Mycologia, 104(6), 2012, pp. 1443–1455. DOI: 10.3852/11-378

Two new species of *Hydnum* with ovoid basidiospores: *H. ovoideisporum* and *H. vesterholtii*

Ibai Olariaga[1]

Department of Plant Biology and Ecology (Botany), University of the Basque Country (UPV/EHU), Apdo 644, E-48080 Bilbao, Spain

Tine Grebenc

Slovenian Forestry Institute, Večna pot 2, SI-1000 Ljubljana, Slovenia

Isabel Salcedo

Department of Plant Biology and Ecology (Botany), University of the Basque Country (UPV/EHU), Apdo 644, E-48080 Bilbao, Spain

María P. Martín

Departamento de Micología, Real Jardín Botánico, RJB-CSIC, Plaza de Murillo 2, E-28014 Madrid, Spain

Abstract: Two new species of *Hydnum*, characterized by slender *Hydnum rufescens*-like basidiomes and ovoid to broadly ellipsoid basidiospores, are described from the Iberian Peninsula based on morphological and ITS molecular data. *Hydnum ovoideisporum* is distinguished by pilei with deep orange tones and strong preference for calcareous soil. It is widespread in the Iberian-Mediterranean area. *Hydnum vesterholtii* is characterized by its ocher to light ocher pileus, and nearly all the collections were made in the Pyrenees. Both ovoid-spored species are monophyletic well supported groups in the maximum parsimony and Bayesian ITS phylogenies, while the remainder of the samples assigned to *H. rufescens* s.l. and having globose basidiospores split into six well supported clades. The need to typify the name *Hydnum rufescens* is discussed, and a provisional key is given for the European taxa of *Hydnum*.

Key words: Cantharellales, cantharelloid clade, ITS nrDNA, phylogeny, stichic basidia, taxonomy

Introduction

Hydnum L. : Fr. is an ectomycorrhizal genus characterized by stipitate and pileate basidiomata with spiny hymenophore, suburniform basidia of stichic nuclear division (Donk 1933, Maas Geesteranus 1971, Pegler et al. 1997) and ampullate septa on the mycelial hyphae (Raidl and Agerer 1992, Agerer et al. 1996). Molecular phylogenetic studies have shown that *Hydnum* is nested in the cantharelloid clade (Pine et al. 1999, Moncalvo et al. 2006), for which the stichic basidia are a synapomorphy. The genus is distributed mainly over temperate and tropical areas of Europe, North America and Asia, but reports also are known from Australia and New Zealand (Cooke 1890, Maas Geesteranus 1971). Although the number of published *Hydnum* species is considerably greater (www.mycobank.org), based on morphological characters, about 10 morphological species currently are accepted by the mycological community. However, the actual number of *Hydnum* species worldwide is certainly higher. Knowledge of species concepts, continental speciation and diversity is poor. *Hydnum* species, popularly called ''hedgehogs'' or ''wood urchins'', are harvested and even commercialized (Pegler et al. 1997, Murrin 2008).

Despite being a common genus having edible species in several geographic areas, species delimitation in *Hydnum* is problematic (Hall and Stuntz 1971; Maas Geesteranus 1971, 1976; Grebenc et al. 2009). Three *Hydnum* species have been recognized conventionally in Europe (viz. *Hydnum albidum* Peck, *Hydnum repandum* L. : Fr. and *Hydnum rufescens* Pers. : Fr.). Whereas *H. albidum* is well characterized by pale basidiomata and small basidiospores, morphologically intermediate forms occur between *H. repandum* and *H. rufescens* (Maas Geesteranus 1976, Otto 1997, Huhtinen and Ruotsalainen 2006). Ostrow and Beenken (2004) demonstrated with morphological and ITS data that *H. repandum* and *H. rufescens* are separate species and described *Hydnum ellipsosporum* Ostrow & Beenken, characterized by ellipsoid basidiospores. Huhtinen and Ruotsalainen (2006) distinguished three *H. rufescens*-like taxa based on spore characters: *H. ellipsosporum*, *H. rufescens* and *Hydnum umbilicatum* Peck. The latter name, described from North America, was used for large globose-spored northern European collections distinct from *H. rufescens*. In addition to the basidiospore variability, Agerer et al. (1996) obtained different RFLP restriction patterns in *H. rufescens* samples from different areas in Europe. The ITS nrDNA analyses by Grebenc et al. (2009) yielded 11 well supported clades, of which six corresponded to specimens resembling *H. rufescens* (referred to as RU1–RU6) and two more clades for specimens with the typical morphological features of *H. repandum* (as RE1, RE2). In general, no specific characters could be

Submitted 16 Nov 2011; accepted for publication 30 Apr 2012.
[1] Corresponding author. E-mail: ibai.olariaga@nrm.se

assigned to any clade. However, other morphological species such as *H. albidum* and *H. ellipsosporum* yielded monophyletic clades.

A number of macroscopic characters have been used for *Hydnum* species delimitation, such as the basidioma habit, pileus color, presence of umbilicus in the pileus, spine shape and attachment to the stipe, and a central or excentric stipe. Some of these characters are variable and plastic. In this framework, microscopic data appear to be more constant and objective. The spore characters, especially the shape, seem to constitute the most reliable character to delimit some *Hydnum* species (Ostrow and Beenken 2004), such as *H. albidum* and *H. ellipsosporum*. However, in view of the high basidiospore diversity and the fact that it is not always easy to correlate spore characters with the clades obtained from the phylogenetic analyses of the ITS region (Ostrow and Beenken 2004, Grebenc et al. 2009), more thorough morphological studies are needed to compare to molecular data. Some of the further characters that might be taxonomically informative in *Hydnum* are the pileus color, shape of the spines, attachment to the stipe and number of sterigmata in the basidia.

During a morphological study of *Hydnum* focusing on the Iberian Peninsula (Olariaga, 2009), two undescribed morphological species that produce slender fruiting bodies of the *H. rufescens* type with ovoid basidiospores were found. Thus, the aims of this work were (i) to achieve a better understanding of species delimitation in *Hydnum*, drawing attention to the spore characters, and (ii) to describe two new species based on morphological and molecular data.

MATERIALS AND METHODS

Morphological study.—The morphological examination was based on 10 fresh specimens collected 2002–2009 in the Iberian Peninsula and the bordering French Pyrenees. Twenty-one additional dried specimens sequenced by Grebenc et al. (2009), including the holotype of *H. ellipsosporum* (M 139587), were examined (TABLE I). Color codes of fresh material were based on the charts of the Royal Horticultural Society (1995) and those of dried material on Munsell Color Corp. (1990). Microscopic characters were studied on dry material with a Nikon light microscope, with a 100× objective. To measure basidiospores a spine from the hymenophore was mounted in 5% KOH. Young, anomalous or aberrant basidiospores were disregarded, and well developed free basidiospores were measured in lateral view. Abbreviations describing basidiospore measurements are: L_m = mean length, W_m = mean width, $Q_m = L_m/W_m$; 25 basidiospores were measured per collection. The number of collections measured is indicated by an ''n''. The means of each collection were plotted in a graph for a more thorough comparison. Basidia measurements exclude sterigmata. The material is deposited at BIO-Fungi, GDAC, JA, LJU and MA-Fungi herbaria (Holmgren and Holmgren 1998).

DNA extraction, PCR amplification and sequencing.—DNA was extracted with a DNeasy Plant Mini Kit (QIAGEN, Hilden, Germany), and the ITS regions were amplified with Ready-To-Go™ PCR Beads (GE Healthcare, UK) (Martín and Winka 2000). The primer pair ITS1F/ITS4 was used for amplification of the ITS1-5.8S-ITS2 region, as described by White et al. (1990) and Gardes and Bruns (1993). Before sequencing, products were cleaned from the gel with QIAquick PCR purification kit (QIAGEN, Chatsworth, California). Both strands were sequenced separately at Macrogen (Seoul, South Korea). All samples were sequenced in both directions with the same primers as in the amplification. Sequencher™ 4.2 (Gene Codes Corp., Ann Arbor, Michigan) was used to assemble the consensus sequence from the two strands of the ITS nrDNA of each isolate. Sequences were submitted to the EMBL/GenBank/DDBJ (Cochrane et al. 2011) and UNITE (Abarenkov et al. 2011, http://unite.ut.ee/cite.php) databases (TABLE I). Sequences were compared with other available sequences at GenBank with Se-Al 2.0a11 Carbon (Rambaut 2002). The alignment was optimized visually. Alignment gaps were indicated as ''–'', and ambiguous nucleotides were marked ''n''.

