RESEARCH ARTICLE

Decrypting the *Hebeloma crustuliniforme* complex: European species of *Hebeloma* section *Denudata* subsection *Denudata* (*Agaricales*)

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Abstract   *Hebeloma* subsection *Denudata* includes the type of *H.* section *Denudata*, *Hebeloma crustuliniforme*, as well as the majority of the taxa commonly included in the *Hebeloma crustuliniforme* complex. Complementing the work of D.K. Aanen and co-workers, and using refined morphological and molecular methods we were able to recognize further individual taxa within the section. Fifteen species occurring in Europe are assigned to *H.* subsect. *Denudata*. Of these, we describe eight species as new, namely *H. aanenii*, *H. aurantioumbrinum*, *H. geminatum*, *H. louiseae*, *H. luteicystidiatum*, *H. pallidolabiatum*, *H. perexiguum* and *H. salicicola*. *Naucoria bellotiana*, a species very similar to *H. alpinum* is recombined into *Hebeloma*. A key to *Hebeloma* subsect. *Denudata* is provided. We demonstrate that within this subsection there is good overall consistency between morphological, phylogenetic and biological species concepts. In contrast to current opinion, in this group there is little species overlap, particularly when also considering species frequencies, between arctic and alpine floras on one hand and temperate on the other.

INTRODUCTION

Hebeloma is a genus of ectomycorrhizal fungi occurring in many different habitats in the northern hemisphere (Marmeisse et al. 1999) and indeed worldwide, with the possible exception of regions, where *Fagales* are not endogenous, such as Northern South America (Tedersoo et al. 2010) or Africa. However, as typical nursery fungi, *Hebeloma* spp. are likely to have been introduced through human activity (see Sulzbacher et al. 2013).

Hebeloma crustuliniforme is one of the most often recorded (Vesterholt et al. 2014) species of the genus *Hebeloma*, but it is widely recognised that what has in the past been referred to as *H. crustuliniforme* is among the most notorious species complexes that have long defied recognition of individual taxa. In Vesterholt et al. (2014) we proposed an epitype for *H. crustuliniforme* so as to tie this name to a particular taxon within this complex, which we then suggested should be referred to as *H. crustuliniforme* (Bull.) Quél. emend. Vesterh., U. Eberh. & Beker to avoid confusion with earlier applied concepts of the taxon. As we stated at the time, this was the first step towards unravelling this complex of species within sect. *Denudata.*

More than 10 years ago, D.K. Aanen and others (Aanen & Kuyper 1999, 2004, Aanen et al. 2000) carried out a profound study of the *H. crustuliniforme* complex, using three different approaches, sporocarp morphology, molecular studies and intercompatibility tests, testing for dikaryotization between pairs of monokaryotic strains. They found 20 intercompatibility groups (ICGs) within the complex. A small number of strains were intercompatible with some strains of other ICGs or could not be unambiguously assigned to a unique ICG.

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It is tempting to consider ICGs as biological species and they may well represent biological species, but as Aanen & Kuyper (1999) point out, the production of basidiospores in the dikaryotic mycelia generated in the intercompatibility tests could not be tested, therefore we do not know what the implications of the observed intercompatibility in nature are. In general, on the population level, partial intercompatibility may correspond to incomplete speciation (Aanen & Kuyper 1999). Almost all of a quite high number of strains stemming from 110 collections could be unambiguously assigned to a single ICG, thus supporting the notion that distinct biological taxa have already formed in this species aggregate.

Aanen & Kuyper (1999) linked this finding of partial compatibility between some ICGs with the difficulty of morphologically separating ICGs into morpho-species, suggesting that partial intercompatibility might contribute to the failure to form distinct morphological and ecological syndromes. Accordingly, Aanen and co-workers (Aanen 1999, Aanen et al. 2000, Aanen & Kuyper 2004) adopted wide species concepts, i.e. *H. crustuliniforme* including *H. alpinum* with six ICGs and *H. pusillum* (four ICGs), partially overlapping with *H. helodes* (at least six ICGs). In the later work (Aanen & Kuyper 2004) *H. helodes* and *H. pusillum* were merged.

Molecular studies showed that three of the ICGs of the *H. crustuliniforme* complex were molecularly quite distinct from the other 17 ICGs. This supported a view published initially by Boekhout (1982), then molecularly supported (Aanen et al. 2000, Boyle et al. 2006), suggesting that there are indeed two distinct groups within this complex, one species complex around *H. velutipes* (syn. *H. leucosarx* acc. Grilli 2007) and another in sect. *Denudata*, around *H. crustuliniforme*. It has found its way into the classification system by Vesterholt (2005), which recognized two distinct sections *Velutipes* and *Denudata*, each including taxa that were formerly considered representatives of the *H. crustuliniforme* complex.

The focus of the present study is on *H.* sect. *Denudata* and particularly on members of the *H. crustuliniforme* complex and related taxa assigned to subsect. *Denudata* (described more fully below) of which *H. crustuliniforme* is the type. The delimitation of *H.* subsect. *Denudata* adopted in this paper is based on morphological characters. Within the scope of this paper we do not demonstrate the molecular delimitation of *H.* subsect. *Denudata*. A separate publication (Eberhardt et al. in prep.) will be concerned with the classification of subsections of *H.* sect. *Denudata* and species from these other subsections.

With regard to species delimitation, we follow de Queiroz (2007) unified species concept that treats different criteria such as morphological distinctness, monophyly, evolutionary distance or intercompatibility as independent lines of evidence for recognizing separately evolving lineages, i.e. species. This implies that not all lines of evidence necessarily support a species or the assignment of a particular specimen to a species, particularly in young species or species with a recent history of range changes. Hybridization and deep coalescence are additional processes, which may prevent representatives from the same biological species from forming monophyletic clades in phylogenetic analyses. In practice, we recognize species that are morphologically distinct and/or which form a monophyletic group in phylogenetic analysis of one or several loci, which is not contradicted by supported monophyletic groupings in phylogenetic results of any other locus.

We obtained data from the ITS, two nuclear coding genes and two variable regions of the mitochondrial SSU to investigate species limits within *H.* subsect. *Denudata*. The goal was to obtain data from all DNA regions for all collections on which species descriptions were based. Taxonomic types were not only included in the descriptions, but as far as possible also in the sequence analyses in order to link molecular results to traditional taxonomy.

Morphological methods have been refined. A large number of morphological characters have been parameterised in order to allow a relatively complete description and easy comparison between collections. These morphological characters span both macroscopic and microscopic detail. We have made extensive use of the work of Vesterholt (2005) and studies cited therein who adopted a classification to describe spore characters and formalised cheilocystidia descriptions. For the cheilocystidia we have further refined their classification to better describe their shape.

Most of the material used by Aanen and co-workers for their ICG studies has kindly been made available by Th.W. Kuyper. Thus, we are now able not only to recognize taxon clusters, but also to relate them to existing species and, thanks to the previous work of Aanen and others, to relate them to ICGs. The rigorous statistical approach of analysing numerous collections and their characters has also helped in the recognition and understanding of ecological preferences.

Within *H.* subsect. *Denudata* we include fifteen species occurring in Europe, eight of which are new to science. *Hebeloma crustuliniforme* was described in a recent publication (Vesterholt et al. 2014); this paper provides descriptions of the remaining fourteen taxa encountered in Europe and a key to all fifteen species, allowing the reader to appreciate species distinctions. Eleven of the fifteen species are likely to correspond to eleven ICGs identified by Aanen and Kuyper (Aanen 1999, Aanen & Kuyper 1999, 2004). As discussed above three ICGs relate to species outside *H.* sect. *Denudata* and the remaining ICGs relate to species in other subsections of *H.* sect. *Denudata* and will be addressed more fully in Eberhardt et al. and Grilli et al. (in prep.). We demonstrate that within this subsection – in spite of occasional problems in morphologically distinguishing between two species, rare mismatches between morphological and molecular evidence and gaps in the molecular data matrix when older specimen could not be sequenced for certain loci – that there is good overall consistency between morphological, molecular and seemingly also biological species circumscriptions.

Implications of earlier taxonomic decisions (Aanen 1999, Aanen & Kuyper 2004) with regard to the *H. crustuliniforme* complex and results based on environmental sequencing studies (reviewed by Timling & Taylor 2012) supported the view that agarics, including *Hebeloma* spp., of the arctic or alpine regions are essentially the same as temperate taxa at the species level. According to the results presented here for the *H. crustuliniforme* complex and *H.* subsect. *Denudata*, this assumption is debatable. Though taxa of both biomes are doubtlessly closely related, qualitative and quantitative differences can be observed between the arctic/alpine flora as opposed to floras of lower latitudes and altitudes.

