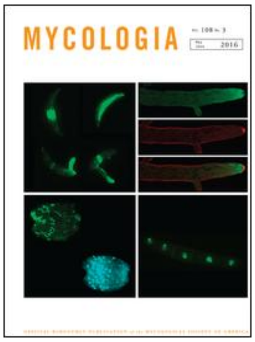

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Identifying and naming the currently known diversity of the genus *Hydnum* with an emphasis on European and North American taxa

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ABSTRACT

In this study 49 species of *Hydnum* are recognized worldwide. Twenty-two of them are described here as new species. Epitypes are proposed for *H. repandum* and *H. rufescens*. The majority of the species are currently known only from a single continent. The barcodes produced in this study are deposited in the RefSeq database and used as a basis to name species hypotheses in UNITE. Eleven infrageneric clades recovered in a phylogenetic analysis are supported by morphological characteristics and formally recognized: subgenera *Albi*, *Hydnum, Pallidi*, and *Rufescentes*; sections *Hydnum*, *Olympici*, *Magnorufescentes*, and *Rufescentes*; and subsections *Mulsicolores, Rufescentes*, and *Tenuiformia*.

KEY WORDS: Cantharellales, commercial mushrooms, cryptic species, EcM, fungal diversity, ITS, type specimens, 29 new taxa, 2 new typifications

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INTRODUCTION

In recent years the application of molecular methods has revolutionized our view of fungal species diversity. In many fungal genera, even in presumably well-known ones, new species have been revealed, not only in the tropics, but also in the supposedly intensively researched boreal and temperate areas of Europe and North America. This has led to a situation where we are not able to describe species with the same speed as which they are found. Scientific names, however, are urgently needed for unambiguous communication and delivery of information (Hibbett et al. 2011; Kõljalg et al. 2013, 2016; Hibbett 2016). Furthermore, the interpretation and application of previously described names are often problematic. Molecular studies of type specimens and the designation of epi- and neotypes are also needed to clarify which species already have been named and which ones should be described as new.

Hydnum L., the focal group of this study, is a genus in the Cantharellales Gäum with a worldwide distribution. Although species presumably number in the dozens, only 12 are currently recognized (Feng et al. 2016). All species are ectomycorrhizal with trees such as members of the Pinaceae and Fagales. *Hydnum* species typically produce white to brownish orange basidiomata with spinose hymenophores. Collected and consumed by humans for centuries, they are popularly called “hedgehogs”, “sweet tooth”, or “wood urchins”.

In Europe three species — *H. albidum* Peck, *H. repandum* L., and *H. rufescens* Pers. — have been traditionally recognized. Of these, *H. albidum* can easily be recognized by the small subglobose basidiospores, but identification of *H. repandum* and, especially, *H. rufescens* has sometimes been challenging due to variable morphological characters and lack of knowledge of the true diversity of the genus. Typically large fleshy basidiomata with whitish to orange ochraceous pilei and decurrent spines have been identified as *H. repandum* and more slender deeper orange basidiomata as *H. rufescens*.

The molecular detection of several distinct RFLP restriction patterns in *Hydnum* samples by Agerer et al. (1996) implied there were more species of *Hydnum* in Europe than previously assumed. Subsequently, Ostrow and Beenken (2004) described a new species, *H. ellipsosporum* Ostrow & Beenken, based on morphological and nuc rDNA ITS1-5.8S-ITS2 (ITS barcode) data. Based on basidiospore characteristics, Huhtinen and Ruotsalainen (2006) suggested the presence of *H. umbilicatum* Peck in Europe, a hypothesis earlier postulated by Maas Geesteranus (1976) and Ryman and Holmåsen (1984).

A more thorough molecular study of European *Hydnum* species by Grebenc et al. (2009) identified 10 clades from Europe: *H. albidum*, *H. ellipsosporum*, two *H. repandum*-like species (RE1, RE2), and six *H. rufescens*-like species (RU1–RU6). However, the presence of *H. umbilicatum* was not confirmed in Europe, while a specimen from Oregon (USA) stood out as a distinct species in the phylogenetic tree. Although *H. albidum* is described from North America, all collections ascribed to this species were from Europe. Olariaga et al. (2012) later recognized the same 11 species but incorporated four others in their phylogeny: *H. albomagnum* Banker from eastern North America, *H*. aff. *ellipsosporum* from Europe and North America, and *H*. aff. *vesterholtii* and *H. ovoideisporum* Olariaga et al. from Europe. Furthermore, clade RE2 was described as *H. vesterholtii* Olariaga et al. (Grebenc et al. 2009). More recently Vizzini et al. (2013), who studied the *H. rufescens*-like species in Italy, described a new species, *H. magnorufescens* Vizzini et al. corresponding to clade RU3 of Grebenc et al. (2009). Only two studies include material from areas outside of Europe and North America. Yanaga et al. (2015), who studied the white species of *Hydnum* in Japan, recognized three species: *H. albomagnum*, *H.*

repandum, and *H. minum* Yanaga & N. Maek. Feng et al. (2016) recognized at least 31 species worldwide, among which about half were sequenced for the first time. They found that most species from Australasia, including the Australasian *H. crocidens* Cooke and *H. elatum* Massee, differed substantially from Northern Hemisphere species. Based on analysis of three loci (nrLSU, *rpb*1, *tef*1), Feng et al. (2016) also discovered four well-supported clades within *Hydnum*, namely /Albomagnum, /Vesterholtii, /Rufescens, and /Repandum.

The process of naming species is mainly hampered by two factors: i) descriptions, as traditionally done, are time consuming, and ii) molecular analysis of type materials is needed for verifying already described species. Furthermore, neotypes should be chosen for "old" names without type material, or epitypes designated for those with uninterpretable holotypes or lectotypes. Grebenc et al. (2009) and Olariaga et al. (2012) considered the clades recovered in their phylogenetic analysis as species. However, since the identity of the names *H. rufescens* and *H. repandum* was unclear (and no adequate morphological data from all the species were available), the species remained unnamed. Furthermore, morphological characteristics suitable for species identification in *Hydnum* are few: mainly pileus color and robustness of the basidiomata, presence of a depression on the pileus, form and attachment of the spines, and size and shape of basidiospores. Morphological characters overlap between species, especially in the *H. rufescens* complex, making morphological recognition difficult or impossible.

The aim of this study is to evaluate the taxonomy of *Hydnum* based on ITS and morphological data. We also want to stabilize the European names by proposing epitypes for *H. repandum* and *H. rufescens* and to describe the remaining species as new. Furthermore, we provide an infrageneric classification of the genus to serve as a framework for future studies.

MATERIALS AND METHODS

Morphological studies.—The morphological descriptions of the species are based on notes taken from fresh collections, associated photographs, and fungarium specimens, or in the case of *H. cremeoalbum*, *H. mulsicolor*, *H. repando-orientale,* and *H. slovenicum* on previously published descriptions of the holotype specimens and other sequenced materials. In the latter case the materials have not been studied by us, but the original source of information is cited (see TAXONOMY), and the fungaria LJF and TUMH have been informed that their specimens are selected as type materials. The specimens from LJF were not available for loan at the time of this study. Color notations in the descriptions of *H. zongolicense* follow Kornerup and Wanscher (1978). Basidiospores and basidia were observed from dried material mounted in 10% KOH, although lactic acid and Melzer's reagent were tested for some specimens. Twenty basidiospores were measured from the spines of each basidioma discarding the smallest (presumably immature) basidiospores. Length and width were recorded, and length/width ratios (Q value) were calculated. Numbers in parentheses represent outliers. Herbarium acronyms follow Thiers [continuously updated]. The (M) after TU and K refers to the mycology collections of those herbaria.

DNA extraction, PCR amplification and sequencing.—46 ITS sequences from 18 species were produced for this study. DNA was extracted from dried material (spines) with the NucleoSpin Plant kit (Macherey-Nagel, Düren, Germany). Primers ITS1F and ITS4 (White et al. 1990; Gardes and Bruns 1993) were used for amplification and direct sequencing. Polymerase chain reaction amplification and sequencing followed Liimatainen et al. (2014).

Data analyses.—Sequences were assembled and edited with SEQUENCHER 4.1 (Gene Codes, Ann Arbor, Michigan). We combined our own sequences with published *Hydnum* sequences in the phylogenetic analysis. The published sequences were obtained through PLUTOF (Abarenkov et al. 2010b) and included all sequences of good quality over 400 bp long from the UNITE database (Abarenkov et al. 2010a) and GenBank (http://www.ncbi.nlm.nih.gov). Identical sequences from the same geographical region (country, or in USA/Canada states or provinces/territories) were excluded. Also most Australasian species (including *H. crocidens* Cooke and *H. elatum* Massee) were excluded because Feng et al. (2016) showed they were distinct from Northern Hemisphere species and impossible to analyze together with other ITS sequences of the genus. *Sistotrema muscicola* (GenBank nos. AJ606040 and AJ606041) was chosen as outgroup species following Olariaga et al. (2012), and sequences of six other closely related species were also included in the analysis. The 132 ITS sequences were aligned with the program MUSCLE (Edgar 2004) under default settings. The ITS alignment was manually adjusted in SEAVIEW (Galtier et al. 1996). The alignment comprised 695 nucleotides (including gaps) and is available at TreeBASE under S21634 (http://www.treebase.org/treebase-web/home.html). Sequences were subjected to Maximum Likelihood (ML) analysis as implemented in RAXML 8 (Stamatakis 2014) with 1000 bootstrap replicates using the GTRGAMMA model as recommended by the manual.

Genetic differences within and between species were calculated by dividing the number of differences (indels and/or substitutions) found in the ITS1+5.8S+ITS2 regions by the length of the region (about 560–590 bases long).

RESULTS

***Molecular analysis*.**—The phylogenetic tree resulting from the analysis of the ITS region is shown in FIG. 1. Our phylogenetic analysis recovered the same main groups as in Feng et al. (2016), although the support values in their study were significantly higher probably because sequences from three different loci were used for the analysis. The groups supported were (BS value from our analysis / PP value from Feng et al. (2016)): *Hydnum* subg. *Albi* (52%/1.00, as /Albomagnum), *H.* subg. *Hydnum* (67%/1.00 as /Repandum), *H.* subg. *Pallidi* (79%/1.00 as /Vesterholtii), and *H.* subg. *Rufescentes* (100%/1.00 as /Rufescens). Within *H.* subg. *Rufescentes* no clades were marked in the phylogenetic tree of Feng et al. (2016), but the groups we currently recognize received the following support values: *H.* sect. *Magnorufescentes* (75%/1.00), *H.* sect. *Rufescentes* (79%/0.99), *H.* subsect. *Rufescentes* (93%/1.00), *H.* subsect. *Tenuiformia* (68%/1.00) and *H.* /Ovoideispori (100%/1.00). In addition we recognize *H.* subsect. *Mulsicolores* (89%) and *H.* sect. *Olympici* (100%) and not included in Feng et al. (2016). These authors, however, found several other well supported Australasian groups not represented in our tree. All the groups mentioned above are also supported by morphological characters. The recognized groups are described as new taxa (see TAXONOMY) except *H.* /Ovoideispori of which only two species are currently known.

In all species the intraspecific variation is smaller (< 0.5%) than the interspecific variation (at least 1%, in many species > 1.5%) when only including sequences with available chromatograms from which the differences could be reliably confirmed. They also received over 90% BS in our analysis, and most species also had distinguishing morphological characteristics. We recognize four species that do not fulfill all the criteria above, namely *H. repandum*, *H. ovoideisporum*, *H.* cf. *umblicatum*, and *H. melitosarx*.

In the first case, closely related sister species, *H. neorepandum, H. boreorepandum,* and *H. repando-orientale*, each form a monophyletic group with over 90% BS, while *H. repandum* itself remains a paraphyletic lineage (FIG. 1). In all of these four species, however, the intraspecific variation (< 0.5%) is clearly smaller than the interspecific one (1%), and three of the four species can also be distinguished based on morphology and/or distribution pattern. Also, treating these as one species would lead to very large morphological and genetic variation within one species, which is not in line with the other *Hydnum* groups treated here. Therefore, we consider them as four separate species.

In the second case, two sister species *H. ovoideisporum* and *H. subovoideisporum* were not separated in the phylogenetic analysis (FIG. 1) despite an interspecific distance over 1.5% and differences in morphology and ecology. Here about 60% of the differences between the ITS sequences are indels, which may explain why the *H. ovoideisporum* clade was poorly recovered in the ML analysis, which only counts base changes unless indels are separately coded in another matrix.

The third case is *H.* cf. *umbilicatum* where the infraspecific variation (> 2%) is greater than in other *Hydnum* species, and our phylogenetic analysis supported some subclades (FIG. 1). These nested groups are also somewhat supported by the morphology and distribution patterns. Because the differences are not clear enough to separate the different taxa, we here treat *H.* cf. *umbilicatum* as one species that is morphologically clearly separated from a sister species, *H. ellipsosporum*. Lastly, although the infraspecific variation of *H. melitosarx* s. l. is also high (> 1%), we could not make further divisions at this time due to the sparse materials from North America.

We do not describe some of the unnamed taxa of the 49 recognized ones for the following reasons: i) because the ITS sequence originates from an environmental sample and lacks a voucher specimen to serve as a type, it cannot be described as new per the International Code of Nomenclature for algae, fungi, and plants (ICN); ii) the ITS sequence is either too short or of poor quality, thus re-sequencing is needed; iii) the number of differences in the ITS region in relation to the closest sister species is so small that more materials and/or more DNA regions should be sequenced to establish the species limits; iv) the identity of *H. crocidens* and *H. elatum* should be clarified before describing more species from Australia; and finally, v) Feng et al. (pers. comm.) intend to describe the majority of the nameless taxa at a future date.

After excluding species belonging to any category listed in the previous paragraph 32 species remain. Five of these have a name that is verified based on an ITS sequence from holotype materials. Epitypes are proposed for two old names, *H. repandum* and *H. rufescens.* Three old names from North America—*H. albidum*, *H. albomagnum,* and *H. umbilicatum*—are applied without having a sequence from a type specimen for comaprison and therefore referred to as "cf." or "fide" awaiting further study. The remaining 22 species are here described as new.

TAXONOMY

Only the type or a representative specimen of each species is listed below. Additional materials are reported in SUPPLEMENTARY FILE 1.

Hydnum L., Sp pl 2:1178. 1753.

Sanctioning citation: Fr., Syst Mycol 1:397. 1821.

Type species: *Hydnum repandum* L. 1753.

Description: Basidiomata small, medium, or large (pileus 15–120(–200) mm diam). Pileus whitish to orange to brownish orange. Stipe whitish to very pale yellowish brown, staining yellowish to orange-brown when handled. Spines not decurrent or decurrent. Basidiospores globose, subglobose, broadly ovoid, or ellipsoid, smooth, thin-walled, hyaline, inamyloid. Basidia stichic. Clamp connections present. Ectomycorrhizal.

Currently included subgenera: *Albi*, *Pallidi, Hydnum*, and *Rufescentes*, presented below in this order reflecting the diversity of the group (smallest groups first) and morphological similarity.

Notes: Most species from Australasia were excluded from our study because Feng et al. (2016) showed that they were distinct from the Northern Hemisphere species and impossible to analyze together with other ITS sequences of the genus. Further studies are needed to clarify how many new subgenera the omitted taxa would represent.

Hydnum subgen. *Albi* Niskanen & Liimat., subgen. nov. FIGS. 2, 3

IndexFungorum: IF553874

Type species: *Hydnum cremeoalbum* Liimat. & Niskanen

Etymology: *Albi* (L.), referring to the nearly white color of the basidiomata.

Description: Basidiomata small to large (pileus 20–80(–200) mm diam). Pileus whitish to cream-colored. Stipe often short, <40 mm long, whitish at first, staining yellowish when handled. Spines not or somewhat decurrent. Basidiospores globose, subglobose to broadly ovoid or ellipsoid, very small to small, on av. <7 × 7 μm, Q av.=1.00–1.10. Known from Eurasia, North America, and Oceania (Papua New Guinea).