Phylogenetic analyses.—The alignment was analyzed as in Grebenc et al. (2009) with PAUP* 4.0b10 for Macintosh (Swofford 2002) and MrBayes 3.0 (Huelsenbeck and Ronquist 2001). We included three *Sistotrema* species as outgroup: *Sistotrema muscicola* (Pers.) S. Lundell (AJ606040) and *Sistotrema alboluteum* (Bourdot & Galzin) Bondartsev & Singer (AJ606042), both ectomycorrhizal and closely related to *Hydnum* (Moncalvo et al. 2006, Di Marino et al. 2008) and the saprotroph *Sistotrema coronilla* (Höhn.) Donk (DQ397337). The first maximum parsimony analysis (MP) was carried out using the heuristic searches with TBR branch-swapping and MULPARS option in PAUP* and saving the best 1000 trees. Gaps were treated as missing data. Branch lengths equal to zero were collapsed to polytomies. For the assessment of branch confidence, nonparametric bootstrap (BP) support was estimated based on 10 000 replicates with the fast-step option (in each replication tree searches are performed with one random-sequence-addition replication and no branch swapping; Felsenstein 1985). The second analysis was conducted with a Bayesian approach (Larget and Simon 1999, Huelsenbeck and Ronquist 2001). It was performed assuming the HYK + G model as suggested by hierarchial likelihood ratio test (hKRTS) and Akaike information criterion (AIC). Best-fitting evolutionary model was estimated with MrModeltest 2.3 (Nylander 2004). Posterior probabilities (PP) were approximated by sampling trees with Markov chain Monte Carlo (MCMC). Posterior probabilities of each branch were calculated by counting the frequency of trees that were visited during MCMC analysis. A 10 000 000 generation run, starting at a random tree and employing two chains, was executed. A tree was saved every 100th generation, with a burn-in at 1000 sampled trees. AWTY (Nylander et al. 2008) was used to determine when the chains reached the stationary stage (Wilgenbusch et al.

TABLE I. Specimens included in the phylogenetic and spore diagram. New sequences are marked with an asterisk

Identification	Location	$L_m \times W_m$	Q_m	Voucher	GenBank	Clade
H. albidum	Slovenia, Divača, Divaški gabrk	5.2 × 3.7	1.43	LJU GIS 1341	AJ534974	AL
H. ellipsosporum	Germany, Thuringen, Steinach (west)	10.2 × 6.7	1.54	M 139587	AY817138	EL
H. ellipsosporum	Slovenia, Grajski Boršt	9.3 × 8.6	1.08	LJU-GIS 1327	AJ535304	–
*H. ovoideisporum**, holotype	Spain, Araba, Barrio	9.0 × 7.1	1.27	BIO-Fungi 12683	HE611081	OV
*H. ovoideisporum**	Spain, Gipuzkoa, Zumaia, Artadi	8.2 × 6.3	1.29	BIO-Fungi 14130	HE611083	OV
*H. ovoideisporum**	Spain, Araba, Kanpezu	9.3 × 6.8	1.37	BIO-Fungi 12902	HE611082	OV
*H. ovoideisporum**	Spain, Huesca, Villanúa	8.9 × 6.9	1.30	BIO-Fungi 12317	HE611080	OV
*H. vesterholtii**	Spain, Huesca, Cañón de Añisclo	8.2 × 6.5	1.27	BIO-Fungi 10429	HE611084	RE2
*H. vesterholtii**	Spain, Huesca, Barranco Garmo Negro	8.4 × 6.6	1.28	BIO-Fungi 10452	HE611085	RE2
*H. vesterholtii**, *holotype*	France, Pyrénées atlantiques, Forêt d'Issaux	8.7 × 6.8	1.29	BIO-Fungi 12904	HE611087	RE2
*H. vesterholtii**	Spain, Huesca, Villanúa	8.2 × 6.4	1.28	BIO-Fungi12330	HE611086	RE2
H. vesterholtii	Andorra, Estany de Engolateus	8.6 × 6.6	1.30	MA-Fungi 47726	AJ547887	RE2
H. repandum	Slovenia, Idrija, Gore	7.3 × 6.2	1.18	LJU GIS 1322	AJ547877	RE1
H. repandum	Slovenia, Idrija, Čekovik	7.5 × 6.6	1.13	LJU GIS 1321	AJ547878	RE1
H. repandum	Slovenia, Vače,	8.1 × 6.9	1.18	LJU GIS 1326	AJ547881	RE1
H. repandum	Slovenia, Šmartno pri Litiji, Pusti Javor	8.0 × 6.9	1.16	LJU GIS 1325	AJ547883	RE1
H. repandum f. *amarum*	Slovenia, Velike Lašče	8.4 × 7.1	1.27	LJU GIS 1337	AJ547871	RE1
H. rufescens	Slovenia, Ilova gora	7.7 × 6.2	1.24	LJU GIS 1324	AJ547869	RU1
H. rufescens	Slovenia, Polica, Grosuplje	9.1 × 7.0	1.32	LJUGIS 1340	AJ547884	RU1
H. rufescens	Slovenia, Idrija, Pringl	7.7 × 7.1	1.10	LJU GIS 1320	AJ535301	RU2
H. rufescens	Slovenia, Pusti Javor	7.5 × 7.0	1.08	LJU GIS 1328	AJ535302	RU3
H. rufescens	Slovenia, Pusti Javor, Šmartno pri Litiji	7.6 × 7.1	1.07	LJU GIS 1329	AJ535303	RU3
*H. rufescens**	Spain, Araba, Kanpezu	8.0 × 7.2	1.11	BIO-Fungi 12901	HE611089	RU3
H. rufescens	Slovenia, Rajhenavski Rog virgin forest, Žaga-Rog	8.5 × 7.5	1.15	LJU GIS 1332	AJ547868	RU4
H. rufescens	Slovenia, Velike Lašče	8.8 × 7.5	1.17	LJU GIS 1336	AJ547885	RU4
H. rufescens	Slovenia, Radovna, Mežjanca	8.1 × 7.2	1.14	LJU GIS 1331	AJ783969	RU4
H. rufescens	Slovenia, Idrija, Ilovce	7.7 × 7.1	1.08	LJU GIS 1330	AJ547872	RU5
*H. rufescens**	Portugal, Tras Os Montes, Macedo de Cavaleiros	8.9 × 7.3	1.22	BIO-Fungi 12760	HE611088	RU5
H. rufescens	Slovenia, close to Velike Lašče	8.4 × 7.0	1.21	LJU GIS 1333	AJ535305	RU6
H. rufescens	Slovenia, Nova Vas	8.5 × 7.7	1.10	LJU GIS 1339	AJ547867	RU6
H. rufescens	Andorra, El Serrat	7.8 × 7.4	1.06	MA-Fungi 47728	AJ547889	RU6

2004). The 50% majority rule consensus tree was calculated with the SUMT command of MrBayes. Phylogenetic trees were viewed with FigTree 1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/) and edited with Adobe® Illustrator CS3 13.0.1. (Adobe Systems Incorporated).

A combination of both bootstrap proportion and posterior probabilities was used to assess the level of confidence for a specific node (Lutzoni et al. 2004). The alignment matrix and the 50% majority rule consensus tree from the Bayesian analysis are available in TreeBASE (http://www.trebase.org) under TB2:S12109. Clades are named according to Grebenc et al. (2009).

RESULTS

Morphological study.—The L_m, W_m and Q_m spore values of the 31 specimens are provided (TABLE I).

The L_m and W_m of each collection were plotted (FIG. 1) for comparison. The two undescribed species and those *H. rufescens* samples placed in clade RU1 in Grebenc et al. (2009) form a group with ovoid to broadly ellipsoid basidiospores (Q_m 1.24–1.37). A second group with globose to subglobose basidiospores (Q_m 1.07–1.22) chiefly contains the samples identified as *H. rufescens* s.l. and shows no overlap with the first group. *Hydnum repandum* samples (RE1) show an intermediate spore type (Q_m 1.16–1.21) between both groups but overlapping the globose to subglobose-spored group. The dimensions of the *H. albidum* collection are the smallest among the studied material (L_m 5.2, W_m 3.7). On the contrary, those of *H. ellipsosporum* were ellipsoid, with the highest L_m (10.2) and Q_m (1.54) values, which differ from the rest of the samples. Collection LJU GIS 1327 (AJ535304), assigned to *H. ellipsosporum* in Grebenc et al. (2009), has large subglobose basidiospores that differ from those of the holotype of *H. ellipsosporum*. The spore shape is constant within all clades, with the exception of RU5, where the Q_m range is broad (1.06–1.22).

