## Circumscription of species of Hodophilus (Clavariaceae, Agaricales) in North America with naphthalene odours

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<th>Journal:</th>
<th>Botany</th>
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<tr>
<td>Manuscript ID</td>
<td>cjb-2016-0091.R2</td>
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<tr>
<td>Manuscript Type:</td>
<td>Article</td>
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<tr>
<td>Date Submitted by the Author:</td>
<td>14-Jun-2016</td>
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<tr>
<td>Complete List of Authors:</td>
<td>Adamčík, Slavomír; Slovenska Akademia Vied Botanicky Ustav, Looney, Brian; University of Tennessee, Ecology and Evolution Biology Birkebak, Joshua; University of Tennessee, Ecology and Evolution Biology Jančovičová, Soňa; Comenius University in Bratislava, Faculty of Natural Sciences, Department of Botany Adamčíková, Katarína; Slovak Academy of Sciences, Institute of Forest Ecology, Branch for Woody Plants Biology Nitra Marhold, Karol; Slovenska Akademia Vied Botanicky Ustav, Vascular plants Matheny, P.; University of Tennessee, Ecology and Evolution</td>
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<td>Keyword:</td>
<td>agaricoid, Clavariaceae, multi-locus phylogeny, morphology, type studies</td>
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Circumscription of species of *Hodophilus* (Clavariaceae, Agaricales) in North America with naphthalene odours

Slavomír Adamčík\(^1\), Brian P. Looney\(^a\), Joshua M Birkebak\(^a\), Soňa Jančovičová\(^b\), Katarína Adamčíková\(^c\), Karol Marhold\(^d\) and P. Brandon Matheny\(^a\)

\(^a\)Department of Ecology and Evolution Biology, University of Tennessee, 332 Hesler Biology Building, Knoxville, TN 37996-1610. Phone: 1-865-974-8896. Email: blooney@vols.utk.edu (BPL), jbirkeba@utk.edu (JMB), pmatheny@utk.edu (PBM)

\(^b\)Comenius University in Bratislava, Faculty of Natural Sciences, Department of Botany, Révová 39, SK-811 02 Bratislava, Slovakia; jancovicova@fns.uniba.sk

\(^c\)Institute of Forest Ecology SAS, Branch for Woody Plants Biology Nitra, Akademická 2, SK-949 01, Nitra, Slovakia; katarina.adamcikova@savzv.sk

\(^d\)Department of Vascular Plant Taxonomy, Institute of Botany, Slovak Academy of Sciences, Dúbravská cesta 9, SK-845 23 Bratislava, Slovakia; Karol.Marhold@savba.sk

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\(^1\) Corresponding author, current address: Department of Cryptogams, Institute of Botany, Slovak Academy of Sciences, Dúbravská cesta 9, SK-845 23 Bratislava, Slovakia. Phone: 421-37-6943130. Fax: 421-37- 59426100. Email: slavomir.adamcik@savba.sk (SA)
Abstract

Five North American Hodophilus species with a naphthalene-like odour are now recognized based on sequence and/or morphological data and molecular annotation of type collections. Two well-supported eastern North American species do not match any of the studied types and are described here as new: Hodophilus hesleri and Hodophilus smithii. The previously described Hodophilus paupertinus is found to represent an autonomous species and appears restricted to western North America. Hodophilus subfuscens is found to be an independent lineage in eastern North America. A morphological type study of Hodophilus peckianus shows that it is a distinct species and not represented among recent collections. Multi-locus phylogenetic analyses of European and North American material of species with naphthalene odours reveal no species with transatlantic distributions. Overall, Hodophilus comprises two superclades (the Hodophilus foetens superclade and the Hodophilus micaceus superclade) and 16 terminal clades that correspond to phylogenetic species. This study introduces a new approach for morphological delimitation of agaricoid Clavariaceae combining shape and dimensions of particular elements in the pileipellis and caulocystidia. All previously described taxa included in this study, which were previously treated in the genera Hygrophorus, Camarophyllopsis or Hygrotrama, are formally transferred to Hodophilus.

Keywords: agaricoid, Clavariaceae, multi-locus phylogeny, morphology, type studies

Introduction

Hodophilus foetens (W. Phillips) Birkebak & Adamčík is a well-known species characterized by its unpleasant camphor-like odour together with skatol and methyl mercaptan-like components, which persists for some years in dried herbarium specimens (Arnolds 1990).
Based on its phylogenetic position, it has been recently transferred from the genus *Camarophyllopsis* Herink (*Ca.*) to the genus *Hodophilus* R. Heim (Birkebak et al. 2016). Members of both genera had been previously treated within the genus *Hygrophorus* Fr. (Dennis 1953, Singer 1959, Hesler and Smith 1963). The genus *Hodophilus*, typified by *Hygrophorus foetens* W. Phillips (Heim 1966), is characterized by a hymeniderm pileipellis composed of globose, obpyriform to sphaero-pendunculate terminal elements and absence of clamp connections (Birkebak et al. 2016).

In Europe all *Camarophyllopsis* collections with such strong odours have been identified as a single species, *Ca. foetens* (W. Phillips) Arnolds (Boertman 2012, Kovalenko et al. 2012), originally described from Wales in the U.K. (Phillips 1878). Hesler and Smith (1963) reported four *Hodophilus* taxa with strong odours from North America (treated in the genus *Hygrophorus*), including the European type species (Smith and Hesler 1954). They distinguished *Hygrophorus foetens* from other North American taxa based on a darker brown colour of the pileus, a stipe covered by squamules, and a hymeniderm pileipellis composed of enlarged cells. *Hygrophorus subfuscescens* var. *odora* A.H. Sm. & Hesler is the second North American taxon with strong odours. It was described with a hymeniderm pileipellis and distinguished from previous species based on a paler overall colour of the basidiomata. The remaining two North American taxa described with strong odours, *Hygrophorus peckianus* Howe and *Hygrophorus paupertinus* A.H. Sm. & Hesler, are both distinguished by their trichoderm pileipellis with less inflated and less dense terminal cells. They differ from each other by narrower lamellae of the latter.

In this study we taxonomically revise species with strong odours because it is easy to sort them out among the 27 species described in the genus *Camarophyllopsis*.
Some of these have been combined recently in the genus *Hodophilus* (Birkebak et al. 2016), but others are of uncertain systematic position. The odour of European collections of *Hodophilus foetens* is most frequently described as similar to *Tricholoma sulphureum* (Bull.) P. Kumm. or *Thelephora palmata* (Scop.) Fr. (e.g. Phillips 1878, Heim 1969, Moser 1978), but also as strong, fetid, gas-like (Boertman 2012) or naphthalene-like (Courtecuisse & Duhem 1994). Hesler and Smith (1963) described the odours of North American taxa as pungent (*Hygrophorus foetens*); exceedingly strong, penetrating, disagreeable (*Hygrophorus paupertinus*); strong, offensive (*Hygrophorus peckianus*); and very distinctly disagreeable when the flesh is bruised (*Hygrophorus subfuscenscens* var. *odora*). Ghyselinck (2003) analysed odour descriptions of *Hodophilus foetens* by various authors and concluded that the best fitting term to describe them as naphthalene-like (similar to the odour of moth balls). We further refer to the strong odours among these taxa as of naphthalene.