Currently included species: *H. albomagnum* fide Matheny et al. (2007), *H. albidum ss*. Grebenc et al. (2009), *H. cremeoalbum,* and *H. subcremeoalbum*. Also the following species with similar morphology but unresolved phylogenetic position are here treated as *H.* subg. *Albi s. l.*: *H. treui*, *H. minum,* and *H. zongolicense*. Furthermore, *H. neoguineense* Henn. 1894 may also belong in to this section.

Notes: *H. albomagnum* Banker and *H. albidum* Peck were both described from the United States. Based on the original descriptions and currently available ITS sequence data, these species would seem to fit in the subgenus *Albi*. Also Papua New Guinean *H. neoguineense* may belong to this subgenus based on the original description. Type material of these species, however, has not been studied, and further studies and/or typifications are needed before making final conclusions.

The species in *H.* subg. *Albi* resemble those in *H.* subg. *Pallidi* and *H.* subg. *Hydnum*, and those in the *H.* sect. *Magnorufescentes* (subg. *Rufescentes*), which all include whitish to cream-colored species. The species in *H.* subg. *Albi*, however, are easily characterized by basidiospore size and shape; in *H.* subg. *Pallidi*, *H.* subg. *Hydnum*, and *H.* subg. *Magnorufescentes*, the basidiospores are larger and in most cases also relatively longer (Q av. value > 1.15 in *Pallidi* and *Hydnum* and 1.06–1.13 in *Magnorufescentes*).

Hydnum cremeoalbum Liimat. & Niskanen, sp. nov.

IndexFungorum: IF553875

Typification: JAPAN. TOTTORI: Tottori City, Kokoge, under *Quercus myrsinifolia* in mixed forest, 27 Oct 2010, *E. Nagasawa 60740* (**holotype** TUMH 60740). GenBank: ITS=AB906678.

Etymology: cremeoalbum (L.), in reference to the color of the basidiomata.

Misappl.: *H. albomagnum* ss. Yanaga et al. Mycoscience 56:438. 2015.

Illustrations: Yanaga et al. (2015: 437)

Description (from Yanaga et al. 2015): Pileus 30–70 mm diam, whitish. Stipe 25–35 × 15–30 mm whitish. Spines not or slightly decurrent. Basidiospores 5–7 × 3.5–5.5 um, broadly ellipsoid. Basidia 24–40 × 4–9 um, with (4–)5 sterigmata. ITS (AB906678) unique within *H.* subg. *Albi*; sister to *H. subcremeoalbum* (UNITE UDB013289), which deviates in the ITS region by at least five substitutions and indel positions.

Ecology and distribution: In mixed forests with *Quercus myrsinifolia*. Producing basidiomata in autumn. Asia (China, Japan).

Notes: *Hydnum cremeoalbum* is most similar to its sister species *H. subcremeoalbum*, which is distinguished by somewhat broader basidiospores (5.5–6.0 × 4.7–5.5 µm) and occurrence in Papua New Guinea in association with *Castanopsis acuminatissima*.

The species was initially called *H. albomagnum* in Yanaga et al. (2015), a species originally described from the United States. Since *H. cremeoalbum* occurs in Asia and our phylogeny does not support shared species between North America and Asia in *H.* subg. *Albi,* we here describe the species as new.

Hydnum subcremeoalbum Tedersoo, Liimat. & Niskanen, sp. nov. FIG. 3A

IndexFungorum: IF553876

Typification: PAPUA NEW GUINEA. EASTERN HIGHLANDS: Lutave, 2133 m elev, in undisturbed *Castanopsis acuminatissima* forest, *L. Tedersoo* (**holotype** TU110688). UNITE: ITS=UDB013289.

Etymology: *subcremeoalbum* (L.), indicating the close relationship to *H. cremeoalbum*.

Description: Basidiomata small to medium. Pileus 40 mm diam, at first convex, later more or less plane with somewhat incurved margin, surface whitish to cream-colored. Stipe 25 mm long, 6 mm diam. at apex, cylindrical, whitish, becoming more yellowish when bruised. Spines somewhat decurrent, crowded, acute, whitish. Basidiospores 5.5–6.0 × 4.7–5.5 µm, av.=5.6 × 5.2 µm, Q=1.04–1.17, Q av.=1.09, globose to subglobose, thin-walled. Basidia 33–40 × 5.7–7.0 µm, 4- or 5-spored, sometimes 6-spored, sterigmata 4–5.5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, hyaline, with cylindrical ends 2.5–3.5 µm diam. ITS sequence (UNITE

UDB013289) unique within *H.* subg. *Albi* and sister to *H. cremeoalbum* (AB906678), from which the ITS region deviates by at least 5 substitutions and indel positions.

Ecology and distribution: In *Castanopsis acuminatissima* forests. Oceania (Papua New Guinea).

Notes: *Hydnum subcremeoalbum* is most similar to *H. cremeoalbum*, which differs by the somewhat narrower basidiospores (5–7 × 3.5–5.5 µm), distribution in Japan, and association with *Quercus*. *Hydnum treui*, another species of *H.* subgenus *Albi s. l.* that occurs in Papua New Guinea, is easy to distinguish from *H. subcremeoalbum* by having larger spores (av.=6.3 × 6.1 µm). A third potential species in the *H.* subgenus *Albi*, *H. neoguineense*, has, based on the original description (Hennings 1894), whitish yellow pileus, and very small spores 3–4 µm. Further studies are needed to clarify the identity of this species.

Hydnum treui Tedersoo, Liimat. & Niskanen, sp. nov. FIG. 3B

IndexFungorum: IF553877

Typification: PAPUA NEW GUINEA. CENTRAL PROVINCE: Varirata National Park, Varirata Gare's lookout, 885 m a.s.l., subtropical/tropical moist *Castanopsis acuminatissima*-dominated ridge forest, *L. Tedersoo* (**holotype** TU110403). UNITE: ITS=UDB013043.

Etymology: *treui* (L.), in honour of Ronald Treu for his pioneer work on the fungi of Papua New Guinea.

Description: Basidiomata small (to medium). Pileus 30–35 mm diam, at first convex, later more or less plane with somewhat incurved margin, surface whitish. Stipe 15–20 mm long, 4–5 mm diam at apex, cylindrical to somewhat narrower towards the base, whitish. Spines non-decurrent, crowded, acute, whitish. Basidiospores 5.5–7.0 × 5.5–7.0 µm, av.=6.3 × 6.1 µm, Q=1.00–1.08, Q av.=1.04, globose to subglobose, thin-walled. Basidia 35–42 × 6.0–7.0 µm, 4-

spored, sterigmata 2.5–3.5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, yellowish, with cylindrical or some with clavate ends 3–4.5 µm diam. ITS sequence (UNITE UDB013043) unique within *H.* subg. *Albi;* sister to *H. zongolicense* (KC152121, holotype), which deviates in the ITS region by 14 substitutions and indel positions.

Ecology and distribution: In tropical forests. Oceania (Papua New Guinea).

Notes: The two species of *Hydnum* subg. *Albi s. l.* known from Papua New Guinea can be distinguished by basidiospore size: *H. subcremeoalbum* has smaller basidiospores on average (av.=5.6 × 5.2 µm) than *H. treui* (av.=6.3 × 6.1 µm). A third potential species in the *H.* subgenus *Albi* from Papua New Guinea, *H. neoguineense*, has, based on the original description (Hennings 1894), whitish yellow pileus, and very small spores 3–4 µm, but further studies are needed to clarify the identity of this species.

Hydnum zongolicense Garibay-Orijel, sp. nov. FIGS. 2A, 3C

IndexFungorum: IF553878

Typification: MEXICO. VERACRUZ: State road 123, 5 km from Zongolica to Texhuacan, in subtropical moist mixed forest with *Pinus patula*, *Liquidambar styraciflua*, *Quercus* spp., and *Alnus acuminata* on chromic luvisol, 1 Sep 2010, *Garibay-Orijel-2010-142a* (**holotype** MEXU 26248). GenBank: ITS=KC152121.

Etymology: *zongolicense* (L.), in reference to Zongolica, the municipality where it was collected.

Description: Basidiomata small to medium. Pileus 17–35 mm diam, fleshy, initially plane-convex, afterward depressed in the center, margin incurved, somewhat sinuous and lobed; surface velutinous, slightly rugulose; white to whitish orange (5A2), whitish yellow (3A2) toward the margin, staining salmon (6A3) or reddish orange (7A7); when dry, whitish yellow

(4A3). Stipe 40–64 × 10–14 mm, wider at the base to slightly radicate, central or somewhat eccentric, solid, smooth, white (3A1), staining whitish yellow (3A2) when handled; when dry, whitish yellow (4A3) to orange (6B8). Spines subdecurrent, ending with small decurrent spines, conical to cylindrical, not flattened, acute, not fimbriate, crowded, 0.5–2 × 0.1– 0.3 mm, initially white (6A1), as a whole pale salmon (6A2), staining whitish yellow (3A2), when dry orange (6B8). Context white (3A1), staining light brown (6C4) at the apex. Odor weak, sweet. Taste not distinctive. Basidiospores (6–)6.5–7.5(–8) × (6–)6.5–7(–8) µm, av.=6.9 × 6.8 µm, Q=0.92–1.08, Q av.=1.00, globose to subglobose, thin-walled. Basidia (20–)35–45(–53) × (3–)6–7(–10) µm, mostly 2- or 4-spored, sometimes 3- or 5-spored, sterigmata 3–5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, hyaline, with cylindrical ends 2.5 µm diam. ITS sequence (KC152121) distinct within *Hydnum* subg. *Albi*. Sister to *H. treui* (UNITE UDB013043, holotype) and deviating from it in the ITS region by 14 substitutions and indel positions.

Ecology and distribution: In subtropical mixed forests. Central America (Mexico).

Notes: With its whitish to cream-colored basidiomata and globose to subglobose basidiospores, *H. zongolicense* is a typical representative of *H.* subg. *Albi*. Its sister species *H. treui* occurs in Papua New Guinea and has smaller basidiospores (av.= 6.3 × 6.1 µm).

Hydnum subgen. *Pallidi* Niskanen & Liimat., subgen. nov. FIG 2, 3

IndexFungorum: IF553879

Type species: *Hydnum vesterholtii* Olariaga, Grebenc, Salcedo & M.P. Martín, Mycologia 104:1449. 2012.

Etymology: *Pallidi* (L.), referring to the pale color of its species.

Description: Basidiomata small to medium (pileus 15–30(–50) mm diam). Pileus whitish ochraceous to cream-colored to ochraceous with very pale orange tints. Stipe at first whitish, staining pale brownish orange when handled. Spines not or somewhat decurrent. Basidiospores ovoid to broadly ellipsoid, Q value usually >1.25. Thus far only known from Eurasia.

Currently included species: *H. vesterholtii* and *H. ibericum*. In addition, several undescribed species are known from China.

Notes: Species of subgenus *Albi* are most similar to species of subgenus *Pallidi*, but *H.* subg. *Albi* species have small globose to subglobose basidiospores (on av. <7 × 7 µm, Q av. value usually 1.00–1.10). Some species of *H.* subg. *Hydnum* and *H.* sect. *Magnorufescentes* (*H.* subg. *Rufescentes*) are also whitish, but the basidiomata are usually larger and basidiospores relatively shorter (Q av. 1.06–1.20).

Hydnum ibericum Olariaga, Liimat. & Niskanen, sp. nov.

IndexFungorum: IF553880

Typification: SPAIN. HUESCA: Villanúa, Fuente el Paco, under *Abies alba* and *Pinus sylvestris* on rich ground, 10 Oct 2006, *I. Olariaga* (**holotype** BIO:Fungi:12330). GenBank: ITS=HE611086.

Etymology: *ibericum* (L.), first found in the Iberian Peninsula.

=*Hydnum* aff. *vestertholtii* ss. Olariaga et al. Mycologia 104:1453. 2012.

Description: Basidiomata small to medium, with the stipe equal to or somewhat longer than pileus diameter. Pileus 22–30 mm diam, convex, sometimes depressed in the center, surface ocher with pale orange tints, especially in the center, nearly white at the margin in young basidiomata. Stipe 20–35 mm long, 5–8 mm diam at apex, cylindrical or with a slightly broader base, white to very pale ocher, slightly darker ocher when bruised. Spines usually decurrent, crowded, conical, acute, white to pale ocher. Basidiospores 7.5–8.5(9) × (5.5)6–7 µm, av. 8.2 × 6.4, Q av. 1.28, ovoid to broadly ellipsoid, thin-walled. Basidia 3- to 5-spored. Hyphae of the apex of the spines cylindrical, thin-walled, with clavate to cylindrical ends 3–4.5 µm diam. ITS sequence (HE611086) distinct from other species of subgenus *Pallidi*. Sister to *H. vesterholtii* (HE611087, holotype), which deviates by eight substitutions and indel positions.

Ecology and distribution: In coniferous forests (*Abies, Pinus*) and with *Castanea sativa*. Producing basidiomata in late autumn and winter. Europe (Spain).

Notes: This species was treated as *H.* aff. *vesterholtii* by Olariaga et al. (2012), who did not find distinct morphological characteristics for it. ITS molecular data, however, distinguish *H. vesterholtii* from *H. ibericum*. Furthermore, the holotype specimen of *H. ibericum* possesses pale orange tints unlike the typical material of *H. vesterholtii*. Additional *H. ibericum* collections should be checked to determine whether the presence of orange tones in the pileus is constant. At the moment, ITS sequence data are needed for reliable identification.

Hydnum subgen. *Hydnum* L. FIGS. 4, 5

Type species: Hydnum repandum L. 1753.

Description: Basidiomata medium to large (pileus (30–)40–110 mm diam), fleshy. Pileus whitish, cream-colored, ochraceous to orange ochraceous. Stipe at first whitish, staining brownish orange when handled. Spines non-decurrent to decurrent. Basidiospores subglobose to very broadly ellipsoid, usually ranging from roundish to more ellipsoid within one individual, 7–9.2 x 5.5–8 µm, Q av. value usually 1.15–1.20. Known from Eurasia and North and Central America.

Currently included sections: *Hydnum* and *Olympici*.

Notes: Whitish species of *H.* subg. *Hydnum* resemble species of subgenus *Albi* and *Pallidi,* and the whitish to orange ochraceous species are similar to those of subgenus *Rufescentes* section *Magnorufescentes.* The four groups can most easily be distinguished by the size and shape of the basidiospores. The species in subgenus *Albi* have small globose to subglobose basidiospores (av. <7 × 7 µm, Q av. value usually 1.00–1.10), and the species of subgenus *Pallidi* ovoid to broadly ellipsoid and relatively longer basidiospores (Q av. > 1.25). In addition, many species of subgenus *Albi*, and all of subgenus *Pallidi*, have small- to medium-sized basidiomata. The species of *H.* sect. *Magnorufescentes* have only subglobose basidiospores, and broadly ellipsoid basidiospores are not present (Q av. 1.07–1.13).

Hydnum sect. *Hydnum* L.

Type species: Hydnum repandum L. 1753.

Description: Basidiomata medium to large (pileus 40–110 mm diam), fleshy. Pileus whitish to pale ochraceous brown to orange ochraceous. Spines more or less decurrent, seldom non-decurrent. Stipe at first whitish, becoming pale brownish to orange ochraceous when scratched. Basidiospores subglobose to elongate subglobose, usually a range from roundish to more ellipsoid within one individual, Q av. usually 1.14–1.17.

Currently included species: *H. repandum*, *H. boreorepandum*, *H. neorepandum*, and *H. repando-orientale*. In addition some undescribed species from China belong here.

Notes: Species of *H.* sect. *Hydnum* are characterized by usually large fleshy basidiomata, whitish to orange ochraceous pilei, more or less decurrent spines, and subglobose to ellipsoid basidiospores. See also notes under *H.* subg. *Hydnum* on how to distinguish these species from those of *H.* subg. *Albi H.* subg. *Pallidi*, and *H.* sect. *Magnorufescentes*.

Hydnum repandum L., Sp pl 2:1178. 1753. FIGS. 4A, 5A

IndexFungorum: IF552885 (lectotype), IF553881 (epitype)

Sanctioning citation: Fr., Syst Mycol 1:400. 1821.