ITS sequence analyses.—Ten new sequences belonging to the genus *Hydnum* were generated (TABLE I). The complete alignment of 71 sequences contained a total of 717 unambiguously aligned nucleotides, of which 443 were constant, 99 variable but parsimony uninformative and 175 parsimony informative. The maximum parsimony analysis and the Bayesian inference produced congruent results gathered in the 50% majority rule consensus tree (FIG. 2). The genus was divided into 12 well supported clades (bs ≥ 75% or pp ≥ 0.95). The clades are named as in Grebenc et al. (2009), except a strongly supported new clade (bs = 100%, pp = 1.0), referred to as OV, that includes sequences obtained from collections BIO-Fungi 12317, BIO-Fungi 12683, BIO-Fungi 12902 and BIO-Fungi 14130. Sequences from collections BIO-Fungi 10429, BIO-Fungi 10452, BIO-Fungi 12330 and BIO-Fungi 12904 group with sequences in clade RE2 in Grebenc et al. (2009) with strong support (bs = 91%, pp = 1.0) as well. This clade comprises two smaller, well supported groups, one of which is assigned to *H. vesterholtii* (bs = 98%, pp = 1.0) and the other one to *H.* aff. *vesterholtii* (bs = 85%, pp = 0.91). The unique molecular and morphological features of the specimens in the OV and *H. vesterholtii* clades let us propose two new species in the genus *Hydnum*. The remaining new sequences from this study, BIO-Fungi 12901 and BIO-Fungi 12760, grouped respectively in the clades RU3 and RU5 (Grebenc et al. 2009). The collections assigned to *Hydnum albidum* and *H. ellipsosporum*, characterized respectively by small ovoid and large ellipsoid basidiospores, formed monophyletic groups, in agreement with Ostrow and Beenken (2004) and Grebenc et al. (2009).

TAXONOMY

Hydnum ovoideisporum Olariaga, Grebenc, Salcedo & M.P. Martín, sp. nov. FIGS. 3, 4

MycoBank MB563524

Basidiomata small to medium, growing isolated or fasciculate. Pileus 12–40 mm diam, generally non-fleshy, initially convex, plane afterward, sometimes depressed or umbilicate in the center, regular, seldom dimidiate. Surface velutinous, sometimes with small and erect scales at the margin, non-staining, not zoned. Color brownish orange (26A) to deep reddish orange (169C, 169D), pale orange in unexposed zones or basidiomata (23D, 26C), pale orange (23D) or white (155A, 159D) toward the margin. Margin initially involute, soon straight, somewhat sinuous and lobed with age. In exsiccatum ocher (10YR 6/6, 7/6). Stipe 20–40 × 2.5–9 mm, cylindrical or broader at the base, central or somewhat excentric, solid, velutinous, white (155D) to pale ocher (20C). Staining ocher (26A) when handled, sometimes conspicuous. In exsiccatum ocher (10YR 6/6, 7/6). Spines normally non-decurrent, sometimes leaving a bare zone around the stipe and with small decurrent spines, conical, not flattened, acute, not fimbriate, sometimes joined at the base, crowded, 2.0–3.1 × 0.2–0.4 mm, initially orange white (159D), pale orange ocher (19D, 20D) afterward. In exsiccatum brownish orange (7.5YR 5/8). Context white (155D), staining. Odor weak, fruity, citric-like; flavor mild, bitter afterward. Macrochemical reactions: KOH + context = pale greenish ocher.

Basidiospores ovoid to broadly ellipsoid, sometimes some cylindrical, apiculus cubic, thin-walled, non-amyloid, (7.5–)8–10(–10.5) × 6–7.5 μm (L_m = 8.1–9.3; W_m = 6.4–7.1; Q_m = 1.27–1.38; n = 4). Basidia suburniform to claviform, 4–5-spored, sometimes with scattered one, two or three-spored ones, clamped, 36–56 × 7–9.5(–12) μm. Hyphae of the apex of the spines arranged in parallel, cylindrical, thin-walled, yellow, clamped, with cylindrical to subclaviform ends (3–5 μm wide), without crystals. Pileipellis composed of hyphae forming a cutis-trichoderm, cylindrical to swollen, thin-walled, colorless to yellowish, clamped, 5.5–14 μm wide, with cylindrical and blunt ends. Stipitipellis composed of hyphae forming a trichoderm, cylindrical, thin-walled, with orange content, clamped, 3–5 μm wide, with cylindrical to narrowly claviform ends. Hyphae of the context woven, cylindrical to swollen, thin-walled, colorless to yellowish, clamped, 4–14 μm wide. Basal mycelium white, composed of woven hyphae, cylindrical, thin-walled, clamped, 4–5.5(–7) μm wide, with some ampullate at septa (6.5–8.5 μm).

Holotype: SPAIN. ARABA PROVINCE: Gaubea-Valdegobía, Barrio, under *Pinus sylvestris* on calcareous ground, 8

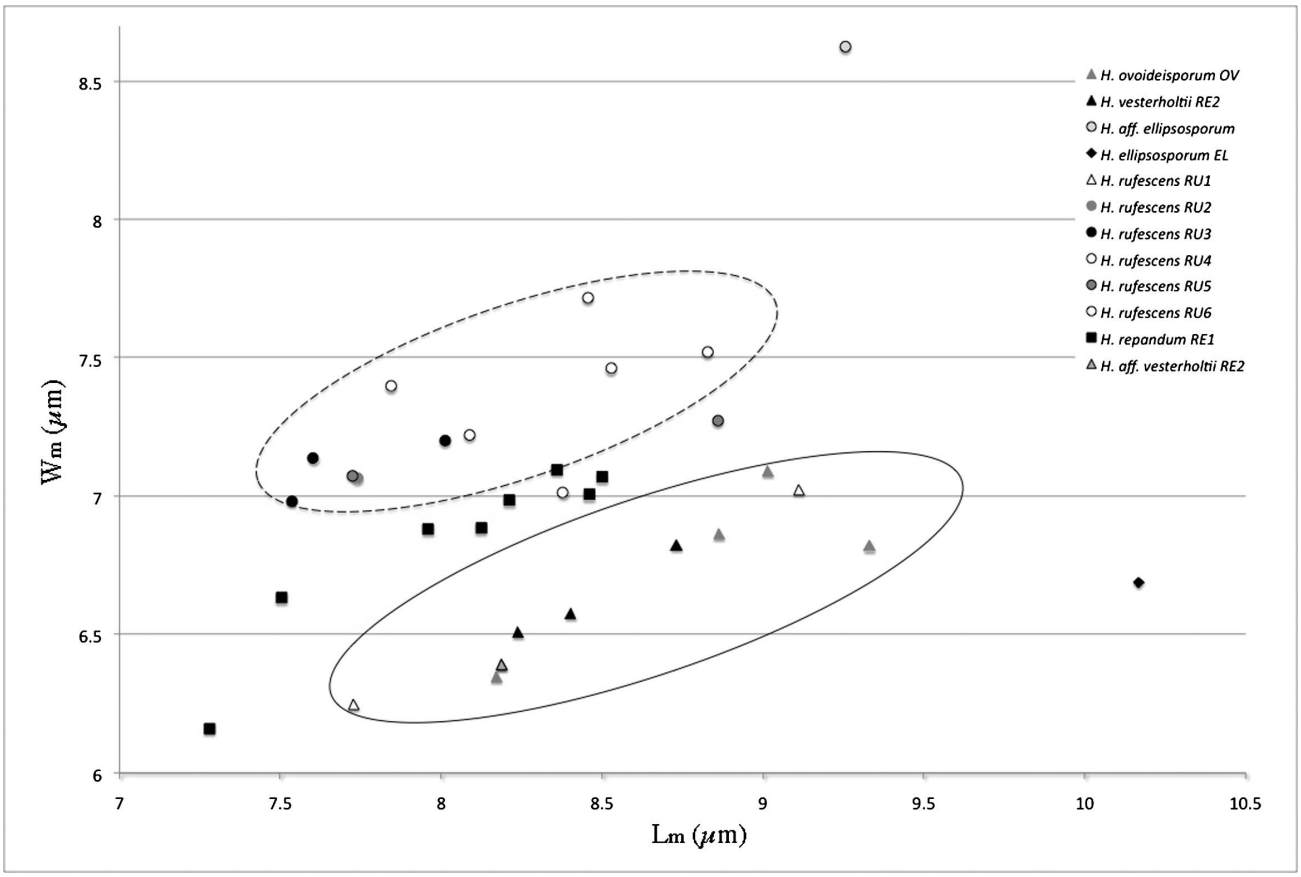

FIG. 1. Spore diagram of the *Hydnum* collections examined. *Hydnum albidum* is not plotted to allow the basidiospores of the rest of species to be compared in more detail. The continuous oval shows the ovoid-spored group, and the dashed oval indicates the globose-subglobose-spored group.

