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

Slavomír Adamčík, Brian P. Looney, Joshua M. Birkebak, Soňa Jančovičová, Katarína Adamčíková, Karol Marhold, and P. Brandon Matheny

**Abstract:** Five North American *Hodophilus* species with naphthalene-like odours 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 subfuscescens* 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. Multilocus 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*.

**Key words:** agaricoid, Clavariaceae, multilocus phylogeny, morphology, type studies.


**Mots-clés** : agaricoïdes, Clavariaceae, phylogénie multi-locus, morphologie, études de type.
Introduction

*Hodophilus foetens* (W. Phillips) Birkebak & Adamčík is a well-known species characterized by its unpleasant camphor-like odour together with skatol and methylmercaptan-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 (Cam.) to the genus *Hodophilus*. R. Heim (Ho.) (Birkebak et al. 2016). Members of both genera had been previously treated within the genus *Hygrophorus* Fr. (Hyg.) (Dennis 1953; Singer 1959; Hesler and Smith 1963). The genus *Hodophilus*, typified by *H. 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, *Cam. foetens* (W. Phillips) Arnolds (Boertman 2012; Kovalenko et al. 2012), originally described from Wales in the UK. (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 *H. foetens* from other North American taxa based on a darker brown colour of thepileus, 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 basidioomata. The remaining two North American taxa described with strong odours, *Hy. peckianus* Howe and *Hy. paupertinus* A.H. Sm. & Hesler, were 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* (http://www.mycobank.org/). 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 *H. 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 and Duhem 1994). Hesler and Smith (1963) described the odours of North American taxa as pungent (*Hy. foetens*); exceedingly strong, penetrating, disagreeable (*Hy. paupertinus*); strong, offensive (*Hy. peckianus*); and very distinctly disagreeable when the flesh is bruised (*Hy. subfuscescens* var. *odora*). Ghyselinck (2003) analysed odour descriptions of *Ho. 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 *Ho. 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 naphthalene odours based on morphological observations and a multilocus phylogenetic analysis using authentic (including type) material and recent well-documented collections. We seek to confirm whether the European species *Ho. 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 *Hy. foetens*, *Hy. peckianus*, *Hy. paupertinus*, and *Hy. subfuscescens* var. *subfuscescens* and *Hy. subfuscescens* var. *odora* were included together with 14 other North American collections of *Hodophilus* (Supplementary data, Table S1). Sequences from GenBank related to North American *Hodophilus* species with naphthalene odours were also used. Twenty European collections identified as *Ho. foetens* were used to test the transatlantic distribution of species with naphthalene odours. Twenty other *Hodophilus* specimens without this smell were included in our phylogenetic taxon scheme to clarify relationships within the genus *Hodophilus* (Supplementary data, Table S1). Six other Clavariaceae species were added as outgroups, including *Cam. atrovelutina* (Romagn.) Argaud, *Cam. schulzeri* (Bres.) Herink, *Cam. deceptiva* (A.H. Sm. & Hesler) Bon, *Clavaria fuscata* Oudem., *Clavaria pullei* Donk, and *Ramarriopsis 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

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3Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjb-2016-0091.
Phylogenetic analyses

Alignments for individual regions were created in ClustalX (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 the RAxML GUI (Silvestro and Michalak 2012) with 1000 bootstrap replicates. Bayesian inference (BI) was performed in MrBayes version 3.2.2 (Ronquist et al. 2011) running 10 000 000 generations and sampling parameter states every 10 000 generations. To ensure convergence had been reached, the mean standard deviation of split frequencies was monitored to ensure that it fell below 0.01, and trace files of the parameters were examined to ensure proper mixing. A burn-in of 25% was used. We consider bootstrap values >70% and posterior probabilities >0.95 as strong support for clades. States and provinces for the USA 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 characteristics were observed under an Olympus CX-41 light microscope with an oil-immersion lens at a magnification of 1000×. All drawings of microscopic structures, with the exception of basidiospores, were made with a camera lucida using an Olympus U-DA drawing attachment at a projection scale of 2000×. Basidiospores were scanned with an Artray Artcam 300MI camera and measured using 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. The Q-value is the length:width ratio of basidiospores. Measurements exclude ornamentation. Statistics for measurements of microscopic characteristics are based on 30 measurements and given as the mean ± SD; values in parentheses are the measured minimum or maximum values. Basidiospores were tested in Melzer’s reagent for amyloid or dextrinoid reactions (Moser 1978).

