (0.87)1.06–1.87(3.36), av. *Q* = 1.46; subterminal cells usually distinctly narrower, cylindrical, occasionally also inflated, occasionally branched, (2)3.5–20.5(45) × (2.5)3–9.5(26) μm, av. 11.9 × 6.3 μm; small cells (shorter than 5 μm) frequent. Terminal cells near the pileus centre (Fig. 25) similar in size and shape to those near the pileus margin, (17)25.5–48(85) × (6)16.5–35.5(57) μm, av. 36.8 × 26 μm, *Q* = (0.95)1.1–1.87(3.31), av. *Q* = 1.48; subterminal cells also similar to those near the pileus margin, (2)4–19.5(41) × (2)3–9.5(26) μm, av. 11.7 × 6.2 μm. *Caulocystidia* (Fig. 26) without dark pigments, thin-walled, repent or ascending; terminal cells mainly narrowly clavate to clavate, occasionally broadly clavate, often pedunculate and flexuous, occasionally nodulose, obtuse, (15)26.5–56.5(102) × (4.5)6.5–11.5(17) μm, av. 41.4 × 9 μm. *Clamp connections* absent in all parts.

Additional material examined: UK: England. Shropshire, Benthall Edge, on soil, 24 September 2008, G Kibby (K(M)159737); West Sussex, Staplefield, on soil among sparse vegetation near yew, 30 October 2013, V C Hodge (K(M)190819); *Wales*. Merionethshire, Bala, Llanuwchllyn, Trawscoed, in short, sheep-grazed "waxcap grassland," 28 November 2006, A Graham (K(M)146133); Anglesey, Red Wharf Bay, on banking ground in broad leaved woodland, 31 July 2012, C E Aron (K(M)187335); Pembrokeshire, Somerton farm, semi-improved neutral grassland, on soil in area grazed by cattle, 13 October 2016, D Harries (SAV F-20086).

Hodophilus phaeoxanthus (Romagn.) Adamčík & Jančovičová, comb. nov. (Figs. 9–11 and 31–37)

≡ *Hygrophorus phaeoxanthus* Romagn., Bulletin de la Société Mycologique de France 86(4): 873. 1971 (Basionym).

≡ *Hygrotrama phaeoxantha* (Romagn.) Bon, Documents Mycologiques 7 (27–28): 47. 1978.

≡ *Camarophyllopsis phaeoxantha* (Romagn.) Arnolds, Mycotaxon 25 (2): 643. 1986.

= *Camarophyllopsis albofloccipes* Kovalenko, E.F. Malysheva & O.V. Morozova, Mycologiya i Fitopatologiya 46: 64. 2012.

≡ *Hodophilus albofloccipes* (Kovalenko, E.F. Malysheva & O.V. Morozova) Looney & Adamčík, in Adamčík et al., Mycol. Progr. 16(1): 50. 2017.

MycoBank No.: MB 825024.

Holotypus: France. Forêt de Laigue (Oise), "dans mousse d'un petit marécage" (in moss of a small swamp), sous *Alnus*, *Fraxinus*, 22 September 1954, H. Romagnesi *54.268* (PC0139813).

Pileus (Figs. 9–11) 6–21 mm broad, convex, with age almost applanate, often indistinctly depressed near the centre; margin inflexed, soon straight, when moist weakly translucently striate up to half the diameter; surface smooth, matt, when mature rough-bumpy, when young with fine granulose covering, hygrophanous, when moist and fresh uniformly yellowish brown (clay 5D5) to brown (6E4), when dry near the margin yellowish brown (hair brown 5E4), greyish brown (milk coffee 6D3), orange grey to brownish orange (5B2–5C3), near the centre paler, orange grey (birch bark 6B2), brownish grey (6C2), pale orange (5A3–5B3) to greyish brown (nougat 5D3). *Stipe* 13–33 × 1–3 mm, cylindrical, flexuous, often narrowed towards the base, rarely compressed; near the lamellae almost along entire length slightly pruinose or sometimes distinctly white farinose, towards the base smooth and shiny, at the base with white tomentum; usually two-coloured (yellow and brown)—yellow (yolk 4B8), golden yellow (4C6), brownish orange (golden blonde 5C4), light brown (honey yellow 5D6), yellowish brown (hair brown 5E4, mustard brown 5E6), greyish brown (milk coffee 6D3), brown (6E4)—the position and intensity of the yellow tints is variable but the base is usually brown. *Lamellae* 1.5–2.5 mm deep, $L = (13)16–22(25)$, $l = 0–1$, shortly or deeply decurrent; young yellowish brown to olive (3D4), soon brownish orange (5C3), light brown (dark blond 5D4) to greyish brown (milk coffee 6D3), when old brown (fawn 7E4) to dark brown (7F4); edges concolorous or slightly paler, entire. *Flesh* elastic; odour indistinct but unpleasant with age.