Nov 2007, *A. Laza & I. Olariaga*, (BIO-Fungi 12683). Isotype. F-207037 (S).

Etymology: In reference to the ovoid basidiospores.

Commentary: Hydnum ovoideisporum is characterized by slender basidiomata with deep orange tones in the pileus, in combination with ovoid to broadly ellipsoid basidiospores. The deep orange tones of the pileus, normally non-decurrent spines and occurrence in forests with rich ground are good characters for a tentative identification in the field, at least in the Mediterranean area. *Hydnum rufescens* s.l. shares a similar macroscopic appearance but differs in having globose to subglobose basidiospores. Furthermore, some of the taxa subsumed under *H. rufescens* seem to have paler tones in the pileus and decurrent or spathulate spines. *Hydnum vesterholtii*, described below, shares with *H. ovoideisporum* a similar habit and basidiospores, but it is primarily distinguished from *H. ovoideisporum* by the pileus devoid of orange tones. The rest of the taxa with ovoid basidiospores are to be found among the species producing larger fleshy basidiomata, such as *H. repandum*. However, the latter is delimited from *H. ovoideisporum* on the basis of the involute pileus that often has paler pinkish orange tones, decurrent spines and robust fruiting bodies with a thicker stipe.

Hydnum ovoideisporum has been observed to fruit abundantly in some localities of the northern Iberian Peninsula (e.g. Artadi and Barrio, Basque Country), where it seems to be a common and widespread species. The only records of *Hydnum ovoideisporum* that we are aware of are by Palazón (2001, as *H. rufescens*), and Mycokey (http://www.mycokey.org,), where ovoid basidiospores are shown for *H. rufescens*-like collections. Huhtinen and Ruotsalainen (2006) cited some *H. rufescens* populations that had elongate and narrower basidiospores than the typical collections. The spore shape of these collections would match *H. ovoideisporum*, as does the macroscopical appearance. *Hydnum ovoideisporum* has proved to be a widespread and common species in the Iberian Peninsula that has been overlooked and mistaken for other taxa of the *H. rufescens* complex. No older name that can be applied with certainty to *H.*

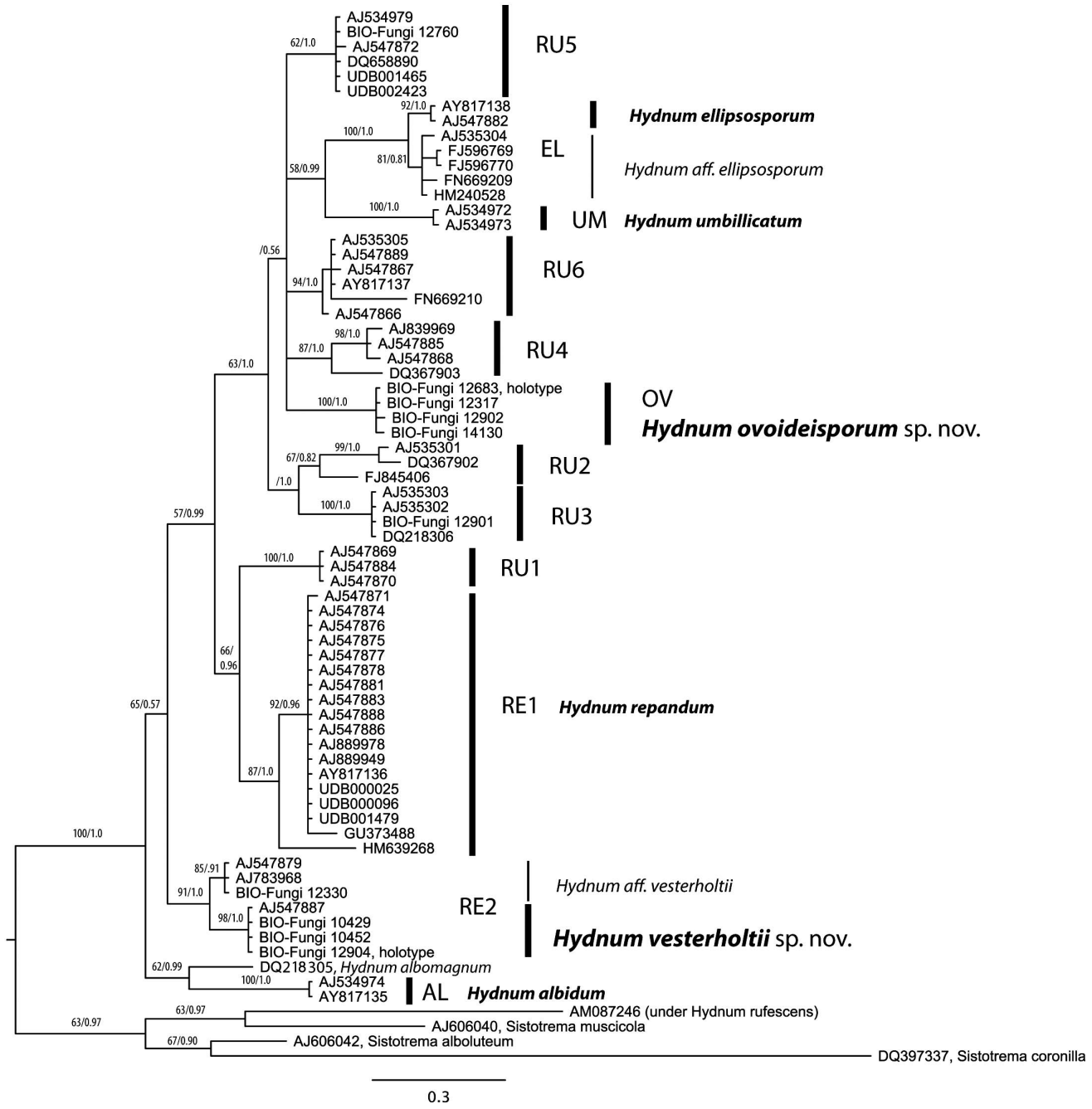

FIG. 2. The 50% majority rule Bayesian tree of *Hydnum* inferred from the ITS region assuming the HYK + G model. Parsimony bootstrap values (≥ 50%) and Bayesian posterior probabilities (≥ 95%) are indicated on the branches. AL, *H. albidum*; EL, *H. ellipsosporum*; OV, *H. ovoideisporum* sp. nov.; RE1, *H. repandum*; RU1 to RU6, *H. rufescens*; UM, *H. umbilicatum* and RE2, *H. vesterholtii* sp. nov.

ovoideisporum could be found in the literature. *Hydnum carnosum* Batsch was described making reference to a Schaeffer plate (Tab. 141, 1763), in which a taxon of *H. rufescens*-like appearance and globose spores is shown. Neither Batsch nor Schaeffer are known to have made herbarium specimens (Stafleu and Cowan 1976, 1985). Two names described by Raddi (1807), *Hydnum bicolor* Raddi and *H. bulbosum* Raddi, are also *H. rufescens*-like, but no type material is kept at his herbarium, and it will remain unknown whether they are ovoid-spored. Furthermore, *H. bicolor* Raddi is illegitimate (Art. 53.1) due to being a later homonym of *H. bicolor* Alb. & Schwein. : Fr. Another taxon described from France, *Hydnum repandum* var. *serotinum* (Quél.) Bourdot & Galzin, also has *H. rufescens*-like basi-

FIG. 3. *Hydnum ovoideisporum* sp. nov. (BIO-Fungi 12683). In situ basidiomata.

diomes and depressed hymenium around the stipe (probably due to a umbilicate pileus), The pileus, described as reddish in the protolog (Bourdot 1899) and later as ochraceous tawny (Bourdot and Galzin 1928), does not appear to match the deep orange tones of *H. ovoideisporum*. Bourdot and Galzin (1928) stated that the spores were similar to those of *H. repandum*, which were described as subglobose and not ovoid as in *H. ovoideisporum*. No other name that conforms to *H. ovoideisporum* could be traced following the extensive synonym lists provided by Maas Geesteranus (1976) under *H. repandum* and *H. rufescens*.

Most of the records were made in localities from the Mediterranean biogeographic region, often occurring together with *H. albidum*. However, it also has been found in the Pyrenees. *Hydnum ovoideisporum* appears to show preference for calcareous soils, rather than for a certain ectomycorrhizal partner. Almost all the collections were made on calcareous sites, and it has been found, for instance, in pure stands of *Quercus rotundifolia* or *Pinus sylvestris*. Although almost no extra-Iberian material that can be attributed to *H. ovoideisporum* has been traced, the Danish record displayed in Mycokey and ovoid-spored collections reported by Huhtinen and Ruotsalainen (2006) suggest that *H. ovoideisporum* occurs further north in Europe.