Typification: Sowerby (1799) Coloured Figures of English Fungi or Mushrooms, second volume: t. 176 (**lectotype** here designated). FINLAND. VARSINAIS-SUOMI: Turku, Ruissalo, Nature Reserve area near Botanical Garden, under *Pinus sylvestris*, near also *Quercus*, on dryish ground, 13 Sep 2008, *K. Liimatainen & T. Niskanen 08-098* (**epitype** H6003710, here designated, **isoepitype** K(M)248973). GenBank: ITS=KX388650.

Description: Basidiomata (medium) large, fleshy. Pileus 40–110 mm diam, at first convex, later more or less plane with somewhat incurved margin; surface cream-colored to orange ochraceous, usually paler towards the margin. Stipe 35–60 mm long, 7–14 mm diam. at apex, cylindrical to slightly clavate, sometimes with a pointed base, at first white, becoming pale ochraceous brown when bruised. Spines decurrent to somewhat decurrent, rarely non-decurrent, crowded, acute, or sometimes spathulate, cream-colored. Basidiospores 7.0–8.5 × 6.2–7.5 µm, av.= 7.8 × 6.8 µm, Q=1.08–1.25, Q av.=1.15, subglobose to elongated subglobose, thin-walled. Basidia 35–45 × 6–8 µm, 4-spored, sterigmata 3–6 µm long. Hyphae of spine apex cylindrical, thin-walled, hyaline to somewhat yellowish, with cylindrical to slightly clavate ends 2.5–5 µm diam. ITS sequence (KX388650) distinct within *H.* sect. *Hydnum*; sister to *H. boreorepandum* (KX388657, holotype), which deviates by five substitutions and indel positions.

Ecology and distribution: In *Picea abies* dominated forests mixed with *Betula, Pinus, Populus, Corylus,* and/or *Quercus*. Also in *Abies* and *Fagus* forests. Producing basidiomata late summer to late autumn. Europe. One sequence (JQ063050) from an ectomycorrhizal root tip of *Pakaraimaea dipterocarpacea* in Venezuela deposited in GenBank requires further confirmation given its extralimital distribution and host plant data.

Notes: *Hydnum repandum* is characterized by large, fleshy basidiomata, cream-colored to orange ochraceous pilei, decurrent to somewhat decurrent spines, and subglobose to elongated subglobose basidiospores. It is a rather common species currently verified only from Europe. The sister species *H. neorepandum* occurs in North America and *H. repando-orientale* in Japan. The two sympatric species in *H.* subgen. *Hydnum* that can be confused with *H. repandum* are *H. slovenicum* and *H. boreorepandum*. *Hydnum slovenicum* has orange ochraceous pileus but can be distinguished from *H. repandum* by smaller spores (av.=7.5 × 6.4 μm). *Hydnum boreorepandum* can be confused with the whitish basidiomata of *H. repandum* and for an unambiguous identification, an ITS sequence is needed.

Hydnum repandum was described by Linnaeus (1753) from Sweden. In northern Europe the name has consistently been used for the species presented here (e.g. Hansen and Knudsen 1997, Nylén 2001), and therefore we propose an epitype for the species, and also select a lectotype among the figures referred to by Fries in his sanctioning treatment (1821).

Hydnum boreorepandum Niskanen, Liimat. & Niemelä, sp. nov. FIGS. 4C, 5D

IndexFungorum: IF553882

Typification: FINLAND. VARSINAIS-SUOMI: Kisko, south of Lake Määrjärvi, Aitsaari, near the pond Vähä Myllylammi, in submesic coniferous (*Picea abies, Pinus sylvestris*) forest with some *Betula*, 16 Aug 2008, *K. Liimatainen & T. Niskanen 08-005* (**holotype** H6003711, **isotype** K(M)248974). GenBank: ITS=KX388657.

Etymology: *boreorepandum* (L.), for the affinity with *H. repandum* and distribution in the boreal zone.

Description: Basidiomata (medium) large, fleshy. Pileus 40–90 mm diam, at first convex, later more or less plane with somewhat incurved margin, surface cream-colored. Stipe 40–70 mm long, 6–14 mm diam at apex, more or less cylindrical, at first white, becoming pale ochraceous brown when bruised. Spines more or less decurrent, crowded, acute or sometimes spathulate, white to cream-colored. Basidiospores 7.0–8.5 × 6.2–7.5 µm, av.= 7.7 × 6.6 µm, Q=1.05–1.24, Q av.=1.16, subglobose to elongated subglobose to very broadly ellipsoid, thin-walled. Basidia 35–43 × 6.5–8.5 µm, 4- to 5-spored, sterigmata 3.5–5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, hyaline, with cylindrical to slightly clavate ends, 3–5.5 µm diam. ITS sequence (KX388657) unique within *H.* sect. *Hydnum* and sister to *H. repandum* (KX388650, neotype), which deviates by five substitutions and indel positions.

Ecology and distribution: In coniferous forests during autumn. Eurasia (Finland, Sweden, and China).

Notes: *Hydnum boreorepandum* is a white to cream-colored species that in the field can be confused with the whitish basidiomata of *H. repandum*. An ITS sequence is needed for unambiguous identification.

Maas Geesteranus (1959) described *H. heimii*, a species morphologically similar to *H. repandum*. The name was introduced as a nomen novum for *Sarcodon abietinus* R. Heim (nom. inval., Art. 39.1), originally described from France but without a Latin description. According to Geesteranus (1959) it differs from *H. repandum* by the olivaceous color at the center of the pileus, a pileus surface that becomes viscid when moist, longer spines, and narrower basidiospores. Typification follows Heim, however, Maas Geesteranus never saw the type specimen but studied a specimen collected at the type locality in 1953. Elements in the description of *H. heimii*, including narrower basidiospores and similarity to *H. repandum*, match *H. boreorepandum*, but the olivaceous coloration and a viscid pileus are not in concordance with our observations. Also we do not have materials of *H. boreorepandum* from France or adjacent areas. Therefore, we describe *H. boreorepandum* as new. *Hydnum heimii* is not discussed here more in detail and more studies are needed to clarify its identity.

Hydnum neorepandum Niskanen & Liimat., sp. nov. FIGS. 4D, 5C

IndexFungorum: IF553883

Typification: CANADA. NEWFOUNDLAND AND LABRADOR: west coast, Gros Morne National Park, north end of the Bonne Bay's eastern Arms, James Callaghan hiking trail to Gros Morne mountain, in mesic to moist *Abies balsamea* dominated forest with some *Picea*, *Alnus* and *Betula*, 18 Sep 2010, *K. Liimatainen & T. Niskanen 10-095* (**holotype** H7043726, **isotype** K(M)248975, **isotype** NY). GenBank: ITS=KX388659.

Etymology: *neorepandum* (L.), for the affinity with *H. repandum* and distribution in the New World.

Description: Basidiomata (medium to) large, fleshy. Pileus 40–110 mm diam, at first convex, later more or less plane, sometimes with incurved margin, surface cream-colored, sometimes with an orange tint. Stipe 30–50 mm long, 9–14 mm diam at apex, more or less cylindrical, at first white, becoming pale ochraceous brown when bruised. Spines more or less decurrent, crowded, acute, white to cream-colored. Basidiospores 6.8–8.0 × 6.0–7.2 μm, av.= 7.5 × 6.5 μm, Q=1.06–1.24, Q av.=1.16, subglobose to elongated subglobose, some broadly ellipsoid, thin-walled. Basidia 35–42 × 7.0–8.2 μm, 4- to 5-spored, sterigmata 3.5–5 μm long. Hyphae of the apex of the spines cylindrical, thin-walled, hyaline, with cylindrical to slightly clavate ends 3.5–5.5 μm diam. ITS sequence (KX388659) unique within *H.* sect. *Hydnum* and sister to *H. repandum* (KX388650, epitype), which deviates by seven substitutions and indel positions.

Ecology and distribution: With coniferous trees (*Abies, Picea, Pinus*). Producing basidiomata in autumn. Eastern and western North America (Newfoundland and Labrador, California).

Notes: *Hydnum neorepandum* is currently the only known member of *H.* sect. *Hydnum* that occurs in North America. It resembles the European *H. repandum*, but the basidiospores are slightly smaller (av.= 7.8 × 6.8 µm in *H. repandum*). The pileus is usually cream-colored with an orange tint. The brighter ochraceous orange colors found on some basidiomata of *H. repandum* are lacking.

Hydnum repando-orientale Liimat. & Niskanen, sp. nov.

IndexFungorum: IF553884

Typification: JAPAN. TOTTORI: Saihaku-gun, in broad-leaved forest (*Fagus crenata, Quercus serrata, Quercus crispula*), 2 Oct 2010, *K. Yanaga 60745* (**holotype** TUMH60745). GenBank: ITS=AB906683.

Etymology: repando-orientale (L.), for the affinity with *H. repandum* and distribution in Asia.

Misappl.: *H. repandum* var. *album* ss. Yanaga et al. Mycoscience 56:438. 2015.

Illustrations: Yanaga et al. (2015: 437)

Description (according to Yanaga et al. (2015)): Pileus 40–70 mm diam, whitish to pale cream. Stipe 30–75 mm long, 10–30 mm wide, whitish. Pileus and stipe becoming slowly pale yellowish brown when scratched. Spines whitish, non-decurrent to decurrent. Basidiospores 7–9 × 5.5–8 µm. ITS sequence (AB906683) unique within *H.* sect. *Hydnum* and deviating from other species in the section by a minimum of eight substitutions and indel positions.

Ecology and distribution: In broad-leaved forests with *Fagus crenata, Quercus serrata*, and *Quercus crispula*. Producing basidiomata in autumn. Asia (Japan).

Notes: This whitish species occurring in east Asia is most easily distinguished from other members of *H.* sect. *Hydnum* by distribution and ITS sequence.

Hydnum sect. *Olympici* Niskanen & Liimat., sect. nov.

IndexFungorum: IF553885

Type species: *Hydnum olympicum* Niskanen, Liimat. & Ammirati

Etymology: *Olympici* (L.), named after the type species of the section.

Description: Basidiomata medium to large (pileus 30–70 mm diam), fleshy. Pileus pale ochraceous brown to orange ochraceous. Stipe at first whitish, becoming pale brownish to orange ochraceous when scratched. Spines non-decurrent to decurrent. Basidiospores very broadly ellipsoid to subglobose, usually ranging from roundish to more ellipsoid within one basidioma, Q av. value usually 1.15–1.20. Some species characterized by utriform to sublageniform pleurocystidia.

Currently included species: *H. olympicum, H. slovenicum*, and *H. subolympicum*.

Notes: Section *Olympici* formed a distinct well supported monophyletic group in our phylogenetic analysis (100% BS) and is the sister group to *H*. sect. *Hydnum* (FIG. 1), therefore we here describe it as new. Currently there are no morphological characteristics to distinguish the two sister sections, and more material will need to be collected and studied to better understand the morphological limits of the section.

Hydnum olympicum Niskanen, Liimat. & Ammirati, sp. nov. FIGS. 4E, 5D

IndexFungorum: IF553886

Typification: USA. WASHINGTON: Olympic National Park, Sol Duc, hiking trail, in old growth coniferous forest (*Tsuga heterophylla, Pseudotsuga mentziesii*), 25 Oct 2009, *K. Liimatainen & T. Niskanen 09-134* (**holotype** H7043715, **isotype** K(M)248976, **isotype** NY). GenBank: ITS=KX388661.

Etymology: *olympicum* (L.), in reference to the first location found in Olympic National Park, named after Mt. Olympus in Washington.

Description: Basidiomata medium to large, fleshy. Pileus 30–65 mm diam, at first convex, later more or less plane with somewhat incurved margin, surface very pale ochraceous brown with more whitish areas intermixed. Stipe 40–60 mm long, 8–12 mm diam at apex, cylindrical, at first white, becoming pale brownish when bruised. Spines somewhat decurrent to decurrent, crowded, acute, whitish. Basidiospores 8.0–9.2 × 6.5–7.5(–7.8) µm, av.= 8.6 × 7.3 µm, Q=1.08–1.30(–1.40), Q av.=1.19, very broadly ellipsoid to subglobose, thin-walled. Basidia 37–43 × 6.6–8.6 µm, 4-spored, sterigmata 4.5–5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, hyaline to somewhat yellowish, with clavate to cylindrical ends 3–7 µm diam. Pleurocystidia present, utriform to sublageniform, 7–7.8 µm diam at the center, 3–4 µm wide close to the apex. ITS sequence (KX388661) unique within *H.* sect. *Olympici*; sister to *H. subolympicum* (MH174257, holotype), which deviates by seven substitutions and indel positions.

Ecology and distribution: In coniferous forest. Producing basidiomata in autumn. Western North America (Washington).

Notes: *Hydnum olympicum* is easily identified by basidiospores that are the largest within *H.* subg. *Hydnum*. The basidiospore size also separates *H. olympicum* from *H. neorepandum* (av. 7.6 × 6.6 µm), another species of subgenus *Hydnum* that grows in western North America.

Hydnum slovenicum Liimat. & Niskanen, sp. nov.

IndexFungorum: IF553887

Typification: SLOVENIA. VELIKE LASCE: *Picea abies, GIS 1338* (**holotype** LJF1059). GenBank: ITS=AJ547870.

= *Hydnum* RU1 ss. Grebenc et al. Anales Jard. Bot. Madrid 66S1:126 and 129. 2009.

Etymology: *slovenicum* (L.), in reference to the nation Slovenia where first found.

Description: (according to Grebenc et al. (2009)): Basidiomata medium to large. Pileus 40–100 mm diam, orange ochraceous. Stipe 30–70 mm long, cylindrical. Spines non-decurrent. Basidiospores 7.0–8.0 × 5–7 µm, av. 7.5 × 6.3 µm. ITS sequence (AJ547870) unique within *H.* sect. *Olympici*; sister *H. olympicum* (KX388661, holotype), which deviates by at least 13 substitutions and indel positions.

Ecology and distribution. In *Picea abies* forests and in mixed forests of *Picea* and *Fagus*. Europe (Slovenia).

Notes: *Hydnum slovenicum* is characterized by its medium to large size and orange ochraceous pileus. Among European species, *H. repandum* is the most similar but can be distinguished by larger (av. 7.8 × 6.8 µm) basidiospores. Its sister species, *H. olympicum* and *H. subolympicum*, occur in North America.

Hydnum subolympicum Liimat., Niskanen, R. E. Baird & Voitk, sp. nov. FIG. 4F

IndexFungorum: IF553888

Typification: CANADA. NEWFOUNDLAND AND LABRADOR: Near Humber Village, trail to Barry’s Lookout, mature secondary growth of *Betula papyrifera* and *B. alleghaniensis*, also with *Cantharellus amethysteus*, 2 Sept 2012, *A. Voitk 12.09.02.av12* (**holotype** DAOM744368, **isotype** K(M)249002). GenBank: ITS=MH174257.

Etymology: *subolympicum* (L.), for the affinity with *H. olympicum*.

Description: Basidiomata medium to large, fleshy. Pileus 40–80 mm diam, at first convex, later more or less plane with often irregular margin, surface very pale ochraceous brown to orange ochraceous, usually paler towards the margin. Stipe 30–50 mm long, 8–15 mm diam at apex, usually eccentric to lateral, cylindrical, sometimes with a pointed base, at first white, becoming ochraceous to reddish brown with bruising, exposure or age. Spines decurrent to somewhat decurrent, rarely non decurrent, crowded, acute, cream-colored. Basidiospores 7.0–8.2 × 5.8–7.3 µm, av.= 7.4–7.5 × 5.9–6.6 µm, Q=1.07–1.26, Q av.=1.13–1.14, very broadly ellipsoid to subglobose, thin-walled. Basidia 39–45 × 7.5–8 µm, 4- to 5-spored, sterigmata 4.5–5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, hyaline to somewhat yellowish, with clavate to cylindrical ends 3–7 µm diam. ITS sequence (MH174257) unique within *H.* sect. *Olympici*; sister to *H. olympicum* (KX388661, holotype), which deviates by seven substitutions and indel positions.