To find micro-morphological differences among studied taxa, the 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 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 Hy. paupertinus, and the other two are named as the new species Ho. hesleri and Ho. smithii below. In addition to these three clades, the type ITS sequence of Hy. 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 Hy. subfuscescens var. subfuscescens.

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

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**Ho. foetens superclade**

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**Ho. micaceus superclade**
Table 1. Mean values of 30 measurements of selected micro-morphological characteristics observed on Hodophilus taxa with unpleasant odours.

<table>
<thead>
<tr>
<th>Species</th>
<th>Herbarium No.</th>
<th>Spores</th>
<th>Caulocystidia</th>
<th>TC margin</th>
<th>TC centre</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ho. foetens</td>
<td>K(M) 0009276*</td>
<td>5.9</td>
<td>4.3</td>
<td>1.39</td>
<td>31.6</td>
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<tr>
<td>Ho. hesleri</td>
<td>JMB10252013-01*</td>
<td>4.8</td>
<td>4.0</td>
<td>1.21</td>
<td>21.8</td>
</tr>
<tr>
<td>Ho. peckianus</td>
<td>NYS F3880*</td>
<td>5.5</td>
<td>4.4</td>
<td>1.26</td>
<td>26.1</td>
</tr>
<tr>
<td>Ho. smithii</td>
<td>JMB10052013-02*</td>
<td>4.5</td>
<td>4.5</td>
<td>1.21</td>
<td>32.0</td>
</tr>
<tr>
<td>Ho. paupertinus</td>
<td>MICHI0923*</td>
<td>5.4</td>
<td>5.2</td>
<td>1.25</td>
<td>27.4</td>
</tr>
<tr>
<td>Ho. hesleri var. subfuscescens</td>
<td>MICH10952*</td>
<td>5.4</td>
<td>5.2</td>
<td>1.25</td>
<td>27.4</td>
</tr>
<tr>
<td>Ho. hesleri var. odora</td>
<td>MICH 10953*</td>
<td>5.4</td>
<td>5.2</td>
<td>1.25</td>
<td>27.4</td>
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<table>
<thead>
<tr>
<th></th>
<th></th>
<th>L</th>
<th>W</th>
<th>Q</th>
<th>L</th>
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<tr>
<td>Ho. foetens</td>
<td>5.9</td>
<td>4.3</td>
<td>1.39</td>
<td>31.6</td>
<td>8.7</td>
<td>27.2</td>
<td>14.3</td>
<td>2.10</td>
<td>23.4</td>
<td>11.4</td>
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<tr>
<td>Ho. hesleri</td>
<td>4.8</td>
<td>4.0</td>
<td>1.21</td>
<td>21.8</td>
<td>5.9</td>
<td>28.6</td>
<td>12.3</td>
<td>2.40</td>
<td>20.1</td>
<td>12.7</td>
</tr>
<tr>
<td>Ho. peckianus</td>
<td>5.4</td>
<td>4.5</td>
<td>1.21</td>
<td>32.0</td>
<td>6.1</td>
<td>32.8</td>
<td>14.0</td>
<td>2.40</td>
<td>28.7</td>
<td>14.3</td>
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<tr>
<td>Ho. smithii</td>
<td>5.1</td>
<td>4.2</td>
<td>1.23</td>
<td>27.9</td>
<td>5.4</td>
<td>31.8</td>
<td>12.3</td>
<td>2.70</td>
<td>30.0</td>
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<td>Ho. paupertinus</td>
<td>5.5</td>
<td>4.4</td>
<td>1.26</td>
<td>26.1</td>
<td>6.4</td>
<td>30.0</td>
<td>14.6</td>
<td>2.10</td>
<td>26.3</td>
<td>15.1</td>
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<tr>
<td>Ho. hesleri var. subfuscescens</td>
<td>6.6</td>
<td>5.0</td>
<td>1.33</td>
<td>32.0</td>
<td>4.7</td>
<td>25.2</td>
<td>11.0</td>
<td>2.62</td>
<td>25.2</td>
<td>8.8</td>
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<tr>
<td>Ho. hesleri var. odora</td>
<td>6.5</td>
<td>5.3</td>
<td>1.24</td>
<td>32.3</td>
<td>5.7</td>
<td>29.7</td>
<td>9.8</td>
<td>3.16</td>
<td>31.6</td>
<td>9.9</td>
</tr>
</tbody>
</table>

Note: * 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.