MATERIALS AND METHODS

The majority of collections cited in species descriptions and used for molecular studies are included in the private herbarium of H.J. Beker. Some collections were obtained from other collectors and their private collections. Additional collections were obtained from public herbaria. The latter are referred to by their acronym, followed by a gap and a collection number. Private collection or collection numbers do not include gaps. Collections not contained in the herbarium of H.J. Beker are also referred to by their HJB database record number. This database contains all data pertaining to the collections and is intended for publication at a later stage.

Molecular analyses

Sequence data were obtained of five different DNA regions, ITS, *RPB2*, *MCM7* (a DNA replication licensing factor) and the variable regions V6 and V9 of the mitochondrial SSU r-DNA. Not all data could be obtained for all collections; for some collections, mostly older collections, none or only partial ITS sequences could be obtained. Sequences were submitted to GenBank with the accession numbers KM390027–KM390104, KM390107–KM390759, KM390763–KM390775 (newly obtained for this study) and AY312982, JN943848–JN943881, KF309396–KF309406 and KF309426–KF309498.

Details of DNA extraction, PCR and sequencing primers have been provided earlier (Eberhardt et al. 2009, 2013, Eberhardt & Beker 2010, Vesterholt et al. 2014). Raw sequence data were edited in Sequencher (v. 4.9, Gene Codes Corporation, Ann Arbor, MI, USA). Ambiguous base calls were regularly encountered in sequences from nuclear ribosomal and protein-coding loci. Length deviant ITS copies within the same amplicon were treated as described in Eberhardt et al. (2013). In these cases the attempt was made to segregate the two constituent sequences, presumably representing different nuclei (Aanen et al. 2001), separately. Sequences with more than one indel were treated under the assumption that the two most likely constituent sequences were the two most similar ones, i.e. minimizing the number of assumed base exchanges. For analyses of concatenated alignments, the intragenomic consensus with the least number of ambiguous positions was used.

Sequence alignments were done in Mafft v. 7 (Katoh & Standley 2013) as implemented on http://mafft.cbrc.jp/alignment/software/, using the FFT-NS-i option for coding genes and the ITS and E-INS-i option for the variable mitochondrial SSU regions. Gap recoding following Simmons & Ochoterena (2000) was done using FastGap v. 1.2 (Borchsenius 2009) for the V6 and V9 sequence alignments. PartitionFinder (Lanfear et al. 2012)

in combination with RAxML (v. 7.2.8-alpha, Stamatakis 2006) was used to determine the most efficient partitioning scheme for protein coding data and concatenated alignments. Concatenation of alignments was done in SequenceMatrix (Vaidya et al. 2011), using only one sequence per collection and locus, i.e. the consensus sequence in case of heterokaryotic data. Prior to the concatenation of different datasets, their compatibility was tested following the principle of Kauff & Lutzoni (2002), assuming a conflict to be significant if two different relationships for the same set of taxa, one being monophyletic and the other non-monophyletic, are supported by bootstrap with more than 70 % in ML analyses.

ML analyses for the compatibility test were done with RAxML v. 7.2.8-alpha on a local computer or RAxML-HPC BlackBox (v. 7.6.3) (Stamatakis 2006, Stamatakis et al. 2008) through the CIPRES Science Gateway (Miller et al. 2010). Maximum likelihood searches for tree building were carried out locally with 100 replicates using the GTRGamma model, selecting the best solution for each analysis. Fast Bootstrap searches were done locally or on the CIPRES server, with 1 000 replicates. Trees were visualized using FigTree v. 1.4.0 (Rambaut 2012). The assignment of collections and sequences to species follows morphology.

Distance values of ITS sequences were calculated in Mesquite (v. 2.75, Maddison & Maddison 2011, http://mesquiteproject. org) as 'uncorrected p' distances based on ambiguity differences, discounting gaps, and on the same alignment, that was also used for concatenation, considering the spacer regions and the 5.8 S rRNA (650 bp).

Morphological analysis

Morphological analysis is carried out with the help of a Biolomics-based database system (v. 7, http://www.bio-aware.com). Except where stated otherwise, all descriptions and measurements given are based on a number of collections. Wherever possible all macroscopic information is collected through the input of parametric data, either directly to the database or via the use of a standardised form. Where this is not possible, for example for old material and often for type material, original descriptions, and where possible photographs, are used to assemble this macroscopic information. All microscopic analysis was carried out on dried material and unless stated otherwise measurements given are average measurements.

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. Additional measurements (not included in any of our keys) included spore area, circumference and colour.

The assessment of spore characters follows Vesterholt (2005): spore ornamentation on a scale from O0 (smooth) to O4 (ornamentation fairly strong, and always visible without immersion), the loosening of the perispore P0 (not loosening) to P3 (strongly and constantly loosening) and the dextrinoidity of the spores in Melzer's reagent from D0 (indextrinoid) to D4 (strongly dextrinoid, immediately becoming dark brick to dark reddish brown).

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. These were measured while still on the lamella edge and by measuring *all* cystidia where the apex could be properly

focused and measured. 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 (A), width at narrowest point in central region (M) and maximum width in lower half (B). The measurements are given in this order and an average value was calculated for each of these measurements. Further, the ratios A/M, A/B and B/M are calculated for each cystidium and then these too are averaged. The measurements were made in 5 % KOH.

All microscopic measurements are made using a Leica DM-RXA2 microscope system with a Leica DC300 camera connected to a computer running Leica IM1000 image capture software and Leica QWin image analysis software. Photographs of all relevant characters are taken and then all measurements and analysis is carried out on the computer system using the image analysis software, fed into spread sheets, where statistics are calculated, and then automatically transferred into the database. An advantage of this approach is that all measurements are repeatable and all information relating to these measurements, including all photographs, is stored with the rest of the collection information in the database.

Keys were built on the database as a set of complex queries. More than 1 250 collections of *H.* sect. *Denudata* amid more than 4 000 collections of *Hebeloma*, including their collection details, ecology and, for more than half these collections, morphometric parameters and results have been entered into the database. By having all data fully parameterised, collections can be compared with ease and database queries can be used to isolate those collections with similar features. This in turn enables keys to sections and to species to be built and continually be tested across a large number of collections. Principal component analyses were done in R (R Core Team 2014, Vu 2011).

RESULTS

All collections cited in the species descriptions of this paper were included in the molecular studies. The minimum goal was to obtain ITS sequences. For known species, collections were selected from a wide variety of habitats throughout Europe and in some cases also from other continents. We were able to locate and obtain type material for each of these taxa, as well as type material for a number of species that we believed were related to these taxa and might belong to this subsection, and this was also included in our studies. In total, ITS sequence data were obtained for over 550 collections and 271 collections were subjected to further and more detailed analysis. *Hebeloma mediorufum* was used as outgroup. This taxon, up to now only known from New Zealand, is, according to all DNA regions included in the analyses and the study of Rees et al. (2013), the closest relative of all known European members of *H.* sect. *Denudata*, without being inside the clade representing the European species of *H.* sect. *Denudata*.

No molecular data could be obtained for the lectotype of *H. helodes* (G 00053920; database record HJB1000054) and the holotype of *H. eburneum* (MPU GM1122; database record HJB1000095). The same applies to one collection used in the description of *H. aanenii* (collected by G. Bresadola, S F14406, database record HJB13470); *H. eburneum* (collected by G. Malencon, MPU GM1415, database record HJB12229); and for *H. pusillum* (collected by D. Aanen WBS 9648, database record HJB12518), though for the latter a V6 sequence could be obtained. For *H. pusillum* GLM GL42941 (database record HJB10993) the ITS sequence published by Boyle et al. (2006), AY312982, was used. In two cases only partial ITS sequences could be obtained: for the lectotype collections of *H. alpinum*

Table 1 Inter- and intraspecific 'uncorrected p' distances of ITS-sequences (alignment 650 bp). Min(inter) – minimum of the interspecific distances; Max(intra) – maximum of the intraspecific distances; no. – number of collections considered; *H.* – *Hebeloma*.