Ecology and distribution: In coniferous, deciduous (birch), and mixed forests. Eastern North America (Indiana, North Carolina, Québec, and Newfoundland and Labrador).

Notes: Two representatives of *H.* sect. *Olympici* are currently known from North America: *H. olympicum* (from western North America) and *H. subolympicum* (from eastern North America). They are most easily distinguished by basidiospore size; the spores of *H. olympicum* are larger (av.=8.6 × 7.3 µm) than those of *H. subolymicum*. Paler basidiomata of *H. subolympicum* are very similar to the ones of co-occuring *H. neorepandum*, and an ITS sequence is needed for unambiguous identification.

Hydnum subgen. *Rufescentes* Niskanen & Liimat., subgen. nov. FIGS. 6–9

IndexFungorum: IF553889

Type species: *Hydnum rufescens* Pers., Observ mycol (Lipsiae) 2:95. 1800.

Etymology: *Rufescentes* (L.), named after its type species.

Description: Basidiomata small to large (pileus 20–100 mm diam), in many species fleshy, but some species more slender. Pileus pale ochraceous brown to orange ochraceous, only in some species cream-colored, plane or with a small depression in the center. Stipe at first whitish, becoming pale brownish to orange ochraceous where scratched. Spines usually non-decurrent to decurrent. Basidiospores subglobose to broadly ellipsoid. Known from Eurasia and North and Central America.

Currently included sections: *H.* sect. *Magnorufescentes* and *H.* sect. *Rufescentes*.

Notes: The species of *H.* sect. *Rufescentes* are characterized by small to medium basidiomata and pale ochraceous brown to orange ochraceous pilei. The species are usually easy to distinguish from those representing other subgenera. The species of *H.* sect. *Magnorufescentes* can resemble those of *H.* subg. *Hydnum*, which is distinguished by subglobose to very broadly ellipsoid basidiospores and a Q av. value of 1.15–1.20 (vs. 1.06–1.13 in *H.* sect. *Magnorufescentes*.)

Hydnum sect. *Magnorufescentes* Niskanen & Liimat., sect. nov.

IndexFungorum: IF553890

Type species: *Hydnum magnorufescens* Vizzini, Picillo & Contu, Mycosphere 4:37. 2013.

Etymology: *Magnorufescentes* (L.), named after the type species of the section.

Description: Basidiomata medium to large (pileus 35–100 mm diam), rarely small (pileus 20–35 mm diam), fleshy. Pileus cream-colored to very pale ochraceous brown to medium orange ochraceous. Stipe at first more or less white, becoming pale brownish to orange ochraceous when scratched. Spines non-decurrent to decurrent. Basidiospores subglobose, Q av. value 1.06–1.13.

Currently included species: *H. albertense, H. jussii, H. magnorufescens,* and *H. melleopallidum*.

Notes: *Hydnum* sect. *Magnorufescentes* is characterized by usually medium to large and fleshy basidiomata with cream-colored to very pale ochraceous brown to medium orange ochraceous pilei, and subglobose basidiospores. Its species resemble those of *H.* subg. *Hydnum*, which differ in their subglobose to more ellipsoid and relatively longer basidiospores (Q av. value usually 1.14–1.17). Basidiomata representing the sister section *H.* sect. *Rufescentes* are smaller (small to medium) and more slender, the pilei often have a small depression in the center, and the spines are non-decurrent. In addition, basidiospores produced within in *H.* subsect. *Rufescentes* have an average Q-value >1.19 whereas the basidiospores in *H.* subsect. *Tenuiformia* and *H.* subsect. *Mulsicolores*, with the exception of *H. mulsicolor*, are usually larger, av. >8.4 × 7.4 µm.

Hydnum albertense Niskanen & Liimat., sp. nov. FIGS. 6A, 7A

IndexFungorum: IF553891

Typification: CANADA. ALBERTA: Hinton, in coniferous forest, 4 Sep 2011, anonymous, *T. Niskanen 11-354* (**holotype** H7043704, **isotype** K(M)248964, **isotype** NY). GenBank: ITS=KX388664.

Etymology: *albertense* (L.), in reference to the province Alberta, Canada, in which the species was first found.

Description: Basidiomata medium- to large, often fleshy. Pileus 45–100 mm diam, fleshy, at first convex, later more or less plane, sometimes with somewhat incurved margin, surface cream-colored to very pale ochraceous brown, paler towards the margin. Stipe 40–65 mm long, 7–14 mm diam at apex, cylindrical to somewhat clavate, whitish, becoming pale ochraceous brown when bruised. Spines non-decurrent to decurrent, crowded, acute, whitish. Basidiospores 7.0–8.0 × 6.2–7.1 µm, av.= 7.6 × 6.8 µm, Q=1.06–1.22, Q av.=1.13, subglobose, thin-walled. Basidia 40–47 × 6.5–8.0 µm, 4- to 5-spored, sterigmata 4–5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, hyaline to yellowish, with cylindrical ends 3–5 µm diam. ITS sequence (KX388664) unique within *H.* sect. *Magnorufescentes;* sister to *H. melleopallidum* (FJ845406, holotype), which deviates in the ITS region by 11 substitutions and indel positions.

Ecology and distribution: In coniferous forests. Producing basidiomata in autumn. Western North America (Alberta).

Notes: *Hydnum albertense* is characterized by medium to large basidiomata with cream-colored to very pale ochraceous brown pilei and medium-sized subglobose basidiospores. It is morphologically difficult to distinguish from its sister species, *H. melleopallidum*, which has a somewhat more colorful pileus but similar sized basidiospores. The distributions of the two species differ, however; currently *H. melleopallidum* is only known from the western coast of British Columbia, Canada, whereas *H. albertense* grows in the interior on the eastern side of the Rocky Mountains. In addition, because the interspecific difference in the ITS region is >1.5%, we accept them as two different species.

Hydnum jussii Niskanen, Liimat. & Kytöv., sp. nov. FIGS. 6B, 7B

IndexFungorum: IF553893

Typification: FINLAND. VARSINAIS-SUOMI: Kisko, Liuhto, Viiramäki, in mesic partly damp spruce forest (*Picea abies*) on calcareous ground with *Betula*, *Populus tremula*, and *Pinus sylvestris*, 23 Jul 2007, *K. Liimatainen & T. Niskanen 07-027* (**holotype** H6003709, **isotype** K(M)248977). GenBank: ITS=KX388665.

Etymology: *jussii* (L.), named after Juhani (Jussi) Ruotsalainen, Finnish amateur mycologist.

Description: Basidiomata medium to large, fleshy. Pileus 35–60 mm diam, fleshy, at first convex, later more or less plane with incurved margin, surface very pale to medium orange ochraceous. Stipe 30–60 mm long, 5–13 mm diam at apex, cylindrical to clavate, whitish, becoming pale orange brownish when bruised. Spines somewhat decurrent, crowded, acute, at first whitish to very pale ochraceous later pale brownish ochraceous. Basidiospores 7.2–8.0 × 6.6–7.5 μm, av.=7.5 × 7.0 μm, Q=1.03–1.18, Q av.=1.07, subglobose, thin-walled. Basidia 43–48 × 7.0–9.0 μm, 4-spored, sterigmata 4.5–5 μm long. Hyphae of the apex of the spines cylindrical, thin-walled, hyaline to yellowish, with cylindrical ends 3–4 μm diam. ITS sequence (KX388665) unique within *H.* sect. *Magnorufescentes* and deviates by 13 substitutions and indel positions from DQ367902.

Ecology and distribution: In coniferous forests. Producing basidiomata in late summer and autumn. Eurasia (Finland and Tibet).

Notes: *Hydnum jussii* is typical within *H.* sect. *Magnorufescentes*. The basidiomata are medium to large and fleshy with pilei that lack very bright orange colors. The species is widely distributed known from Finland and China in Tibet. The other known European species of this section, *H. magnorufescens*, has non-decurrent spines and larger basidiospores (av.= 7.9 × 7.5 μm).

Hydnum melleopallidum Kranab., Liimat. & Niskanen, sp. nov. FIG. 7C

IndexFungorum: IF553894

Typification: CANADA. BRITISH COLUMBIA: McDonnell Lake, McDonell Forest Research Road, Smithers, mixed old-growth coniferous forest, 21 Aug 2008, *M. Kranabetter & J. Friesen SMI 356* (**holotype** UBC F17492). GenBank: ITS=FJ845406.

Etymology: melleopallidum (L.), refers to the pale honey color of the basidiomata.

Description: Basidiomata small to medium. Pileus 20–35 mm diam, at first convex, later more or less plane, surface cream-ochraceous to very pale brownish ochraceous. Stipe 25–35 mm long, 4–7 mm diam at apex, cylindrical, whitish, becoming pale yellowish brown when bruised. Spines decurrent, crowded, acute, whitish. Basidiospores 7.0–8.0 × 6.5–7.3 μm, av.= 7.5 × 6.7 μm, Q=1.04–1.18, Q av.=1.12, subglobose, thin-walled. Basidia 42–48 × 7.5–8.5 μm, 4- to 5-spored, sterigmata 3–4.5 μm long. Hyphae of the apex of the spines cylindrical, thin-walled, hyaline to yellowish, with cylindrical to somewhat clavate ends 3–4.7 μm diam. ITS sequence (FJ845406) unique within section *Magnorufescentes,* sister to *H. albertense* (KX388664, holotype), which deviates by 11 substitutions and indel positions.

Ecology and distribution: In mixed coniferous forests. Producing basidiomata in autumn. Western North America (British Columbia).

Notes: *Hydnum melleopallidum* produces medium-sized basidiomata with cream-ochraceous to very pale brownish ochraceous pilei and medium-sized subglobose basidiospores. See additional discussion under *H. albertense*.

Hydnum sect. *Rufescentes* Niskanen & Liimat., sect. nov.

IndexFungorum: IF553895

Type species: *Hydnum rufescens* Pers., Observ mycol. (Lipsiae) 2:95.1800.

Etymology: *Rufescentes* (L.), named after the type species of the section.

Description: Basidiomata small to medium (pileus 25–45 mm diam), rarely large (pileus up to 65 mm diam), often slender. Pileus pale cream-ochraceous to ochraceous brown to yellow-orange to deep reddish orange, most species with a small depression in the center. Stipe at first more or less white, becoming pale brownish to orange ochraceous when bruised. Spines usually non-decurrent. Basidiospores subglobose to broadly ellipsoid.

Currently included subsections: *Hydnum* subsect. *Mulsicolores, H.* subsect. *Rufescentes, H.* subsect. *Tenuiformia,* clade /Ovoideispori, and *H. melitosarx* (incertae sedis).

Notes: *Hydnum* sect. *Rufescentes* is characterized by usually small to medium and slender basidiomata, pilei that are cream-ochraceous to deep reddish orange and in most species feature a small depression in the center, and non-current spines. As a rule of thumb, one could say that all more or less small and slender species with a colorful pileus in North America and Europe belong to this section. The species of *H.* sect. *Rufescentes* are most similar to those in the sister section *H.* sect. *Magnorufescentes,* which are distinguished by usually larger basidiomata, pilei lacking a central depression, and subglobose (Q av. value 1.06–1.13) and generally smaller (av. < 7.6 × 7.0 µm) basidiospores.

Hydnum subsect. *Mulsicolores* Niskanen & Liimat., subsect. nov.

IndexFungorum: IF553896

Type species: *Hydnum mulsicolor* Liimat. & Niskanen.

Etymology: *Mulsicolores* (L.), named after the type species of the subsection.

Description: Basidiomata small to medium (pileus 18–50 mm diam), often slender. Pileus pale ochraceous brown to yellow-orange, often with a small depression in the center. Stipe at first whitish, becoming pale ochraceous brown to pale orange brownish where scratched. Spines non-decurrent. Basidiospores rather small, subglobose (7.5–8.6 × 6.6–7.7 µm, Q av. <1.15).

Currently included species: *H. canadense, H. mulsicolor,* and *H. submulsicolor*. In addition, one as yet undescribed species from China (GenBank no. KU612601) is recognized.

Notes: The species in *H.* subsect. *Mulsicolor* are most similar to those in *H.* subsect. *Tenuiformia*, most of which are distinguished by either larger subglobose basidiospores (av. > 8.6 × 7.9 µm) or distinctly ellipsoid basidiospores. Most similar is *H. quebecense*, distinguished by differently shaped (somewhat more ovoid subglobose) basidiospores. *Hydnum melitosarx* (incertae sedis) is morphologically also very similar to species in *H.* subsect. *Mulsicolores*. The average spore size of *H. melitosarx* (7.9 × 7.2 µm), however, does not overlap with the known species of subsection *Mulsicolores* and can be used to separate the species from one another. Species in *H.* subsect. *Rufescentes* and /Ovoideispori have relatively longer basidiospores (Q av. > 1.15).

Hydnum canadense Niskanen & Liimat., sp. nov., FIGS. 8A, 9A

IndexFungorum: IF553897

Typification: CANADA. NEWFOUNDLAND AND LABRADOR: near Grand Falls, south of the Exploits River, west of Hwy 360, south of Hwy 1, along a gravel road beside Moccasin Lake, in conifer dominated forest, 9 Sep 2009, *K. Liimatainen & T. Niskanen 09-006* (**holotype** H7043727, **isotype** K(M)248978, **isotype** NY). GenBank: ITS=KX388681.

Etymology: *canadense* (L.), in reference to the type locality country, Canada.

Description: Basidiomata rather small and slender. Pileus 20-40 mm diam, at first convex, later more or less plane with somewhat incurved margin, often with a small depression in the center, surface pale ochraceous brown. Stipe 25–45 mm long, 4–8 mm diam at apex, cylindrical to somewhat clavate, sometimes with a pointed base, white to very pale ochraceous, becoming pale ochraceous brown when bruised. Spines non-decurrent, crowded, acute, at first whitish, later pale ochraceous brown. Basidiospores 7.8–9.2 × 7.0–8.3 µm, av.=8.6 × 7.7 µm, Q=1.03–1.26, Q av.=1.12, subglobose, some very broadly, short ellipsoid, thin-walled. Basidia 47–52 × 8.5–9.5 µm, 3- or 4-spored, sterigmata 5.5–7.5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, yellowish, with cylindrical ends 3–4 µm diam. ITS sequence (KX388681) unique within *H.* subsect. *Mulsicolores,* the other species of which deviate by at least 17 substitutions and indel positions.

Ecology and distribution: In coniferous forests. Producing basidiomata in autumn. Eastern North America (Newfoundland and Labrador).

Notes: Hydnum canadense is a typical member of *H.* subsect. *Mulsicolores*. The co-occurring *H. mulsicolor*, which also occurs in Europe, produces distinctly smaller basidiospores (av. 7.5 × 6.6 µm). The third eastern North American species in this subsection, *H. submulsicolor,* is morphologically very similar to *H. canadense*, and ITS barcoding is needed for an unambiguous identification of the species.

Hydnum mulsicolor Liimat. & Niskanen, sp. nov.

IndexFungorum: IF553898

Typification: SLOVENIA. VELIKE LAŠČE: in forest of *Picea abies, Fagus sylvatica,* and *Corylus avellana, GIS 1336* (**holotype** LJF1057). GenBank: ITS=AJ547885.

Etymology: *mulsicolor* (L.), color of honey wine or mead (*mulsum*), in reference to the yellow-orange color of the pileus.

= *Hydnum* RU4 in Grebenc et al. Anales Jard. Bot. Madrid 66S1:126 and 129. 2009.

Description (according to Grebenc et al. (2009)): Basidiomata rather small to small. Pileus 18–32 mm diam, intense yellow-orange. Stipe 3–5 mm diam at apex. Spines non-decurrent. Basidiospores on av. 7.5 × 6.6 µm. ITS sequence (JX093560) unique within *H.* subsect. *Mulsicolores;* sister to *H. submulsicolor* (KX388682, holotype), which deviates by eight substitutions and indel positions.

Ecology and distribution: In Europe collected from different types of mixed forests (*Picea, Abies, Fagus, Corylus, Quercus*); in North America from a mixed deciduous forest. Producing basidiomata in late summer and autumn. Eastern North America (Tennessee, Ohio) and northern and central Europe (Finland, Slovenia, Switzerland).