Specimens examined: SPAIN. ARABA: Gaubea-Valdegobía, Barrio, 30TVN9340, 700 m, under *Pinus sylvestris* on calcareous ground, 08 Nov 2007, *leg. A. Laza & I. Olariaga* (HOLOTYPE, BIO-Fungi 12683); 12 Nov 2002, BIO-Fungi 9683. Kanpezu, 30TWN6325, under *Quercus rotundifolia* on calcareous ground, 04 Dec 2008, *leg. E. Sarrionandia*, BIO-Fungi 12902. Trespuentes, under *Quercus rotundifolia*, 10 Nov 2007, *leg. I. Salcedo*, BIO-Fungi 12672. Zigoitia, Apodaka, under *Quercus rotundifolia* on calcareous soil, 10 Nov 2007, *leg. I. Salcedo*, BIO-Fungi 12669. ÁVILA: El Tiemblo, Garganta de la Yedra, 30TVK7168, 1100 m, under *Castanea sativa*, 7 Jun 1997, *leg. P.P. Daniëls*, MA-Fungi 37522 (as *Hydnum rufescens*). BURGOS: from Río de Losa to Oteo, Valle de Losa, 30TVN7657, 700 m, under *Pinus sylvestris* on rich soil, 12 Nov 2002, *leg. I. Olariaga*, BIO-Fungi 9676. GRANADA: Llano de la Perdiz, under *Quercus rotundifolia*, 7 Feb 1980, leg. A. Ortega & R. Galán, GDAC 10508 (as *Hydnum rufescens*). GIPUZKOA: Zumaia, Artadi, 30TWN6193, 50 m, under *Quercus ilex* on calcareous ground, 26 Dec 2009, *leg. J.L. Teres*, BIO-Fungi 14130. HUELVA: Camino de los Molinillos, Aracena, under *Quercus suber*, 4 Dec 1989, *leg. M.T. Vizoso*, GDAC 35130 (as *Hydnum rufescens*). Galaroza, Talenque-La Suerte, 29SQC0400, 660 m, forest with *Quercus suber*, *Castanea sativa*, *Quercus pyrenaica*, *Pinus* sp., 28 Nov 2002, *leg. L. Romero de la Osa*, JA 235 (as *Hydnum rufescens*). HUESCA: Villanúa, Fuente el Paco, under *Abies alba* and *Pinus sylvestris* on rich ground, 10 Oct 2006, *leg. I. Olariaga*, BIO-Fungi 12317. Jaca, Bernués, 30TXN9806, 1000 m, under *Quercus rotundifolia* on rich soil, 21 Oct 2003, *leg. I. Olariaga*, BIO-Fungi 9982. JAÉN: Cazorla, Linarejos, 30SW0897, 1100 m, forest with *Quercus*, *Pinus*, *Populus*, *Fraxinus*, *Betula*, 15 Nov 2002, *leg. A. Martínez Macarro*, JA 2272 (as *Hydnum rufescens*). ZARAGOZA: Venta Garrica, Sigüés, 30TXN6220, 510 m, under *Quercus rotundifolia* on rich soil, 21 Oct 2003, *leg. I. Olariaga*, BIO-Fungi 9980; BIO-Fungi 9987.

Hydnum vesterholtii Olariaga, Grebenc, Salcedo & M.P. Martín, sp. nov. FIGS. 5, 6

MycoBank MB563525

Basidiomata small to medium, growing isolated or fasciculate. Pileus 10–30(–50) mm diam, non-fleshy, initially convex, plane afterward, often depressed in the center, seldom umbilicate, sometimes irregular or dimidate. Surface velutinous, not radially fibrillose, slightly hygrophanous, non-staining, sometimes vaguely zoned. Color ocher (22B), lighter ocher (158A, 158C) toward the margin. In dry conditions light ocher (158A, 158B). Margin initially involute, soon straight, somewhat sinuous and lobed with age, sometimes slightly fimbriate, excedent. In exsiccatum ocher (10YR 7/6, 8/6, 5/4). Stipe 15–55 × 3.5–5.5(–10) mm, cylindrical, sometimes tapering or broader at the base, central to completely excentric, solid, velutinous, white (155D). Staining often ocher when handled. In exsiccatum ocher (10YR 7/6, 8/6, 5/4). Spines non-decurrent to slightly decurrent, sharply delimited, conical, acute to subacute, fimbriate or not, not flattened, crowded, 1–1.7 × 0.2–0.25 mm, pale ocher (158A, 158C). In exsiccatum brownish ocher (10YR 5/8, 6/8). Context white (155D), ocher in the surface of the stipe, non-staining or staining ocher toward the base. Odor weak, fruity, citric-like; flavor mild, slightly bitter-acrid afterward. Macrochemical reactions: KOH + context = 0; TL4 + context = 0.

Basidiospores ovoid to broadly ellipsoid in lateral view, apiculus cubic, thin-walled, non-amyloid, (7–)8–9(–9.5) × 6–7.5(–8) µm (L_m = 8.2–8.7; W_m = 6.4–6.8; Q_m = 1.27–1.30; n = 4). Basidia suburniform to claviform, 3–5-spored, sometimes with scattered 1–2-

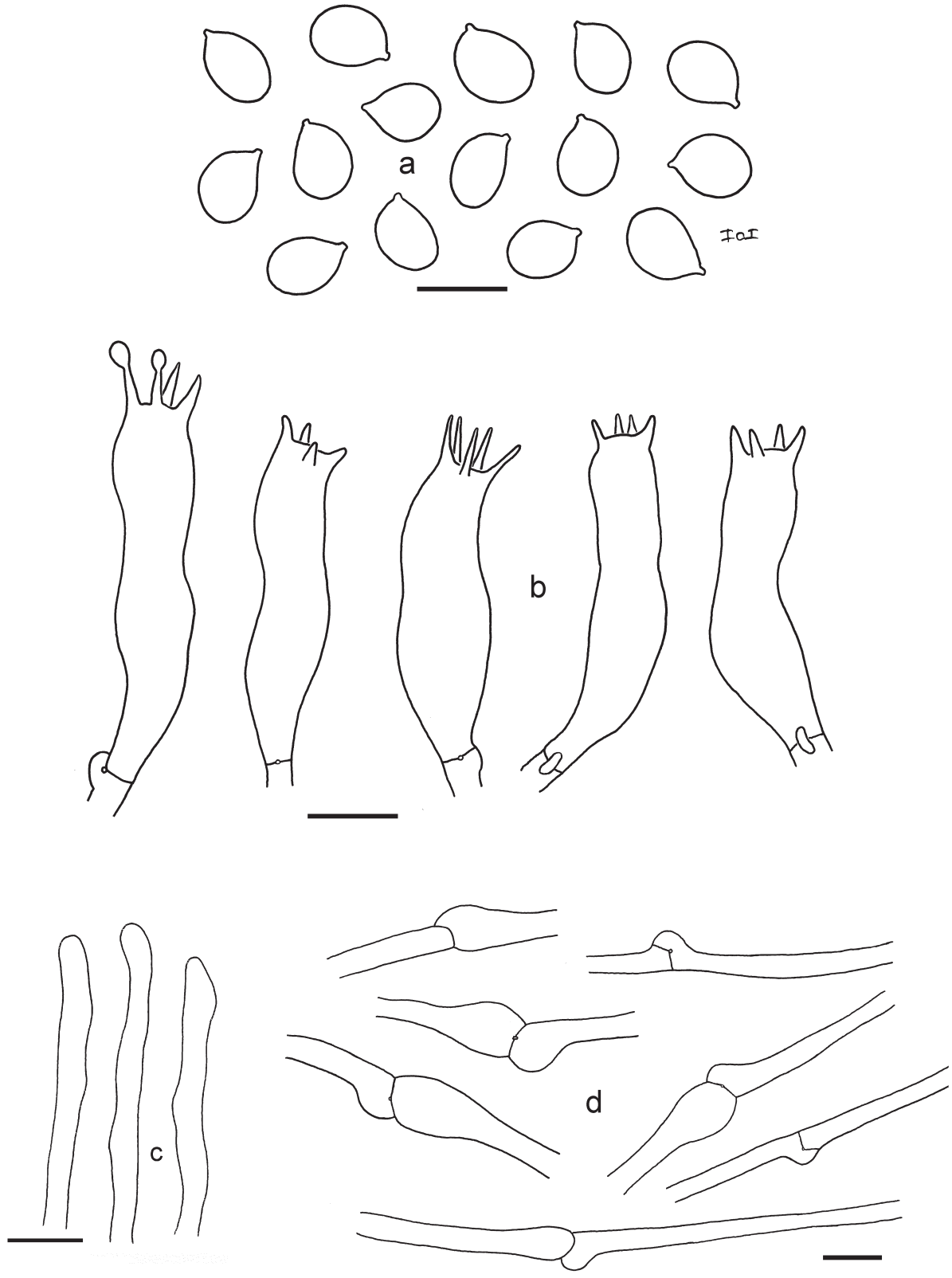

FIG. 4. *Hydnum ovoideisporum* sp. nov. (BIO-Fungi 12683). Bar = 10 mm approx. A. Basidiospores. B. Basidia. C. Hyphae of the apex of the spines. D. Mycelial hyphae. Bar = 10 μm.