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 characteristics are labelled in Table 1. Mean basidiospore length of Ho. hesleri and Ho. subfuscescens do not exceed 5.5 μm. Mean caulocystidia width of Ho. foetens, Ho. peckianus, and Ho. smithii is broader than 8 μm. Terminal cells of hyphae in the pileipellis near the pileus margin are shorter with a length:width ratio; The shaded boxes indicates important differences.

Contributes to its smallest mean width (up to 10 μm). This species and Ho. smithii have the greatest length:width ratio of the terminal cells near the pileipellis centre.

The shape of the terminal cells differ between the margin and the centre of the pileus in Ho. hesleri and Ho. smithii. The length:width ratio of the first is smaller near the pileus centre, whereas 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 characteristics do not seem to exhibit much difference among the studied species other than the olive-buff tints of Ho. subfuscescens (Table 2).

Taxonomy

Artificial key to North American Hodophilus species with an unpleasant odours

1A. Caulocystidia on average wider than 8 μm .................................................. 2
1B. Caulocystidia on average narrower than 8 μm ............................................. 3
2A. Terminal cells of hyphae near the pileus centre sphaero-pedunculate, capitate, obpyriform or clavate, towards the base usually distinctly pedunculate .................................................. 3. Hodophilus smithii
2B. Terminal cells of hyphae near the pileus centre mostly globose, obpyriform and not distinctly pedunculate .......................................................... 4
3A. Pileipellis near the pileus centre with frequent non-inflated cylindrical or clavate terminal cells. 4. Hodophilus paupertinus
3B. Pileipellis near the pileus centre with obpyriform, globose, or sphaero-pedunculate terminal cells .......................................................... 4
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) ............................................. 4. Hodophilus subfuscescens
4B. Terminal cells of hyphae near the pileus centre obpyriform or sphaero-pedunculate with a ratio of length:width >1.7, subterminal cells rarely short and small (mostly >10 μm). 5. Hodophilus hesleri

Hodophilus hesleri Adamčík, Birkebak & Looney, sp. nov., Figs. 2C, 3A–3C, 4A, 5A, and 6A
MycoBank no.: MB815983.
Etymology: In honor of Dr. Lexemuel Ray Hesler.
Table 2. Comparison of field characteristics observed on *Hodophilus* taxa with unpleasant odours as interpreted by Hesler and Smith (1963), Howe (1874), and according to *Isabella colour to pale olive buff*.

<table>
<thead>
<tr>
<th>Species epithet</th>
<th>Lamellar colour</th>
<th>Odour</th>
<th>Width of lamellae</th>
<th>Stipe surface</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>fasciculata</em></td>
<td>Pale olive buff</td>
<td>Fleshy, becoming granulose and cracking when old, matt, hygrophanous, colour when moist near the margin dark brown (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 mm × 0.75–2.00 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 brown (5D4) to chocolate brown (6F4), near the base first dark brown (5D4), later hair brown (5E4) or chocolate brown (6F4), flexuous, sometimes narrowed near base. <strong>Lamellae</strong> 1–2 mm wide, <em>L</em> = 12–23, <em>l</em> = 0–1, short decurrent, brownish orange to grey brown (5C3–6C3–6D3, 5B3–5D2). <strong>Flesh</strong> elastic, with a naphthalene odour but also mixed with other farinaceous or unpleasant components, dry orange grey (5B3), wet greyish brown (6E3).</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>subfuscescens</em> var. <em>Isabella</em></td>
<td>Pale olive buff</td>
<td>Fleshy, becoming granulose and cracking when old, matt, hygrophanous, colour when moist near the margin dark brown (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 mm × 0.75–2.00 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 brown (5D4) to chocolate brown (6F4), near the base first dark brown (5D4), later hair brown (5E4) or chocolate brown (6F4), flexuous, sometimes narrowed near base. <strong>Lamellae</strong> 1–2 mm wide, <em>L</em> = 12–23, <em>l</em> = 0–1, short decurrent, brownish orange to grey brown (5C3–6C3–6D3, 5B3–5D2). <strong>Flesh</strong> elastic, with a naphthalene odour but also mixed with other farinaceous or unpleasant components, dry orange grey (5B3), wet greyish brown (6E3).</td>
<td></td>
<td></td>
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<tr>
<td><em>Isabella</em></td>
<td>Pale olive buff</td>
<td>Fleshy, becoming granulose and cracking when old, matt, hygrophanous, colour when moist near the margin dark brown (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 mm × 0.75–2.00 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 brown (5D4) to chocolate brown (6F4), near the base first dark brown (5D4), later hair brown (5E4) or chocolate brown (6F4), flexuous, sometimes narrowed near base. <strong>Lamellae</strong> 1–2 mm wide, <em>L</em> = 12–23, <em>l</em> = 0–1, short decurrent, brownish orange to grey brown (5C3–6C3–6D3, 5B3–5D2). <strong>Flesh</strong> elastic, with a naphthalene odour but also mixed with other farinaceous or unpleasant components, dry orange grey (5B3), wet greyish brown (6E3).</td>
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</table>