Notes: *Hydnum mulsicolor* can be distinguished from other co-occurring species in *H.* subsect. *Mulsicolor* (*H. submulsicolor*, *H. canadense)* and from *H.* cf. *umbilicatum* by smaller basidiospores.

Hydnum submulsicolor Niskanen & Liimat., sp. nov. FIG. 9B

IndexFungorum: IF553899

Typification: CANADA. QUÉBEC: Saint-Come, Chute-a-Bull, in conifer dominated forest (*Abies*, *Picea*) with some *Betula*, on mossy ground, 22 Sep 2010, *K. Liimatainen & T. Niskanen 10-132* (**holotype** H7043716, **isotype** K(M)248979, **isotype** NY). GenBank: ITS=KX388682.

Etymology: *submulsicolor* (L.), for the affinity to *H. mulsicolor*.

Description: Basidiomata rather small to medium. Pileus 30–50 mm diam, at first convex, later more or less plane, often with a depression in the center, orange ochraceous to more brownish ochraceous. Stipe 20–40 mm long, 4–7 mm diam at apex, cylindrical or somewhat clavate, white to pale ochraceous, becoming pale orange brown when scratched. Spines usually non-decurrent, crowded, acute, at first whitish, later very pale ochraceous brown. Basidiospores 7.8–9.0 × 7.0–8.2 μm, av.= 8.5 × 7.5 μm, Q=1.05–1.22, Q av.=1.13, subglobose, a few very broadly ellipsoid, thin-walled. Basidia 44–49 × 7.0–8.0 μm, 3- to 4-spored, sterigmata 3.5–5 μm long. Hyphae of spine apex cylindrical, thin-walled, yellowish, with cylindrical ends 3–5.5 μm diam. ITS sequence (KX388682) unique within *H.* subsect. *Mulsicolores;* sister to *H. mulsicolor* (JX093560, holotype), which deviates by eight substitutions and indel positions.

Ecology and distribution: In coniferous forests. Producing basidiomata in autumn. Eastern North America (Québec).

Notes: Hydnum submulsicolor is an eastern North American species producing small to medium slender basidiomata with non-decurrent spines and subglobose basidiospores. Its sister species, *H. mulsicolor,* is distinguished by smaller basidiospores (av. 7.5 × 6.6 µm), while the third eastern North American species of this subsection, *H. canadense,* is morphologically very similar to *H. submulsicolor*, and ITS barcoding is needed for an unambiguous identification of the species. *Hydnum* cf. *umbilicatum* from *H*. sect. *Tenuiformes* has larger basidiospores (av.= 8.9 × 8.1 µm).

Hydnum /Ovoideispori

Description: Basidiomata usually small to medium (pileus 15–40 mm diam). Pileus pale cream-ochraceous, pale orange to deep reddish orange, often with a small depression in the center. Spines usually non-decurrent. Stipe at first white, becoming pale orange brown, pale ochraceous brown when bruised. Basidiospores subglobose to ovoid to broadly ellipsoid basidiospores (Q av. value usually > 1.15).

Currently included species: *H. ovoideisporum* and *H. subovoideisporum*.

Notes: Species in */Ovoideispori* produce relatively long basidiospores similar to those in *H.* subsect. *Rufescentes,* but in the field they look more like the species in *H.* subsect. *Mulsicolores* and *H.* subsect. *Tenuiformia*. The latter species, however, produce basidiospores with an average Q-value less than 1.15, except *H. ellipsosporum*, which produces large (av. 10.0 x 6.6 µm) ellipsoid basidiospores.

Hydnum subovoideisporum Niskanen & Liimat., sp. nov. FIGS. 8B, 9C

IndexFungorm: IF553900

Typification: FINLAND. VARSINAIS-SUOMI: Turku, Ruissalo, Nature Reserve near the Botanical Garden, under *Quercus* (also near *Pinus* and *Betula*) in a primarily deciduous forest, on mull soil, 13 Sep 2008, *K. Liimatainen & T. Niskanen 08-097* (**holotype** H6003707, **isotype** K(M)248980). GenBank: ITS=KX388680.

Etymology: subovoideisporum (L.), due to the affinity with *H. ovoideisporum*.

Description: Basidiomata rather small and slender. Pileus 15-40 mm diam, thin, at first convex, later more or less plane with somewhat incurved margin, with a small depression in the center, surface pale cream-ochraceous to pale orange-ochraceous. Stipe 25–40 mm long, 3–7 mm diam at apex, more or less cylindrical, white to very pale ochraceous, becoming more pale ochraceous brownish where scratched. Spines non-decurrent, sometimes leaving a bare zone around the stipe, crowded, acute, cream-colored. Basidiospores 7.0–8.6 × 6.0–7.5 µm, av.= 7.9 × 6.5 µm, Q=1.05–1.42, Q av.=1.21, ovoid subglobose to broadly ellipsoid, thin-walled. Basidia 36–45 × 7–7.5 µm, 4-spored, sterigmata 3–5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, more or less yellowish, with cylindrical ends (3–5 µm diam). ITS sequence (KX388680) unique within *H.* sect. *Rufescentes;* sister to *H. ovoideisporum* (NR119818, holotype), which deviates by nine substitutions and indel positions.

Ecology and distribution: In mixed forests (*Quercus*, *Pinus*, *Betula*). Producing basidiomata in autumn. Europe (Finland).

Notes: *Hydnum subovoideisporum* resembles its sister species *H. ovoideisporum,* which according to the type description by Olariaga et al. (2012) is distinguished by its usually deep orange tones in the pileus and longer (av. 8.1–9.3 µm) and often wider (av. 6.4–7.1 µm) basidiospores. More recent observations of *H. ovoideisporum* by Vizzini et al. (2013; two sequenced specimens from Italian material with a spore size averaging 7.4 × 6.9 µm), however, suggest that the variation in the shape and length of the basidiospores is rather large. Thus far *H. ovoideisporum* has been found in the Mediterranean area (despite one specimen collected under *Abies alba* from a forest with boreal affinity in the Pyrenees), whereas *H. subovoideisporum* is currently only known from the hemiboreal zone in Finland.

Hydnum subsect. *Rufescentes* Niskanen & Liimat., subsect. nov.

IndexFungorum: IF553901

Type species: *Hydnum rufescens* Pers., Observ mycol (Lipsiae) 2:95 .1800 [1799].

Etymology: *Rufescentes* (L.), named after the type species of the subsection.

Description: Basidiomata usually medium-sized, rarely large (pileus 20–65 mm diam). Pileus margin often irregular, surface more or less lumpy, pale to medium brownish ochraceous to deep reddish orange, most species with a small depression in the center. Stipe at first white, becoming pale orange brown pale ochraceous brown when bruised. Spines usually non-decurrent. Basidiospores subglobose to broadly ellipsoid (Q av. value usually >1.19, rarely 1.1).

Currently included species: *H. rufescens* and *H. subrufescens*. There are additional undescribed species known from China.

Notes: Species in *H.* subsect. *Rufescentes* can be distinguished from those in *H.* subsect. *Mulsicolores* and *H.* subsect. *Tenuiformia*, and from *H. melitosarx*, by basidiospore size and shape. Species of *H.* subsect. *Mulsicolores* and *H. melitosarx*, produce basidiospores with an average Q-value of less than 1.15, as do species of *H.* subsect. *Tenuiformia* (excluding *H. ellipsosporum*, distinguished by large ellipsoid basidiospores (av. 10.0 × 6.6 μm). Species in /Ovoideispori are characterized by relatively long basidiospores (Q av. value usually > 1.15) but with smaller and more slender basidiomata reminiscent of species in *H.* subsect. *Mulsicolores* and *H.* subsect. *Tenuiformia.*

Hydnum rufescens Pers., Observ mycol (Lipsiae) 2:95. 1800. FIGS. 8C, 9D

IndexFungorum: IF553856 (lectotype), IF553902 (epitype)

Sanctioning citation: Fr., Syst mycol 1:401.1821.

Typification: Schaeffer (1800) Fung. bav. Erlangae. Tab. CXLI, fig. II and III (**lectotype**, here designated). FINLAND. VARSINAIS-SUOMI: Karjaa, Mustio, Kohagen, herb-rich spruce (*Picea abies*) forest with some *Corylus, Betula* and *Populus*, 02 Sep 2008, *K. Liimatainen & T. Niskanen 08-050* (**epitype** H6003708, **isoepitype** K(M)248981). GenBank: ITS=KX388688.

= *Hydnum* RU5 ss. Grebenc et al. Anales Jard Bot Madrid 66S1:126 and 129. 2009.

Description: Basidiomata medium, sometimes small or large, often fleshy. Pileus 20–65 mm diam, fleshy, often irregular in shape, at first convex, later more or less plane, sometimes with a small depression in the center, surface uneven (lumpy), colorful, deep reddish orange to medium brownish orange, paler towards the margin. Stipe 28–55 mm long, 4–15 mm diam at apex, cylindrical or somewhat clavate, base often pointed, white to pale ochraceous, becoming more pale orange brown where bruised. Spines usually non-decurrent, crowded, acute or sometimes spathulate, whitish to very pale orange-ochraceous.

Basidiospores 7.0–8.5(9) × 6.0–7.2(7.5) µm, av.= 8.0–8.2 × 6.4–6.8 µm, Q=(1.03)1.10–1.28(1.35), Q av.=1.19–1.28 (since there was large variation among different collections, the range of average values are given for this species), subglobose to broadly ellipsoid, thin-walled. Basidia 35–40 × 7.5–9.0 µm, 4-spored (rarely 3- or 5-spored), sterigmata 3–5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, more or less yellowish, with cylindrical ends 3–4.5 µm diam. ITS sequence (KX388688) unique within *H.* subsect. *Rufescentes*; sister to *H. subrufescens* (KX388649, holotype), which deviates by 18 substitutions and indel positions.

Ecology and distribution: Associated with many different tree species; collected from *Picea abies* dominated forests and under *Fagus, Corylus, Quercus,* and *Tilia cordata*. Producing basidiomata in autumn. Europe.

Notes: Hydnum rufescens produces medium-sized basidiomata and is best characterized by the combination of rather bright-colored, often irregular pilei that lack a distinct depression, non-decurrent spines, and basidiospores usually with an average Q-value >1.19. The variation in basidiospore shape within and between individuals is rather large (e.g., Olariaga et al. (2012) reported an average Q value of 1.08 for specimen LJF GIS 1330, GenBank AJ547872), but the average values in combination with other characteristics often suffice for unambiguous species identification. The eastern North American sister species, *H. subrufescens*, is distinguished by a less colorful, pale to medium, brownish ochraceous pileus and wider basidiospores (av. 8.1 × 7.0 μm).

There has been much confusion regarding application of the name *H. rufescens*, as the name has until now been untypified complicating a clade assignment (Grebenc et al. 2009; Olariaga et al. 2012; Vizzini et al. 2013). By studying the original description and collections of Persoon, however, it is now possible to fix unambiguously the application of the name. Persoon (1800) described *H. rufescens* as a fleshy fungus with a brownish-orange pileus growing in *Fagus* forests. Persoon's herbarium in Leiden includes three collections labeled as *H. rufescens*: L0116294 from Italy, (Calabria), L0116295 from France, and L0116296 from an unknown location. The basidiomata in collection L0116294 do not include any measurable basidiospores, but L0116295 and L0116296 were suitable for micromorphological studies. The basidiospores in those collections were subglobose to broadly ellipsoid. The spore measurements for L0116295 were 7.4–8.8 × 5.7–7.2 μm, av. 8.2 × 6.7 μm, Q=1.10–1.35, Q av. 1.23, and for L0116296 (7.0–)7.3–9.3(–9.6) × (5.3–)5.7–8.1 (8.8) μm, av. 8.4 × 7.0 μm, Q=1.05–1.40 (1.47), Q av. 1.21. In *H.* subg. *Rufescentes* the only groups containing species with basidiospores averaging a Q value >1.20 are /Ovoideispori and *H.* subsect. *Rufescentes*. In these two groups three species are known from Europe, namely *H. ovoideisporum, H. subovoideisporum,* and *H. rufescens*. *Hydnum ovoideisporum*, currently known from the Mediterranean area, is distinguished by a basidiospore Q av. value of 1.27–1.38 (Olariaga et al. 2012). *Hydnum subovoideisporum*, currently known only from southern Finland, produces the smallest (av.= 7.9 × 6.5 μm) basidiospores of the three species. *Hydnum rufescens*, as described here, is a widespread species in Europe and grows in many kinds of forests including *Fagus*. The basidiospores are on average 8.0–8.2 × 6.4–6.8 μm, and the Q av. value is 1.19–1.28. Based on the ecology, distribution, and spore size, we conclude that this intepretation best fits the original description of Persoon (1800). Because there is no information on when the *H. rufescens* collections in Persoon's herbarium were made, before or after the description of the species, there is no obligation to consider any of them as a potential type. To keep further interpretation of the name as unambiguous as possible, we did not select a type among Persoon's collections but instead selected a lectotype among the figures referred to in the protologue and propose collection H6003708 as an epitype.

Hydnum subrufescens Niskanen & Liimat., sp. nov. FIGS. 8D, 9E

IndexFungorm: IF553903

Typification: CANADA. QUÉBEC: Montebello, in mixed forest (mainly *Tsuga*, some *Abies, Pinus, Quercus, Populus* and *Betula*), 24 Sep 2010, *K. Liimatainen & T. Niskanen 10-154* (**holotype** H7043705, **isotype** K(M)248982, **isotype** NY). GenBank: ITS=KX388649.

Etymology: subrufescens (L.), in reference to the affinity with *H. rufescens.*

Description: Basidiomata medium-sized to sometimes large, often fleshy. Pileus 25–60 mm diam, often irregular, fleshy, at first convex, later more or less plane with somewhat incurved margin, sometimes with a small depression in the center, surface somewhat lumpy, pale to medium brownish ochraceous, paler towards the margin. Stipe 25–40 mm long, 4–13 mm diam, at apex, cylindrical, white to very pale ochraceous, darkening to pale orange brownish where scratched. Spines usually non-decurrent, crowded, acute, whitish to very pale ochraceous. Basidiospores 7.4–8.8 × 6.4–7.8 µm, av.= 8.1 × 7.0 µm, Q=1.05–1.24(–1.30), Q av.=1.15, subglobose, some broadly ellipsoid, thin-walled. Basidia 40–51 × 7.5–9.0 µm, 3- or 4-spored, sterigmata 4.5–6 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, more or less yellowish, with cylindrical ends 3–4.5 µm diam. ITS sequence (KX388649) unique within *H.* subsect. *Rufescentes;* sister to *H. rufescens* (KX388688, neotype), which deviates by 18 substitutions and indel positions.

Ecology and distribution: In mixed forests (*Tsuga*, *Abies*, *Pinus*, *Quercus*, *Populus*, *Betula*). Producing basidiomata in autumn. Eastern North America.

Notes: The eastern North American *H. subrufescens* resembles its European sister species *H. rufescens* in size and shape, but the pileus of *H. rufescens* is more colorful (deep reddish orange to medium brownish orange), and the basidiospores are narrower (av.= 8.0 × 6.6 µm).

Hydnum subsect. *Tenuiformia* Niskanen & Liimat., subsect. nov.

IndexFungorum: IF553904

Type species: *Hydnum ellipsosporum* Ostrow & Beenken, Z Mykol 70:139. 2004.

Etymology: *Tenuiformia* (L.), referring to the slender basidiomata characterizing this subsection.

Description: Basidiomata small to medium (pileus 20–45 mm diam), often slender species. Pileus pale orange ochraceous to pale orange-brown to orange-brown, often with a small depression in the center. Stipe at first white, becoming orange brown to ochraceous brown when scratched. Spines non-decurrent. Basidiospores rather large subglobose to ovoid-subglobose (av. > 8.5 × 7.5 µm) or ellipsoid (av. 10.0 × 6.6 µm).

Currently included species: *H. ellipsosporum, H. oregonense, H. quebecense,* and *H*. cf. *umbilicatum* (our current interpretation of *H. umbilicatum*).

