

Hebeloma vesterholtii, a new species in section *Theobromina*

Ursula Eberhardt · Henry J. Beker

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Abstract The species *Hebeloma vesterholtii* spec. nov. is described. It is morphologically and molecularly closely related to *Hebeloma theobrominum* from which it can be distinguished using either morphological or molecular characters. Both of these species belong to section *Theobromina*. The new species is known from 13 collections from six European countries.

Keywords *Hebeloma theobrominum* · Ectomycorrhizal fungi · Agaricales · Basidiomycota

Introduction

Hebeloma section *Theobromina* was proposed by Vesterholt (2005) and includes *H. theobrominum* (the section type), *H. erumpens* and potentially another taxon that cannot be clearly differentiated from *H. erumpens* (Eberhardt et al. 2009). In this paper we describe a new species, *H. vesterholtii* spec. nov., that fits both morphologically in the sect. *Theobromina* and molecularly in the clade / theobromina. We also provide molecular evidence using ITS sequence data that *H. vesterholtii* is a taxon distinct from the other members of its section. In addition, we include a morphological key to separate this species from the two

other species of sect. *Theobromina* mentioned above and *H. plesiocistum* which shares a number of characters with the members of sect. *Theobromina*.

Materials and methods

ITS sequence data were obtained from all known collections of *Hebeloma vesterholtii* and all collections of *H. theobrominum* examined in the context of this study. Sequences were produced by direct sequencing following the protocols detailed in Eberhardt et al. (2009) and references therein. In some of the tracefiles evidence was found for length variation within the template PCR products. These were taken into account by including both length variants as separate sequences into GenBank and into the phylogenetic analyses. Collection details and GenBank accession numbers of new accessions are listed in Table 1. Additional sequences considered in the molecular analyses were EU570163—EU570189, EU693013, EU881922, and EU887517 (GenBank acc. numbers) for which collection details were published by Eberhardt et al. (2009). To avoid confusion stemming from the application of different species concepts we did not include sequences in the analysis for which the corresponding collections have not been morphologically examined within this project. Sequence alignment was carried out using Se-al (vs. 2.0a11; Rambaut 2002). Maximum likelihood analyses were carried out as a heuristic search (100 replicates) in RAxML (vs. 7.0.3; Stamatakis 2006) under the GTRMIX model including bootstrap analyses (500 replicates). FigTree (vs. 1.1.2; Rambaut 2008) was used to visualize the results, relying on njplot (vs. 2.2; Perrière and Gouy 1996) for the correct placement of the bootstrap values.

U. Eberhardt (✉)
CBS-KNAW Fungal Biodiversity Centre,
Uppsalalaan 8,
NL-3584 CT Utrecht, Netherlands
e-mail: u.eberhardt@cbs.knaw.nl

H. J. Beker
Rue Père de Deken, 19,
1040 Bruxelles, Belgium

Table 1 Collection details and GenBank accession no. of new *Hebeloma* spp. ITS sequences included in the phylogenetic analyses