**Basidiospores** (4.2–4.8–6.0–(7.2) µm × (3.8–4.0–4.8–(5.8) µm, mean = 5.4 µm × 4.4 µm, Q (length: width) = (1.04–)1.13–1.40–(1.55), mean Q = 1.26, broadly ellipsoidal to ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hiral appendage 0.4–0.6–(1.0) µm long. **Basidia** 4-spored, (31.0–34.5–40.5–(43.0) µm × (4.5–15.0–6.5–(7.0) µm, mean = 37.5 µm × 5.6 µm, hyaline, narrowly clavate, attenuated and flexuous toward base. **Basidioles** cylindrical to narrowly clavate, often flexuous, obtuse, (19.0–)26.0–38.0–(45.0) µm × 4.0–6.0–(6.5) µm, mean = 31.9 µm × 5.0 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, hyphae 4–10–(15) µm wide, composed of cells 20–100 µm long. **Subhymenium** pseudoparenchymatic, 20–25 µm deep, composed of branched, dense, hyphae 2–4 µm wide. **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) µm × (10.5–)11.0–18.0–(24.5) µm, mean = 30.0 µm × 14.6 µm, Q = (1.19–)1.57–2.63–(2.92), mean Q = 2.1; subterminal cells rarely inflated, usually cylindrical or fusiform, short and small cells (shorter than 10 µm) occasional, usually not branched, often bearing incrusted pigments, measuring (3.5–)8.5–13.0–(17.0) µm × (1.8–)2.6–4.0–(5.0) µm, mean = 31.3 µm × 6.6 µm. Terminal cells of hyphae in pileipellis near the pileus centre comparatively shorter, mainly obpyriform, (15.5–)19.5–33.0–(44.0) µm × (10.5–)12.0–18.0–(22.0) µm, mean = 26.4 µm × 14.9 µm, Q = (1.06–)1.39–2.21–(2.83), mean Q = 1.8. Pileus trama of interwoven hyphae, 3–10 µm wide, subparallel, irregularly inflated and often branched. **Capillitium** fascided, thin-walled, repent or ascending, with terminal cells clavate or obpyriform, obtuse or rarely apically constricted, occasionally flexuous towards septum, measuring (10.0–)15.0–36.0–(58.0) µm × 4.5–8.5–(11.0) µm,
Fig. 2. Basidiomata field aspect of (A) *Hodophilus smithii* sp. nov. (JMB10051302, holotypus) photo by B.P. Looney. (B) *Hodophilus smithii* (PBM3930) photo by P.B. Matheny. (C) *Hodophilus hesleri* sp. nov. (ECV4175) photo by S. Trudell. (D) *Hodophilus peckianus* (labelled as "Hygrophorus Peckii Howe") drawing by C.H. Peck. Courtesy New York State Museum, Albany, New York, USA. (E) *Hodophilus paupertinus* (Ceska020704 from the 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. Scale bar = 1 cm. All photos and drawings reproduced with permission. [Colour online.]
mean = 25.7 μm × 6.5 μm, subterminal cells occasionally short and small (shorter than 10 μm). Stipe trama of hyphae 4–12(–15) μm wide, parallel, and composed of cells 15–90 μm long. Clamp connections absent in all tissues.


COMMENTARY: Hodophilus hesleri is similar in field aspect and in microscopy to Ho. 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 Ho. hesleri misidentified as Ho. peckianus.

Hodophilus paupertinus (A.H. Sm. & Hesler) Adamčík, Birkebak & Looney, comb. nov., Figs. 2E, 3D–3F, 4B, 5B, and 6B

MYCOBANK NO.: MB815984.