Notes: The species of *H.* subsect. *Tenuiformia* most closely resemble species in *H.* subsect. *Mulsicolores* and *H. melitosarx* that usually can be distinguished by smaller subglobose basidiospores (ave. 7.5–8.6 × 6.6–7.7 µm). Within the subsection, only *H. quebecense* (see below) can be difficult to separate from species in *H.* subsect. *Mulsicolores*. The shape of the basidiospores of *H. quebecense*, however, is different from those of *Mulsicolores*, tending towards ovoid or subglobose. The species in *H.* subsect. *Rufescentes* and *H.* /Ovoideispori differ by having relatively longer basidiospores (Q av. >1.15).

Hydnum oregonense Norvell, Liimat. & Niskanen, sp. nov. FIG. 9G

IndexFungorum: IF553905

Typification: USA. OREGON: Benton County, Green Peak, under *Pseudotsuga menziesii* with *Tsuga heterophylla*, 595–600 m elev, 2 May 2001, *L. Norvell and R. Exeter g2010502h1-09* (**holotype** OSC). GenBank: ITS=AJ534972.

Etymology: oregonense (L.), referring to the state in which the type locality occurs.

Misappl.: *H. umbilicatum* ss. Grebenc et al. (2009), Olariaga et al (2012), Vizzini et al. (2013), Yanaga et al. (2015), Feng et al. (2016).

Description: Basidiomata rather small and slender. Pileus up to 45 mm diam, at first convex, later more or less plane, surface very pale brownish orange to ochraceous cream-colored. Stipe up to 45 mm long, 5–6 mm diam at apex, cylindrical, white at first, becoming very pale brownish ochraceous where scratched. Spines non-decurrent, crowded, acute, ochraceous white when young, becoming orange in age. Basidiospores 8.4–10.5(–12.9) × 7.3–10.4 µm, av.= 9.5 × 9.0 µm, Q=0.95–1.32, Q av.=1.06, globose to subglobose (rarely broadly ellipsoid), thin-walled. Basidia clavate, hyaline, 60–62 × 8–11 µm tapering to a 4–4.7 µm diam base, 2-spored, sterigmata 4–5.7 µm long. Hyphae of the apex of the spines ± cylindrical, thin-walled, with cylindrical to spathulate ends 2.5–4.6 µm diam. ITS sequence (AJ534972) distinct from other species in *H.* subsect. *Tenuiformia* differing by over 30 substitutions and indel positions.

Ecology and distribution: In coniferous forests (*Pinus muricata*, *Pseudotsuga menziesii*, *Tsuga heterophylla*). Fruiting in late spring and autumn. Western North America (California, Oregon).

Notes: *Hydnum oregonense* can easily be distinguished from other species in *H.* subg. *Rufescentes* by the large globose to subglobose basidiospores. The name *H. umbilicatum* was misapplied to this species by Grebenc et al. (2009), Olariaga et al (2012), Vizzini et al. (2013), Yanaga et al. (2015), and Feng et al. (2016). *Hydnum umbilicatum*, however, was described from eastern North America, and the spore measurements from the type specimen are on average 8.4 × 8.0 µm. Since *H. oregonense* has larger spores and is currently only known from western North America, we conclude that it very unlikely represents *H. umbilicatum* Peck and describe here it as new.

Hydnum quebecense Niskanen & Liimat., sp. nov. FIGS. 8F, 9H

IndexFungorum: IF553906

Typification: CANADA. QUÉBEC: Saint-Donat, in coniferous forest (*Tsuga*, *Abies*, *Picea*, *Betula*, and *Populus*), 5 Sep 2010, anonymous, *T. Niskanen 10-064* (**holotype** H7043948, **isotype** K(M)248983, **isotype** NY). GenBank: ITS=KX388662.

Etymology: *quebecense* (L.), in reference to the original location of Québec, Canada.

Description: Basidiomata medium-sized, slender, often with a long stipe compared to the pileus diameter. Pileus 25–45 mm diam, at first convex, later plane with somewhat incurved margin, often with a depression in the center, surface pale orange-brown to orange-brown. Stipe 30–65 mm long, 4–9 mm diam at apex, cylindrical to clavate, white to very pale ochraceous, becoming more orange brown where scratched. Spines non-decurrent, crowded, acute, at first whitish, later pale brownish ochraceous. Basidiospores 7.8–9.5 × (6.5–)7.0–8.2 µm, av.= 8.5 × 7.5 µm, Q=1.05–1.23, Q av.=1.13, primarily subglobose (some broadly ellipsoid), thin-walled, inamyloid. Basidia 50–57 × 6.8–8.2 µm, usually 2-spored, sterigmata 4–5.5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, more or less yellowish, with cylindrical ends 3–4.7 µm diam. ITS sequence (KX388662) distinct from other species of subsection *Tenuiformia*, which differs by about 30 substitutions and indel positions.

Ecology and distribution: In coniferous forests among *Sphagnum*. Producing basidiomata in autumn. Eastern North America (Québec).

Notes: Hydnum quebecense resembles a very brightly colored *H*. cf. *umbilicatum*, but *H.* cf. *umbilicatum* has larger basidiospores (av. 8.9 × 8.1 µm).

Hydnum cf. *umbilicatum* FIGS. 8G, 9I

= *H. umbilicatum* ss. Huhtinen and Ruotsalainen, Karstenia 46:19. 2006.

Misappl.: *H. ellipsosporum* p.p. ss. Grebenc et al. (2009), Feng et al. (2016)

Misappl.: *H.* aff. *ellipsosporum* Olariaga et al. (2012), Vizzini et al. (2013)

Description: Basidiomata rather small and slender. Pileus 20–40 mm diam, at first convex, later more or less plane with somewhat incurved margin, often with a distinct depression in the center, surface pale orange ochraceous to orange ochraceous. Stipe 40–65 mm long, 4–7 mm diam at apex, cylindrical to somewhat clavate, white, becoming very pale brownish ochraceous when bruised. Spines non-decurrent to somewhat decurrent, crowded, acute, at first whitish, later pale ochraceous brown.

Basidiospores in eastern North American (ENA) specimens 8.4–9.6 × 7.8–8.8 μm, av.= 8.9 × 8.1 μm, Q=1.07–1.13, Q av.=1.10, in western North American (WNA) specimens 8.0–9.5 × 7.2–9.0 μm, av.= 8.7 × 8.1 μm, Q=1.00–1.15, Q av.=1.08, in Eurasian (EUR) specimens 7.8–9.2 × 7.4–8.8 μm, av.=8.6 × 8.0 μm, Q=1.00–1.16, Q av.=1.08, subglobose to somewhat elongated, thin-walled. Basidia in ENA specimens 47–55 × 9.0–11.5 μm, 2- or 3-spored, sterigmata 6.3–13.3 μm long, in WNA specimens 47–52 × 7.5–9.5 μm, 2- or 3-, rarely 4-spored, sterigmata 4–7 μm long, in EUR specimens 43–47 × 7.5–9.5 μm, basidiospores 2- or 3-spored, sterigmata 4.5–6 μm long. Hyphae of the apex of the spines in all groups similar, cylindrical, thin-walled, yellowish, with cylindrical to somewhat clavate ends 2.5–5 μm diam. ITS sequence (KX388681). The intraspecific variation (nine substitutions and indel positions, >1.5% between the two most divergent specimens) observed in *H.* cf. *umbilicatum* is so large that *H.* cf *umbilicatun* probably represents a species complex. The group can tentatively be divided into four taxa that would seem to have a non-overlapping distribution: Eurasia, central Europe, eastern North America, and western North America. The *H.* cf. *umbilicatum* complex deviates from the closest species, *H. ellipsosporum*, by nine substitutions and indel positions (> 1.5%).

Ecology and distribution: In conifer dominated forests, among mosses or on damp ground amongst *Sphagnum*. Producing basidiomata in autumn. Circumboreal in distribution.

Notes: Hydnum cf. *umbilicatum* is rather small and slender. The pileus is pale orange ochraceous to orange ochraceous and often with a distinct depression in the center. It can be distinguished from all other similar species by the large subglobose basidiospores.

Hydnum umbilicatum was described from eastern North America, and the type locality is Hague, New York. Huhtinen and Ruotsalainen (2006), who examined the type specimen of *H. umbilicatum* morphologically, cited spore measurements of 7.4–9.0 × 7.0–8.7 μm, av.=8.2 × 7.6

µm, Q=1.0–1.2, Q av.=1.0 based on basidiospores obtained randomly from the spines. Our measurements of *H.* cf. *umbilicatum* were calculated by discarding the smallest (presumably immature) basidiospores; Q-values have been calculated to two decimals instead of one. By treating the original spore measurements of Huhtinen and Ruotsalainen (2006) from the type specimen of *H. umbilicatum* the same way as we have done for the other species in this paper, the resulting values are 7.5–9.0 × 7.4–8.7, av. 8.4 × 8.0 µm, Q=1.00–1.14, Q av.=1.06, more comparable with our other measurements in this paper.

Grebenc et al. (2009), Olariaga et al (2012), Vizzini et al. (2013), Yanaga et al. (2015), and Feng et al. (2016) applied the name *H. umbilicatum* to the species here described as *H. oregonense*, known only from western North America. As such, we concluded that the western species does not represent Peck's *H. umbilicatum*. Potential candidates for *H. umbilicatum* currently known from eastern North America are *H. canadense, H. mulsicolor,* and *H. submulsicolor* in *H.* subsect. *Mulsicolores* and *H.* cf. *umbilicatum* and *H. quebecense* in *H.* subsect. *Tenuiformia*. In the first three species, basidiospores average 8.5 × 7.5 µm with a maximum width of 8.3 µm. *Hydnum quebecense* has on average slightly larger basidiospores 8.6 × 7.7 µm with an observed maximum width of 8.2 µm. The only species, however, to produce at least some basidiospores > 8.3 µm diam (as observed in the type specimen) is *H*. cf. *umbilicatum*. We therefore conclude that among the currently known eastern North American species, the one presented here best fits the type material of *H. umbilicatum*. Huhtinen and Ruotsalainen (2006) applied the name *H. umbilicatum* to this species. However, more studies on North American material and sequencing of type material, or designation of an epitype, are needed for an unambiguous interpretation of *H. umbilicatum*.

Grebenc et al. (2009) and Feng et al. (2016) included *H*. cf. *umbilicatum* as circumscribed here in *H. ellipsosporum,* whereas Olariaga et al (2012) and Vizzini et al. (2013) treated it as *H.* aff. *ellipsosporum.* The two clades are clearly distinct morphologically and easy to identify. The basidiospores of *H. ellipsosporum* are ellipsoid (av. 10 × 6.6 μm), whereas the basidiospores of *H*. cf. *umbilicatum* are subglobose (av. 8.6–8.9 × 8.0–8.1 μm). The intraspecific variation in ITS region within *H*. cf. *umbilicatum* is rather large, and some subclades were formed in the current phylogenetic analysis. These groups also correlate with small differences in basidiospore size in specimens from different geographical areas. Further studies are needed to clarify the taxonomy of *H*. cf. *umbilicatum*.

TAXA OF UNCERTAIN POSITION

Hydnum melitosarx Ruots., Huhtinen, Olariaga, Niskanen, Liimat. & Ammirati, sp. nov. FIGS. 8H, 9J

IndexFungorum: IF553907

Typification: USA. ALASKA: Fairbanks, Ballaine Lake trails, northeast of University campus, in *Picea* dominated forest with *Betula, Alnus, Salix*, and *Populus*, on rich ground, 14 Aug 2011, *K. Liimatainen & T. Niskanen 11-056* (**holotype** H7043937, **isotype** K(M)248984, **isotype** NY). GenBank: ITS=KX388683.

= *Hydnum* RU6 ss. Grebenc et al. Anales Jard Bot Madrid 66S1:126 and 129. 2009.

Misappl.: *Hydnum rufescens* ss. Ostrow and Beenken (2004).

Etymology: *melitosarx* (L.). in reference to the honey color of the basidiomata.

Description: Basidiomata medium-sized, slender, often with a long stipe compared to the pileus diameter. Pileus 20–50 mm diam, at first convex, later more or less plane with somewhat incurved margin, rarely with a small depression in the center, surface pale orange-brown ochraceous to orange-brown ochraceous, somewhat paler towards the margin. Stipe 30–70 mm long, 4–13 mm diam at apex, cylindrical, white to very pale ochraceous, becoming more orange brownish where scratched. Spines usually non-decurrent, sometimes with scattered small decurrent spines, crowded, acute, whitish. Basidiospores 7.0–8.6 × 6.4–7.8 µm, av.= 7.9 × 7.2 µm, Q=1.01–1.25, Q av.=1.11, subglobose, some broadly ellipsoid, thin-walled. Basidia 40–45 × 8.5–11 µm, usually 3-spored, sterigmata 4–5.5 µm long. Hyphae of the apex of the spines cylindrical, thin-walled, more or less yellowish, with cylindrical ends 3–4.5 µm diam. ITS sequence (KX388683) distinct from other species of *H.* sect. *Rufescentes,* which deviates by over 20 substitutions and indel positions.

Ecology and distribution: In mixed forests (*Pinus*, *Picea, Fagus, Quercus, Corylus*). Producing basidiomata in autumn. Europe, North America, and Asia.

Notes: Basidiomata of *H. melitosarx,* diagnosed by the pale orange brown pileus color and relatively long stipe, resemble species in *H.* sect. *Mulsicolores* and *H.* sect. *Tenuiformia*. The basidiospore average size (7.9 × 7.2 µm) in *H. melitosarx* falls among averages cited in *H.* subsect. *Mulsicolores* and can be used to separate *H. melitosarx* from the species of *H.* subsect. *Mulsicolores*. Species in *H.* subsect. *Tenuiformia* have larger (av. > 8.5 × 7.5 µm) basidiospores. The phylogenetic relationships of *H. melitosarx* within *H.* sect. *Rufescentes* remain unresolved based on ITS sequence data. However, the current phylogenetic analysis places it, although without support, as sister to *H.* subsect. *Tenuiformia*, a placement that also seems morphologically acceptable.

KEY TO THE SUBGENERA, SECTIONS, AND SUBSECTIONS OF *HYDNUM*

A key to subgenera, sections, and subsections is provided here, and a key to all currently known species is provided in SUPPLEMENTARY FILE 2. The diversity of the genus from many geographical areas is still poorly known, and new species will likely be discovered. Even though the groups and species do not look similar, there is considerable overlap in the morphological characteristics that makes constructing a key and identification of certain species difficult. The subgenera, sections, and subsections of *Hydnum* can, in most cases, be rather easily separated from another.

1. Basidiomata more or less white or cream-colored 2

1. Basidiomata ochraceous to orange brown 5

2. Basidiospores av. <7 × 7 µm *H.* subg. *Albi*

2. Basidiospores av. >7 × 7 µm 3

3. Q av. value >1.25 *H.* subg. *Pallidi*

3. Q av. value <1.20 4

4. Basidiospores subglobose to very broadly ellipsoid, usually ranging from roundish to more ellipsoid, Q av. value usually 1.15–1.20 *H.* subg. *Hydnum*

4. Basidiospores subglobose, no broadly ellipsoid basidiospores present, Q av. value 1.07–1.13 *H.* sect. *Magnorufescentes*

5. Basidiomata small to medium, usually slender; pileus often, but not always, with a small depression in the center; spines usually non-decurrent 6

5. Basidiomata medium to large, fleshy, not slender; pileus without a depression; spines non-decurrent to decurrent 8

6. Q av. value usually >1.15 *H.*subsect. *Rufescentes* and *H.* /Ovoideispori

6. Q av. value usually <1.15 or basidiospores large and ellipsoid, av. 10.0–6.6 µm 7

7. Basidiospores large, subglobose (av. >8.6 × 7.9 µm) or distinctly ellipsoid (av. 10.0–6.6 µm) *H.* subsect. *Tenuiformia*

7. Basidiospores smaller, subglobose, av. 7.5–8.6 × 6.6–7.7 µm *H.* subsect. *Mulsicolores*, *H. melitosarx*

8. Basidiospores subglobose, Q av. value 1.07–1.13 *H.* sect. *Magnorufescentes*

8. Basidiospores subglobose to broadly ellipsoid, Q av. value usually 1.15–1.30 9

9. Spines non-decurrent; basidiomata medium-sized; pileus surface sometimes lumpy *H.* subsect. *Rufescentes*

9. Spines decurrent, rarely non-decurrent; basidiomata medium- to large; pileus surface smooth to only somewhat lumpy *H.* subg. *Hydnum*

DISCUSSION

Species delimitation.—All species recognized in this study have smaller intraspecific variation than interspecific variation in their ITS regions, except for the *H.* cf. *umbilicatum* complex, which may comprise several species. Species separation is also often supported by morphological, ecological, and/or distributional data. Most, about two thirds, of the species can be distinguished by a 98.5% (ITS) threshold value, the default value for species hypothesis in UNITE, but the 99% threshold value is needed in some cases to be able to separate all species. The barcodes produced in this study are deposited in the RefSeq database (Schoch et al. 2014) and used as a basis to name species hypotheses in UNITE (Kõljalg et al. 2013). Through these databases the sequences can be used by the research community.