Hesler and Smith’s monograph (1963) is the most recent comprehensive North American taxonomic study of what are now recognized as *Hodophilus* species. No molecular studies have been published supporting species delimitation of species of *Hodophilus* with naphthalene or otherwise strong odours and testing the transatlantic distribution of *Hodophilus foetens*. A study by Birkebak et al. (2016) suggested that genetic diversity of both North American and European collections corresponds to more than one species with naphthalene odours. Here we seek to circumscribe species of North American *Hodophilus* taxa described with a naphthalene odour based on morphological observations and a multi-locus phylogenetic analysis using authentic (including type) material and recent well-documented collections. We seek to confirm if the European species *Hodophilus foetens* occurs in North America, or if there are any other species with strongly disagreeable or naphthalene-like odours that have transatlantic distributions. We
also seek to evaluate the taxonomic importance of the naphthalene odour for classification within the genus *Hodophilus*.

**Materials and Methods**

*Taxon sampling*

Types of *Hygrophorus foetens*, *Hygrophorus peckianus*, *Hygrophorus paupertinus* and *Hygrophorus subfusescens* var. *subfusescens* and *Hygrophorus subfuscescens* var. *odora* were included together with 14 other North American collections of *Hodophilus* (Supplementary Table S1). Sequences from GenBank related to North American *Hodophilus* species with naphthalene odours were also used. 20 European collections identified as *Hodophilus foetens* were used to test the transatlantic distribution of species with naphthalene odours. 20 other *Hodophilus* specimens without this smell were included in our phylogenetic taxon scheme to clarify relationships within the genus *Hodophilus* (Supplementary Table S1). Six other Clavariaceae species were added as outgroups including *Camarophyllopsis atrovelutina* (Romagn.) Argaud, *Camarophyllopsis schulzeri* (Bres.) Herink, *Camarophyllopsis deceptiva* (A.H. Sm. & Hesler) Bon, *Clavaria fuscata* Oudem., *Clavaria pullei* Donk, and *Ramariopsis corniculata* (Schaeff.) R.H. Petersen based on Birkebak et al. (2016).

*DNA extraction, PCR, and Sequencing*

Three gene regions (nLSU ribosomal RNA, ITS and *rpb2*) were sequenced and analyzed. 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. Sequencing was performed at the UT 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 10,000,000 generations and sampling parameter states and trees every 10,000 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 (S19050).

**Morphological analyses**
Macromorphological descriptions were prepared from fresh material shortly after collection from the field. Colour nomenclature standards follow Kornerup and Wanscher (1967). All micromorphological characters were observed under the 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. Microscopical structures were examined on desiccated herbarium specimens in Congo red solution with ammonia after a short treatment in warm aqueous 10% KOH. Q-value is the length/width ratio of basidiospores. Measurements exclude ornamentation. Statistics for measurements of microscopic characters 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).

In order to find micro-morphological differences among studied taxa, shape and size of the following elements were compared: basidiospores, basidia, caulocystidia, marginal cells on the lamellar edge, and terminal and subterminal cells of hyphae in the pileipellis. Pileipellis elements near the pileus margin and pileus centre were observed and evaluated separately, as several publications suggested that pileipellis structure may change depending on its position from the pileus margin (e.g. Ronikier and Moreau 2007, Adamčík and Buyck 2011).

Results

Phylogenetic analyses
All nodes recovered from the ML inference were also recovered by the BI analysis. All recent collections of North American *Hodophilus* with naphthalene odours are grouped in three well-supported clades (Fig. 1). Only one of these clades is associated with a named species based on the sequence of the type specimen of *Hygrophorus paupertinus*, and the other two are named as the new species *H. hesleri* and *H. smithii* below. In addition to these three clades, the type ITS sequence of *Hygrophorus subfuscescens* var. *odora* type has an isolated position from the rest of *Hodophilus* collections with naphthalene odours and is identical with the ITS sequence of a paratype of *Hygrophorus subfuscescens* var. *subfuscescens*.

European collections of *Hodophilus* with naphthalene odours (putatively identified as *Hodophilus foetens*) form four well-supported clades that correspond to different phylogenetic species. All collections with naphthalene odours, other than the type of *Hygrophorus subfuscescens* var. *odora*, are part of one *Hodophilus foetens* superclade with moderate support. Within this, there is one clade with samples identified as *Hodophilus atropunctus* (an odourless species), and one clade of sequences originating from soil samples from Canada with an unknown odour. Sister to the *Hodophilus foetens* superclade is a second well-supported *Hodophilus* core clade of mostly odourless taxa, designated as the *Hodophilus micaceus* superclade. The one exception to being odourless in this clade is the *Hygrophorus subfuscescens* var. *odora* type collection. Samples morphologically identified as *Ca. atropuncta*, *Ca. phaeoxantha* and *Ca. micacea* all undoubtedly belong to the genus *Hodophilus*, but all contain multiple species under each name.

*Morphological delimitation of genetically defined groups*

Our morphological observations showed several differences among species defined by
the molecular analyses. The most distinct differences represented by micro-morphological characters are labelled in Table 1. Mean basidiospore length of *Hodophilus hesleri* and *Hodophilus subfusescens* do not exceed 5.5 µm. Mean caulocystidia width of *Hodophilus foetens*, *Hodophilus peckianus* and *Hodophilus smithii* is broader than 8 µm. Terminal cells of hyphae in the pileipellis near the pileus margin are shorter with a length/width ration up to 1.7 in *Hodophilus peckianus* and *Hodophilus subfusescens*. In *Hodophilus paupertinus*, the presence of very narrow cylindrical terminal cells in the pileipellis near the pileus centre contributes to its smallest mean width (up to 10 µm). This species and *Hodophilus smithii* have the greatest length/width ratio of the terminal cells near the pileipellis centre.

The shape of the terminal cells differed between the margin and the centre of the pileus in *Hodophilus hesleri* and *Hodophilus smithii*. The length/width ratio of the first is smaller near the pileus centre, while the second species shows an opposite pattern. Both species are similar in the shape of terminal cells near the pileus margin but demonstrate clear differences in terminal cell morphology at the pileus centre. Macro-morphological characters do not seem to exhibit much difference among the studied species other than the olive-buff tints of *Hodophilus subfusescens* (Table 2).

**Taxonomy**

*Artificial key to North American Hodophilus species with an unpleasant odour*

1A. Caulocystidia on average wider than 8 µm 2

1B. Caulocystidia on average narrower than 7 µm 3

2A. Terminal cells of hyphae near the pileus centre sphaeropedunculate, capitate, obpyriform or clavate, towards the base usually distinctly pedunculate *Hodophilus smithii*
2B. Terminal cells of hyphae near the pileus centre mostly globose, obpyriform and not distinctly pedunculate

**Hodophilus peckianus**

3A. Pileipellis near the pileus centre with frequent non-inflated cylindrical or clavate terminal cells

**Hodophilus paupertinus**

3B. Pileipellis near the pileus centre with obpyriform, globose, or sphaeropedunculate terminal cells

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4A. Terminal cells of hyphae near the pileus centre obpyriform or globose with a ratio of length/width <1.5, subterminal cells often very short and small (up to 10 µm)

**Hodophilus subfuscescens**

4B. Terminal cells of hyphae near the pileus centre obpyriform or sphaeropedunculate with a ratio of length/width >1.7, subterminal cells rarely short and small (mostly >10 µm)

**Hodophilus hesleri**

**Hodophilus hesleri** Adamčík, Birkebak & Looney, sp. nov. Figs. 2C, 3A-C, 4A, 5A, 6A

MycoBank No.: MB815983

*Etymology:* in honor of Dr. Lexemuel Ray Hesler

*Holotypus:* TENN 070842 (coll. no. JMB10251301)

**Pileus** (2.5–) 4–11 mm broad, convex, weakly depressed near the centre when old, margin not striated, sometimes slightly crenulated, surface smooth, slightly rough when young, becoming granulose and cracking when old, matt, hygrophanous, colour when moist near the margin dark blond (5D3–5D4), young with white outline, near the centre greyish brown to chocolate brown (6E4–6F4), eye brown (7F4) to black, when dry near the margin orange grey
(5B2–5B3), birch grey (5C2), dry near the centre brownish orange (5C3). **Stipe** 9–24 × 0.75–2 mm, smooth and reflective except where slightly pruinose near lamellae, upper part bronze (5E5), brownish orange (5C3) or brown (6D3-6E4) when young, becoming darker with age dark blond (5D4) to chocolate brown (6F4), near the base first dark blond (5D4), later hair brown (5E4) or chocolate brown (6F4), flexuous, sometimes narrowed near base. **Lamellae** 1–2 mm wide, L=12-23, l=0-1, short decurrent, brownish orange to grey brown (5C3–6C3–6D3, 5B3–5D2). **Flesh** elastic, with a naphthalene odour but also mixed with other farinaceous or unpleasant components, dry orange grey (5B3), wet greyish brown (6E3).