ORIGINAL DESCRIPTION: Pileus (5) 10–20 mm, latus, subplanus, siccus, isabellinus demum umbrinus; caro cinerea, odor

Fig. 3. Hymenium elements and spores of three Hodophilus species with naphthalene odours. Hodophilus hesleri sp. nov. (holotypus): (A) Basidia. (B) Basidiola. (C) Spores. Hodophilus paupertinus (holotypus): (D) Basidia. (E) Basidiola. (F) Spores. Hodophilus smithii sp. nov. (holotypus): (G) Basidia. (H) Basidiola. (I) Spores. Scale bar = 10 μm.

Fig. 4. Hyphal terminations in pileipellis near the pileus margin of three Hodophilus species with naphthalene odours. (A) Hodophilus hesleri sp. nov. (holotypus). (B) Hodophilus paupertinus (holotypus). (C) Hodophilus smithii sp. nov. (holotypus). Scale bar = 10 μm.
subnauseosa; lamellae angustatae, distantes vel diādistantes, 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) μm × (4.3–)4.7–5.4 (–6.0) μm, mean = 6.4 μm × 5.0 μm, Q = (1.09–)1.16–1.36(–1.51), mean Q = 1.26, broadly ellipsoid to ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage up to 1 μm long. Basidia 4-spored, 47.0–56.0 μm × 5.0–7.5 μm, hyaline, narrowly clavate, attenuated and flexuous toward base. Basidioles cylindrical to narrowly clavate, obtuse, often flexuous, ca. 3.5–7.0 μm wide. Pleurocystidia absent. Marginal cells on the lamellar edge not well-differentiated, similar to basidioles on lamellar sides. Lamellar trama composed of subparallel 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 (12.0–)17.0–49.0(–108.0) μm × (5.0–)7.0–15.0 (–23.5) μm, mean = 32.1 μm × 10.9 μm, Q = (1.89–)1.72–4.55(–7.35), mean Q = 3.13; subterminal cells often narrower, cylindrical or fusiform, often also inflated, never short (i.e., shorter than 10 μm), often branched, measuring (10.0–)18.5–51.0(–86.5) μm × (3.5–)5.5–13.0(–23.0) μm, mean = 34.7 μm × 9.3 μm, Q = (0.74–)1.78–5.34(–11.4), mean 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 (8.0–)12.0–34.0(–54.0) μm × (3.0–)4.5–11.0(–18.0) μm, mean = 23.0 μm × 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 (15.0–)20.5–40.5(–57.0) μm × (2.0–)3.5–6.0(–7.5) μm, mean = 30.5 μm × 4.7 μm. Clamp connections absent in all tissues.


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 Columbia confirms that Ho. paupertinus is likely widely distributed along the West Coast.

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

MYCOBANK NO.: MB815985.


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, .002 in. in diameter.
Plant 1–2 inches high (1 inch = 2.54 cm), 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 (Chrysotha). 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–(7.0) µm × (4.0–)4.4–5.1 (–5.6) µm, mean = 6.1 µm × 5.8 µm, Q = (1.13–)1.21–1.34–(1.40), mean Q = 1.28, broadly ellipsoid to ellipsoid, hyaline, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage 0.6–0.9–(1.0) µm long. Basidia 4-spored, (30.0–)36.5–45.0–(50.0) µm × 5.0–6.5–(7.5) µm, mean = 40.8 µm × 5.9 µm, hyaline, narrowly clavate, attenuated and flexuous toward base. Basidioles cylindrical to narrowly clavate, often flexuous, and apically constricted, ca. 2.5–6.0 µm wide. Pleurocystidia absent. Marginal cells on the lamellar edge well differentiated, clavate to obpyriform, pedunculate or not, (10.0–)15.0–28.0–(35.0) µm × (5.5–)6.5–12.5–(15.5) µm, mean = 21.5 µm × 9.3 µm.