Feng et al. (2016) considered several of the species we recognize here as one species. For example, they treated *H. ellipsosporum*, *Hydnum* sp. 1, and *H.* cf. *umbilicatum* as one species – *H. ellipsosporum*. These three taxa, however, formed well supported clades in the ITS analysis (PP >0.97), and two, for which sequence data were available before 2013, had already been recognized in Olariaga et al. (2012) and Vizzini et al. (2013). Furthermore, Ostrow and Benken (2004), Huhtinen and Ruotsalainen (2006), and our study show that *H. ellipsosporum* and *H.* cf. *umbilicatum* can be readily separated by basidiospore shape and size and differences in ecology. Therefore, based on the other closely related sister species with morphological, ecological, and/or distributional differences studied, we conclude that species limits in *Hydnum* should be narrower than those used in Feng et al. (2016) and their conclusions on the species diversity, distribution, endemism, and ecological patterns should be, at least partly, re-evaluated.

Infrageneric classification.— Morphological and molecular data support the division of North American, European, Asian, and some Oceanic species into four subgenera: *Albi*, *Pallidi*, *Hydnum*, and *Rufescentes*. Additional groups from Australasia are also known (Feng. et al. 2016), but they are not treated here in detail since Feng et al. (2016) showed that they were substantially distinct from Northern Hemisphere species and impossible to analyze together with other ITS sequences of the genus.

Hydnum subg. *Albi* includes small to large whitish to cream-colored species with small, subglobose to broadly ovoid basidiospores (av. < 7 × 7 μm, Q av. value usually 1.00–1.10). *Hydnum* subg. *Pallidi* is characterized by ochraceous to cream-colored, small to medium species with ovoid to broadly ellipsoid basidiospores (Q av. value usually >1.25).

Hydnum subg. *Hydnum* includes species traditionally identified as *H. repandum* and characterized by medium to large fleshy basidiomata with whitish to cream-colored or rarely orange ochraceous pilei, and subglobose to very broadly ellipsoid basidiospores (Q av. value usually 1.15–1.20). Within *H.* subg. *Hydnum*, two sections, *Hydnum* and *Olympici*, are recognized.

The most diverse subgenus is *H.* subg. *Rufescentes*, which includes the species primarily identified as *H. rufescens* in the past. The subgenus is further divided into sections *Magnorufescentes* and *Rufescentes*, with *H.* subg. *Magnorufescentes* including mainly medium to large fleshy basidiomata with cream-colored to orange ochraceous pilei and subglobose basidiospores (Q av. value 1.06–1.13) and *H.* subg. *Rufescentes* with mainly small to medium and often slender basidiomata with pale cream-ochraceous to deep reddish orange pilei (often with a small depression in the center) and subglobose to broadly ellipsoid basidiospores. Within

H. sect. *Rufescentes* three groups distinguished by morphology are recognized: subsections *Mulsicolores, Rufescentes*, and *Tenuiformia*.

***Usefulness of non-molecular characters in* Hydnum *taxonomy*.**—Although characters suitable for classification within *Hydnum* are few, the majority of species and infrageneric classifications are, at least to some extent, supported by morphological characteristics. The most useful are shape, average length, width, and Q-value of basidiospores combined with the size, color, and appearance of the basidiomata. Information on attachment of the spines and whether or not there is a depression at the center of the pileus may or may not be taxonomically useful. Many species appear geographically restricted and have specific ecological requirements that also help in identification. Nonetheless, sequencing the ITS region is often necessary for reliable identification.

Although the number of basidiospores per basidium varies even within one basidiocarp, it provides some indication of the group. For example, the large-spored *H.* subsect. *Tenuiformia* species (section *Rufescentes*, subgenus *Rufescentes*) typically have 2- to 3- or rarely 4-spored spored basidia. In other somewhat smaller-spored groups of section *Rufescentes*, the basidia are 3- or 4-spored. In *H.* sect. *Magnorufescentes* (subg. *Rufescentes*) the basidia are 4–5-spored. The hyphae of the spine apex may also provide some information. In *H.* subg. *Rufescentes* hyphae in the apical part of spine apex are cylindrical and rarely clavate, whereas in *H.* subg. *Hydnum* they are more often clavate and somewhat wider in diameter.

***Species diversity*.**— Recent molecular studies of *Hydnum* have focused mainly on European species (Ostrow and Beenken 2004; Grebenc et al. 2009; Olariaga et al. 2012; Vizzini et al. 2013). Of the 15 species recognized in the current study from Europe, 14 were already recognized by Olariaga et al. (2012), indicating that the majority, or at least the most common, of the species might now be known. So far, only two studies have been conducted outside of Europe: Yanaga et al. (2015) from Japan and Feng et al. (2016) with global sampling, including an emphasis on Asian and Australasian taxa. Based on these studies and our data, 22 species are confirmed from North America. In contrast, no species of *Hydnum* have been confirmed from South America, although an ITS sequence from an ECM root tip of *Pakaraimaea dipterocarpacea* (Cistaceae) in Venezuela representing *H. repandum* exists. However, this kind of distribution and ecology of the species is highly doubtful, thus we cannot exclude a possibility of some kind of error in this case. In addition, 10 species have been found in Australasia and 32 from Asia. At the moment we presumably have a rather good sampling from Europe, mediocre sampling from Asia, Australasia and North America, and poor or no sampling from Central America, South America, and Africa. Given that further exploration of poorly studied regions will lead to the discovery of additional new species, we estimate that less than half of the global diversity of *Hydnum* has been discovered.

***Ecology and distribution*.**—Very little is currently known about the ecology of *Hydnum* species, since for most only a few verified collections are known, and there are little root tip or metagenomics data readily available. The Northern Hemisphere species, at least in Europe and North America, would seem to associate primarily with plant hosts in the Pinaceae and/or Fagaceae. In addition, one *H. repandum* collection was made under *Populus* (Salicaceae.) *Hydnum rufescens* is known from *Tilia cordata* (Malvaceae) plantations and under *Corylus* (Betulaceae). Furthermore, *H. vesterholtii* is also known to occur with *Corylus*. While several species are known to associate with hosts in both the Pinaceae and Fagaceae, some species, like *H. rufescens*, might be less host-specific than, for example, species of *Russula* (Russulales) and *Cortinarius* (Agaricales). Many species seem to prefer (if not require) rich to calcareous soils, and we speculate that their diversity is highest in the Mediterranean-temperate areas of the Northern Hemisphere and in the richer forests at more northerly latitudes. According to Feng et al. (2016) some lineages of Australasian species associate mainly with Dipterocarpaceae and Myrtaceae. The two species from Papua New Guinea described in this paper associate with *Castanopsis* (Fagaceae).

In contrast with Feng et al. (2016), we conclude that species distribution patterns seem rather restricted at a global scale. Thus far, only *H. mulsicolor* and *H.* cf. *umbilicatum* are known from both Europe and North America, whereas *H. boreorepandum* and *H. magnorufescens* occur in Eurasia. *Hydnum melitosarx* is the first *Hydnum* species confirmed with a circumboreal distribution. Another potential circumboreal species is *Hydnum* sp. 3 (FIG. 1) currently known only from Alberta, Canada, and China but which might very well also occur in Europe. Overall the most widespread species seem to be those with distributions extending to boreal areas, a pattern also seen in *Cortinarius* (Niskanen et al. 2016). All other species in this study are currently only known from a single continent.

At the subgenus, section, and subsection levels, species from different continents (Europe, Asia, Oceania, and North America) do not, in most cases, form distinct evolutionary lineages, suggesting the importance of historical intercontinental dispersal processes. The only exception is part of the Oceanic-southeast Asian species. In Feng et al. (2016) several of them, forming two clades, diverged deeply from the Northern Hemisphere groups. Feng et al. (2016) suggested that these species could be ancient relics isolated in this region for a long period of time.

Obstacles in naming* Hydnum *diversity.— Of the 49 species recognized in this study, 39 were undescribed. Using the species concept applied here, the Feng et al. (2016) data most likely include another 27 new species from Oceanic-southeast Asia and Australasia not included in our analyses, amounting to a total of 66 *Hydnum* species worldwide. In the era of molecular taxonomy, seven *Hydnum* molecular studies have been published in the past 12 years (Agerer et al. 1996; Ostrow and Beenken 2004; Grebenc et al. 2009; Olariaga et al. 2012; Vizzini et al. 2013; Yanaga et al. 2015; Feng et al. 2016) in which only five new species were described. At that rate it would take approximately 160 years and 95 publications before the currently known diversity would be named. Most likely all agree that there has to be a quicker way for naming new species, but a consensus on how that should be done is still lacking, despite recent suggestions on how to speed up the description of new species known only from sequence data (Hawskworth et al. 2016).

Pre-DNA era taxonomy set forth rigid morphological standards for species descriptions that prevented the proposal of taxonomically superfluous names (synonyms) and provided an accurate tool for identification. Although species recognition has changed dramatically with the arrival of molecular taxonomy, our standards have not changed. For instance, in all European studies on *Hydnum* to date, authors found more species than they actually named and the delimitation of most species was the same from study to study. Thus, there already was a consensus among European authors concerning the number and delimitation of *Hydnum* species, but the naming of new taxa did not take place, because the identity of *H. rufescens* had not been clarified, and there was an absence of reliable morphological characters for separating the species.

Therefore, we should first quickly stabilize the application of widely used old names by selecting a neotype or, where required, an epitype. The starting point in taxonomic studies should be an Index Fungorum search of published names of the research group in focus. Following that, studies should include type materials or, when no type materials exist, specimens that fit the morphology, ecology and geographical origin cited in the original protologue to serve as a later neotype or epitype. Unfortunately, taxonomists usually start with a study of diversity and how to identify the species they have found. Only later do they start to consider how to apply the already described names when the diversity has been shown to be greater than previously thought, and one cannot apply the names based only on morphology.

Furthermore, species should be described sooner rather than later, including cryptic species, since DNA barcoding now provides a much more reliable tool for identification than morphology. Also, there are not that many people who are able to recognize the majority of *Hydnum* species based on morphology because gaining that expertise usually takes several years. Most likely while there are only a few hundred mycologists who can recognize the easiest species in a genus, like *H. ellipsosporum*, all other professional and amateur mycologists may be able to recognize only species groups. Therefore, our target audience should not only include expert mycologists but also others, like ecologists, who can use sequences for identification.

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Figure 1. Phylogram resulting from the RAxML analysis of ITS regions. Bootstrap values greater than 50% are indicated above branches. Sequences originating from type specimens are in boldface.

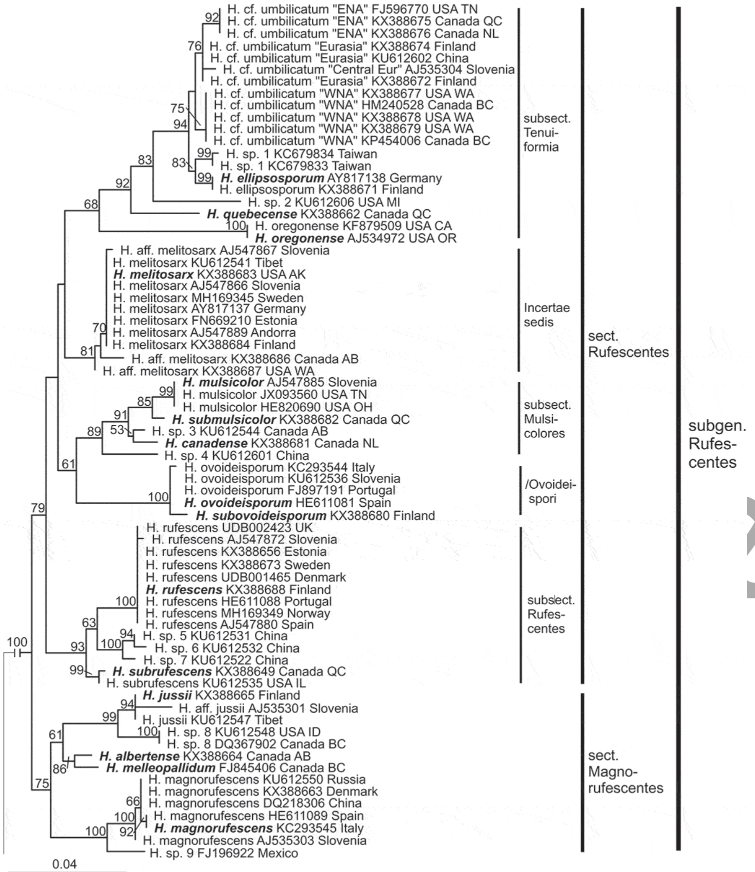


Figure 2. Basidiomata of species of subgenera *Albi* and *Pallidi*. A. *H. zongolicense* (MEXU 26248, type). B. *H. vesterholtii* (H6069769). Photograph A Roberto Garibay-Orijel, B Kare Liimatainen. Bar=10 mm.

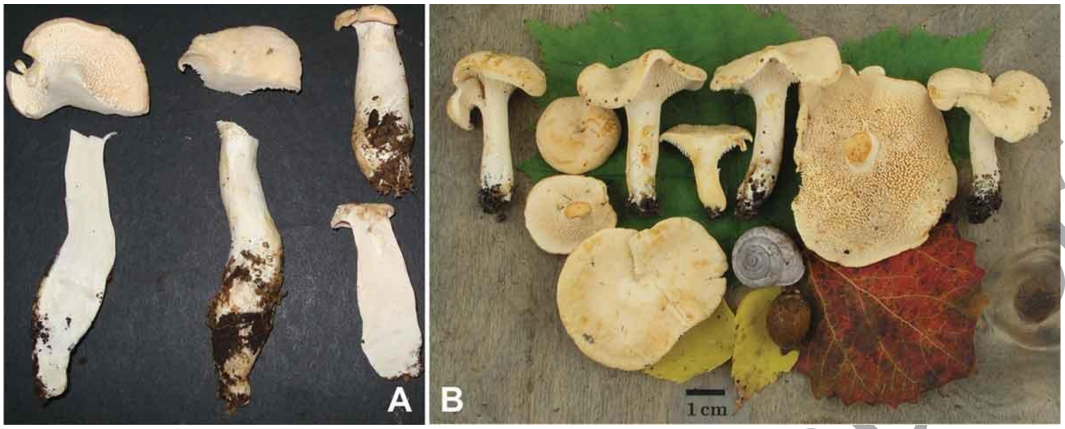


Figure 3. Basidiospores of species of subgenera *Albi* and *Pallidi*. A. *H. subcremeoalbum* (TU110688, type). B. *H. treui* (TU110403, type). C. *H. zongolicense* (MEXU 26248, type). D. *H. vesterholtii* (H6069769). Photographs A–C Tuula Niskanen and Ross Scambler, D Roberto Garibay-Orijel. Bar=10 µm.