Taxon	Collection code ^a and herbarium number	GenBank acc. no.	Origin	Host plants
<i>H. erumpens</i>	C, 41584, double HJB, HJB12301	FJ816618	ITALY: Prov Foggia, Mattinata, Tratturita	<i>Cistus monspeliensis</i> ; <i>Quercus coccifera</i> ; <i>Q. ilex</i>
<i>H. theobrominum</i>	HJB, HJB10467	FJ816619	ENGLAND: Derby, Coombsdale	<i>Helianthemum</i> sp.
<i>H. theobrominum</i>	HJB, HJB10679	FJ816620	ENGLAND: East Sussex, St Dunstan's	broadleaves
<i>H. theobrominum</i>	C, JV00-435, double HJB, HJB10909	FJ816621	DENMARK: LFM, Hamborg Skov, Lolland: Fuglsang Storskov UTM PF 812,741 TBU 36.	<i>Fagus</i> sp.
<i>H. theobrominum</i>	C, JV00-314, double HJB, HJB10908	FJ816622	NORWAY, Leikanger, Sanden by Klyvi	broadleaves
<i>H. theobrominum</i>	HJB, HJB10063	FJ816623	BELGIUM: Luxembourg, Han sur Lesse	broadleaves
<i>H. theobrominum</i>	HJB, HJB11382	FJ816624	SPAIN: Catalunya, Brunyola	<i>Quercus</i> sp.
<i>H. theobrominum</i>	C, JV06-1095, double HJB, HJB11848	FJ816625	ITALY: Grosseto, Cala Violina NW of Grosseto	<i>Quercus cerris</i> ; <i>Q. ilex</i> ; <i>Q. suber</i>
<i>H. vesterholtii</i> ^b	BR, BR-MYCO 166528-76, double, HJB, HJB1000133, double C	FJ816626, FJ816627	BELGIUM: Luxembourg, Han sur Lesse	<i>Carpinus</i> sp.; <i>Corylus</i> sp.; <i>Fagus</i> sp.; <i>Quercus</i> sp.
<i>H. vesterholtii</i>	HJB, HJB10117	FJ816628	BELGIUM: Luxembourg, Han sur Lesse	<i>Carpinus</i> sp.; <i>Corylus</i> sp.; <i>Fagus</i> sp.; <i>Quercus</i> sp.
<i>H. vesterholtii</i>	HJB, HJB10339	FJ816629, FJ816630	ITALY: Carpegna	<i>Castanea</i> sp.; <i>Quercus</i> sp.
<i>H. vesterholtii</i>	HJB, HJB11206	FJ816631	BELGIUM: Luxembourg, Han sur Lesse	<i>Carpinus</i> sp.; <i>Fagus</i> sp.; <i>Quercus</i> sp.
<i>H. vesterholtii</i>	HJB, HJB11199	FJ816632	BELGIUM: Luxembourg, Han sur Lesse	<i>Carpinus</i> sp.; <i>Fagus</i> sp.; <i>Quercus</i> sp.
<i>H. vesterholtii</i>	HJB, HJB11195	FJ816633, FJ816634	BELGIUM: Luxembourg, Han sur Lesse	<i>Carpinus</i> sp.; <i>Fagus</i> sp.; <i>Quercus</i> sp.
<i>H. vesterholtii</i>	HJB, HJB11377	FJ816635	SPAIN: Pais Vasco, Urdiain	<i>Quercus rubra</i>
<i>H. vesterholtii</i>	C, JV08-132, double HJB, HJB12321	FJ816636, FJ816637	DENMARK, Eastern-Jylland: Elbæk Skov Elbæk Skov E of Horsens, N of Horsens Fjord	<i>Fagus sylvatica</i> ; <i>Quercus robur</i>
<i>H. vesterholtii</i>	C, JV08-133, double HJB, HJB12331	FJ816638, FJ816639	DENMARK, Eastern-Jylland: Elbæk Skov E of Horsens, N of Horsens Fjord	<i>Fagus sylvatica</i> ; <i>Quercus robur</i>
<i>H. vesterholtii</i>	C, DB8207, double HJB, HJB12344	FJ816640, FJ816641	BULGARIA, Sarantsi	<i>Quercus cerris</i> ; <i>Q. frainetto</i> ; <i>Q.</i> sp.
<i>H. vesterholtii</i>	HJB, HJB12696	FJ816642, FJ816643	ENGLAND, Calke Abbey	<i>Fagus sylvatica</i> , <i>Quercus</i> sp.
<i>H. vesterholtii</i>	HJB, HJB10674	FJ943237, FJ943238	ENGLAND, East Sussex, St Dunstan's	broadleaves
<i>H. vesterholtii</i>	HJB, HJB11869	FJ943239, FJ943240	ITALY, Sardinia, Mount Limbara	not specified

^a Collection codes: C, Copenhagen; HJB, personal herbarium H. J. Beker; BR Meise, Belgium.

^b type of *H. vesterholtii*

Details of the morphological analyses are given in Eberhardt et al. (2009). For each collection at least 50 spores were measured in Melzer's reagent, excluding the apiculus. The maximum length and width of each spore was measured and its Q value (ratio of length to width) calculated. Average length, width and Q value were calculated and recorded alongside the median, standard deviation and 5% and 95% percentiles. The assessment and coding of spore characters follows Vesterholt (2005). The average width of the cheilocystidium apex appears to be an important character in the separation of species within *Hebeloma*