Basidiospores (Fig. 37) (4.1)4.7–5.5(6.6) × (3.4)3.9–4.5(5) μm, av. 5.1 × 4.2 μm, Q (length/width) = (1.09)1.15–1.3(1.45), av. $Q = 1.22$, broadly ellipsoid, hyaline, smooth, thin-walled; hilar appendage 0.6–0.9 μm long. *Basidia* (Fig. 35) 4-spored, hyaline, narrowly clavate, usually flexuous towards the base, (23)30.5–42(48) × (5)6–7.5(9) μm, av. 36.4 × 6.7 μm. *Basidiola* (Fig. 34) cylindrical to narrowly clavate, often flexuous, obtuse, (15)20.5–35.5(49) × (3)4–6.5(8) μm, av. 28 × 5.4 μm. *Pleurocystidia* absent. *Marginal cells* (Fig. 36) on the lamellar edges usually well differentiated, narrowly clavate to clavate, usually not flexuous, obtuse, (14)22.5–39(48) × (5)6.5–10(15) μm. *Pileipellis* a transition between hymeniderm and epithelium; terminal cells near the pileus margin (Fig. 31) mostly subglobose, obpyriform or ellipsoid, less frequently broadly clavate, often thick-walled (walls up to 1 μm), (7.5)21.5–48(78) × (4)14.5–32.5(57) μm, av. 34.8 × 23.5 μm, $Q = (0.83)0.92–2.22(7.69)$, av. $Q = 1.57$; subterminal cells usually distinctly narrower, mainly cylindrical, some clavate or ventricose, occasionally branched, (2)5.5–30(60) × (2.5)3–12(35) μm, av. 17.9 × 7.6 μm; small cells (shorter than 5 μm) rare or occasional. Terminal cells near the pileus centre (Fig. 32) similar in shape to those near the pileus margin but usually somewhat larger, (10)21.5–50.5(102) × (7.5)16–34.5(68) μm, av. 36.2 × 25.2 μm, $Q = (0.83)1.07–1.85(2.94)$, av. $Q = 1.46$; subterminal cells similar in size to those near the pileus margin, but more frequently branched and inflated, (2)8–29(50) × (2)3.5–12(22.5) μm, av. 18.5 × 7.8 μm. *Caulocystidia* (Fig. 33) without dark pigments, thin-walled, usually in dense fascicles and ascending, some single and repent; terminal cells mostly narrowly clavate to clavate, occasionally subcylindrical or ventricose, flexuous, occasionally curved or twisted, often nodulose, in some collections irregularly nodulose-lobate (e.g. the type of *H. albofloccipes*), mostly obtuse, (6)21–51.5(108) × (3)5.5–10.5(20) μm, av. 36.3 × 7.9 μm. *Clamp connections* absent in all parts.