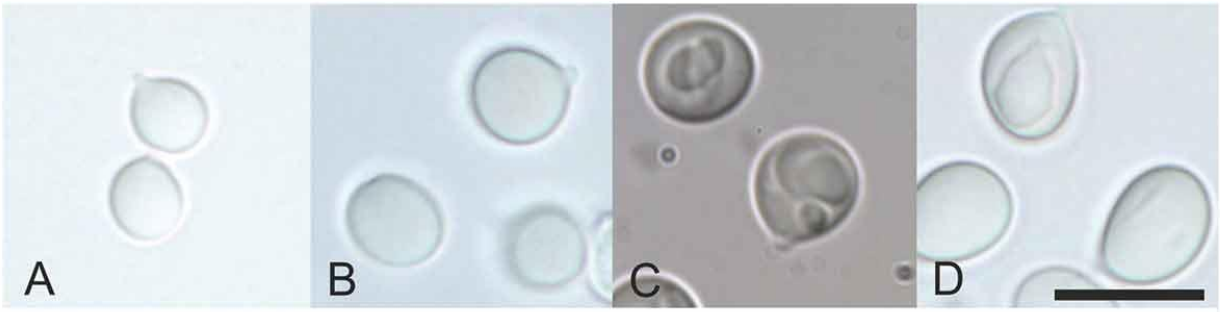


Figure 4. Basidiomata of species of subgenus *Hydnum*. A. *H. repandum* (H6003710, type). B. *H. repandum* (H6001840). C. *H. boreorepandum* (H6003711, type). D. *H. neorepandum* (TN 10-095, H, type). E. *H. olympicum* (H7043715, type). F. *H. subolympicum* (DAOM744368, type). Photographs A–E Kare Liimatainen, F Maria Voitk. Bar=10 mm.

Figure 5. Basidiospores of species of subgenus *Hydnum*. A. *H. repandum* (H6003710, type). B. *H. boreorepandum* (H6003711, type). C. *H. neorepandum* (H7043726, H, type). D. *H. olympicum* (H7043715, type). Photographs Tuula Niskanen and Ross Scambler. Bar=10 µm.

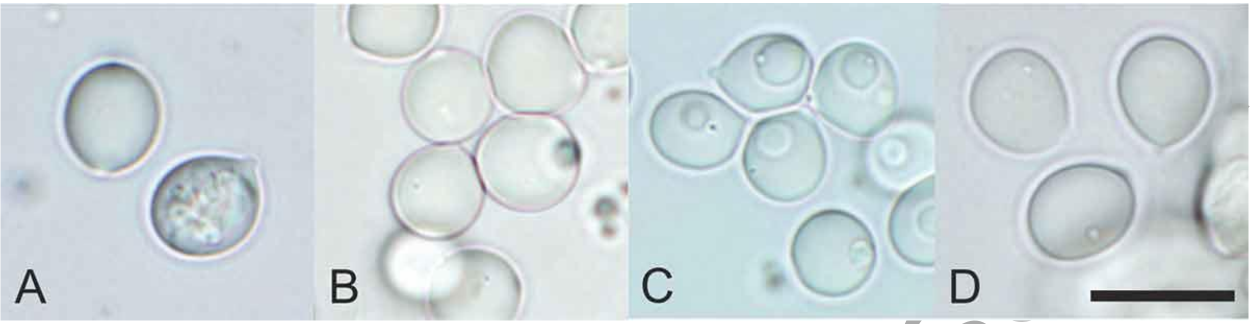


Figure 6. Basidiomata of species of section *Magnorufescentes*. A. *H. albertense* (H7043704, type). B. *H. jussii* (H6003709, type). Photograph Kare Liimatainen. Bar=10 mm.

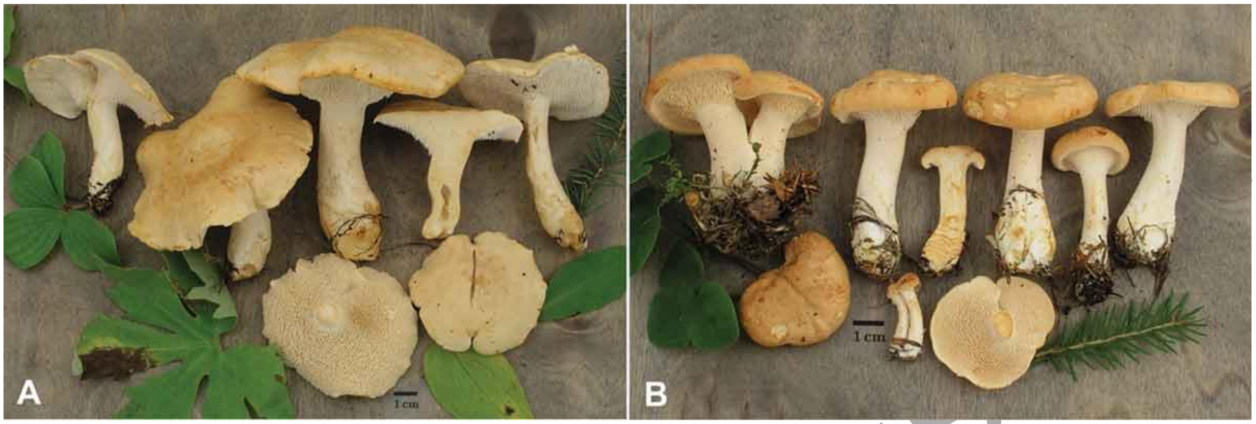


Figure 7. Basidiospores of species of section *Magnorufescentes*. A. *H. albertense* (H7043704, type). B. *H. jussii* (H6003709, type). C) *H. melleopallidum* (UBC F17492, type). Photographs Tuula Niskanen and Ross Scambler. Bar=10 µm.

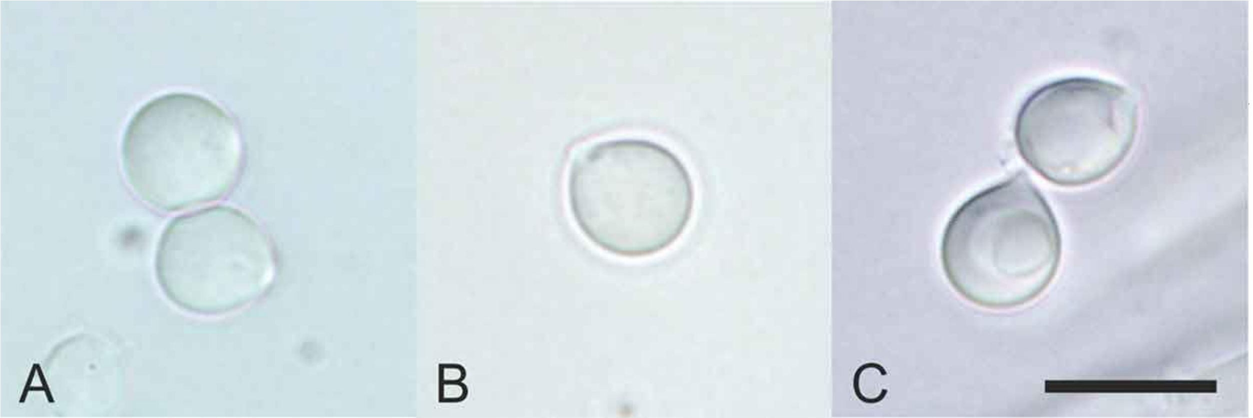
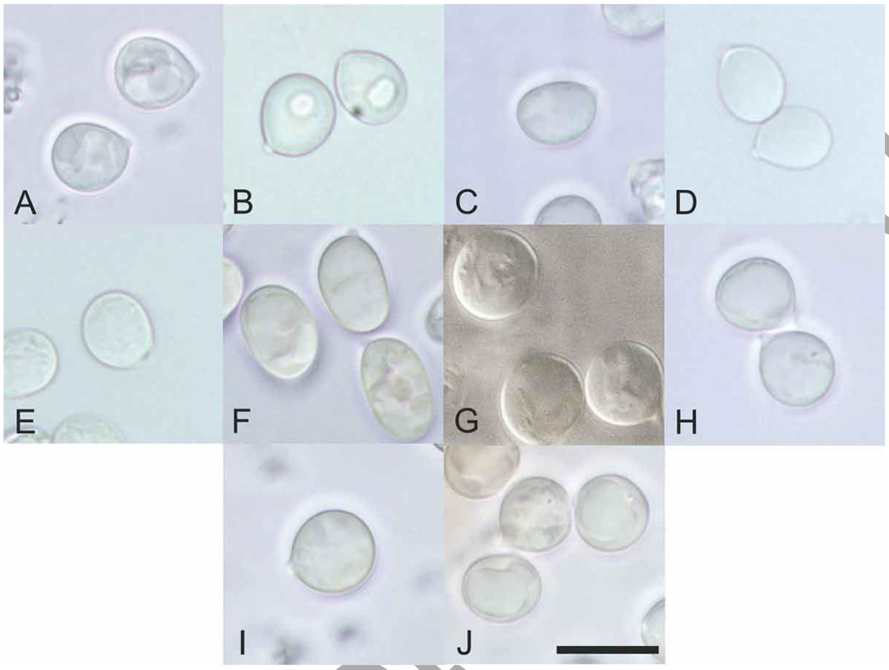
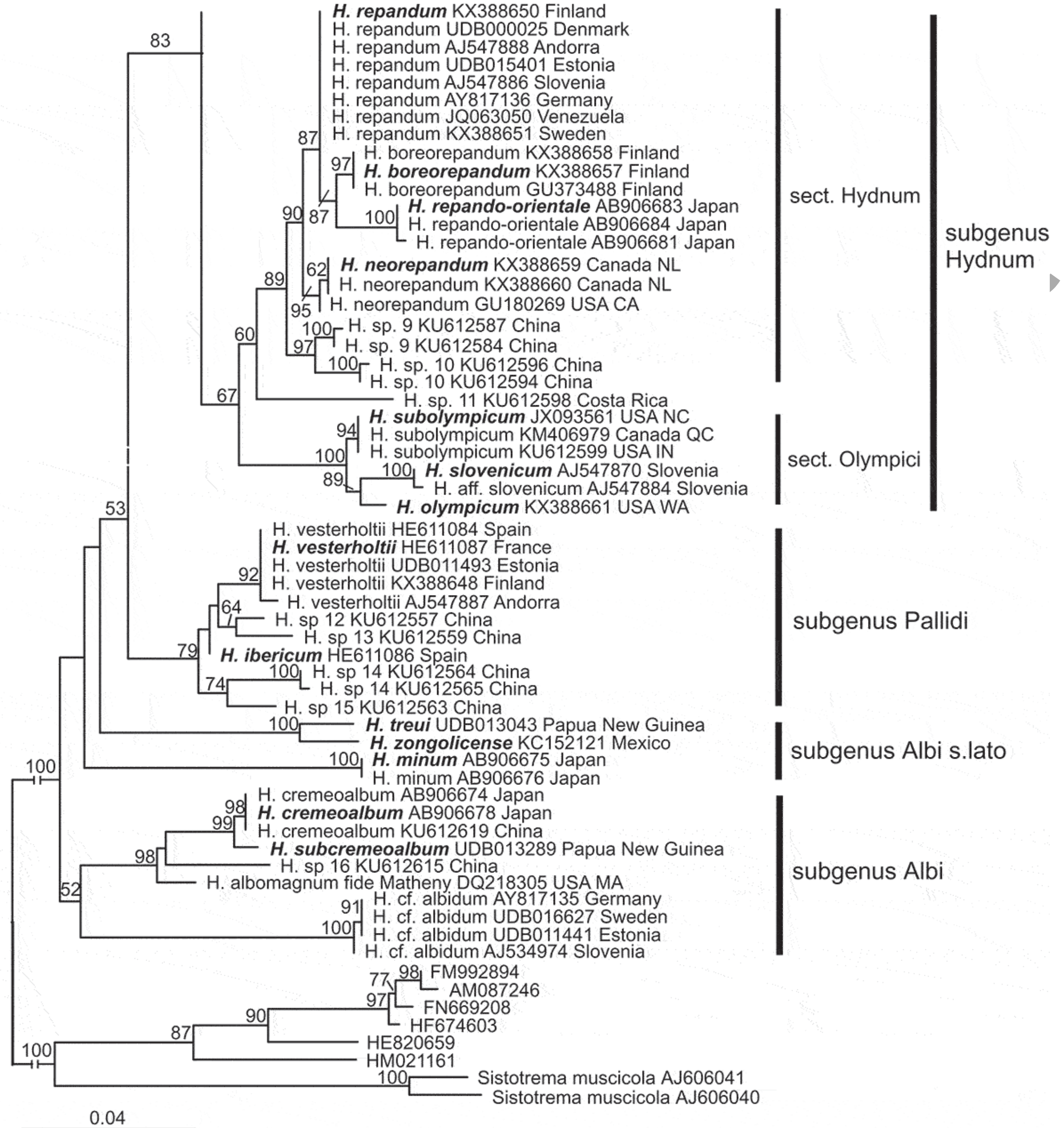


Figure 8. Basidiomata of species of section *Rufescentes*. A. *H. canadense* (H7043727, type). B. *H. subovoideisporum* (H6003707, type). C. *H. rufescens* (H6003708, type). D. *H. subrufescens* (H7043705, type). E. *H. ellipsosporum* (H6069758). F. *H. quebecense* (H7043948, type). G. *H.* cf. *umbilicatum* (H6003706). H) *H. melitosarx* (H7043937, type). Photographs Kare Liimatainen. Bar=10 mm.

Figure 9. Basidiospores of species of section *Rufescentes*. A. *H. canadense* (H7043727, type). B. *H. submulsicolor* (H7043716, type). C. *H. subovoideisporum* (H6003707, type). D. *H. rufescens* (H6003708, type). E. *H. subrufescens* (H7043705, type). F. *H. ellipsosporum* (H6069758). G. *H. oregonense* (OSC, g2010502h1-09, type). H. *H. quebecense* (H7043948, type). I. *H.* cf. *umbilicatum* (H6003706). J. *H. melitosarx* (H7043937, type). Photograph G Lorelei Norvell, other photographs Tuula Niskanen and Ross Scambler. Bar=10 µm.




H. repandum KX388650 Finland
H. repandum UDB000025 Denmark
H. repandum AJ547888 Andorra
H. repandum UDB015401 Estonia
H. repandum AJ547886 Slovenia
H. repandum AY817136 Germany
H. repandum JQ063050 Venezuela
H. repandum KX388651 Sweden
H. boreorepandum KX388658 Finland
H. boreorepandum KX388657 Finland
H. boreorepandum GU373488 Finland
H. repando-orientale AB906683 Japan
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H. repando-orientale AB906681 Japan
H. neorepandum KX388659 Canada NL
H. neorepandum KX388660 Canada NL
H. neorepandum GU180269 USA CA
H. sp. 9 KU612587 China
H. sp. 9 KU612584 China
H. sp. 10 KU612596 China
H. sp. 10 KU612594 China
H. sp. 11 KU612598 Costa Rica
H. subolympicum JX093561 USA NC
H. subolympicum KM406979 Canada QC
H. subolympicum KU612599 USA IN
H. slovenicum AJ547870 Slovenia
H. aff. slovenicum AJ547884 Slovenia
H. olympicum KX388661 USA WA
H. vesterholtii HE611084 Spain
H. vesterholtii HE611087 France
H. vesterholtii UDB011493 Estonia
H. vesterholtii KX388648 Finland
H. vesterholtii AJ547887 Andorra
H. sp 12 KU612557 China
H. sp 13 KU612559 China
H. ibericum HE611086 Spain
H. sp 14 KU612564 China
H. sp 14 KU612565 China
H. sp 15 KU612563 China
H. treui UDB013043 Papua New Guinea
H. zongolicense KC152121 Mexico
H. minum AB906675 Japan
H. minum AB906676 Japan
H. cremeoalbum AB906674 Japan
H. cremeoalbum AB906678 Japan
H. cremeoalbum KU612619 China
H. subcremeoalbum UDB013289 Papua New Guinea
H. sp 16 KU612615 China
H. albomagnum fide Matheny DQ218305 USA MA
H. cf. albidum AY817135 Germany
H. cf. albidum UDB016627 Sweden
H. cf. albidum UDB011441 Estonia
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sect. Olympici
subgenus Hydnum
subgenus Pallidi
subgenus Albi s.lato
subgenus Albi
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