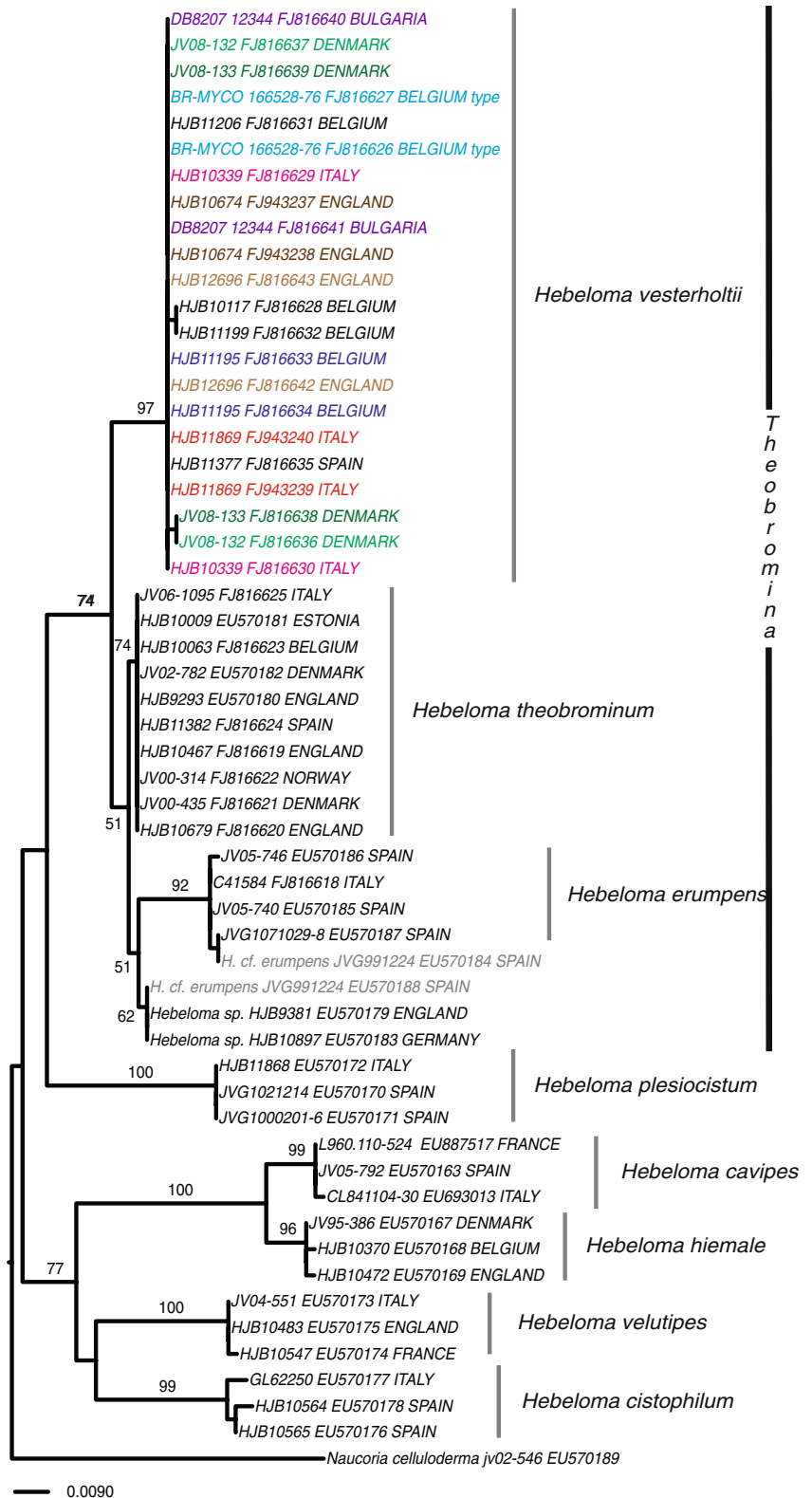
(Vesterholt 2005). It is also important, when determining the average apex width, not to be selective with regard to the cystidia chosen for measurement. To determine the average width at the apex about 100 cheilocystidia were measured on the lamellae edge. For other measurements, at least 20 cheilocystidia, separated from the lamella edge, were measured from each collection. Because of the complex shapes of the cheilocystidia four measurements were made: length, width at apex, width at narrowest point in central region and maximum width in lower half. The measurements are given in this order and an average value was calculated for

each of these measurements. The measurements were made in 5% KOH. Unless mentioned otherwise, cited specimens are presently located in the personal collection of H.J. Beker (HJB).

Results and discussion

The sequences of the currently known collections belonging to the species described below as *Hebeloma vesterholtii*

Fig. 1 Best of 100 ML tree of from a heuristic search with 100 replicates based on ITS data; bootstrap support was calculated with 500 replicates. For specimens showing length variation in the ITS, both variants were included in the tree and indicated by the same shade font. Single sequences are in black



(i.e. all collections on which the description is based) form a well-supported clade in the ITS analyses (Fig. 1). Judging from direct sequence data, evidence of intragenomic variation (ambiguous readings in both strands; overlapping peaks as the result of length variation among amplicons) was found in ten of thirteen specimens, implicating seventeen positions in the alignment of all *H. vesterholtii* sequences. Only one additional position is variable in between-specimen comparisons, but unambiguous within all sequenced specimens. However, counting only clear mismatches and disregarding the length variation, the intraspecific variation is restricted to two sites, which explains the very short terminal branches in the clade. The observation and extent of the intragenomic ITS variation is not uncommon in *Hebeloma* (Aanen et al. 2001; Matheny et al. 2007; Eberhardt et al. 2009; unpublished data). Likewise, the clade of the closely related *H. theobrominum* is well-supported. In contrast, *H. erumpens*, forms a mixed clade with sequences of the insufficiently known *Hebeloma* sp. For a more detailed discussion see Eberhardt et al. (2009). These two species and one species complex are European representatives of the /theobromina clade, corresponding to *Hebeloma* sect. *Theobromina*. From a morphological point of view *H. plesiocistum* should also be included in this section. In Fig. 1 it is associated with the /theobromina clade, but in a more inclusive analysis including ITS sequences from all purported *Hebeloma* species occurring in Europe (not published) it appears in a separate clade. A study including genes other than the ITS is underway.

Taxonomy

Hebeloma vesterholtii Beker & U. Eberh., *sp. nov.*—
Mycobank MB 515246;
Figs. 2, 3, 4 and 5

Figures 2, 3, 4 and 5

Etymology—in honour of Jan Vesterholt who has made a significant contribution to our understanding of the genus *Hebeloma*.