**Basidiospores** (4.2–) 4.8–6 (–7.2) × (3.8–) 4–4.8 (–5.8) µm, av. 5.4 × 4.4 µm, Q (length/width) = (1.04–) 1.13–1.40 (–1.55), av. Q = 1.26, broadly ellipsoid to ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage 0.4–0.6 (–1) µm long. **Basidia** 4-spored, (31–) 34.5–40.5 (–43) × (4.5–) 5–6.5 (–7) µm, av. 37.5 × 5.6 µm, hyaline, narrowly clavate, attenuated and flexuous toward base. **Basidioles** cylindrical to narrowly clavate, often flexuous, obtuse, (19–) 26–38 (–45) × 4–6 (–6.5) µm, av. 31.9 × 5 µm. **Pleurocystidia** absent. **Marginal cells** on the lamellae not well differentiated, similar to basidiola on lamellar sides. **Lamellar trama** of strongly intricate, subparallel, scarcely branched and irregularly inflated, 4–10 (–15) µm wide hyphae, composed of 20–100 µm long cells. **Subhymenium** pseudoparenchymatic, 20–25 µm deep, composed of branched, dense, 2–4 µm wide hyphae. **Pileipellis** near the pileus margin a hymeniderm, composed of sphaero-pedunculate or obpyriform cells arranged in one rank, terminal cells measuring (16.5–) 22.5–37.5 (–45.5) × (10.5–) 11–18 (–24.5) µm, av. 30 × 14.6 µm, Q = (1.19–) 1.57–2.63 (–2.92), av. Q = 2.1; subterminal cells rarely inflated, usually cylindrical or fisiform, short and small cells (shorter than 10 µm) occasional, usually not branched, often bearing incrusted pigments, measuring (3.5–
8.5–34 (–63) × (3–) 4–9 (–12) µm, av. 21.3 × 6.6 µ. Terminal cells of hyphae in pileipellis near the pileus centre comparatively shorter, mainly obpyriform, (15.5–) 19.5–33 (–44) × (10.5–) 12–18 (–22) µm, av. 26.4 × 14.9 µm, Q = (1.06–) 1.39–2.21 (–2.83), av. Q = 1.8. Pileus trama of interwoven, 3–10 µm wide, subparallel, irregularly inflated and often branched hyphae.

**Caulocystidia** fascicled, thin-walled, repent or ascending, with terminal cells clavate or obpyriform, obtuse or rarely apically constricted, occasionally flexuous towards septum, measuring (10–) 15–36.5 (–58) × 4.5–8.5 (–11) µm, av. 25.7 × 6.5 µm, subterminal cells occasionally short and small (shorter than 10 µm). Stipe trama of 4–12 (–15) µm wide, parallel, hyphae, composed of 15–90 µm long cells. **Clamp connections** absent in all tissues.

**Material examined**: USA. Arkansas. Stone County. Gunner pool recreation area, in deciduous forest on riverbank of North Sylamore Creek, 35°58'57.5"N; 92°28'33.5"W, on naked soil, 25 October 2013, JM Birkebak and S Adamčík JMB10251301 (TENN 070842, holotype); North Carolina. Haywood County. Along Highway 32 near Big Creek, 9 October 2010, EC Vellinga ECV4175 (TENN 065670); Tennessee. Cambell County. Norris Dam State Park, Andrews Ridge Trail, 36°14'30.2"N; 84°07'30.6"W, 10 October 2013, JM Birkebak and S Adamčík JMB10101301, JMB10101302 (TENN 070837, TENN 070838).

**Commentary**: *Hodophilus hesleri* is similar in field aspect and in microscopy to *Hodophilus peckianus* from which it differs by narrower caulocystidia and by the absence of globose terminal cells in the pileipellis. It is possible that there are some historical reports of *Hodophilus hesleri* misidentified as *Hodophilus peckianus*.

**Hodophilus paupertinus** (A.H. Sm. & Hesler) Adamčík, Birkebak & Looney, comb. nov.

Figs. 2E, 3D-F, 4B, 5B, 6B
MycoBank No.: MB815984


≡ *Armillariella paupertina* (A.H. Sm. & Hesler) Singer, Lilloa 22: 216. 1951


≡ *Camarophyllopsis paupertina* (A.H. Sm. & Hesler) Boertm., Bibliothca Mycol. 192: 75. 2002

Holotypus: MICH 10923 (coll. no. *A.H. Smith* 3793).

**Original description:**

Pileus (5) 10-20 mm, latus, subplanus, siccus, isabellinus demum umbrinus; caro cinerea, odore subnauseosa; lamellae angustatae, distantes vel dibdistantes, decurrentes, subcinereae; stipes 1-2 (3) cm. longus, 3-6 mm. crassus, fragilis, solidus demum cavus, isabellinus demum umbrinus, glaber; sporae 5-6 × 4-5.5 µm, subglobosae.

**Basidiospores** (4.6–) 5.7–6.7 (–7.5) × (4.3–) 4.7–5.4 (–6) µm, av. 6.4 × 5 µm, Q (length/width) = (1.09–) 1.16–1.36 (–1.51), av. Q = 1.26, broadly ellipsoid to ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage up to 1 µm long. **Basidia** 4-spored, 47–56 × 5–7.5 µm, hyaline, narrowly clavate, attenuated and flexuous toward base. **Basidioles** cylindrical to narrowly clavate, obtuse, often flexuous, ca. 3.5–7 µm wide. **Pleurocystidia** absent. **Marginal cells** on the lamellar edge not well differentiated, similar to basidiola on lamellar sides. **Lamellar trama** composed of sub-parallel hyphae of very variable width, 3–17 µm wide, septa usually more distant than 100 µm. **Pileipellis** near the pileus margin transition from hymeniderm to trichoderm, composed of hyphal terminations very variable in shape, oriented mainly upward but some also repent, often with 1-3 irregularly inflated cells and
some without inflated cells, terminal cells cylindrical, clavate, ellipsoid, globose, obpyriform, occasionally also lobate, measuring (12–) 17–49 (–108) × (5–) 7–15 (–23.5) µm, av. 32.1 × 10.9 µm, Q = (1.89–) 1.72–4.55 (–7.35), av. Q = 3.13; subterminal cells often narrower, cylindrical or fusiform, often also inflated, never short (shorter than 10 µm), often branched, measuring (10–) 18.5–51 (–86.5) × (3.5–) 5.5–13 (–23) µm, av. 34.7 × 9.3 µm. Pileipellis near the pileus centre showing more distinct contrast between cellular structure and narrow cylindrical hyphae, composed of often smaller and more irregular nodulous-flexuous-lobate elements, some terminal cells sphaeropedunculate, obpyriform, and globose, others clavate or subcylindrical, terminal cells measuring (12.5–) 16.5–41.5 (–74) × (4–) 5–13 (–24.5) µm, av. 29.2 × 9.2 µm, Q = (0.74–) 1.78–5.34 (–11.4), av. Q = 3.56; subterminal cells sometimes inflated but sometimes very narrow cylindrical, often also inflated, occasionally flexuous or nodulous, never short (shorter than 10 µm), often branched, measuring (8–) 12–34 (–54) × (3–) 4.5–11 (–18) µm, av. 23 × 7.7 µm.