Lamellar trama composed of strongly undulate and intricate, parallel, scarcely branched, and irregularly inflated hyphae 2–8–(10) µm wide, 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 (12.0–)15.5–35.0–(45.0) µm × (7.5–)11.5–21.0–(30.0) µm, mean = 26.0 µm × 16.3 µm, Q = 0.94–2.42–4.50, mean 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 (23.0–)30.0–50.5–(70.0) µm × (4.5–)6.5–11.0–(13.0) µm, mean = 40.1 µm × 8.6 µm. Pileipellis elements near the pileus centre very similar to those near the margin, terminal cells of hyphae measuring (9.0–)15.0–31.5–(42.0) µm × (6.0–)8.0–21.0–(31.0) µm, mean = 23.3 µm × 14.7 µm, Q = (0.82–)1.05–2.36–(3.35), mean Q = 1.71. Caulocystidia fascicled, thin-walled, repent or ascending, clavate, obtuse, usually pedunculate and flexuous towards septum, with terminal cells measuring (9.0–)12.5–31.5–(50.0) µm × 4.5–14.0–(23.0) µm, mean = 22.2 µm × 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 Ho. foetens, but Ho. peckianus was not widely accepted because of the European bias for accepting a single species (Ho. foetens) with a strong disagreeable odour. Smith and Hesler (1954) reported Ho. foetens from Michigan, and later from Idaho (in Hesler and Smith 1963), and discussed its differences from Ho. peckianus. They also recognized two more species with unpleasant odours (in Hesler and Smith 1963). Comparing the descriptions of Ho. 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 Camarophyllopis because the hyphae are not oriented perpendicularly to form a hymenidem. 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 characteristic 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”, which is a combination that Howe did not make. Although not linked to a particular collection, it is likely that this represents Hy. peckianus rather than Ho. 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., Figs. 2A–2B, 3G–3I, 4C, 5C, and 6C

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), nought 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) mm × 0.75–1.50 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 1.0–1.5 mm wide, L = 12–18, 1 = 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 (5.0–)5.4–6.3–(7.2) µm × (3.8–)4.1–4.8–(5.2) µm, mean = 5.9 µm × 4.5 µm, Q = (1.08–)1.22–
hyphal, smooth, inamyloid, not dextrinoid, thin-walled, hilar appendage 0.45–0.80 μm long. Basidia 4-spored, (28.0–)33.0–42.5–(49.0) μm × (5.0–)6.0–7.5–(8.0) μm, mean = 37.7 μm × 6.8 μm, hyaline, narrowly clavate, attenuated and flexuous toward base. Basidioles cylindrical to narrowly clavate, often flexuous, obtuse, (17.0–)24.5–37.5–(49.0) μm × (3.0–)4.0–6.5–(8.0) μm, mean = 31.0 μm × 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 cells 10–90 μm long. Subhymenium pseudoparenchymatic, 20–25 μm deep, composed of branched, dense, hyphae 3–5 μm wide. Pileipellis near the pileus margin a hymeniderm, mainly composed of sphaero-pedunculate, occasionally also obpyriform cells arranged in one rank, terminal cells measuring (10.0–)20.0–39.5–(58.0) μm × (7.0–)10.0–17.5–(24.0) μm, mean = 29.8 μm × 13.7 μm, Q = (1.00–)1.47–3.01–(4.00), mean Q = 2.24; subterminal cells rarely inflated, usually cylindrical, short and small cells (shorter than 10 μm) very rare, usually unbranched, measuring (5.0–)13.5–35.0–(53.0) μm × (3.0–)3.5–13.0–(30.0) μm, mean = 21.2 μm × 8.1 μm. Terminal cells of hyphae in pileipellis near the pileus centre usually somewhat longer, mainly clavate-pedunculate or sphaero-pedunculate, rarely obpyriform, (15.0–)23.0–42.0–(66.0) μm × (6.0–)8.0–14.5–(21.0) μm, mean = 32.5 μm × 11.3 μm, Q = (1.18–)2.06–3.99–(5.67), mean Q = 3.03. Pileus trama of interwoven, 3–10 μm wide, subparallel, irregularly inflated hyphae, composed of cells 10–80 μm long. Caulocystidia repent and dispersed or fascicled and ascending, thin-walled, often inflated, obpyriform or sphaero-pedunculate, others broadly clavate, usually not flexuous, with terminal cells measuring (13.0–)21.0–44.0–(78.0) μm × (4.0–)7.0–11.5–(17.0) μm, mean = 32.6 μm × 9.1 μm, with darker parietal and sometimes also dark incrusted pigments. Stipe trama hyphae 4–10 μm wide, parallel, often anastomosed, composed of cells 10–120 μm long. Clamp connections absent in all tissues.