Additional material examined: Denmark. N Jutland, Hanstholm, Biowide 010 Kællingdal, deep in grass turf on calcareous soil, 3 September 2014, E A Thomsen *Atlas DMS-679291* (C). France. Nord-Pas-de-Calais, Nœux-lès-Auxi, réserve naturelle régionale du Mont de Boffles, coteaux calcaires (limestone hills) à *Juniperus communis*, 23 November 2004, C Lécuru *CL/F04.874* (LIP); Pyrénées, Bagnères-de-Bigorre, Conservatoire botanique national des Pyrénées—Allées dramatiques, on soil, 3 September 2014, Z Egertová (SAV F-4442). *Germany*. A Gminder, strain H07_AT_H8; Thuringia, Hainich Naturpark, on soil, 15 September 2014, T Böhning (14229-C14); ibid., 15 September 2014, T Böhning (14233-C10). *Norway*. Oslo, Bygdøy, Dronningberget, in deciduous forest, on clayey calcareous soil, associated with clavarioids, 3 September 2011, A Molia & T Læssøe (O-F-21057); Oslo, Bygdøy, Oscarshall, in deciduous forest, on clayey soil, 3 September 2011, T Læssøe (O-F-21064). *Russia.* Samara region, Zhiguliеvsky Nature Reserve, meadow on soil, 20 August 2004, E Malysheva (LE214946, holotypus of *Camarophyllopsis albofloccipes*). *Slovakia.* Belianske Tatry Mts., Kopské sedlo (saddle)—slopes under the saddle, subalpine meadow, among grass, 15 September 2009, V Kučera (SAV F-3032); Poľana Mts., Zvolen city, Arborétum Borová hora, on soil among the grass, 30 September 2009, I Kautmanová (SAV F-3098); Podunajská nížina Lowland, Banka village, near the Koliba pod Ahojom, mossy soil, under *Crataegus* sp., *Acer campestre*, 26 September 2014, S Jančovičová (SLO781). *Sweden.* Bohuslän, Tanum, Svenneby, on soil, 27 August 1992, L & A Stridvall *LAS92085* (GB0060390).

Discussion

Distinguishing morphological characters and their phylogenetic significance

This study confirmed the plesiomorphy of some characters previously treated in the literature as important for species grouping, particularly odour and the covering of the stipe surface. The naphthalene odour is more typical for the phylogenetically defined *H. foetens* superclade, but it was reported and confirmed also within the *H. micaceus* superclade recently (Adamčík et al. 2016, 2017a). The present study demonstrates that, based on the sequence data, the naphthalene smell *H. albofloccipes* (Kovalenko et al. 2012) is a synonym of *H. phaeoxanthus* originally described without a strong odour (Romagnesi 1971). According to our observations, the naphthalene-like odour may occur occasionally in any species of the *H. micaceus* superclade, but we experience it as less offensive than that found in *H. foetens*. The odour of *H. micaceus* superclade members may become more distinctive after drying (in herbarium specimens).

Adamčík et al. (2017b) demonstrated that the not very closely related species, *H. atropunctus* and *H. variabilipes*, have a very similar stipe covering composed of dark dots. We observed white granulations or squamules as reported in *H. albofloccipes* by Kovalenko et al. (2012) and in other collections of *H. phaeoxanthus* (SAV F-3098), but also in a collection of *H. variabilipes* (Adamčík et al. 2017b).

Our morphological observations demonstrate that the shape of the terminal cells of the hyphae in the pileipellis is an important character with a strong phylogenetic signal. The terminal cells near the pileus centre of the *H. foetens* superclade are relatively narrow, with an average ratio of length and width 1.9–4.5 (Adamčík et al. 2016, 2017a, b). The range for the *H. micaceus* superclade is 1.31–2.12; there is only one collection of *H. anatinus* with a higher *Q* value than 1.9 (SAV F-20084), but this has wider terminal cells (in av. 14.8 μm) than any collection of the *H. foetens* superclade.

An interesting discovery is that the presence of a yellow colour could be a synapomorphic character. Within the clade of seven European and three North American species, only the single collection of *H. rugulosus* has no yellow colour on the stipe, but this species is represented only by a single LSU sequence and its further placement requires more sequence data. The placement of yellow tints on the stipe and their development during maturation also proved to be a character of crucial importance for distinguishing individual species.

Yellow-stiped *Hodophilus* species in the European literature

Our recent studies on *Hodophilus* in Europe focused on *H. foetens* defined by a naphthalene odour (Adamčík et al. 2017a) and on *H. atropunctus* defined by dark dots on the stipe (Adamčík et al. 2017b) both treated in widely used identification keys (e.g. Boertmann 2012; Horak 2005) as individual species each defined by one of these unique characters. The first appeared to be a species complex of four and the second of two phylogenetically defined species. In this study, we focused on yellow-stiped species which were often treated in the literature as a single species *H. micaceus*. Our study revealed six phylogenetic species with a yellow stipe of which four are described morphologically in this study. Not only the number of species is higher within the complex, but also the nomenclature is more difficult compared with previous studies. The oldest published name applied to a yellow-stiped *Hodophilus* is *H. micaceus* (Berkeley and Broome 1879) which was described from a collection from North Wales (UK). The name had been continuously used in the British Isles (Cooke 1888; Rea 1922; Dennis 1948; Orton and Watling 1969; Orton 1988) but remained virtually unknown to mycologists in continental Europe. Romagnesi (1971) described a new species *H. phaeoxanthus* (as *Hygrophorus*), comparing its yellow and brown colouration with *Craterellus tubaeformis*, but without any reference to the only previously described species *H. micaceus*. Recently, *H. albofloccipes* with a yellow stipe was described (Kovalenko et al. 2012) based on white granulations on the stipe and odour of *H. foetens*.