Species	No.	Min(inter)	Max(intra)
H. aanenii	35	0	1.1
H. alpinum	34	0	0.2
H. aurantioumbrinum	12	0	0.3
H. crustuliniforme	20	0.2	0.2
H. eburneum	35	0	1.2
H. geminatum	26	0	0.3
H. helodes	21	0	0.5
H. louiseae	3	0.5	0
H. luteicystidiatum	4	0.2	0
H. lutense	23	0.2	0
H. mediorufum	4	3.4	0
H. minus	10	0	1.0
H. pallidolabiatum	2	0	0.2
H. perexiguum	1	0.3	n.a.
H. pusillum	36	0.6	1.1
H. salicicola	21	0	0.2

(G GK13674; database record HJB1000060) only the ITS1; for the isotype of *H. lutense* (L 0054088, database record HJB1000011) only the ITS2; the ITS sequence of the holotype of *H. lutense* (P 59.232, database record HJB1000253) is complete.

Table 1 summarizes the minima of the interspecific distances and maxima of the intraspecific distances of ITS – barcode – sequences. If the former value is lower than the latter value, correct species identification solely based on sequence similarity of the ITS barcode is bound to fail at least in some cases. Single locus alignments and trees for all DNA regions used were submitted to TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S15738). Fig. 1 and 2 show 5 representations of the phylograms, colour-coded by species, with the position of type collections indicated at the side of the tree for loci for which sequence data could be obtained.

In total, 314 ITS sequences represent 271 collections, because length deviant ITS copies retrieved from single collections were entered separately to see whether they would be part of different clusters supported by bootstrap of ≥ 75 %. This was

not the case, so that for the concatenated alignment a single consensus sequence represents the 43 collections concerned (see below).

The ML result of the ITS analysis (Fig. 1a) shows only two species (*H. louiseae* and *H. luteicystidiatum*) are supported by bootstrap of ≥ 75 %. The clade, which contains the majority of *H. minus* ITS sequences, though supported, does not include all sequences from this species. Some clades are constituted predominantly by sequences of a single taxon (*H. aanenii*, *H. aurantioumbrinum*, *H. eburneum*, *H. helodes*, *H. lutense*, *H. pusillum* and *H. salicicola*). The placement of the isotype of *H. lutense* in the middle of the main *H. aanenii* cluster is due to missing data; complete sequences of *H. lutense* (also the sequence of the holotype) differ mostly in the ITS1 from *H. aanenii* sequences. The obtained ITS2 sequence of the isotype shows no differences from any of the *H. lutense* sequences.

For the variable region V6 of the mitSSU, 190 sequences from the same number of collections were obtained. The alignment spans 408 DNA positions and 24 positions for recoded gap information. Bootstrap support is better with this region, with the species clades of *H. crustuliniforme*, *H. louiseae*, *H. luteicystidiatum*, *H. lutense*, *H. pallidolabiatum* and *H. pusillum* receiving bootstrap support of 86 % or more. Part of the *H. crustuliniforme* complex (Vesterholt et al. 2014), without *H. crustuliniforme* but including *H. louiseae* and *H. pallidolabiatum* (which were not included in the former publication) receive 90 % bootstrap support. There are additional supported clades (Fig. 1b), but neither of these represent species clades in the sense that all sequences of a given taxon are included.

For the other variable region of the mitSSU analysed here (Fig. 2a), V9, 106 sequences from the same number of collections were analysed. The alignment consists of 502 DNA positions and 20 positions represent recoded gaps. Four species (*H. crustuliniforme*, *H. luteicystidiatum*, *H. lutense*, *H. pusillum*) form bootstrap-supported species clades, the species clade of *H. pallidolabiatum* is unsupported.

Among the analysed loci, *RPB2* (103 sequences of 103 collections, alignment 702 bp) is the one that on its own supports the species concepts described below best. Nine species clades receive bootstrap support, among them clades of *H. aurantioumbrinum* and *H. helodes*, *H. minus* and *H. salicicola* in addition

Table 2 Clades supported by bootstrap support values higher than 70 % in single locus analyses. In **bold** are support values supporting clades incompatible between some of the single locus ML results. n.a. – not applicable. Clades consisting of sequences assigned to a single species, but not containing all sequences of the respective species, are not listed

Clade	ITS	V6 of mitSSU	V9 of mitSSU	RPB2	MCM7
H. aurantioumbrinum				90	97
H. helodes				91	100
H. aurantioumbrinum & *H. helodes*	89	100	90		70
H. luteicystidiatum	93	100	99	n.a.	100
Ingroup excluding *H. luteicystidiatum* & *H. perexiguum*		**73**			
H. lutense		96	100	98	99
H. pusillum	77	88	100	99	100
H. perexiguum & *H. pusillum*			**91**		
H. crustuliniforme	74	100	99	96	99
H. crustuliniforme complex excluding *H. crustuliniforme*		90			
H. louiseae	99	84		100	99
H. minus				88	
H. minus & *H. louiseae*			77		
H. louiseae & *H. pallidolabiatum* & *H. minus*					**78**
H. salicicola				**82**	
H. salicicola excluding HJB13087 & HJB9072		78			
H. pallidolabiatum				95	97
H. pallidolabiatum & HJB13087 (*H. salicicola*) & HJB12204 (*H. alpinum*)		**81**			
H. salicicola & *H. pallidolabiatum*				**98**	
HJB9072 (*H. salicicola*) & HJB11986 (*H. alpinum*)		80			
HJB12806 (*H. aanenii*) and HJB10290, HJB12537, HJB12996 & HJB12804 (*H. eburneum*)	76				
H. aanenii (excluding HJB10450) & *H. eburneum*	81				
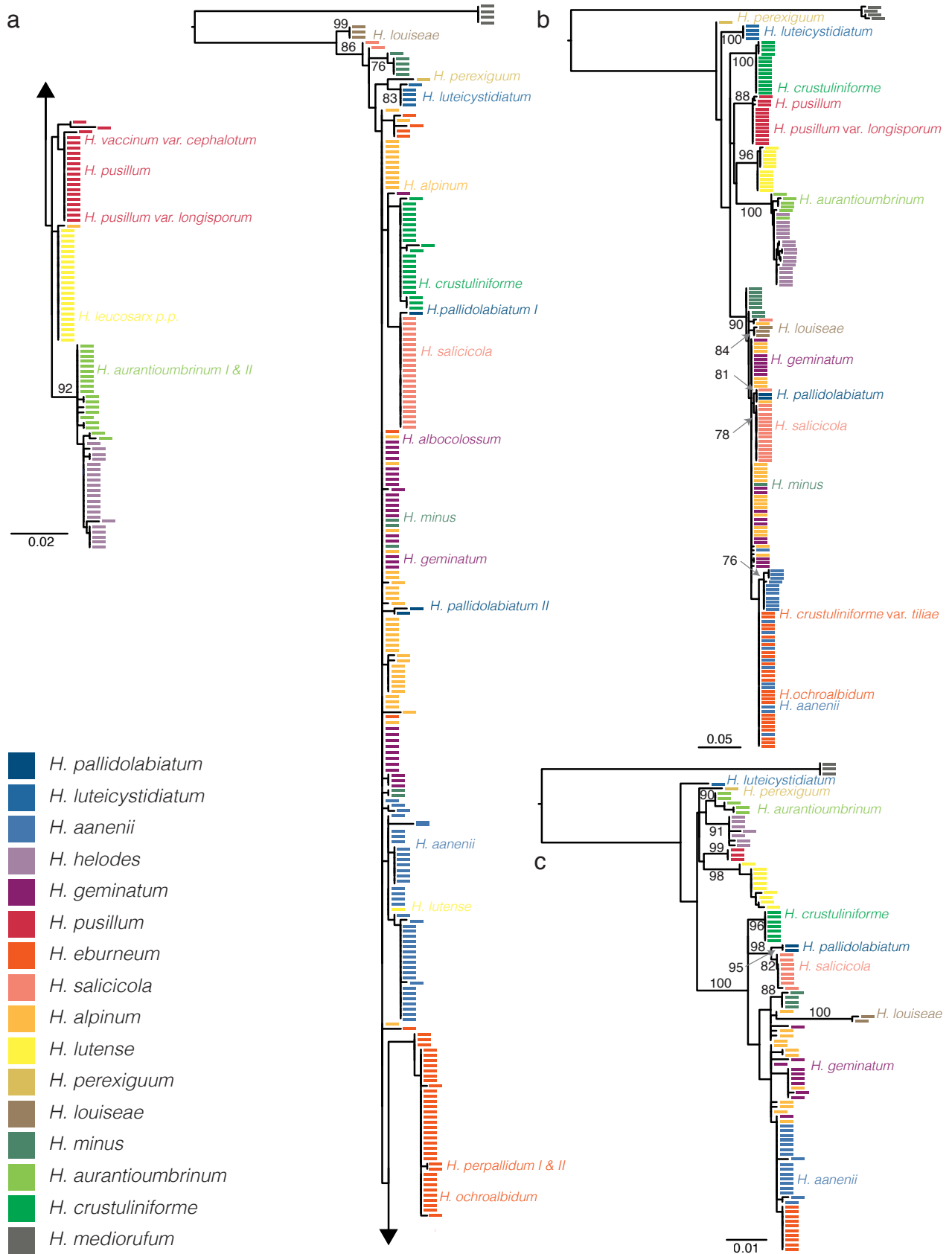
Fig. 1 Best of 100 ML results of European *Hebeloma* subsect. *Denudata* of single gene analyses with 1 000 bootstrap replicates and *H. mediorufum* as outgroup. Only bootstrap values of ≥ 75 % are given. Species are colour coded (see legend). *H. – Hebeloma*. The placement of type collections is indicated by the name of the respective species at the side of the clade; the colour of the font matches the current taxonomic placement of the species. a. ITS; b. V6 region of the mitSSU; c. *RPB2*. For the ITS, length variant copies of the ITS from the same specimen were both included in the analysis and indicated by 'I' and 'II'.