Material Examined: USA. North Carolina. Big Creek, at very beginning of Baxter Creek trail, 9 August 2012, E.C. Vellinga JMB08091202 (TENN 067461); Macon County, Highlands, Horse Cave Road, Rusty Falls area, 15 July 1991, D.E. 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, E.B. Lickey DJL04TN23 (TENN); 11 miles (1 mile = 1.6 km) up Schoolhouse Gap trail, 19 July 2013, P.B. 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, J.M. Birkebak and S. Adamčík JMB10051302 (TENN 070839, holotype); Anderson County.

COMMENTARY: In determining the identity of North American collections of Ho. foetens (Smith and Hesler 1954, Hesler and Smith 1963), Ho. 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 Ho. 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 Ho. smithii have comparatively smaller basidiomata with pilei not exceeding 10 mm, whereas pilei of Ho. foetens are described as 10–40 mm wide. The identity of North American collections of Ho. 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, and 10

**Mycobank no.:** MB815987.

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


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.

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


Original description: Pileus 6–25 mm latus, connexus, glaber, odorous; stipes 2–4 cm. longus, 1.5–3 mm. crassus, glaber, pallide luteus, distantes, decurrentes, subluteae, demum sordide avellaneae; Sporae 5–6 × 4–5 μm, mean = 4.9 μm, mixed with dispersed basidia. Lamellar trama composed of undulate and intricate but parallel, scarcely branched and irregularly inflated hyphae 3–9 μm wide. 

Subhymenium pseudoparenchymatic, 15–25 μm deep, composed of branched, dense hyphae 2–4 μm wide. Pileipellis near the pileus margin hymeniderm, composed of sphaero-pedunculate or obpyriform cells arranged usually in 1 rank, terminal cells measuring (15.0–)20.0–35.5(–53.0) μm × (8.5–)14.0–26.0(–36.5) μm, mean = 28.0 μm × 20.1 μm, Q = (0.86–)0.92–2.04(–4.50), mean Q = 1.48; subterminal cells mainly narrow cylindrical, short and small cells (shorter than 10 μm) occasional, branched or not, measuring (2.0–)7.5–31.0(–58.5) μm × (3.5–)4.0–19.0(–24.0) μm, mean = 19.4 μm × 8.4 μm. Pileipellis elements near the pileus centre very similar to those near the margin, terminal cells of hyphae measuring (15.0–)19.0–33.5(–47.0) μm × (12.0–)14.0–24.5(–35.0) μm, mean = 26.0 μm × 19.4 μm, Q = (0.83–)1.04–1.70(–2.70), mean Q = 1.37. Pileus trama of interwoven hyphae 3–15 μm wide, subparallel, irregularly inflated and often branched. Caulocystidia in dense fascicles, thin-walled, usually ascending or erect, clavate or cylindrical, obtuse, flexuous and often also moniliform, with terminal cells measuring (10.0–)20.0–40.5(–61.5) μm × (3.5–)4.0–7.0(–9.5) μm, mean = 33.3 μm × 5.4 μm. Trama of stipe parallel, unbranched hyphae 5–10 μm wide, composed of cells often shorter than 30 μm and rarely longer than 100 μm. Stipe trama hyphae 2–11 μm wide, parallel, composed of cells 20–100 μm long. Clamp connections absent in all tissues.