Pileus usque ad 55 mm in diam., convexus vel obtuse umbonatus; superficies sicca vel leviter viscida, interdum hygrophana, haud striata, ochracea vel bruno ochracea, praeter marginem pallidum cum coloribus cremeis vel roseis. Lamellae adnatae vel emarginatae, parce densae, tenues; color saturate cremeus, alutaceus vel brunneo-alutaceus pallidus vel brunneus, demum brunneo-olivaceus. Acies fimbriata. Stipes centralis, interdum attenuatus vel clavatus basin versus, usque ad 75 mm longus et 10 mm crassus, candidus vel alutaceus; superficies sicca, pruinosa vel floccosa. Cortina non visa. Caro cremea vel pallide



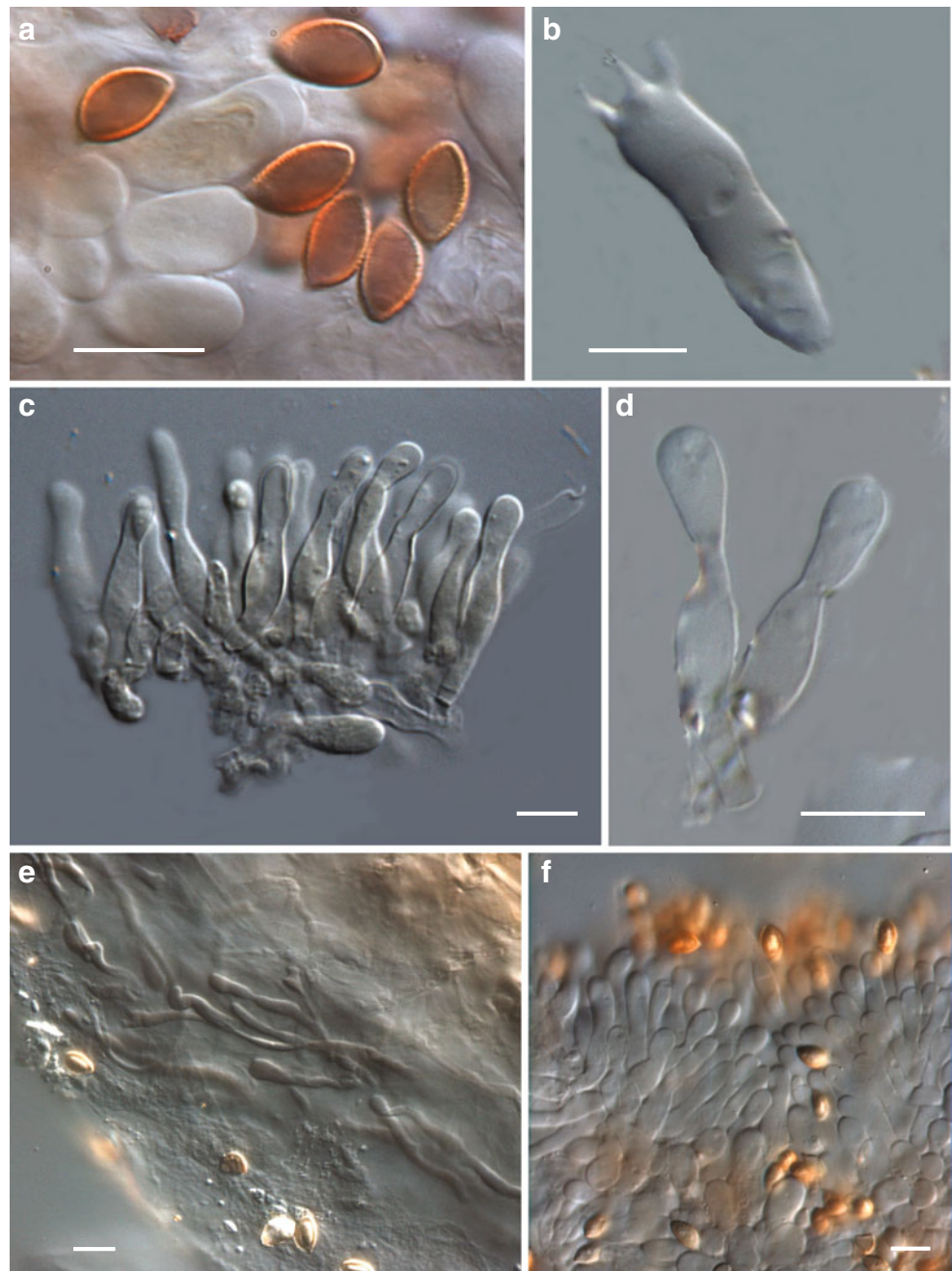
Fig. 2 Collection BR-MYCO 166528-76 (holotype) of *Hebeloma vesterholtii* growing on calcareous ground under deciduous trees. Photograph H.J. Beker

brunnea; odor compositus (cacao et raphanoideus). Sporae amygdaloideae, fere laeves vel inconspicue ornamentatae, valde dextrinoideae; $7.8\text{--}9.5 \times 4.7\text{--}5.6 \mu\text{m}$. Basidia tetrasporica, $21\text{--}33 \times 5.6\text{--}8.4 \mu\text{m}$, cylindrica vel clavata. Pleurocystidia non visa. Cheilocystidia subclavata, in parte inferiori incrassata, apex $4.4\text{--}6.3 \text{ mm}$ latus. Caulocystidia cheilocystidiiformia. Fibulae omnipraesentes.