to species clades mentioned before. *Hebeloma eburneum* is monophyletic without support. Only a single sequence could be obtained for *H. luteicystidiatum*, so that we do not know about the clade support. As in V6, the clade of the *H. crustuliniforme* complex receives a high bootstrap support. *Hebeloma aanenii*, *H. alpinum* and *H. geminatum* are paraphyletic.

Sequences for *MCM7* were difficult to obtain, but 120 sequences of the same number of collections could be obtained; alignment length was 667 bp. The analysis supports eight species with bootstrap. *Hebeloma salicicola* forms an unsupported species clade. Sequence variation is rather high within some species of the *H. crustuliniforme* complex (i.e. *H. aanenii*, *H. minus*, *H. salicicola*) and, judging from SNPs, also intragenomically. We assume that the intragenomic variation is the result of heterokaryocity (Aanen et al. 2001). In high quality reads there are not more than two superposed peaks in a position.

Table 2 summarizes bootstrap results of single locus analyses, which were used for testing compatibility of the results of single gene analyses prior to concatenation. Results of single locus analyses are incompatible only with regard to the placement of the clades of *H. perexiguum* and *H. pallidolabiatum*. The results of the two mitochondrial variable regions differ with view to the placement of the *H. perexiguum* sequence, but in one case (V6) the support is rather low with 73 %. *Hebeloma pallidolabiatum* is in a supported clade with *H. louiseae* and *H. minus* for *MCM7*, which is incompatible with the supported *RPB2* clade of *H. pallidolabiatum* and *H. salicicola* or the V6

result, where *H. pallidolabiatum* forms a supported clade with one collection of *H. alpinum* and *H. salicicola* each. This in turn forms a potential incompatibility with the supported *H. salicicola* clade of the *RPB2* result.

In spite of these incompatibilities we decided to concatenate the single locus alignments to see whether species not receiving support or being paraphyletic in single locus analyses would form (supported) monophyla in concatenated analyses. All loci were included in the concatenation, as there was no indication that mitochondrial DNA data show a completely different evolutionary history from nuclear data. Fig. 3 shows the ML result including five loci and all collections (158) for which data were available for at least three of the five concatenated loci. If only collections were included with a full dataset of five sequenced loci, the resulting topology is very similar, but the bootstrap support is better. Only *H. alpinum* (paraphyletic) and *H. minus* do not receive support ≥ 75 % and all other species, apart from *H. geminatum* and *H. aanenii* receive bootstrap support of 90 % or more. With four genes out of five, the result differs from the depicted phylogram by supporting the *H. geminatum* clade with 78 % bootstrap and the *H. aanenii* clade with 77 % bootstrap. With a minimum of two genes out of five, *H. aanenii*, *H. eburneum*, *H. geminatum*, and *H. minus*, in addition to *H. alpinum* that is paraphyletic in all analyses, also become paraphyletic.

In the ML result based on a minimum of three loci, one collection is 'misplaced' with regard to its morphological species
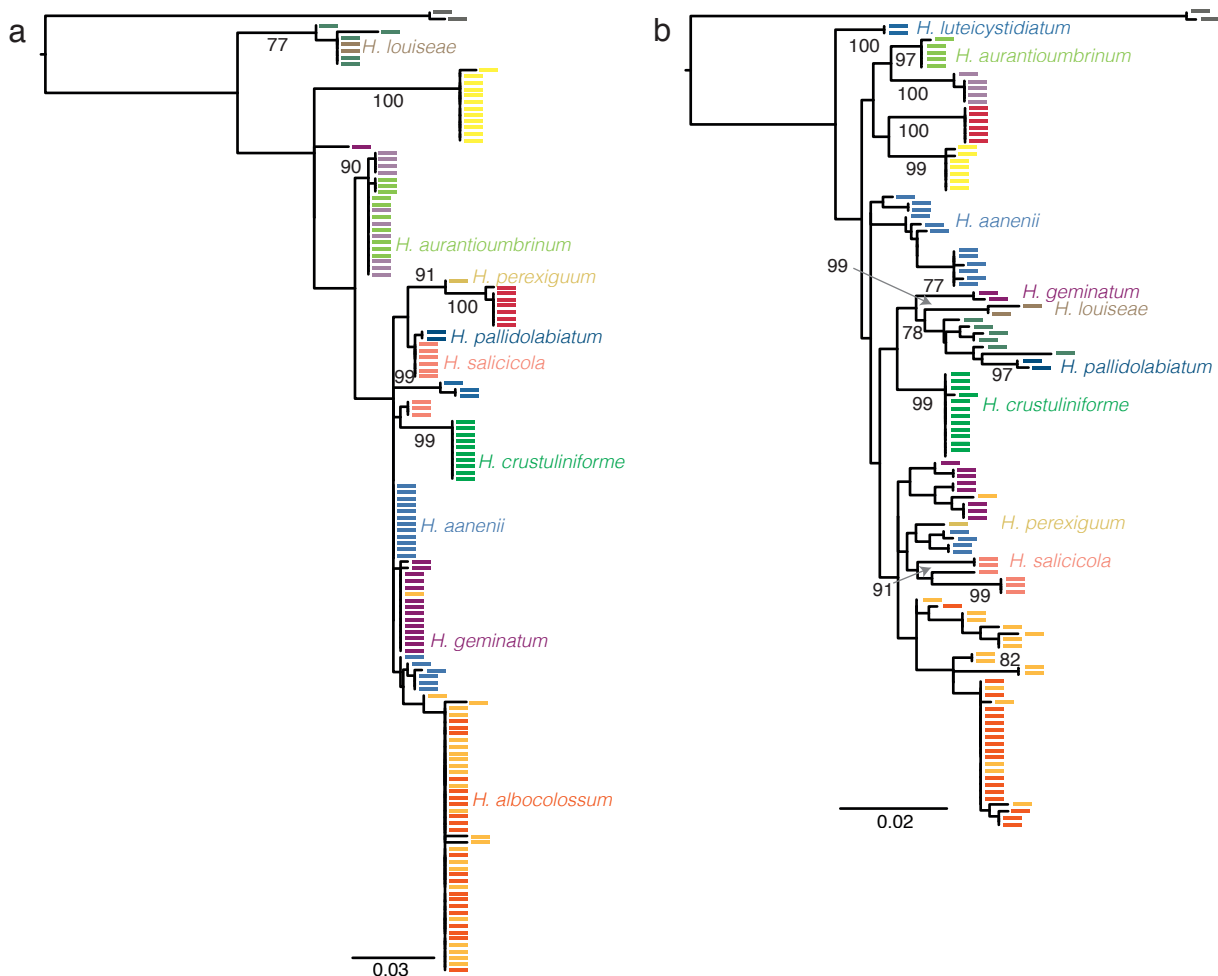
Fig. 2 Best of 100 ML results of *Hebeloma* subsect. *Denudata* of single gene analyses with 1 000 bootstrap replicates and *H. mediorufum* as outgroup. Only bootstrap values of ≥ 75 % are given. Species are colour coded (see legend Fig. 1). *H. – Hebeloma*. The placement of type collections is indicated by the name of the respective species at the side of the clade; the colour of the font matches the current taxonomic placement of the species. a. V9 region of the mitSSU; b. *MCM7*.