**Caulocystidia** dispersed or in small or larger fascicles, thin-walled, repent or ascending, clavate or cylindrical, occasionally with lateral diverticulae, often flexuous at basal part, with terminal cells measuring (15–) 20.5–40.5 (–57) × (2–) 3.5–6 (–7.5) µm, av. 30.5 × 4.7 µm. **Clamp connections** absent in all tissues.

**Material examined:** **Canada.** British Columbia. Capital Regional District. Colwood, Royal roads University property, 3 February 2001, A and O Ceska Ceska11032001 (TENN 070844); **USA.** California. Humboldt County, Orick, on soil, 5 December 1935, A.H. Smith 3793 (MICH 10923, holotype); Mendocino County. Jackson State Forest off Highway 20, 28 January 2012, D Smith MEND16 (TENN 070840).

**Commentary:** *Hygrophorus paupertinus* was described and reported originally from California (Smith and Hesler 1942, Hesler and Smith 1963) and is the only species of
Hodophilus currently known from western North America. Molecular sequence data from the type and two other western collections are in full agreement. A recent collection from British Colombia confirms that H. paupertinus is likely widely distributed along the West Coast.

Hodophilus peckianus (Howe) Adamčík, Birkebak & Looney, comb. nov. Figs. 2D, 7, 8

MycoBank No.: MB815985

≡ Hygrophorus peckianus Howe, Bull. Torrey bot. Club 5: 43. 1874
≡ Camarophyllus peckianus (Howe) Murrill, N. Amer. Fl. (New York) 9(6): 389. 1916
≡ Hygrotrama peckianum (Howe) Singer, Beih. Sydowia 7: 4. 1973
≡ Camarophyllopsis peckiana (Howe) Boertm., Bibliothca Mycol. 192: 75. 2002

Holotypus: NYS f3880

Original description:

Odorous, rather firm, gregarious or subcaespitose; pileus fleshy, convex or slightly depressed in the centre, smooth, hygrophanous, fuliginous when moist, paler buff-brown when dry, the margin curved and sometimes wavy; lamellae subdistant, broad, thick, arcuate, decurrent, pallid when young, becoming darker with age; stem smooth, stuffed or hollow, subflexuous, often compressed and attenuated below, coloured like the pileus; spores subglobose, rough, .0002 in. in diameter.

Plant 1-2 in. high, pileus 5-10 lines broad; stem about 1 line thick.

Ground under Pteris aquilina. Lake Pleasant, August.

Odor quite strong, resembling that emitted by some species of Golden-eyed lace-wing flies (Chrysopha). The colour of the moist plant is almost exactly like that of Lactarius fuliginosus, Fries. Related to Hygrophorus Cantharellus, Schw.
**Basidiospores** (5.4–) 5.6–6.5 (–7) × (4–) 4.4–5.1 (–5.6) µm, av. 6.1 × 5.8 µm, Q (length/width) = (1.13–) 1.21–1.34 (–1.4), av. Q = 1.28, broadly ellipsoid to ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage 0.6–0.9 (–1) µm long. **Basidia** 4-spored, (30–) 36.5–45 (–50) × 5–6.5 (–7.5) µm, av. 40.8 × 5.9 µm, hyaline, narrowly clavate, attenuated and flexuous toward base. **Basidioles** cylindrical to narrowly clavate, often flexuous and apically constricted, ca. 2.5–6 µm wide. **Pleurocystidia** absent. **Marginal cells** on the lamellar edge well differentiated, clavate to obpyriform, pedunculate or not, (10–) 15–28 (–35) × (5.5–) 6.5–12.5 (–15.5) µm, av. 21.5 × 9.3 µm. **Lamellar trama** composed of strongly undulate and intricate but parallel, scarcely branched and irregularly inflated, 2–8 (–10) µm wide hyphae, some hyphae with yellow pigments. **Pileipellis** near the pileus margin transitions from a hymeniderm to an epithelium, composed of globose, sphaero-pedunculate or obpyriform cells arranged in 1-2 (rarely 3) ranks, terminal cells measuring (12–) 16.5–35 (–45) × (7.5–) 11.5–21 (–30) µm, av. 26 × 16.3 µm, Q = 0.94–2.42 (–4.5), av. Q = 1.67.; subterminal cells often inflated, some narrow cylindrical, short and small cells (shorter than 10 µm) rare, usually not branched, often bearing incrusted pigments, measuring (23–) 30–50.5 (–70) × (4.5–) 6.5–11 (–13) µm, av. 40.1 × 8.6 µm. Pileipellis elements near the pileus centre very similar to those near the margin, terminal cells of hyphae measuring (9–) 15–31.5 (–42) × (6–) 8–21 (–31) µm, av. 23.3 × 14.7 µm, Q = (0.82–) 1.05–2.36 (–3.5), av. Q = 1.71. **Caulocystidia** fascicled, thin-walled, repent or ascending, clavate, obtuse, usually pedunculate and flexuous towards septum, with terminal cells measuring (9–) 12.5–31.5 (–50) × 4.5–14 (–23) µm, av. 22.2 × 9.2 µm. **Clamp connections** absent in all tissues.

**Material examined**: USA. New York. Hamilton County. Lake Pleasant, ground, under *Pteris aquilina*, August (NYS f3880, holotype).
Commentary: *Hygrophorus peckianus* is the oldest name of agaricoid Clavariaceae species described and reported from North America (Howe 1874). Coker (1948) suggested a close relationship with the European species *Hodophilus foetens*, but *Hodophilus peckianus* was not widely accepted because of the European bias for accepting a single species (*Hodophilus foetens*) with a strong disagreeable odour. Smith and Hesler (1954) reported *Hodophilus foetens* from Michigan, and later from Idaho (in Hesler and Smith 1963), and discussed its differences from *Hodophilus peckianus*. They also recognized two more species with an unpleasant odour (in Hesler and Smith 1963). Comparing the descriptions of *Hodophilus peckianus* by Coker (1948) and Smith and Hesler (1954) with the original diagnosis suggests that their interpretation of the species was correct. Hesler and Smith (1963) place the species in the section *Camarophyllopsis* because the hyphae are not oriented perpendicularly to form a hymeniderm. In Fig. 8 of their publication (Hesler and Smith 1963) they illustrated and described end-cells in the pileipellis (terminal cells) as pyriform, clavate ovoid, or subglobose, similar to our observation on the type. Because of the poor condition of the type with mostly collapsed microscopic elements, we were not able to judge and confirm the perpendicular orientation of hyphae. However, it is possibly a useful character to distinguish the species from other similar species.