Basidiomes usually in small scattered groups, but occasionally solitary and rarely caespitose. *Pileus* up to 55 mm in diam. (rarely up to 85 mm), convex to broadly umbonate; surface dry or slightly viscid, can be hygrophanous but is not striate; *cuticle colour* fairly uniform across most of the pileus except for a thin paler margin, ochraceous to yellowish brown, occasionally with fawn or cinnamon tones, sometimes even slightly olive at centre while the thin paler margin has cream to pinkish buff tones; *pileus margin* straight, slightly involute in immature basidiomes, wavy (undulate) when old. *Lamellae* adnate to emarginate, 4–6 mm deep at the widest point, moderately dense, thin, with 60–90 full length lamellae and usually between 1 and 3 *lamellules* between lamellae, droplets on the lamellae rarely recorded; *colour* cream, alutaceous or brown when young, later brownish olive following spore maturity; *edge* fimbriate, paler than lamella surface. *Stipe* central, cylindrical but occasionally either attenuate or clavate towards the base, up to 75 mm long and with central width 4–10 mm (rarely up to 20 mm); white or alutaceous, sometimes discolouring from the base upwards, becoming hollow with age; *surface* dry, pruinose to floccose. *Cortina* not observed. *Flesh* cream or pale brown, almost never discolouring when bruised. *Smell* cacao with a raphanoid component but sometimes no smell recorded, *taste* mild. *Spore print* brownish olive. *Exsiccata* often dark or even blackening particularly on the pileus.

Spores amygdaloid, with small apiculus and rounded at the end opposite the apiculus, with a distinct thinning of the

Fig. 3 Collection BR-MYCO 166528-76 (holotype) of *Hebeloma vesterholtii*: **a.** spores $\times 1600$ in Melzer's Reagent; **b.** basidium $\times 500$ in 5% KOH; **c.** cheilocystidia $\times 500$ in 5% KOH; **d.** cheilocystidia $\times 1000$ in 5% KOH; **e.** ixocutis $\times 500$ in 5% KOH; **f.** cheilocystidia on lamella edge $\times 500$ in 5% KOH. Scale bars=10 μm . Photographs H.J. Beker



spore wall and never any sign of papilla, guttulate with one or occasionally more oily drops, almost smooth to weakly ornamented, with no sign of loosening perispore and strongly dextrinoid (O1/2; P0; D3/4); *spore colour* under the microscope from pale yellow to pale brown; *spore size* based on $n=87$ spores of the holotype, 5% to 95% percentile range $7.8\text{--}9.5 \times 4.7\text{--}5.6 \mu\text{m}$, with median $8.6 \times 5.2 \mu\text{m}$ and av. $8.7 \times 5.1 \mu\text{m}$ with S. D. length $0.54 \mu\text{m}$ and width $0.29 \mu\text{m}$, Q value 5% to 95% percentile range 1.54–1.82, with median 1.70 and av. 1.69 with S. D. 0.09; *spore size* based on thirteen collections medians $8.2\text{--}9.8 \times 4.7\text{--}5.4 \mu\text{m}$ and av. $8.2\text{--}9.8 \times 4.7\text{--}5.5 \mu\text{m}$ with S. D. length

$0.45\text{--}0.71 \mu\text{m}$ and width $0.18\text{--}0.31 \mu\text{m}$, av. Q 1.64–1.79. *Basidia* cylindrical to clavate and 4-spored, $21\text{--}33 \times 5.6\text{--}8.4 \mu\text{m}$, with av. $23\text{--}29 \times 6.2\text{--}8.0 \mu\text{m}$. *Pleurocystidia* not found. *Cheilocystidia* mostly hourglass-shaped, i.e. clavate, occasionally cylindrical in the upper part, the majority narrower in their central region but then swollen again in the lower half, very rarely cylindrical in their lower half, occasionally with unclamped septa or some median thickening or with apex mucronate and often bent in the centre; *width of apex* holotype 5% to 95% percentile range $4.4\text{--}6.3 \mu\text{m}$, with median $5.3 \mu\text{m}$ and av. $5.3 \mu\text{m}$ with S.D. $0.64 \mu\text{m}$; across thirteen collections median $4.3\text{--}7.1 \mu\text{m}$ and

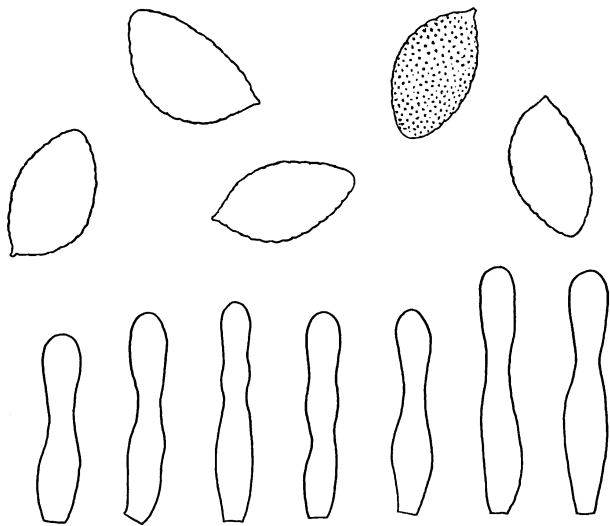


Fig. 4 Spores and cheilocystidia of collection BR-MYCO 166528-76 (holotype) of *Hebeloma vesterholtii*. Scale bar=5 μ m