FIG. 5. *Hydnum vesterholtii* sp. nov. (BIO-Fungi 12904). In situ basidiomata. Bar = 10 mm approx.

spored ones, clamped, 42–68 × 8–9 µm. Hyphae of the apex of the spines arranged in parallel, cylindrical, thin-walled, yellow, clamped, with cylindrical to slightly broader ends (3.5–4.5 µm), without crystals. Pileipellis composed of hyphae forming a cutis-trichoderm, cylindrical, thin-walled, with yellowish content, clamped, 5–9.5(14) µm wide, with cylindrical and blunt ends.

Stipitipellis composed of hyphae forming a trichoderm, cylindrical, thin-walled, with yellow content, clamped, 4–8 µm wide. Hyphae of the context woven, cylindrical to swollen, thin-walled, light yellowish, clamped, 4–13 µm wide. Basal mycelium white, composed of woven hyphae, cylindrical, thin-walled, clamped, 3–4.5 µm wide, with some ampullate inflations at septa (5.5–8.5 µm).

Etymology: After Jan Vesterholt, Danish mycologist.

Holotype: FRANCE. PYRÉNÉES ATLANTIQUES PROVINCE: Forêt d'Issaux, from Col du Labays to Pierre Saint Martin, under *Abies alba* and *Fagus sylvatica* on calcareous ground, 12 Oct 2008, *J.C. Zamora, J.A. Campos, M.A. Ribes, L.A. Parra & I. Olariaga,* (BIO-Fungi 12904). Isotype. F-207038 (S).

Commentary: H. vesterholtii is characterized by slender basidiomata, ocher pilei that are sometimes umbilicate, often having decurrent spines and possessing ovoid basidiospores. The habit of *H. vesterholtii* conforms to the conventional concept of *H. rufescens* due to the relatively thin and long stipe, together with the non-fleshy cap. However, *H. rufescens* s.l. has been treated as having globose to subglobose basidiospores and orange pileus. *Hydnum ovoideisporum*, also described here, is the only species known to us that shares the same habit and same basidiospore shape as *H. vesterholtii*. The orange pileus of *H. ovoideisporum* is a morphologically informative character to distinguish it from *H. vesterholtii*, as supported by ITS analyses (FIG. 2).

Hydnum vesterholtii shares some similarities with *H. repandum* (clade RE1) and *H. heimii* Maas Geest. (may correspond to clade RU1), such as the relatively pale color and the ovoid basidiospores. Both differ in having fleshier basidiomata with a larger pileus and thicker stipe and having a non-umbilicate pileus. Furthermore, *H. repandum* possesses pinkish orange tones in the pileus and a thick involute margin in young basidiomata. *Hydnum pallidum* Raddi, described from Italy, shares with *H. vesterholtii* slender basidiomata and pale color. However, it was described as ''entirely pale-white'', and a completely white basidiocarp is depicted in the plate (Tab. 12, fig. 8, Raddi 1807), which instead might suggest *Hydnum albidum* Peck.

Among the extra-European taxa, *Hydnum albomagnum* Banker, described from North America, also should be compared to *H. vesterholtii* due to having a pale pileus and ovoid spores. However, the protolog of *H. albomagnum* describes a ''fleshy plant'', ''white throughout'', with a thick stipe, ''1–2.5 cm thick'' (Banker 1902), which does not resemble *H. vesterholtii*. Furthermore, the *H. albomagnum* sequence included in the phylogenetic analyses did not show affinity to those of *H. vesterholtii*. *Hydnum crocidens* Cooke is another taxon that shares with *H. vesterholtii* a similar slender basidiomata, pileus tending to be umbilicate and pale (Cooke 1890). The basidiospores of *H. crocidens*, however, are 4–5 µm long and definitely smaller than those of *H. vesterholtii*. *Hydnum crocidens* is considered a synonym of *H. ambustum* Cooke & Massee in Index Fungorum, but the latter differs in the ''testaceous'' to ''almost black'' pileus and considerably larger spores (8–10 µm, Cooke 1887).

Hydnum vesterholtii probably had been reported earlier in the literature under other names. Maas Geesteranus (1971) depicted as *Hydnum repandum* a collection from New Zealand (PLATE 1, FIG. 3) that macroscopically resembles *H. vesterholtii*. However, we prefer to be cautious as to the identity of this fungus due to the antipodal distribution and the lack of microscopic data of this collection. Lüderitz (2005) provided, under the name *H. umbilicatum*, a color photo that shows macroscopic characteristics of *H. vesterholtii* due to the umbilicate and ocher pileus. However, no information regarding the spores was given and the identity of the fungus will remain doubtful until the material can be checked for the spore shape. In any case, the holotype of *H. umbilicatum* has large, globose basidiospores and this name must remain attached to a globose-spored taxon (Huhtinen and Ruotsalainen 2006).

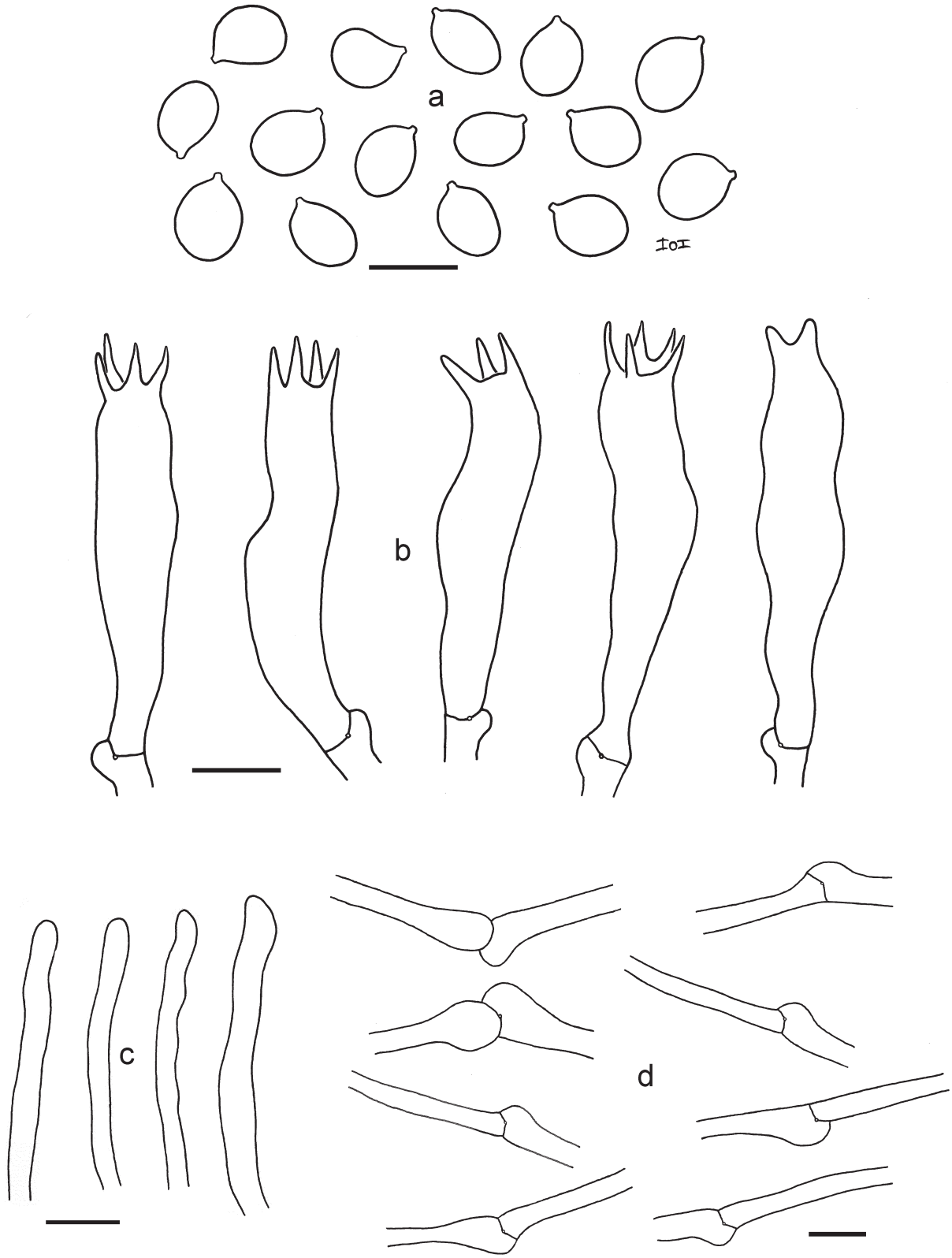

FIG. 6. *Hydnum vesterholtii* sp. nov. (BIO-Fungi 12904). A. Basidiospores. B. Basidia. C. Hyphae of the apex of the spines. D. Mycelial hyphae. Bar = 10 μm.