*Hodophilus peckianus* has been reported from New York (Howe 1874), Massachusetts (Murrill 1916), North Carolina (Coker 1948), Michigan (Smith and Hesler 1942) and Tennessee (Hesler and Smith 1963). The drawing included in Fig. 2 was sketched by C.H. Peck and is labelled as “*Hygrophorus Peckii* Howe”, a combination that Howe did not make. Though not linked to a particular collection, it is likely that this represents *Hygrophorus peckianus* rather than *Hygrophorus peckii* G.F. Atk. based on the colour of stipe, lack of glutinous coating of stipe, and a lack of striations on the pileus margin.
**Hodophilus smithii** Adamčík, Birkebak & Looney, sp. nov.  
MycoBank No.: MB815986

*Etymology:* in honor of Dr. Alexander Hanchett Smith  
*Holotypus:* TENN 070839 (coll. no. JMB10051302)

**Pileus** 2–10 mm broad, convex, margin not striate, sometimes slightly crenulated, surface smooth, matt, hygrophanous, colour when moist near the margin brownish orange (5C3), nougat to grey brown (5D3–6D3), fawn brown (7F4), near the centre concoloured or nutria brown (5F3), when dry near the margin orange grey (5B2), birch grey (5C2), greyish brown (6E3–6E4), dry near the centre concoloured or golden (5C4). **Stipe** (6–) 9–30 (–37) × 0.75–1.5 mm, smooth or with fine blackish punctuations in zones oriented horizontally, near the lamellae camel brown (6D4), greyish brown (6E3), chocolate brown (6F4), towards base sometimes darker, sometimes black or almost so all over, sometimes with white tomentum on base, flexuous, slightly narrowed near base. **Lamellae** 1–1.5 mm wide, L=12-18, l=0–1, deeply decurrent, milk-coffee to greyish brown (6D3–6E3), towards edge paler golden (5C4). **Flesh** elastic, with very strong naphthalene odour but also with farinaceous or other unpleasant components, in pileus orange white (5A2), greyish brown (6C2–6D3).

**Basidiospores** (5–) 5.4–6.3 (–7.2) × (3.8–) 4.1–4.8 (–5.2) μm, av. 5.9 × 4.5 μm, Q (length/width) = (1.08–) 1.22–1.4 (–1.55), av. Q = 1.31, broadly ellipsoid to ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage 0.45–0.8 μm long. **Basidia** 4-spored, (28–) 33–42.5 (–49) × (5–) 6–7.5 (–8) μm, av. 37.7 × 6.8 μm, hyaline, narrowly clavate,
attenuated and flexuous toward base. **Basidioles** cylindrical to narrowly clavate, often flexuous, obtuse, (17–) 24.5–37.5 (–49) × (3–) 4–6.5 (–8) µm, av. 31 × 5.2 µm. **Pleurocystidia** absent.

**Marginal cells** on the lamellae not well differentiated, similar to basidiola on lamellar sides.

**Lamellar trama** of strongly undulate and intricate, subparallel, scarcely branched and irregularly inflated, 3–10 (–15) µm wide hyphae, composed of 10–90 µm long cells.

**Subhymenium** pseudoparenchymatic, 20–25 µm deep, composed of branched, dense, 3–5 µm wide hyphae. **Pileipellis** near the pileus margin a hymeniderm, mainly composed of sphaero-pedunculate, occasionally also obpyriform cells arranged in one rank, terminal cells measuring (10–) 20–39.5 (–58) × (7–) 10–17.5 (–24) µm, av. 29.8 × 13.7 µm, Q = (1–) 1.47–3.01 (–4), av. Q = 2.24; subterminal cells rarely inflated, usually cylindrical, short and small cells (shorter than 10 µm) very rare, usually unbranched, measuring (5–) 13.5–35 (–53) × (3–) 3.5–13 (–30) µm, av. 21.2 × 8.1 µm. Terminal cells of hyphae in pileipellis near the pileus centre usually somewhat longer, mainly clavate-pedunculate or sphaero-pedunculate, rarely obpyriform, (15–) 23–42 (–66) × (6–) 8–14.5 (–21) µm, av. 32.5 × 11.3 µm, Q = (1.18–) 2.06–3.99 (–5.67), av. Q = 3.03.

Pileus trama of interwoven, 3–10 µm wide, subparallel, irregularly inflated hyphae, composed of 10–80 µm long cells. **Caulocystidia** repent and dispersed or fascicled and ascending, thin-walled, often inflated, obpyriform of sphaeropedunculate, others broadly clavate, usually not flexuous, with terminal cells measuring (13–) 21–44 (–78) × (4–) 7–11.5 (–17) µm, av. 32.6 × 9.1 µm, with darker parietal and sometimes also dark incrusted pigments. Stipe trama of 4–10 µm wide, parallel, often anastomosed hyphae, composed of 10–120 µm long cells. **Clamp connections** absent in all tissues.

**Material examined:** USA. North Carolina. Big Creek, at very beginning of Baxter Creek trail, 9 August 2012, EC Vellinga *JMB08091202* (TENN 067461); Macon County. Highlands,
Horse Cave Rd., Rusty Falls area, 15 July 1991, DE Desjardin DED5230 (TENN 050035, as Hygrophorus subfuscescens var. odora); Tennessee, Blount County. Cades Cove, Primitive Baptist Church, 35°36'08"N; 83°48'48"W, 9 August 2005, EB Lickey DJL04TN23 (TENN); 1.1 miles up Schoolhouse Gap trail, 19 July 2013, PB Matheny PMB3930 (TENN 070843); Monroe County. Cherokee National Forest, Walnut Grove Picnic Area, 35°19'36"N; 84°09'41"W, lawn on a strip between parking place and the road, under deciduous trees, 5 October 2013, JM Birkebak and S Adamčík JMB10051302 (TENN 070839, holotype); Anderson County. Norris Dam State Park, Grist Mill trail, naked soil on margin of the trail in deciduous forest, 12 October 2013, JM Birkebak and S Adamčík JMB10121302 (TENN 070841).

Commentary: In determining the identity of North American collections of Hodophilus foetens (Smith and Hesler 1954, Hesler and Smith 1963), Hodophilus smithii presents the best candidate for their original concept. Smith and Hesler (1954) described incrusted pigment on the hyphae of the pileipellis and a scabrous-dotted stipe of Hodophilus foetens that may somewhat correspond to caulocystidia incrusted by dark pigments and arranged in fascicles (thus appearing in the field as darker dots on the stipe surface). However, all of our collections of Hodophilus smithii have comparatively smaller basidiomata with pilei not exceeding 10 mm, while pilei of Hodophilus foetens are described as 10–40 mm wide. The identity of North American collections of Hodophilus foetens has to be revealed by the study of more recent and authentic material.

Hodophilus subfuscescens (A.H. Sm. & Hesler) Adamčík, Birkebak & Looney, comb. nov.

Figs. 2F, 9, 10

MycoBank No.: MB815987

≡ Hygrophorus subfuscescens A.H. Sm. & Hesler, Sydowia 8: 318. 1954
≡ Camarophyllopsis subfuscescens (A.H. Sm. & Hesler) Arnolds, Mycotaxon 25(2): 643. 1986

≡ Hygrotrama subfuscescens (A.H. Sm. & Hesler) Singer, Beih. Sydowia 7: 3. 1973

≡ Camarophyllopsis subfuscescens var. odora (A.H. Sm. & Hesler) Arnolds, Mycotaxon 25(2): 643. 1986

≡ Hygrophorus subfuscescens var. odora A.H. Sm. & Hesler, Sydowia 8: 318. 1954

Holotypus: MICH 10952 (coll. no. A.H. Smith 32894)

Original description:

Pileus 6–25 mm. latus, connexus, glaber, usus, olivaceo-luteus, demum olivaceo-brunneus; lamellae distantes, decurrentes, subluteae, demum sordide avellaneae; stipes 2–4 cm. longus, 1.5–3 mm. crassus, glaber, pallide luteus, dein cinereus; sporae 5–6 × 4–5 μ. Specimen typicum in Herb. Univ. Mich. conservatum; legit prope Mackinaw City, Mich. Aug. 6, 1949, Smith n. 32894.