av. 4.4–7.1 μ m; n=20–30 selected cheilocystidia of each of thirteen collections yields a range for the averages of 27–37 \times 4.4–7.1 \times 3.5–4.9 \times 5.4–6.6 μ m and 30 \times 5.3 \times 3.6 \times 5.6 μ m av. for holotype. *Caulocystidia* resemble cheilocystidia but tend to be larger. *Pileipellis* is an ixocutis with an

epicutis in the range 120–180 μ m, embedded hyphae up to 5 μ m broad, often encrusted, hyaline or occasionally pigmented. *Cutis* orange brown and made up of cylindrical to isodiametric elements. *Clamp connections* present throughout the fruitbody.

Habitat and distribution—all thirteen collections, on which the above description is based, were made in deciduous woodland and with a single exception all habitats were reported as calcareous. There is a range of deciduous trees reported but *Quercus* appears to have been present on every occasion. This species appears widespread in Europe with a more southerly distribution and is already known from Denmark, England, Belgium, Italy, Spain and Bulgaria. The most northerly collection is from Denmark at N55.86 degrees.

Collections examined Belgium, Wallonia, Han-sur-Lesse, Turmont, (N50.1142167;E05.1715000; alt. 153 m) on calcareous soil in a deciduous woodland including *Carpinus betulus*, *Corylus avellana*, *Fagus sylvatica*, *Quercus robur*, 19 Sep. 2004, H. Beker, holotype BR-MYCO 166528-76, BR, double HJB1000133; loc. cit., 19 Sep. 2004, H. Beker, HJB10117; loc. cit., alt. 150–165 m, H. Beker, 1 Sep. 2005, HJB11195; loc. cit., H. Beker, 1 Sep. 2005, HJB11199; loc. cit., H. Beker, 1 Sep. 2005, HJB11206. Bulgaria, Sarantsi

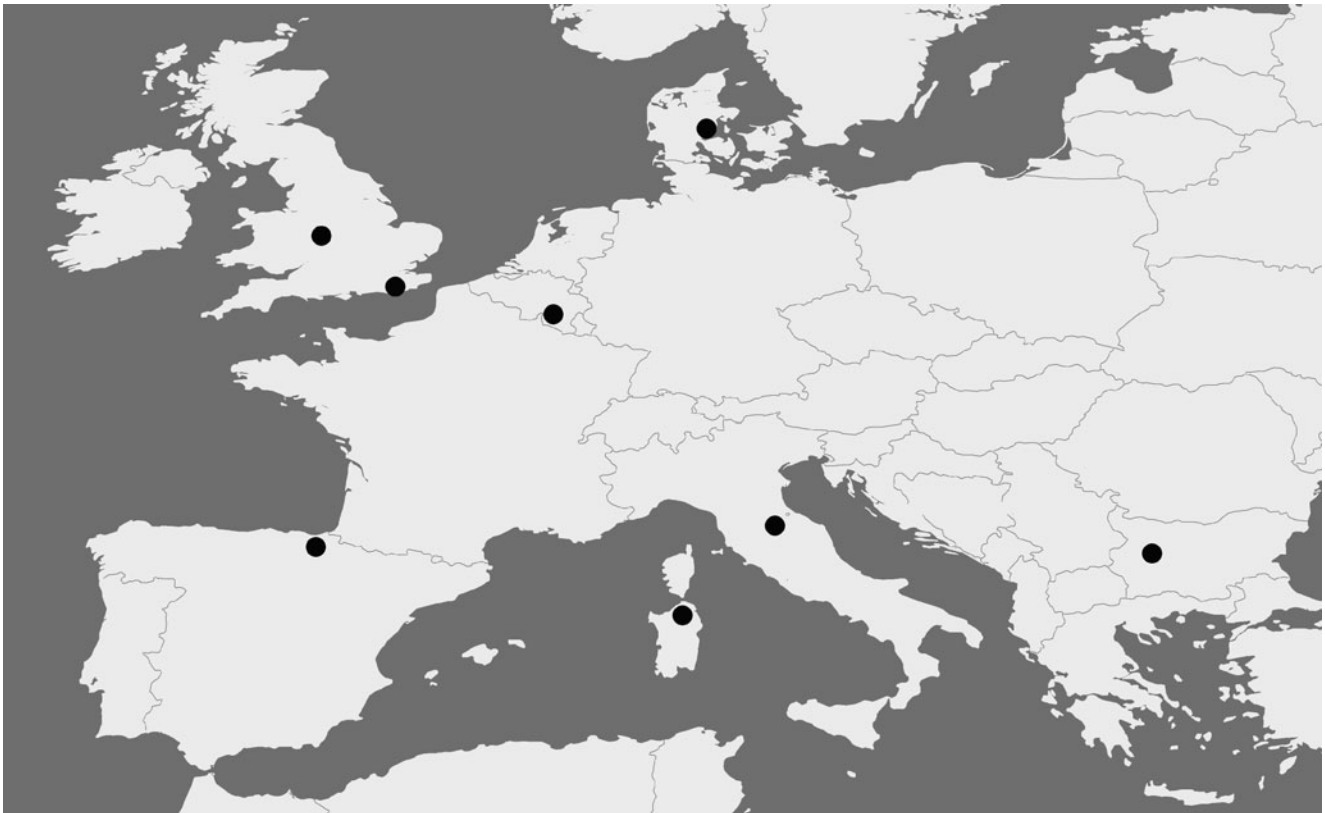


Fig. 5 Distribution map for collections of *Hebeloma vesterholtii*



Fig. 6 Collection JV02-782 of *Hebeloma theobrominum* from Hostemark, Denmark growing in mossy ground under *Picea*