Hence, we propose here *Hydnum vesterholtii* as a new species that can be recognized by morphological and anatomical data as well as molecular data. The sister clade of *H. vesterholtii* might represent a morphologically very similar species that shares a pale pileus and ovoid spores, judging from specimen BIO 12330. The latter collection differed only from the specimens in the *H. vesterholtii* clade in the very pale orange tinges of the pileus. However, further material would be required to address the question whether it can be referred to a different species. We thus prefer to be cautious and restrict our concept of *H. vesterholtii* to the clade where the holotype is included. The material of *H. vesterholtii* examined has been collected in southern Europe, and especially the Pyrenees. The Italian collection studied could not be successfully sequenced, but morphologically it matches the rest of the material examined.

Specimens examined: ANDORRA: Estany de Engolateus, under *Corylus avellana* and *Buxus sempervirens*, 16 Oct 2002, *leg. M.P. Martin & T. Grebenc*, MA-Fungi 47726 (sub *H. repandum)*. FRANCE. PYRÉNÉES ATLANTIQUES (64), Forêt d'Issaux, from Col du Labays to Pierre Saint Martin, under *Abies alba* and *Fagus sylvatica* on calcareous ground, 12 Oct 2008, *leg. J.C. Zamora, J.A. Campos, M.A. Ribes, L.A. Parra & I. Olariaga*, (HOLOTYPE, BIO-Fungi 12904). ITALY. TOSCANA: Cala Violina NW of Grosseto, in *Quercus cerris* dominated forest with scattered *Q. ilex* and *Q. suber*, 7 Nov 1996, *leg. J. Vesterholt*, BIO-Fungi 12353, [dupla ex JV96-447]. SPAIN. HUESCA: Sallent de Gállego, Barranco de Garmo Negro, 30TYN1744, 1700 m, under *Fagus sylvatica*, 16 Sep 2004, leg. *I. Olariaga*, BIO-Fungi 10452. Fanlo, Cañon de Añisclo, 31BHN5717, 1500 m, under *Abies alba*, *Fagus sylvatica* and *Buxus sempervirens*, 17 Sep 2004, *leg. I. Olariaga*, BIO-Fungi 10429. ***Hydnum* aff. *vesterholtii*.**—SPAIN. HUESCA: Villanúa, Fuente el Paco, under *Abies alba* and *Pinus sylvestris* on rich ground, 10 Oct 2006, leg. *I. Olariaga*, BIO-Fungi 12330. CÁCERES: Castañar de Ibor, under *Castanea sativa*, 20 Feb 1977, *leg. M.T. Telleria*, MA-Fungi 3457.

DISCUSSION

The fact that the Q_m (mean length/width ratio) values were consistent in well characterized species, such as in *H. albidum*, *H. ellipsosporum* and *H. repandum*, and were congruent with the ITS nrDNA analyses supports the usefulness of the Q_m as a taxonomically informative character. The Q_m seems likewise useful as a morphological criterion to identify *H. ovoideisporum* and *H. vesterholtii*, although the sample size in both species is still low. On the other hand, several phylogenetic species exist that have globose spores with overlapping dimensions (Grebenc et al. 2009). More focused studies drawing attention to presence of umbilicate pileus, shape and attachment of the spines, number of predominant sterigmata and ecological and distributional data could contribute to morphological characterization of this lineage. The species corresponding to clade RU3, characterized by large basidiomata (Grebenc et al. 2009) or the morphological species that is recognized as *H. umbilicatum* in northern Europe could serve as examples of this (Jeppson 2010), although the latter has not been tested with molecular data.

This scenario, in which several well supported clades comprising morphologically similar specimens are treated under *H. rufescens* s.l. (RU2–RU6), raises the question as to which of the clades should be used to typify *H. rufescens*. The description of *H. rufescens* by Persoon (1799) does not provide information on microscopic characters, and no type specimen seems to remain. However, it conventionally has been considered a globose-spored taxon (Lundell and Nannfeldt 1936, Ostrow and Beenken 2004, Huhtinen and Ruotsalainen 2006) and we agree. This situation requires narrowing the typification of *H. rufescens*, selecting a lectotype from the original material and an adequate epitype collection. A better morphological characterization and distributional data about the globose-spored species needs to be gained to choose the most appropriate clade to typify *H. rufescens*. Likewise, new species will have to be described or available names found when each of the remaining clades is better characterized. In the meantime, we propose a provisional key to the species that can be distinguished morphologically with the current knowledge of the European taxa including the two new species proposed, *H. ovoideisporum* and *H. vesterholtii*.

KEY TO THE EUROPEAN SPECIES OF *HYDNUM*

1. Pileus initially entirely white; L_m = 4.9–6.1 μm; basidia 5–6.5 μm wide . . . . . *H. albidum*
1′ Pileus initially not white $L_m \geq 7$ μm; basidia 7.5–12 μm wide 2
2. Basidiospores broadly to narrowly ellipsoid, Q_m = 1.55–1.75; L_m = 9.8–10.6; spines often spathulate at least around the stipe, non-decurrent . . . . . *H. ellipsosporum*
2′ Basidiospores globose to broadly ellipsoid, Q_m= 1.06–1.38; L_m= 7.7–9.3; spines spathulate or not, decurrent or not 3
3. Basidiomata slender, stipe up to 9 mm diam; basidiospores broadly ellipsoid to ovoid (Q_m = 1.24–1.38) 4
3′ Basidiomata slender to robust; stipe up to 20 mm in diam; basidiospores subglobose to ovoid (Q_m = 1.07–1.22) 6
4. Pileus with deep orange tones . . . . . *H. ovoideisporum*
4′ Pileus pale ocher, without deep orange tones . . . 5

5. Pileus pale ocher, without orange tinge. . . . . *H. vesterholtii*

5′ Pileus with pale orange tinge . . . . . *H.* aff. *vesterholtii*

6′ Basidiomata fleshy; basidiospores Q_m = 1.16–1.21 . . . . . *H. repandum* and clade RU1

6′ Basidiomata slender; if fleshy then basidiospores $Q_m < 1.16$ . . . . . (*H. rufescens* s.l.) 7

7′ Basidiospores $L_m > 9$ µm; spines sharply non-decurrent, spathulate around the stipe and often paler at the apex; pileus often umbilicate; . . . . . *H.* aff. *ellipsosporum*

7′ Basidiospores Lm < 9 µm; spines not sharply delimited, without strong tendency to be spathulate; pileus umbilicate or not. . . . . Clades RU2–RU6

ACKNOWLEDGMENTS

This paper is dedicated to Jan Vesterholt who provided valuable *Hydnum* material that was extremely useful to the first author in the pursuit of the doctorate degree. We thank José Luis Terés for collecting one of the *H. ovoideisporum* specimens. Dagmar Triebel (M) and Mercedes Herrera (BIO) handled the loan of the holotype of *H. ellipsosporum*. We also are grateful for the help of Vincent Demoulin for his nomenclatural advice, as well as for the help of Maria Prieto for her comments on the manuscript. Thanks to Marian Glenn for checking the English. This work has been partially supported (I. Olariaga) by a grant for Training of Researchers from the Basque Government (2002/2003), DGI Flora Micológica Ibérica VI (2007–2009) CGL2006-12732-C02-01. The partner from the Slovenian Forestry Institute was co-financed by the Ministry of Higher Education, Science and Technology through Research Program P4-0107 and research project CRP V4-0492 (Slovenian Research Agency and Ministry of Agriculture, Forestry and Food).