Basidiospores (4.3–) 4.9–5.6 (–6.1) × (3.5–) 3.9–4.3 (–4.6) μm, av. 5.2 × 4.1 μm, Q (length/width) = (1.16–) 1.2–1.34 (–1.49), av. Q = 1.27, broadly ellipsoid to ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage 0.7–1 μm long. Basidia (2-)4-spored, (31–) 34.5–43 (–49) × (5–) 5.5–7.5 (–9) μm, av. 38.6 × 6.6 μm, hyaline, narrowly clavate, attenuated and flexuous toward base. Basidioles cylindrical to narrowly clavate, often slightly flexuous towards the base, ca. 2–7 μm wide. Pleurocystidia absent. Marginal cells on the lamellar edge not well differentiated, similar to basidiola but smaller, cylindrical to clavate, (10–) 10.5–19 (–24) × 2.5–4 (–5.5) μm, av. 14.9 × 3.1 μm, mixed with dispersed basidia. Lamellar trama composed of undulate and intricate but parallel, scarcely branched and irregularly inflated,
3–9 µm wide hyphae. **Subhymenium** pseudoparenchymatic, 15–25 µm deep, composed of branched, dense, 2–4 µm wide hyphae. **Pileipellis** near the pileus margin hymeniderm, composed of sphaero-pedunculate or obpyriform cells arranged usually in 1 rank, terminal cells measuring (15–) 20–35.5 (–53) × (8.5–) 14–26 (–36.5) µm, av. 28 × 20.1 µm, Q = (0.86–) 0.92–2.04 (–4.5), av. Q = 1.48; subterminal cells mainly narrow cylindrical, short and small cells (shorter than 10 µm) occasional, branched or not, measuring (2–) 7.5–31 (–58.5) × (3.5–) 4–19 (–24) µm, av. 19.4 × 8.4 µm. Pileipellis elements near the pileus centre very similar to those near the margin, terminal cells of hyphae measuring (15–) 19–33.5 (–47) × (12–) 14–24.5 (–35) µm, av. 26 × 19.4 µm, Q = (0.83–) 1.04–1.7 (–2.7), av. Q = 1.37. Pileus trama of interwoven, 3–15 µm wide, subparallel, irregularly inflated and often branched hyphae. **Caulocystidia** in dense fascicles, thin-walled, usually ascending or erect, clavate or cylindrical, obtuse, flexuous and often also moniliform, with terminal cells measuring (10–) 20–40.5 (–61.5) × (3.5–) 4–7 (–9.5) µm, av. 33.3 × 5.4 µm. Trama of stipe parallel, unbranched, 5–10 µm wide hyphae, composed of cells often shorter than 30 µm and rarely longer than 100 µm. Stipe trama of 2–11 µm wide, parallel hyphae, composed of 20-100 µm long cells. **Clamp connections** absent in all tissues.

**Material examined:** USA. Michigan. Cheboygan County. Mackinaw City, 45°47'02"N; 84°43'40"W, in hardwoods, 13 July 1947, **A.H. Smith 32894** (MICH 10952, type of **Hodophilus subfuscens** var. **subfuscens**; TENN 023669, paratype); Emmet County. Maple River, Brutus, 13 July 1947, **A.H. Smith 25670** (MICH 10953, type of **Hygrophorus subfuscens** var. **odora**).

**Commentary:** This study gives clear molecular and morphological arguments for the placement of **Hygrophorus subfuscens** in the **Hodophilus micaeus** superclade of the genus **Hodophilus** but fails to confirm odour as an appropriate criterion to recognize it as a distinct
taxon from the typical inodorous variety. After the original description of *Hodophilus subfuscescens* (Smith and Hesler 1954), the species was adopted by later authors (e.g. Romagnesi 1971, Singer 1975) but also treated as a synonym of *Hodophilus micaceus* (Printz and Læssøe 1986). Based on morphological observation of the type specimens of both *Hodophilus subfuscescens* varieties, Kovalenko et al. (2012) considered the species as very similar to *Hodophilus micaceus* in all characters except for the more globose basidiospores of the former. Our phylogenetic analyses suggest *Hodophilus subfuscescens* is different from European *Hodophilus micaceus* collections and also from other North American recognized species within the *Hodophilus micaceus* superclade. The morphological distinction from *Hodophilus foetens* superclade members, i.e. other species with unpleasant odour, is discussed above (different shape of terminal cells and presence of small cells in the pileipellis).

**Discussion**

**Pileipellis structure and infragenetic classification**

Hesler and Smith (1963), in the last North American monograph of the genus *Hygrophorus* (incl. all known North American *Hodophilus* species), used pileipellis structure (that is, the anatomical make up of the pileus cuticle) as the basic character for species classification. *Hygrophorus peckianus* and *Hygrophorus paupertinus*, both having a trichoderm type of pileipellis, were classified in *Hygrophorus* sect. *Camarophyllopsis* Hesler and Smith and *Hygrophorus foetens* and *Hygrophorus subfuscescens* var. *odora* with a hymeniderm (or in some places of the book interpreted as epithelium) type of pileipellis in *Hygrophorus* sect. *Hygrotrama* (Singer) Hesler and Smith. Among our studied material of collections with naphthalene odours, that includes types of the above mentioned taxa, all collections have inflated broadly clavate,
sphaero-pedunculate, obpyriform or globose elements usually arranged in one rank and oriented perpendicularly. These structures correspond more or less to a hymeniderm, sometimes with transitions to an epithelium if the subterminal cells or cells in lower ranks are inflated. According to our observations, the types of *Hygrophorus foetens*, *Hygrophorus peckianus* and *Hygrophorus subfuscenscens var. odora* show a more distinctive transition to an epithelium (with more inflated subterminal cells and subsequent cells) than the *H. paupertinus* type and representatives of the other two species clades of North American *Hodophilus* with naphthalene odours. This does not agree with Hesler and Smith’s concept of sections.

In addition to differences in the overall structure of the pileipellis, we observed differences in the shape and dimensions of its terminal elements. The size of terminal cells near the pileus margin and the pileus centre, together with basidiospore and caulocystidia dimensions, are presented for sequenced North American *Hodophilus* collections with naphthalene odours and types of *Hygrophorus peckianus* and *Hygrophorus foetens* (Table 1). Representatives of the *Hodophilus paupertinus, Hodophilus hesleri*, and *Hodophilus smithii* clades, together with the type of *Hodophilus foetens*, have terminal cells in the pileipellis near the pileus margin that are typically clavate, sphaero-pedunculate or obpyriform, having a length/width ratio greater than 2. In contrast, the types of *Hygrophorus peckianus* and *Hygrophorus subfuscenscens var. subfuscenscens* and var. *odora* have a length/width ratio of the terminal cells near the pileus margin less than 2 (1.67, 1.44 and 1.52 respectively). According to our morphological observations of European representatives of the *Hodophilus micaceus* superclade, and according to our type studies of related North American taxa (unpublished data), representatives of this group typically have shorter and broader (length/width ratio up to 2) terminal cells in the pileipellis. According to our observations, odourless members of the *Hodophilus micaceus*
superclade are also typical by occasional to frequent small (length and width up to 5 µm) subterminal cells or cells at lower ranks of hyphae in pileipellis (Fig. 10). Such small subterminal cells are absent or rare in the *Hodophilus foetens* superclade and might represent an additional and even more stable feature for morphological recognition of two major clades within the genus *Hodophilus*.