(N42.71;W23.77; alt. 650 m), woodland, *Quercus cerris*; *Quercus frainetto*; *Quercus* sp., 7 Oct. 2008, D. Bojantchev, DB8207/HJB12344. Denmark, Eastern-Jylland: Elbæk Skov, East of Horsens, North of Horsens Fjord (N55.8615800; W9.9374770; alt. 4 m), on calcareous clayey soil in dry woodland, *Fagus sylvatica*, *Quercus robur*, 5 Sep. 2008, J. Vesterholt, JV08-132/HJB12321; loc. cit., J. Vesterholt, JV08-133/HJB12331. Italy, Emilia-Romagna, nr Carpegna, (N43.62055;E12.13133; alt. 578) on calcareous soil in a deciduous woodland under *Castanea sativa* and *Quercus spp.*, 15 Oct. 2004, H. Beker, HJB10339; Sardinia, Mount Limbara, (N40.857;E9.168; alt. 1200 m) on calcareous soil under deciduous trees including *Quercus* sp., 10 Nov. 2006, C. Hobart, HJB11869. Spain, Pais Vasco, Urdiain, (N42.9059833;W2.1503333; alt. 489 m) on calcareous soil under *Quercus rubra*, 22 Oct. 2005, H. Beker, HJB11377. United Kingdom, East Sussex, St. Dunstan's Farm (N50.95421;E0.28947; alt. 88 m) in a deciduous woodland under *Quercus* sp., 10 Oct. 2004, A. Andrews, HJB10674; Calke Abbey (N52.59975;W1.99604; alt. 148 m), *Fagus sylvatica*, *Quercus* sp., 18 Sep. 2008. C. Hobart, HJB12696.

Hebeloma theobrominum Quadr., 1987, Mycotaxon 30: 311

Collections examined Belgium, Wallonia, Han-sur-Lesse, Turmont, (N50.11;E05.16; alt. 150 m) on calcareous soil in a deciduous woodland including *Carpinus betulus*, *Corylus avellana*, *Fagus sylvatica*, *Quercus robur*, 5 Sep. 2004, D. Ghyselinck, HJB10063. Denmark, Høstemark Skov, south of Mou (N56.93;E10.21; alt. 6 m) on mossy ground under *Picea abies*, 15 Oct. 2002, J. Vesterholt, JV02-782/HJB10907; Hamborg Skov, Lolland, Fuglsang Storskov (N54.78;E11.31; alt. 7 m) under *Fagus sylvatica*, 6 Oct. 2000, J. Vesterholt, JV00-435/HJB10909. Estonia, Tagamoisa (N58.4611;E22.0089; alt. 25 m), on calcareous soil in a mixed woodland under *Tilia sp.*, 9 Aug. 2004, H. Beker, HJB10009. Italy, Cala Violina, north west of Grosseto (N42.83;E10.77; alt. 20 m) in a deciduous woodland under *Quercus cerris*, *Q. ilex*, *Q. suber*, 9 Nov. 2006, J. Vesterholt, JV06-1095/HJB11848. Norway, Leikanger, Sanden by Klyvi, (N59.77;E9.92; alt. 7 m) in a deciduous woodland, 10 Sep. 2000, J. Heilmann-Clausen, JV00-314/HJB10908. Spain, Catalunya, Brunyola (N41.9001;E2.6595; alt. 187 m) in a mixed woodland under *Quercus* sp., 23 Oct 2005, H. Beker, HJB11382. United Kingdom, Westmorland, Roudsea (N54.2356;W3.0294; alt. 15 m) on calcareous soil in a deciduous woodland, 24 Sep. 2002, H. Beker, HJB9293; Derbyshire, Coombsdale (N53.2706;W1.6446; alt. 140 m) on calcareous soil with *Helianthemum sp.*, 28 Oct. 2004, H. Beker, HJB10467; East Sussex, St. Dunstan's (N50.95; E0.29; alt. 88 m) in a deciduous woodland, 10 Oct. 2004, A. Andrews, HJB10679.