LITERATURE CITED

Abarenkov K, Nilsson KH, Larsson K-H, Alexander IJ, Eberhardt U, Erland S, Høiland K, Kjøller R, Larsson E, Pennanen T, Sen R, Taylor AFS, Tedersoo L, Ursing BM, Vrålstad T, Liimatainen K, Peintner U, Kõljalg U. 1996. The UNITE database for molecular identification of fungi—recent updates and future perspectives. New Phytol 186:281–285, doi:10.1111/j.1469-8137.2009.03160.x

Agerer R, Kraigher H, Javornik B. 1996. Identification of ectomycorrhizae of *Hydnum rufescens* on Norway spruce and the variability of the ITS region of *H. rufescens* and *H. repandum* (Basidiomycetes). Nova Hedwigia 63:183–194.

Banker HJ. 1902. A preliminary contribution to a knowledge of the *Hydnaceae*. Bull Torrey Bot Club 28:199–222, doi:10.2307/2478788

Bourdot H. 1899 (1898). Les hyménomycètes des environs de Moulins. Rev Sci Bourbonnais Centre Fr (suppl.): 1–41.

———, Galzin A. 1928 (1927).Hyménomycètes de France. Sceaux: Société Mycologique de France.

Cochrane G, Karsch-Mizrachi I, Nakamura Y. 2010. The International Nucleotide Sequence Database Collaboration. Nucleic Acids Res 39:D15–18, doi:10.1093/nar/gkq1150

Cooke MC. 1887. Australian fungi. Grevillea 16:30–33.

———. 1890. Australian fungi (cont. from p 5). Grevillea 19:44–47.

Di Marino E, Scattolin L, Bodensteiner P, Agerer R. 2008. *Sistotrema* is a genus with ectomycorrhizal species—confirmation of what sequence studies already suggested. Mycol Prog 7:169–176, doi:10.1007/s11557-008-0562-4

Donk MA. 1933. Revision der Niederländischen Homobasidiomycetae-Aphyllophoraceae II. Meded Ned Mycol Ver 22:1–278.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791, doi:10.2307/2408678

Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118, doi:10.1111/j.1365-294X.1993.tb00005.x

Grebenc T, Martín MP, Kraigher H. 2009. Ribosomal ITS diversity among the European species of the genus *Hydnum* (Hydnaceae). Anal J Bot Madrid 66:121–132, doi:10.3989/ajbm.2221

Hall D, Stuntz DE. 1971. Pileate *Hydnaceae* of the Puget Sound area I. White-spored genera: *Auriscalpium*, *Hericium*, *Dentinum* and *Phellodon*. Mycologia 63: 1099–1128, doi:10.2307/3757988

Holmgren PK, Holmgren NH. 1998. (continuously updated). Index Herbariorum. New York Botanical Garden. (http://sciweb.nybg.org/science2/indexHerbariorum.asp)

Huelsenbeck JP, Ronquist F. 2001. MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755, doi:10.1093/bioinformatics/17.8.754

Huhtinen S, Ruotsalainen J. 2006. Variability of *Hydnum rufescens* in Finland: three taxa hidden under one name and appearance? Karstenia 46:17–24.

Jeppson M. 2010. *Hydnum umbilicatum*—en taggsvamp att leta efter. Svensk Myk Tidskr 31:48–51.

Larget B, Simon DL. 1999. Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. Mol Biol Evol 16:750–759, doi:10.1093/oxfordjournals.molbev.a026160

Lüderitz M. 2005. Svampar i Natura 2000-områden—ett project för identifiering och indikering av naturtyper. Svensk Myk Tidskr 26:90–95.

Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosaka K, Lim YW, Matheny B, Nishida H, Pfister D, Rogers J, Rossman AM, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R. 2004. Assembling the Fungal Tree of Life: progress, classification and evolution of subcellular traits. Am J Bot 91:1446–1480, doi:10.3732/ajb.91.10.1446

Lundell S, Nannfeldt JA. 1936. Fungi exsiccati suecici. Fasc. 7, 8. Uppsala. Sweden.

Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY,

Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johson D, Hambleton S, Crockett M, Shoemaker R, Sung GH, Lücking R, Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosaka K, Lim YW, Matheny B, Nishida H, Pfister D, Rogers J, Rossman AM, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R. 2004. Assembling the Fungal Tree of Life: progress, classification and evolution of subcellular traits. Am J Bot 91:1446–1480, doi:10.3732/ajb.91.10.1446

Maas Geesteranus RA. 1971. Hydnaceous fungi of the eastern Old World. Verh Kon Ned Akad Wetensch Afd Natuurk Tweede Sect 60:1–175.

———. 1976. Notes on Hydnums X. Proc Kon Ned Akad Wetensch C 79:273–289.

Martín MP, Winka K. 2000. Alternative methods of extracting and amplifying DNA from lichens. Lichenologist 32:189–196, doi:10.1006/lich.1999.0254

Moncalvo J-M, Nilsson RH, Koster B, Dunham SM, Bernauer T, Matheny PB, Porter TM, Margaritescu S, Weiß M, Danell E, Langer G, Langer E, Larsson E, Larsson K-H, Vilgalys R. 2006. The cantharelloid clade: dealing with incongruent gene trees and phylogenetic reconstruction methods. Mycologia 98:937–948, doi:10.3852/mycologia.98.6.937

Munsell Color Corp. 1990. Soil color charts. New York, Macbeth Division, Kollmorgen Instruments Corp.

Murrin F. 2008. Commercial wild mushroom harvest in Newfoundland and Labrador. Non-timber forest products workshop. Newfoundland Univ. Canada.

Nylander JAA. 2004. MrModeltest 2. Program distributed by the author. Uppsala, Sweden: Evolutionary Biology Center, Uppsala Univ.

———, Wilgenbusch JC, Warreb DL, Swofford DL. 2008. AWTY (Are there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. Bioinformatics 24:581–583, doi:10.1093/bioinformatics/btm388

Olariaga I. 2009. The order Cantharellales in the Iberian Peninsula and the Balearic Islands [doctoral dissertation]. Univ. Basque Country. Unpubl. 547 p.

Ostrow H, Beenken L. 2004. *Hydnum ellipsosporum* spec. nov. (Basidiomycetes, Cantharellales)—ein Doppelgänger von *Hydnum rufescens* Fr. Z Mykol 70:137–156.

Otto P. 1997. Kommentierter Bestimmungsschlüssel der terrestrischen Stachelpilze Deutschlands mit taxonomischen und nomenklatorischen Anmerkungen. Boletus 21:1–21.

Palazón F. 2001. *Setas para todos*. Editorial Pirineo. Huesca, Spain. 654 p.

Pegler DN, Roberts PJ, Spooner BM. 1997. British chanterelles and tooth fungi. Kew, UK: Royal Botanic Gardens. 114 p.

Persoon DCH. 1799. Observationes mycologicae. Pars Secunda. Leipzig and Luzern.

Pine EM, Hibbett DS, Donoghue MJ. 1999. Phylogenetic relationships of cantharelloid and clavarioid Homobasidiomycetes inferred from mitochondrial and nuclear rDNA sequences. Mycologia 91:944–963, doi:10.2307/3761626

Raddi G. 1807. Memoria delle specie nuove di Funghi ritrovate nei contorni di Firenze e non registrate nel Systema Naturae di Linneo edizioni XIII. Mem Mat Fis Soc Ital Sci 13:345–362.

Raidl S, Agerer R. 1992. Studien an Ektomykorrhizen XLII. Nova Hedwigia 55:279–307.

Rambaut A. 2002. Se-Al. Sequence alignment editor 2.0a11. Oxford, UK: Department of Zoology, Univ. Oxford.

The Royal Horticultural Society. 1995. R.H.S. Color Charts. London.

Schaeffer JC. 1763. Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur icons natives coloribus expressae. Tomus II. Regensburg.

Stafleu FA, Cowan RS. 1976. Taxonomic literature. Vol. 1, A–G. Utrecht, the Netherlands: Bohn, Skeltema & Holkema.

———, ———. 1985. Taxonomic Literature, vol. 5: Sal-Ste. Bohn, Skeltema and Holkema, Utrecht: the Netherlands.

Swofford DL. 2002. PAUP* 4.0: phylogenetic analysis using parsimony (*and other methods). Sunderland, Massachusetts: Sinauer Associates.

White TJ, Bruns T, Lee S, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds. PCR protocols: a guide to methods and applications. San Diego, California: Academic Press. p 315–322.

Wilgenbusch JC, Warren DL, Swofford DL. 2004. AWTY: a system for graphical exploration of MCMC convergence in Bayesian phylogenetic inference. (http://ceb.csit.fsu.edu/awty)