**Species nomenclature and morphological delimitation.**

*Hygrophorus paupertinus* is not only clearly identified by the position of the type sequence in the phylogenetic tree (Fig. 1), but it is probably the most distinctive species studied here. All three studied collections (type and two more recent ones) show a pileipellis composed of typical inflated terminal elements mixed with numerous narrower, clavate, or cylindrical elements. Below, the species is re-described and combined in the genus *Hodophilus*.

The phylogenetic tree also clearly demonstrates that *Hygrophorus subfuscescens* var. *odor*a is very different from other North American *Hodophilus* samples with naphthalene odours. Because of the close sequence identity with the typical variety, the var. *odor*a is not accepted here as a distinct infraspecific taxon and the species is re-described based on the types of both varieties and combined in the genus *Hodophilus*.

The phylogenetic position of the type of *Hygrophorus peckianus* is unknown due to unsuccessful attempts at sequencing, and this species represents a nomenclatural challenge for two unidentified North American clades of *Hodophilus* with naphthalene odours. Our morphological studies demonstrate two differences observed on the *Hygrophorus peckianus* type specimen that distinguish it from both unidentified clades but also from the type of *H. foetens*: length/width ratios of terminal cells in the pileipellis near the pileus margin and the pileus centre are smaller than 2 (Tab. 1, Fig. 8) and subterminal cells are often inflated. Based on the
pileipellis structure of the type specimen, *Hygrophorus peckianus* is re-described here as a distinct species of the genus *Hodophilus* in addition to *Hodophilus paupertinus* and two other new *Hodophilus* species with naphthalene odours. Because of the lack of small subterminal cells (Fig. 8) we expect that *Hygrophorus peckianus* is member of the *Hodophilus foetens* superclade.

In our *Hodophilus* phylogeny, all European collections of *Hodophilus* with naphthalene odours are grouped in well-supported species clades with no overlap with any North American clade. This suggests that the European species *Hodophilus foetens* probably does not occur in North America. Because there are no alternative published names for two so far unidentified clades, they are described here as two new species *Hodophilus hesleri* and *Hodophilus smithii*. The first is distinguished from other studied members of the *Hodophilus foetens* superclade by smaller spores (up to 5.5 µm long on average), narrow caulocystidia (up to 6.4 µm wide on average) and a smaller length/width ratio of terminal cells in near the pileus centre. The second species is defined by a combination of wide caulocystidia (at least 8.4 µm wide on average) and a greater length/width ratio of terminal cells in pileipellis near the pileus centre (on average between 2.77 and 3.17) (Tab. 1).

**Importance of field characters**

Hesler and Smith (1963) used several field characters to recognize four North American taxa with strong unpleasant odours: pileus and lamellar colour, width of lamellae, surface texture of the stipe and the pileus, and the odour of basidiomata. All of these characters are compared in Table 2. Concerning the colour of the pileus, both species described here as new are very similar. They have brown and grey tints of variable intensity because of a hygrophanous surface. We did not observe on our material for the two new species any cinnamon colour reported for *Hygrophorus foetens* by Hesler and Smith (1963) nor Isabella or Olive-Buff colours reported by
them for *Hygrophorus paupertinus* and *Hygrophorus subfuscescens* var. *odora*. The lamellae of both new species are grey brown, which probably corresponds to the pallid lamellae of *Hygrophorus peckianus* and *Hygrophorus paupertinus*. The odour of both new species is somewhat variable, naphthalene mixed with a farinaceous, methyl mercaptan or an unpleasant component. Hesler and Smith (1963) distinguished various odour types that seem to us subjective and difficult to recognize. The odour for *Hygrophorus subfuscescens* var. *odora* seems to be useful, which is described as distinctly disagreeable when bruised. In our experience with both new species, their odour was so strong that they can be located among leaves even before having seen them. Hesler and Smith defined the lamellar width as specifically “very narrow” in *Hygrophorus paupertinus*, which may correspond to the width of the lamellae of *Hodophilus hesleri* and *Hodophilus smithii* (up to 1.5 (–2) mm). However, since no specific size of the lamellae is given, the importance of this character needs to be verified. Possibly a good field character might be darker dots on the upper part of the stipe of *Hodophilus smithii*, probably caused by dark incrusted pigments on caulocystidia. Hesler and Smith reported the presence of a scabrous-dotted stipe surface (with no mention of darker colour) only for American collections of *Hygrophorus foetens*.

**Ecology**

In the North American literature (e.g. Hesler and Smith 1963), the ecology of *Hodophilus* taxa with an unpleasant odour is defined very generally, most frequently in woods and on bare soil, often under bracken ferns. The only mention of grassland is associated with *Hygrophorus peckianus*, reported also from lawns in addition to other forest habitats. Accordingly, we collected only one among seven of our North American collections of *Hodophilus* with naphthalene odours in a lawn on a strip between a parking lot and the road in the Cherokee
National Forest (JMB10052013-02), but this was surrounded by a forest in close vicinity. In Europe, the reports of *Hodophilus foetens* more frequently originate from grasslands, e.g. pastures or meadows (e.g. Arnolds 1990, Boertman 2012). In our experience, *Hodophilus* species with naphthalene odours grow at locally humid places but not on damp soil. The suitable microclimate is probably supported by the shelter provided by various woody or herbaceous vegetation (forest, scrubs, high grass) in combination of either proximity to a water source or humid climate with frequent rains. In both continents, *Hodophilus* with naphthalene odours occur frequently on naked soil, e.g. steep slopes on riverbanks, footprints or paths of large animals, roadsites, etc. They are often associated with other clavaroid Clavariaceae and with *Hygrocybe* species. Most of our North American collections are from riverbanks, roadsides, and embankments next to trails, while our European collections are mainly from scrubs and high grass on forest/pasture margins.
Acknowledgements

The authors would like to thank David Boertmann, Christine Braaten, Adolf and Oluna Ceska, Marisol Sánchez-García, Emma Harrower, D. Jean Lodge, Steve Trudell, and Else Vellinga for their contribution of specimens, DNA sequences, photographs and/or assistance with field work. We also thank the staff and curators of the herbaria at K, MICH, TENN and NYBG for providing loans. Specifically, we would like to thank Lorinda Leonardi at NYBG and Patricia Rogers at MICH for providing historical images to include in our photo plate. This work was supported by an NSF Doctoral Dissertation Improvement Grant (DEB-1210302) to JMB and PBM. The research of SA, KA, KM and SJ was granted by a Centre of Excellence for Protection and Use of Landscape and for Biodiversity (ITMS 26240120014) financed by the European Fund for Regional Development under the Operational programme Research and Development (002/2009/4.1/OPVaV) and the national grant Vega 02/0075/14 to SA and SJ. Constructive comments to an earlier version of this paper were kindly provided by D. Jean Lodge and Bryn Dentinger.

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N. Boubée, Paris.


Tables

Table 1. Average values of 30 measurements of selected micro-morphological characters observed on Hodophilus (Ho.) taxa with an unpleasant odour. * type specimens, TC margin/centre – terminal cells in pileipellis near the pileus margin/centre, L – length, W – width, Q – length/width ratio. The shaded boxes indicates important differences.

<table>
<thead>
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<th>species epithet</th>
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<th>spores</th>
<th>caulocystidia</th>
<th>TC margin</th>
<th>TC centre</th>
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<td>39.5</td>
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<td>Ho. subfuscescens var. odora</td>
<td>MICH 10953 *</td>
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<td>4.1</td>
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Table 2. Comparison of field characters observed on *Hodophilus* taxa with an unpleasant odour as interpreted by a Hesler and Smith (1963), b Howe (1874) and c according to our observations.