In the present study, we have recognised *H. micaceus* based on the constant vivid yellow colour of the stipe. The past interpretation of this character was however unclear, even in the UK, where e.g. Rea (1922) described his collections of the species as having stipes that were light yellow and then brown towards the base. Without knowing the phylogenetic relationships, no attention was paid to position and intensity of yellow colouration on the stipe. Printz and Læssøe (1986) accepted only one species with a yellow stipe, *H. micaceus*, and they treated *H. phaeoxanthus* together with the North American *H. subfuscescens* (A.H. Sm. & Hesler) Adamčík, Birkebak & Looney as synonyms. The concept of a single yellow-stiped species became the most widely adopted opinion (Orton 1988; Printz and Sivertsen 1992; Arnolds 1990; Horak 2005; Boertmann 2012). Only Bon (1977, 1999) and Ghyselinck (2003) accepted *H. phaeoxanthus* as a good species and considered *H. micaceus* a more yellow-coloured species occurring exclusively in Britain. Our study demonstrated that all but one (*H. albofloccipes*) *Hodophilus* names correspond to different species.

The published descriptions of *H. micaceus* correspond to a broad taxonomic concept. The widely used identification keys (Moser 1978; Arnolds 1990; Horak 2005; Boertmann 2012) usually described the stipe of the species briefly as yellow and brown which does not allow species identification of any of the species described in this study, and specifically does not agree with *H. micaceus* itself. The exception is the key by Printz and Silvertsen (1992)) who described the stipe of *H. micaceus* as "fulvous at the apex to yellowish orange at the base and turning brown all over with the age," which perfectly fits with *H. anatinus*. We were able to find only one description of a yellow-stiped *Hodophilus* that, in our opinion, agrees with the concept of a previously described species: that of *H. phaeoxanthus* by Ghyselinck (2003).

Ecology and distribution

Our previous studies (Adamčík et al. 2017a, b) suggested that most of the studied *Hodophilus* species are widely distributed in temperate to boreal areas of Europe. They usually prefer heavy clay soils, often with a very high pH and co-occur with *Clavaria*, *Clavulinopsis*, *Dermoloma*, *Entoloma*, Geoglossaceae, *Hygrocybe* etc. Our sampling confirmed that this is true for *H. phaeoxanthus* reported from the oceanic climate of the UK, Scandinavia (Sweden and Norway) and Northern Baltic (Russia), the mountainous climate of Caucasus (Russia, Kovalenko et al. 2012), Pyrenees Mts. (France/Spain) and Vysoké Tatry Mts. (Slovakia) to the continental climate of Samara Region (Russia). The second such species is *H. anatinus* reported here from areas as far apart as Norway, Sweden, France and the UK. It is possible that *H. micaceus* is endemic to the British Isles such as suggested by Bon (1977). According to the studied material from the UK, this is the most common species with a yellow stipe in this country. In continental Europe, reports of such a distinctive species with a completely and persistently vivid yellow stipe are lacking. It is also possible that due to rare occurrence, and possibly decline of natural habitats, some species may have become even rare and to some extend endangered. In parts of Europe is has become a common practice to clear thorny thickets for so-called nature conservation purposes. *Hodophilus cambriensis* was only collected at two nearby sites in South-West Wales (UK) and the two other undescribed species (in this study called *H.* cf. *phaeoxanthus* and *H.* cf. *micaceus*) were only collected in Central Europe (Germany and Denmark). We think that species of *Hodophilus* are generally overlooked. They often occur in dense thorny thickets or in more open areas with low mycological activity, and we believe that our studies will encourage mycologists to look for this potentially endangered group of fungi.

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