assignment, namely *H. alpinum* HJB11051. DNA extraction, PCR and sequencing were repeated, but several markers place the collections in *H. geminatum*. One collection, *H. geminatum*, HJB11545, is not included in the *H. geminatum* clade and thus implicitly in the paraphyletic part of the tree constituting *H. alpinum*. In this case, the V9 sequence of the collection is odd and differs from the rest of the *H. geminatum* V9 sequences (and all other taxa with long V9 sequences in the alignment) in a number of positions. It differs very clearly from *H. alpinum* V9 sequences, which are considerably shorter than *H. geminatum* V9 sequences.
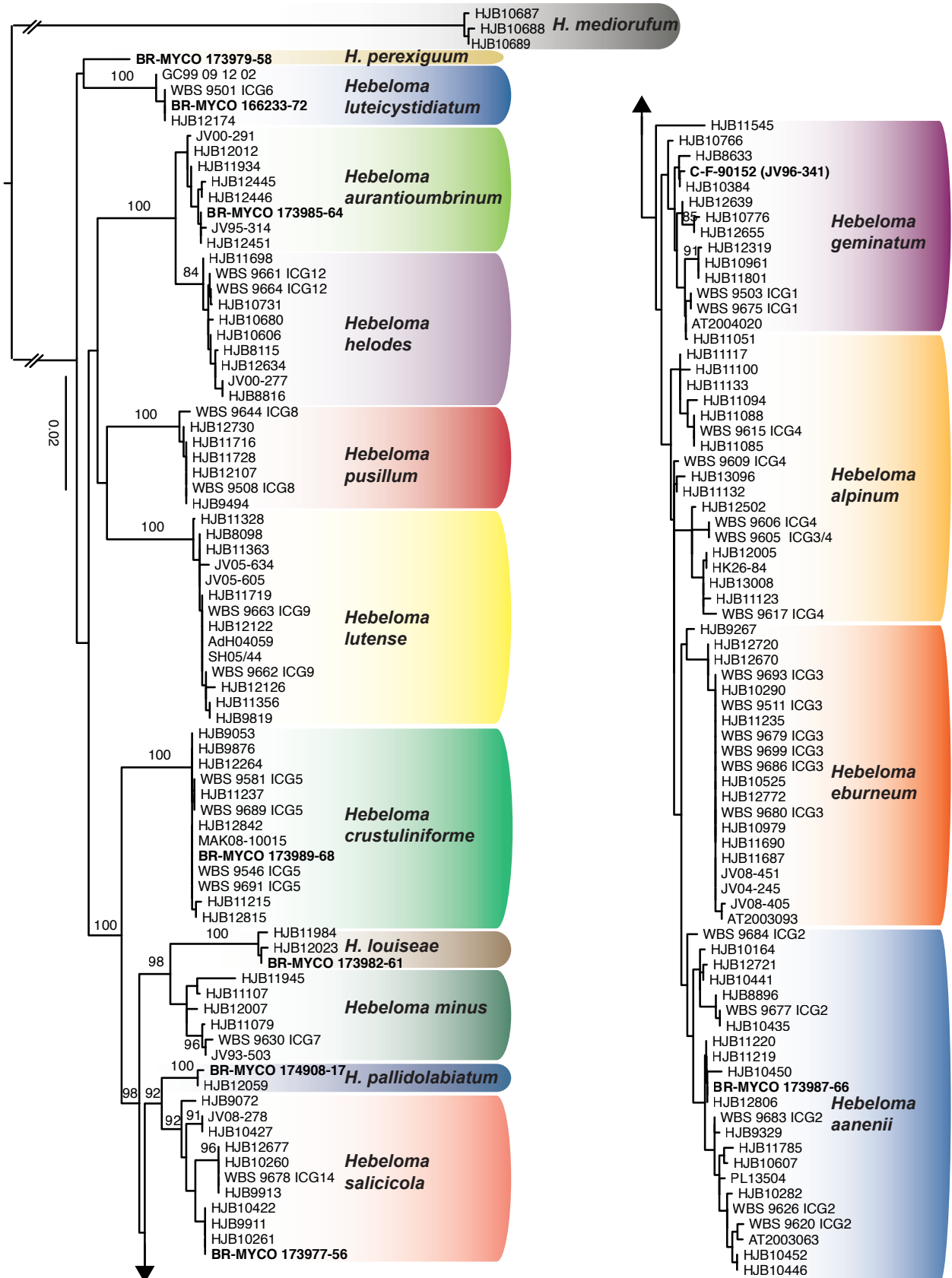
Fig. 3 Best of 100 ML results based on five DNA regions (ITS, V6 and V9 of the mitSSU, partial *RPB2* and *MCM7*), including all collections for which sequences of at least three of the loci were obtained. *Hebeloma mediorufum* is outgroup. Bootstrap analyses are based on 1 000 replicates; only support values of ≥ 75 % are shown. Type collections are in **bold**. ICG – Intercompatibility group (see Aanen & Kuyper 1999).

Table 3 Summary of ecological preferences and the most important morphological characters of the 15 species of *Hebeloma* subsect. *Denudata*. A/M, A/B and B/M refer to the average apex (A), median (M) and B (basal) width of the cheilocystidia. ICG (intercompatibility group) numbers follow (Aanen & Kuyper 1999).

species: *Hebeloma*	*aanenii*	*alpinum*	*aurantioumbrinum*	*crustuliniforme*	*eburneum*	*geminatum*
habitat	woodland; on a variety of soils with a variety of trees; rarely alpine	arctic; alpine; with *Salix* or *Dryas*	arctic; alpine; boreal with *Salix*	woodland; dunes; with various trees	woodland; dunes; with various trees	woodland; on a variety of soils with a variety of trees; rarely arctic/alpine
cap colour	cream to yellow to buff to yellow brown in centre; margin paler	cream to buff, sometimes centre Isabella or yellow brown	from yellow brown to umber but with some orange	cream to buff	pale, cream to yellowish	usually pale, cream to yellow or pale buff
pileus diameter	20–170	12–70	< 21	20–135	20–133	27–120
median stipe width	3.5–13	3–13	2.0–3.1(–3.5)	(6–)7.0–20(–26)	(3–)6–29(–36)	6.5–12.8
stipe Q (5–95%)	2.1–12.0	2.3–6.0	5.5–7.0	1.7–6.9	2.8–9.4	2.5–9.2
slenderness	1.4–20.6	1.2–8.6	5.3–14.7	0.8–12.6	3.1–15.6	1–12.8
number of lamellae (L)	60–110	40–72	26–39	60–100	usually 70–110; but some colls. 40–60	65–100
spore ornamentation	O2,O3	O1,O2(O3)	O1,O2(O3)	(O1)O2,O3	O2,O3	O2,O3
spore perispore	(P0)P1,P2	P0,P1	P0,P1	(P0)P1(P2)	(P0)P1(P2)	(P0)P1(P2)
spore dextrinoidity	D0,D1(D2)	D0,D1,D2	D1,D2	(D0)D1,D2	D1,D2	D0,D1
av spore length	8.8–10.9	11.0–13.7	10.2–11.8	10.8–12.2	(10.2–)10.9–13.7	9.8–10.8(–11.6)
av spore width	5.2–6.3	6.1–7.7	6.2–6.8	6.1–6.7	(5.5–)6.1–7.1	5.4–6.3
av spore Q	1.60–1.95	1.60–1.97	1.60–1.85	1.70–1.89	(1.60–)1.69–2.06	1.65–1.93
av cheilocystidium length (µm)	39–82	40–71	45–61	42–63	45–71	50–72
av cheilocystidium apex width	6.2–9.0	6.8–9.8	7.2–8.4	6.5–7.9	8.0–10.4	8.0–10.4
av cheilocystidium median width	3.6–5.3	3.6–5.1	4.0–4.8	3.4–4.7	3.6–4.9	4.0–4.7
av cheilocystidium basal width	3.5–5.8	3.2–6.1	4.3–5.4	3.5–5.0	3.7–5.1	3.7–5.0
A/M	1.61–2.49	1.61–2.74	1.61–1.99	1.61–2.32	1.78–2.71	1.76–2.57
A/B	1.51–2.48	1.52–2.71	1.62–1.98	1.52–2.32	1.80–2.72	1.68–2.85
B/M	0.85–1.24	0.87–1.24	0.97–1.18	0.90–1.22	0.90–1.19	0.81–1.19
epicutis thickness	100–400	60–160	< 100	150–350	80–120	100–200
ICG	2	4	n.a.	5	3	1

In Fig. 3 the intercompatibility group (ICG) assignment of (Aanen & Kuyper 1999) is stated for all collections for which this information was available. The figure shows that there is full agreement between the ICG, taxon names based on morphology and the molecular results. Collection WBS 9605, compatible with two ICGs belongs to *H. alpinum* morphologically and also clusters with other collections of this taxon.