Comment *Hebeloma vesterholtii* appears to favour deciduous woodland in calcareous areas. It is likely that it forms ectomycorrhizal relationships with species of *Quercus*. The combination of almost smooth to very weakly ornamented and strongly dextrinoid spores indicates an affinity to either sect. *Velutipes* or sect. *Theobromina* (Vesterholt 2005). The known species in the sect. *Velutipes* tend to have more

Fig. 7 Comparison of spores of *Hebeloma vesterholtii* and *Hebeloma theobrominum* $\times 1600$ in 5% KOH: **a.** Collection HJB10339 of *Hebeloma vesterholtii*; **b.** Collection JV06-1095 of *Hebeloma theobrominum*. Scale bars = 10 μ m. Photographs H.J. Beker

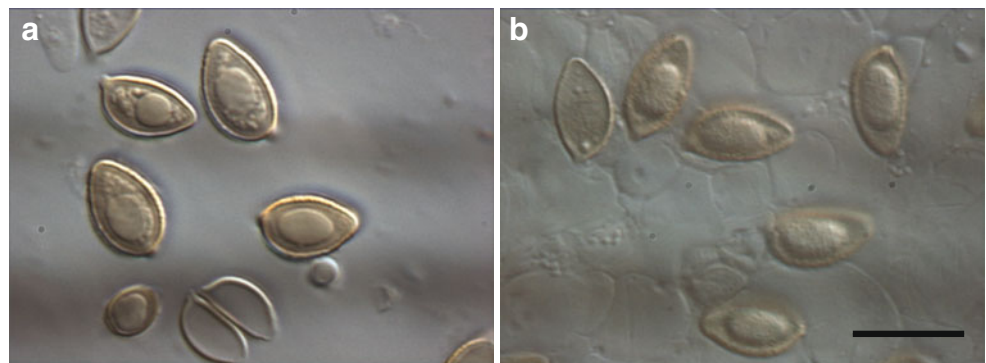


Table 2 Comparison of critical morphological and ecological characters of species of *Hebeloma*, sect. *Theobromina*

	<i>H. theobrominum</i>	<i>H. vesterholtii</i>	<i>H. plesiocistum</i>	<i>H. erumpens</i>
Habitat	Deciduous or mixed woodland on calcareous ground	Deciduous or mixed woodland on calcareous ground	With <i>Cistus</i>	With <i>Cistus</i>
Cap colour	Reddish–brown	Yellowish–brown	Pale brown to ochraceous brown with grey pruina	Orange–brown to reddish–brown often with grey pruina and particles of earth or rock stuck to the cap
Spore ornamentation	O1;O2	O1;O2	O1;O2	O1;O2
Spore perispore	P0;P1	P0	P0	P0
Spore dextrinoidity	D3;D4	D3;D4	D4	D2;D3
Ave. spore length (μ)	8.4–9.9	8.2–9.8	9.9–11.1	9.4–10.3
Ave. spore width (μ)	4.5–5.3	4.7–5.5	6.0–6.1	5.6–6.2
Ave. spore Q (μ)	1.80–1.95	1.54–1.79	1.64–1.82	1.61–1.85
Ave. cheilocystidium length (μ)	30–37	27–37	38–52	31–40
Ave cheilocystidium apex width (μ)	5.3–6.3	4.4–7.1	7.3–8.9	5.6–6.5
Ave. cheilocystidium median width (μ)	3.7–4.6	3.5–4.9	4.4–4.9	3.9–4.4
Ave. cheilocystidium basal width (μ)	5.4–6.3	5.4–6.6	5.9–6.9	5.5–6.4

ornamented spores and/or differently shaped cystidia. Their cheilocystidia are generally much more gently clavate than those of *H. vesterholtii*. The very pale small spores and the shape of the cystidia strongly support that *H. vesterholtii* belongs within sect. *Theobromina*. The new taxon can be readily distinguished both morphologically and molecularly (see above) from the other members of this section. It is likely that previous collections may have been confused with *H. theobrominum*. However, *H. vesterholtii* is distinguishable from the latter species by means of its differently shaped spores and different cap colour (Figs. 2, 6, 7). Based on 10 collections of *H. theobrominum* we find the cap colour to range from deep cinnamon to red–brown to dark brick as opposed to the lighter and often more yellowish to buff colours of *H. vesterholtii*. Based on the same 10 collections (and measuring a minimum of 50 spores in each case) the average spore size ranges from 8.4–9.9×4.5–5.3 μm and av. Q 1.80–1.95. Based on our collections there is no overlap in the average spore Q, though there is only a small gap between the two ranges. Thus a collection of either species with a misleading average spore Q cannot be ruled out. However, in cases where the average spore Q may give an ambiguous identification, the cap colour should help distinguish between the two species. Figure 1 shows the placement of *H. vesterholtii* in the *theobromina* clade based on ITS data. Table 2 summarizes the main

characters of the four species currently included in the section *Theobromina*.

Key to *Hebeloma* sect. *Theobromina* and *H. plesiocistum*:

- 1a Collected on calcareous ground in deciduous or mixed woodland 2
- b. Collected under *Cistus* 3
- 2a Cap reddish brown and ave. spore Q>1.80 ***H. theobrominum***
- b. Cap yellowish brown and ave. spore Q<1.80 ***H. vesterholtii***
- 3a Average cheilocystidium apex>7 μm and spores very strongly dextrinoid, becoming dark brick to dark reddish–brown ***H. plesiocistum***
- b. Average cheilocystidium apex<7 μm and spores strongly dextrinoid, becoming yellow brown to orange–brown or brick ***H. erumpens***

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