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

Commentary: This study gives clear molecular and morphological arguments for the placement of Hy. subfuscescens in the Ho. micaceus 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 Ho. 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 Ho. micaceus (Printz and Læssøe 1986). Based on morphological observation of the type specimens of both Ho. subfuscescens varieties, Kovalenko et al. (2012) considered the species as very similar to Ho. micaceus in all characteristics except for the more globose basidiospores of the former. Our phylogenetic analyses suggest Ho. subfuscescens is different from European Ho.
micaceus collections and also from other North American recognized species within the Ho. micaceus superclade. The morphological distinction from Ho. foetens superclade members, i.e., other species with unpleasant odours, 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 (including all known North American Hodophilus species), used pileipellis structure (that is, the anatomical makeup of the pileus cuticle) as the basic characteristic for species classification. Hygrophorus peckianus and Hy. paupertinus, both having a trichoderm type of pileipellis, were classified in Hygrophorus sect. Camarophyllopsis Hesler & Smith and Hy. foetens and Hy. subfuscens var. odora with a hymeniderm (or in some places of the book interpreted as epithelium) type of pileipellis in Hygrophorus sect. Hygrotrama (Singer) Hesler & Smith. Among our studied material of collections with naphthalene odours, which includes types of the above mentioned taxa, all collections have inflated broadly clavate, sphaero-pedunculate, obpyriform, or inflated subterminal cells and subsequent cells) than the Hy. 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 Hy. peckianus and Hy. foetens (Table 1). Representatives of the Ho. paupertinus, Ho. hesleri, and Ho. smithii clades, together with the type of Ho. foetens, have terminal cells in the pileipellis near the pileus margin that are typically clavate, sphaero-pedunculate, or obpyriform, having a length:width ratio (Q) > 2. In contrast, the types of Hy. peckianus and Hy. subfuscens var. subfuscens and var. odora have a length:width ratio of the terminal cells near the pileus margin < 2 (1.67, 1.44, and 1.52 respectively). According to our morphological observations of European representatives of the Ho. micaceus superclade, and according to our type studies of related North American taxa (unpublished data), representatives of this group typically have shorter and broader (Q ≤ 2) terminal cells in the pileipellis. According to our observations, odourless members of the Ho. micaceus superclade typically have 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 Ho. 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. The species is re-described above, and combined in the genus Hodophilus.

The phylogenetic tree also clearly demonstrates that Hy. subfuscens var. odora is very different from other North American Hodophilus samples with naphthalene odours. Because of the close sequence identity with the typical variety, the variety ‘odora’ 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 Hy. peckianus is unknown, owing 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 Hy. peckianus type specimen that distinguish it from both unidentified clades but also from the type of Hy. foetens; length:width ratios of terminal cells in the pileipellis near the pileus margin and the pileus centre are less than 2 (Table 1; Fig. 8) and subterminal cells are often inflated. Based on the pileipellis structure of the type specimen, Hy. peckianus is re-described here as a distinct species of the genus Hodophilus in addition to Ho. paupertinus and two other new Hodophilus species with naphthalene odours. Because of the lack of small subterminal cells (Fig. 8) we expect that Hy. peckianus is member of the Ho. 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 Ho. 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 Ho. hesleri and Ho. smithii. The first is distinguished from other studied members of the Ho. 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 for terminal cells in pileipellis 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 for terminal cells in pileipellis near the pileus centre (on average between 2.77 and 3.17) (Table 1).

Importance of field characteristics

Hesler and Smith (1963) used several field characteristics to recognize four North American taxa with strong unpleasant odours: pileus and lamellum colour, width of lamellae, surface texture of the stipe and the pileus, and the odour of basidiomata. All of these characteristics 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 odour such as reported for Hy. foetens by Hesler and Smith (1963) nor Isabella or olive-buff colours such as reported by them for Hy. paupertinus and Hy. subfuscescens var. odora. The lamellae of both new species are grey brown, which probably corresponds to the pallid lamellae of Hy. peckianus and Hy. paupertinus. The odour of both new species is somewhat variable, naphthalene mixed with a farinaecous, 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 Ho. subfuscescens var. odora seems to be useful, which is described as distinctly disagreeable when bruised. In our experience, with both new species, their odours were so strong that they could be located among leaves even before having seen them. Hesler and Smith defined the lamellar width as specifically “very narrow” in Hy. paupertinus, which may correspond to the width of the lamellae of Ho. hesleri and Ho. smithii (up to 1.5–2 mm). However, since no specific size of the lamellae is given, the importance of this characteristic needs to be verified. Possibly a good field characteristic might be darker dots on the upper part of the stipe of Ho. smithii, which are probably caused by dark incrusted pigments on the caulocystidia. Hesler and Smith also reported the presence of a scabrous-dotted stipe surface (with no mention of darker colour), but only for American collections of Hy. foetens.

Ecology

In the North American literature (e.g., Hesler and Smith 1963), the ecology of Hodophilus taxa with unpleasant odours is defined very generally, most frequently in woods and on bare soil, often under bracken ferns. The only mention of grassland is associated with Hy. 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 (MB10052013-02), but this was surrounded by a forest in close proximity. In Europe, the reports of Ho. 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, shrubs, high grass) in combination with 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 clavariae Clavariaceae and with Hygrocybe species. Most of our North American collections are from riverbanks, roadsides, and embankments next to trails, whereas our European collections are mainly from lawns and high grass on forest/pasture margins.

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