We have been able to construct queries on the database, based purely on morphological characters, which can select the collections of a single clade (or ICG) as demonstrated in the keys provided below, with the single exception of *H. aaneni* and *H. geminatum* where there is clear evidence for two distinct species but we have been unable, thus far, to find a morphological character or set of characters on which such separation can consistently be unambiguous. Table 3 summarizes the most important morphological properties and ICG assignment (following Aanen & Kuyper 1999) of the recognized species.

Principal component analyses with three parameters (average spore area, cheilocystidia apex width and number of complete lamellae, Fig. 4a), and with two parameters (average spore
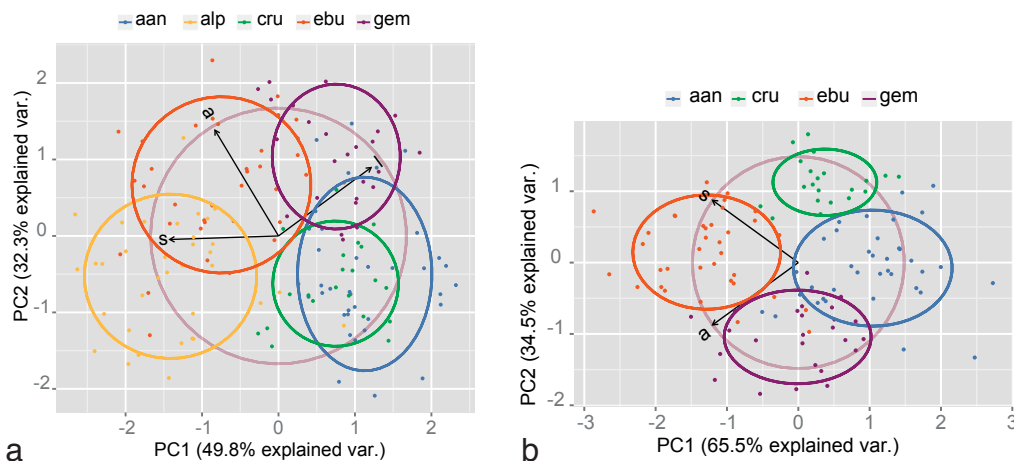
Fig. 4 PCA of *Hebeloma aanenii* (aan), *H. alpinum* (alp), *H. crustuliniforme* (cru), *H. eburnuem* (ebu) and *H. geminatum* (gem). a. Using average apex width (a), average spore area (s) and average number of complete lamellae (l); b. excluding *H. alpinum*, using average apex width (a) and average spore area (s).

helodes	louiseae	luteicystidiatum	lutense	minus	pallidolabiatum	perexiguum	pusillum	salicicola
woodland; dunes; various trees usually wet soil	arctic, with *Salix*	woodland; with *Salix* wet soil	woodland; dunes; with *Salix* usually wet soil	alpine; arctic; subalpine with *Salix*	arctic; with *Salix*	arctic; with *Salix*	woodland; with *Salix* often wet soil	dunes; woodlands; on a variety of soils with *Salix* or *Populus*; rarely arctic
pale, white to cream centre sometimes darker buff or yellowish brown	clay buff to Isabella	zonate: centre honey to dark brown; margin paler to buff	zonate; centre: yellow brown to dark brick; margin: white to cream	Isabella or buff to brown olive or umber, sometimes paler margin	sepia to dark brick in the centre, thin pale margin	uniformly grey brown	zonate: centre cinnamon to sepia to dark brick; margin paler to cream	zonate: centre ochre to red brown, sepia or dark brick; margin clay pink to buff or Isabella
13–38	< 15	< 15	15–58	9–31	12–21	7–25	11–25	10–48
2.9–4.5	2–3(–3.5)	1.0–2.5	3–11	1.0–8.0	2–3.5	2	1.5–3.5	(1.5–)2–7
4.7–20	4.6–7.6	12–17.5	4.2–12.3	4.8–14	6.2–6.6	6.3	10.8–21.6	3.5–11.1
5.4–44.5	4.8–12.9	19.8–65	4.1–23.2	6.6–28	6.4–6.9	8.3	8.5–64.1	2–23.6
37–54	30–38	21–26	32–58	30–34	30–33	24–26	20–38	30–50
O2,O3	O1,O2	O1,O2	(O1)O2,O3	O2,O3	O2	O1	(O1)O2,O3	O2,O3
(P0)P1,P2	P0	P0,P1(P2)	(P0)P1,P2	P0,P1,P2	P0	P0	(P0)P1,P2	(P0)P1,P2
D0,D1(D2)	D0,D1	D1,D2	D1,D2	D1(D2)	(D0)D1,D2	D1	(D0)D1,D2	D2,D3
9.1–10.8	12.3–12.8	11.6–11.9	9.4–11.7	11.2–13.1	12.8–13.5	11.7	11.4–13.6	11.2–13.3
4.9–6.0	7.5–7.7	6.1–6.5	5.4–6.4	6.2–7.7	7.2–7.6	7.2	5.6–6.7	6.1–7.5
1.61–2.02	1.63–1.66	1.80–1.95	1.63–1.91	1.61–1.86	1.69–1.88	1.63	1.91–2.22	1.64–2.00
44–63	49–59	50–62	42–56	40–55	58–59	54	41–70	46–63
8.3–11.4	9.0–9.9	8.8–9.9	6.8–7.9	8.8–10.4	8.6–9.0	8.5	8.0–10.0	7.9–10.7
4.0–4.9	4.4–5.4	4.0–4.3	3.4–4.5	(3.7–)4.2–5.1	5.1–5.4	4.8	3.8–4.8	3.8–5.0
3.3–5.4	4.8–5.6	4.0–4.9	3.5–4.8	(3.0–)4.3–5.9	5.9–6.3	6.4	3.6–4.9	3.6–5.9
1.90–2.86	2.01–2.42	2.27–2.77	1.63–2.39	1.99–2.44	1.61–2.05	1.75	1.71–2.71	1.83–2.63
2.02–3.38	1.99–2.25	2.21–2.68	1.58–2.34	1.82–3.02	1.57–1.69	1.45	1.68–2.52	1.60–2.82
0.77–1.17	0.92–1.24	0.98–1.22	0.95–1.22	0.84–1.24	1.09–1.24	1.33	0.94–1.20	0.96–1.27
100–135	< 100	50–60	100–180	40–100	80	< 30	40–80	85–150
12	n.a.	6	9	7	n.a.	n.a.	8	14

area and cheilocystidia apex width, Fig. 4b) that are important for species identification were run for the four taxa that are most difficult to distinguish from each other morphologically (*H. aanenii*, *H. crustuliniforme*, *H. eburneum* and *H. geminatum*) and *H. alpinum* which is most difficult to distinguish from these four in molecular terms. This analysis shows that these parameters alone are sufficient to group many collections correctly to species.

TAXONOMY

Hebeloma section *Denudata* (Fr.) Sacc.

Type. *Hebeloma crustuliniforme* (Bull.) Quél. emend. Vesterh., U. Eberh. & Beker.

Hebeloma subsection *Denudata*

Within subsect. *Denudata* we recognise the following fifteen taxa:

H. aanenii, *H. alpinum*, *H. aurantioumbrinum*, *H. crustuliniforme*, *H. eburneum*, *H. geminatum*, *H. helodes*, *H. louiseae*, *H. luteicystidiatum*, *H. lutense*, *H. minus*, *H. pallidolabiatum*, *H. perexiguum*, *H. pusillum* and *H. salicicola*

Cortina absent; universal veil not observed; smell usually more or less radish-like but sometimes absent; the lamellae usually with clear droplets but occasionally absent, particularly in dry weather, but then often leaving brown or rusty stains on the lamellae. *Spores* amygdaloid, sometimes with a papilla, O1-3; P0-2; D0-2, occasionally with some spores up to D3, av size 9.1–13.7 × 4.9–7.7 µm, Qav 1.60–2.17. *Cheilocystidia* with a majority capitate-, clavate- or spathulate-stipitate; i.e. swollen at the apex but fairly cylindrical below this apical swollen area but sometimes with a few cheilocystidia a little swollen near the base (capitate-, clavate- or spathulate-lageniform), particularly in smaller, possibly less mature cheilocystidia; average length between 40 µm and 75 µm; av width dimensions (µm): 6.8 < apex A < 11.4; 3.4 < median M < 5.4; 3.2 < base B < 6.4. Ratios: A/M > 1.6; A/B > 1.45; B/M < 1.35.