<table>
<thead>
<tr>
<th>Species epithet</th>
<th>Pileus colour</th>
<th>Lamellar colour</th>
<th>Odour</th>
<th>Width of lamellae</th>
<th>Stipe surface</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>foetens</em> a</td>
<td>cinnamon brown</td>
<td>wood brown</td>
<td>pungent</td>
<td>medium</td>
<td>first scabrous-dotted</td>
</tr>
<tr>
<td><em>subfuscescens</em></td>
<td>Isabella colour to pale olive buff</td>
<td>pale olive buff, greyer at maturity</td>
<td>disagreeable when flesh is bruised</td>
<td>moderately</td>
<td>glabrous</td>
</tr>
<tr>
<td>var. <em>odora</em> a</td>
<td>Isabella colour to pale olive buff</td>
<td>pale olive buff, greyer at maturity</td>
<td>disagreeable when flesh is bruised</td>
<td>moderately</td>
<td>glabrous</td>
</tr>
<tr>
<td><em>paupertinus</em> a</td>
<td>sordid Isabella, soon dark brownish grey</td>
<td>palid to pale drab</td>
<td>strong disagreeable</td>
<td>very</td>
<td>glabrous</td>
</tr>
<tr>
<td><em>peckianus</em> b</td>
<td>fuliginous paler buff-brown dry</td>
<td>palid, becoming darker with age</td>
<td>strong, like lace-wing</td>
<td>broad</td>
<td>smooth</td>
</tr>
<tr>
<td><em>hesleri</em> c</td>
<td>pale grey brown, darker near the centre</td>
<td>brownish grey to grey brown</td>
<td>naphthalene also with other components</td>
<td>1-2 mm</td>
<td>smooth, slightly pruinose near lamellae</td>
</tr>
<tr>
<td><em>smithii</em> c</td>
<td>pale grey brown</td>
<td>milk-coffee to greyish brown</td>
<td>naphthalene also with other components</td>
<td>1-1.5 mm</td>
<td>smooth or with fine blackish punctuations</td>
</tr>
</tbody>
</table>
Figure captions

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*. Collection labels are updated with appropriate taxon labels except where collector identifications disagree. Also included are collection labels, country or state/province, and whether this represents a type collection. Bootstrap values followed by Bayesian posterior probabilities are indicated at nodes.

Fig. 2. Basidiomata field aspect of *A. Hodophilus smithii* (JMB10051302, holotypus) photo by B.P. Looney. B. *Hodophilus smithii* (PBM3930) photo by P.B. Matheny. C. *Hodophilus hesleri* (ECV4175) photo by S. Trudell D. *Hodophilus peckianus* (labelled as “Hygrophorus Peckii Howe”) drawing by C.H. Peck. Courtesy New York State Museum, Albany, NY. E. *Hodophilus paupertinus* (Ceska020704 from same locality as Ceska020301) photo by O. and A. Ceska. F. *Hodophilus subfuscescens* (AHS32894, holotypus) photo by A.H. Smith. This image is the property of the Regents of the University of Michigan. Scale bar = 1 cm. All photos and drawings reproduced with permission.


Fig. 4. Hyphal terminations in pileipellis near the pileus margin of three *Hodophilus* species with

Fig. 5. Hyphal terminations in pileipellis near the pileus centre of three *Hodophilus* species with naphthalene odour. A. *Hodophilus hesleri* (holotypus). B. *Hodophilus paupertinus* (holotypus). C. *Hodophilus smithii* (holotypus). Scale bar = 10 µm.


Fig. 7. *Hodophilus peckianus* (holotypus). A. Caulocystidia. B. Marginal cells on the lamellar edge. C. Basidia. D. Basidiola. E. Spores. Scale bar = 10 µm.

Fig. 8. *Hodophilus peckianus* (holotypus). A. Hyphal terminations in pileipellis near the pileus centre. B. Hyphal terminations in pileipellis near the pileus margin. Scale bar = 10 µm.

Fig. 9. *Hodophilus subfusescens var. odora* (holotypus). A. Caulocystidia. B. Marginal cells on the lamellar edge. C. Basidia. D. Basidiola. E. Spores. Scale bar = 10 µm.

Fig. 10. *Hodophilus subfusescens var. odora* (holotypus). A. Hyphal terminations in pileipellis near the pileus centre. B. Hyphal terminations in pileipellis near the pileus margin. Scale bar = 10 µm.
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. Collection labels are updated with appropriate taxon labels except where collector identifications disagree. Also included are collection labels, country or state/province, and whether this represents a type collection. Bootstrap values followed by Bayesian posterior probabilities are indicated at nodes.

Fig. 1
212x239mm (300 x 300 DPI)
Fig. 2. Basidiomata field aspect of A. Hodophilus smithii (JMB10051302, holotypus) photo by B.P. Looney. B. Hodophilus smithii (PBM3930) photo by P.B. Matheny. C. Hodophilus hesleri (ECV4175) photo by S. Trudell D. Hodophilus peckianus (labelled as "Hygrophorus Peckii Howe") drawing by C.H. Peck. Courtesy New York State Museum, Albany, NY. E. Hodophilus paupertinus (Ceska020704 from same locality as Ceska020301) photo by O. and A. Ceska. F. Hodophilus subfuscens (AHS32894, holotypus) photo by A.H. Smith. This image is the property of the Regents of the University of Michigan. To inquire about copyright restrictions and use permissions, contact the MICH Herbarium curator Timothy James, tyjames@umich.edu. Scale bar = 1 cm.

Fig. 2
215x279mm (300 x 300 DPI)
Fig. 4. Hyphal terminations in pileipellis near the pileus margin of three Hodophilus species with naphthalene odour. A. Hodophilus hesleri (holotypus). B. Hodophilus paupertinus (holotypus). C. Hodophilus smithii (holotypus). Scale bar = 10 µm.
Fig. 5. Hyphal terminations in pileipellis near the pileus centre of three Hodophilus species with naphthalene odour. A. Hodophilus hesleri (holotypus). B. Hodophilus paupertinus (holotypus). C. Hodophilus smithii (holotypus). Scale bar = 10 µm.
Fig. 6. Caulocystidia of three Hodophilus species with naphthalene odour. A. Hodophilus hesleri (holotypus). B. Hodophilus paupertinus (holotypus). C. Hodophilus smithii (holotypus). Scale bar = 10 µm.
Fig. 7. Hodophilus peckianus (holotypus). A. Caulocystidia. B. Marginal cells on the lamellar edge. C. Basidia. D. Basidiola. E. Spores. Scale bar = 10 µm.

Fig. 7
165x235mm (300 x 300 DPI)
Fig. 8. Hodophilus peckianus (holotypus). A. Hyphal terminations in pileipellis near the pileus centre. B. Hyphal terminations in pileipellis near the pileus margin. Scale bar = 10 µm.
Fig. 9. Hodophilus subfuscens var. odora (holotypus). A. Caulocystidia. B. Marginal cells on the lamellar edge. C. Basidia. D. Basidiola. E. Spores. Scale bar = 10 µm.

Fig. 9
160x188mm (300 x 300 DPI)
Fig. 10. Hodophilus subfuscescens var. odora (holotypus). A. Hyphal terminations in pileipellis near the pileus centre. B. Hyphal terminations in pileipellis near the pileus margin. Scale bar = 10 µm.

Fig. 10
157x235mm (300 x 300 DPI)