Notes — The main morphological feature that distinguishes species of *H.* subsect. *Denudata* is the shape of the cheilocystidium, significantly swollen at the apex, constricted in the median part and little swollen, if at all, in the bottom half, except in smaller, possibly less mature cheilocystidia.

Below we give descriptions of all species of *H.* subsect. *Denudata* discussed in this paper, with the exception of *H. crustuliniforme*, which was described in Vesterholt et al. (2014). Although a number of these species have been treated extensively in the literature, our diagnosis may be narrower (based wholly on the collections cited in this paper) and hence we feel a full description is necessary in order to properly define the morphological species concepts.

Key to Hebeloma section Denudata subsection Denudata

We provide a separate key for arctic/alpine collections. While this inevitably means some repetition between the two keys we believe the practical advantages make it worthwhile.

Fig. 5 Photo of: a. *Hebeloma aanenii* BR-MYCO 173987-66 (holotype); b. *H. aurantioumbrinum* BR-MYCO 173985-64 (holotype); c. *H. geminatum* C-F-90152 (JV96-341) (holotype); d. *H. louiseae* BR-MYCO 173982-61 (holotype); e. *H. luteicystidiatum* BR-MYCO 166233-72 (holotype); f. *H. pallidolabiatum* BR-MYCO 174908-17 (holotype); g. *H. perexiguum* BR-MYCO 173979-58 (holotype); h. *H. salicicola* BR-MYCO 173977-56 (holotype). — Photos: a, b, d, f–h. H. Beker; c. J. Vesterholt; e. P. Derboven.

Key to *Hebeloma* subsection *Denudata*

1. Alpine or arctic collection with *Salix* or *Dryas* . . . .   Key 1
1. Not alpine or arctic, whatever the association . . . .   Key 2

Key 1 – *Hebeloma* subsection *Denudata*

1. Av L ≥ 60 and av spore length < 11 µm . . . .
. . . . *Denudata* Key 2 - 11
1. Av L < 60 or av spore length ≥ 11 µm 2
2. Av L ≥ 40, spore length ≥ 11 µm with distinct papilla . . . .
. . . . *H. alpinum*
2. Any of the above conditions not satisfied 3
3. Spores O3 and D2 and not D1 . . . . *H. salicicola*
3. Spores not O3 or not D2 or D1 4
4. Av width of cheilocystidia apex < 8.5 µm. . . . .
. . . . *H. aurantioumbrinum*
4. Av width of cheilocystidia apex ≥ 8.5 µm 5
5. Cheilocystidium ratio A/B > 1.8 6
5. Cheilocystidium ratio A/B ≤ 1.8 7
6. Spores O1 or O2, few if any spores O3. . . . . *H. louiseae*
6. A large number of spores O3. . . . . *H. minus*
7. Majority of spores O1 and av spore length ≤ 12 µm . . . .
. . . . *H. perexiguum*
7. At least some spores at least O2 and av spore length
> 12 µm . . . . *H. pallidolabiatum*

Key 2 – *Hebeloma* subsection *Denudata*

1. L < 60. 2
1. L ≥ 60. 9
2. Av width of cheilocystidia apex < 8 µm and many cheilo-
cystidia sinuate . . . . *H. lutense*
2. Av width of cheilocystidia apex ≥ 8 µm or cheilocystidia not
sinuate 3
3. Av spore length < 11 µm 4
3. Av spore length ≥ 11 µm 5
4. Cheilocystidia without consistent and distinct apical thicken-
ing . . . . *H. aurantioumbrinum*
4. Cheilocystidia with consistent and distinct apical thicken-
ing . . . . *H. helodes*
5. Pileus almost uniformly coloured and pale (usually 3A2 or
4A2) and av stipe width in centre ≥ 6 mm .   *H. eburneum*
5. Pileus distinctly 2-coloured (with brown centre) and av stipe
width in centre ≤ 7 mm. 6
6. L < 30 and cheilocystidia have a thick apical wall often
appearing yellow under the microscope . . . .
. . . . *H. luteicystidiatum*
6. L > 30 or cheilocystidia without such an apical wall . . . 7
7. Av stipe Q < 12, spore dextrinoidity at least D2 . . . .
. . . . *H. salicicola*
7. Av stipe Q ≥ 12 or many spores at most D1 8
8. Av spore Q < 1.9 . . . . *H. minus*
8. Av spore Q ≥ 1.9 . . . . *H. pusillum*
9. Av spore width is ≥ 6.4 µm or av, spore length > 10.75 µm
and av spore width > 6 µm 10
9. Av spore width < 6.4 µm and av, spore length ≤ 10.75 µm
or av spore width ≤ 6 µm 11
10. Av width of cheilocystidia apex ≥ 8 µm . . . . *H. eburneum*
10. Av width of cheilocystidia apex < 8 µm *H. crustuliniforme*
11. Av width of cheilocystidia apex > 9 µm . . . *H. geminatum*
11. Av width of cheilocystidia apex ≥ 8 µm and ≤ 9 µm. . . . .
. . . . *H. aanenii/H. geminatum*
11. Av width of cheilocystidia apex < 8 µm . . . . . . *H. aanenii*

Hebeloma aanenii Beker, Vesterh. & U. Eberh., *sp. nov.* —
MycoBank MB809905; Fig. 5a, 6, 7

Etymology. In honour of Duur Aanen to whom we are deeply indebted for carrying out extensive research on biological mating between *Hebeloma* spp. as well as molecular analysis.

Type. POLAND, Bialowieski Park Narodowytrup (N52.72111 E23.9056; alt. ± 160 m) on acid soil in mixed ancient woodland pathside with *Carpinus betulus*, *Picea* sp., *Populus* sp. and *Quercus* sp., 19 Sept. 2008, *H. Beker, I. Kałucka*, holotype BR BR-MYCO 173987-66; isotype C C-F-90147; data-base record HJB12630.

Diagnosis — *Hebeloma aanenii* has the typical cystidia of *H.* sub-sect. *Denudata*. It differs from *H. alpinum*, *H. crustuliniforme*, *H. eburneum* by the average size of its spores (length < 11 µm and width < 6 µm) and normally from *H. geminatum* by the average width of the cheilocystidium apex which is always < 9 µm and usually < 8 µm and from the rest of the species of its subsection by the average number of lamellae, which is always ≥ 60. It can be differentiated from *H. geminatum* based on sequence comparison of the partial *RPB2* sequences and usually also the internal transcribed spacer of the nuclear ribosomal genes.

Basidiomes usually in scattered groups, sometimes caespitose, sometimes growing gregariously, sometimes solitary. *Pileus* from 18–170 mm diam, convex, often umbonate; *surface* often very viscid in appearance, tacky when moist never hygropha-nous but occasionally spotted; *cuticle colour* usually from cream to buff and sometimes yellowish even ochraceous, yellow brown or clay-coloured in the centre but then becoming paler towards the margin which is always very pale at most light buff; *pileus margin* often involute, particularly in young specimens, sometimes straight but can be serrate, scalloped or crenulate. *Lamellae* emarginate to adnate, crowded (L = 60–110) with a maximum depth of 2.5–9 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore matu-rity; *edge* fimbriate, paler than lamella surface; droplets on the lamella edge are usually present and visible to the naked eye; *lamellules* frequent. *Stipe* central, cylindrical often clavate and occasionally bulbous, (22–)25–108(–130) × 3.5–9(–13) mm and up to 20 mm at the base; white or alutaceous, sometimes but not usually discolouring from the base when handled or with age; *surface* dry, usually strongly floccose particularly towards the apex but at least pruinose; *interior* stuffed when young but sometimes becoming hollow with age and sometimes with a superior wick. *Cortina* not observed. *Flesh* rather thick, cream or pale brown. *Smell* raphanoid. *Taste* bitter. *Spore deposit* brownish olive to greyish brown or umber.

Spores amygdaloid, with small apiculus and rounded at the end opposite the apiculus, with a distinct thinning of the spore wall but rarely with any papilla, guttulate with one or more oily drops, weakly to distinctly ornamented, sometimes with some sign of loosening perispore in a few spores and weakly dextrinoid (O2,O3; (P0)P1,P2; D0,D1(D2)); *spore colour* un-der the microscope yellow-brown to brown; *spore size* based on n = 109 spores of the holotype, 5–95 % percentile range 8.8–11.3 × 5.1–5.9 µm, with median 10.0 × 5.4 µm and av 10.0 × 5.5 µm with SD length 0.73 µm and width 0.29 µm, Q value 5–95 % percentile range 1.66–2.01, with median 1.85 and av 1.83 with SD 0.11; *spore size* based on 36 collections medians 8.7–11.0 × 5.2–6.2 µm and av 8.8–10.9 × 5.2–6.3 µm with SD length 0.42–1.00 µm and width 0.18–0.65 µm, Qav 1.60–1.95. *Basidia* cylindrical to clavate and 4-spored, 21–43 × 6.1–10.2 µm, with av 22–36 × 6.6–9.1 µm. *Pleurocystidia* not found. *Cheilocystidia* usually clavate-stipitate and sometimes spathulate-stipitate, occasionally slightly swollen towards the base (clavate-lageniform) and occasionally with some apical or median thickening, septate, sinuate and occasionally bifurcate;
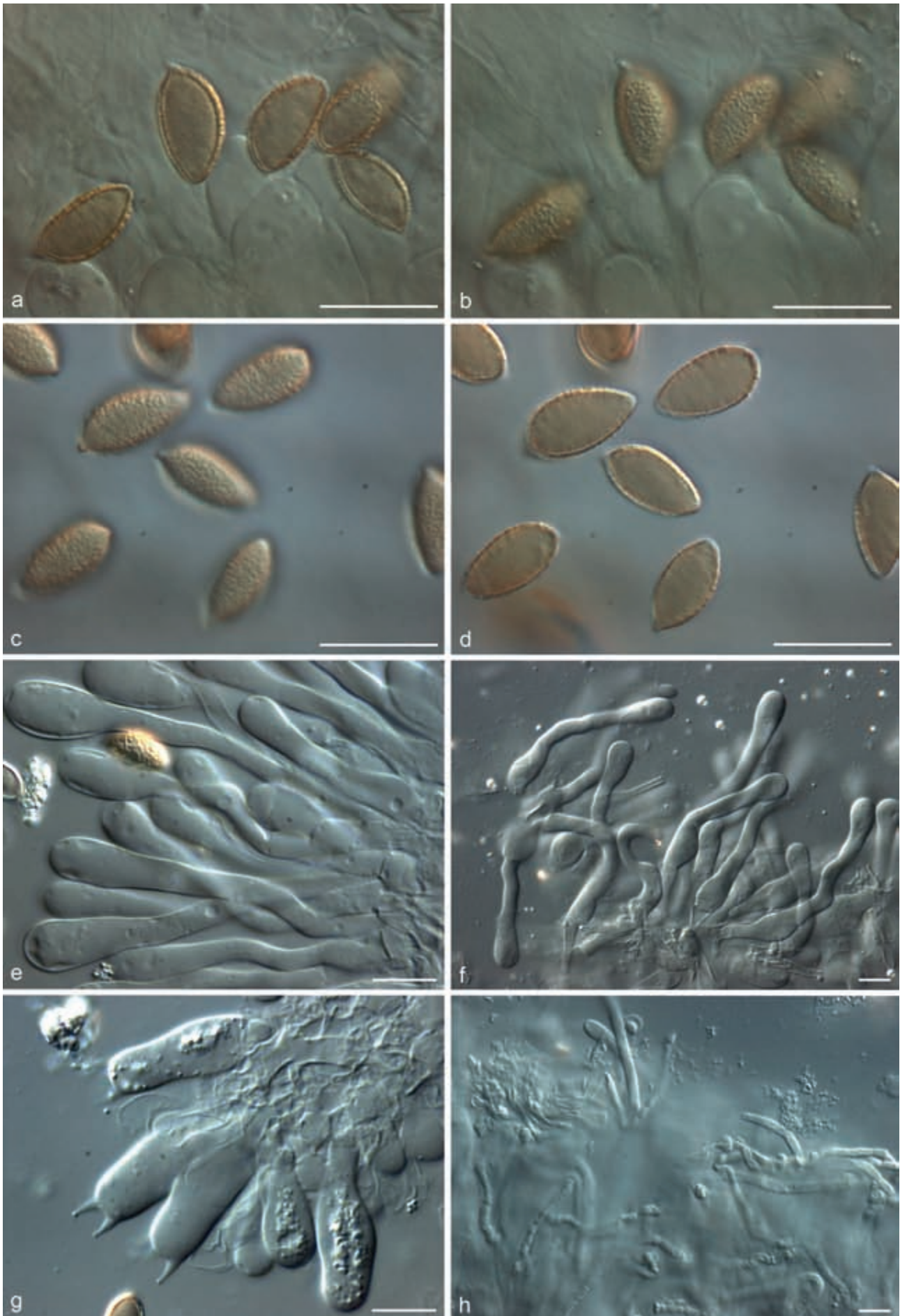
Fig. 6 *Hebeloma aanenii* (BR-MYCO 173987-66, holotype). a, b. Spores and spore ornamentation ×1 600 in 5 % KOH; c, d. spores and spore ornamentation ×1 600 in 5 % Melzer's reagent; e. cheilocystidia ×1 000 in 5 % KOH; f. caulocystidia ×500 in 5 % KOH; g. basidia ×1 000 in 5 % KOH; h. epicutis hyphae ×500 in 5 % KOH. — Scale bars: 10 µm.
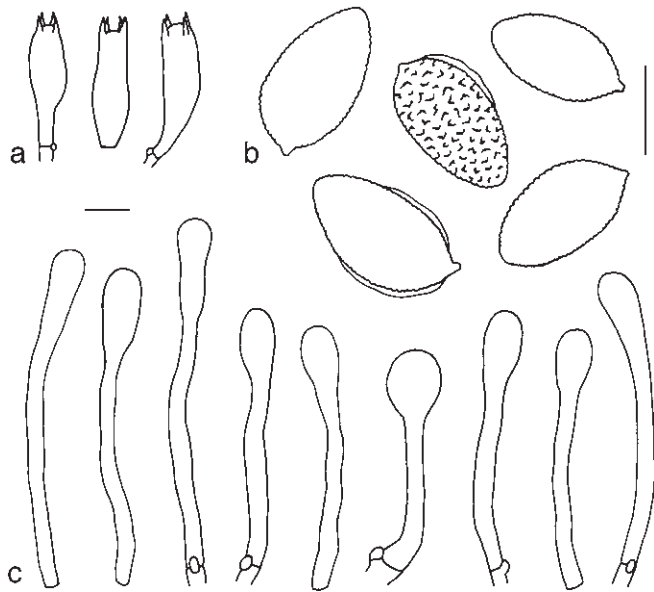
Fig. 7 *Hebeloma aanenii* (BR-MYCO 173987-66, holotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 µm.

width of apex holotype 5–95 % percentile range 5.5–9.0 µm, with median 7.3 µm and av 7.2 µm with SD 1.01 µm; across 36 collections median 6.2–9.0 µm and av 6.2–9.0 µm (of the 36 collections almost 80 % have the cheilocystidium apex av ≤ 8 µm); with n ≥ 20 selected cheilocystidia of 36 collections the 5–95 % percentile ranges are 28–104 × 4.6–12.6 × 2.4–7.4 × 2.3–9.0 µm while the averages are 39–82 × 6.2–9.0 × 3.6–5.3 × 3.5–5.8 µm and 61 × 7.2 × 3.7 × 3.9 µm av for the holotype. The av cheilocystidia ratios for the 36 collections were: A/M = 1.61–2.49; A/B = 1.51–2.48; B/M = 0.85–1.24. *Caulocystidia* resemble cheilocystidia but are often more clavate-lageniform shaped, up to 100 µm long and 11 µm wide at the apex. *Pileipellis* is an ixocutis with a very thick epicutis 100–400 µm, embedded hyphae up to 5–7 µm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* yellowish and made up of cylindrical to isodiametric elements. *Subcutis* contains isodiametric elements and the trama below the subcutis contains cylindrical, ellipsoid and thick sausage shaped elements up to 20 µm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — *Hebeloma aanenii* appears to be widespread across Europe, although we do not have confirmed records from south-west Europe. It appears to grow in a variety of habitats, on both acid and calcareous soils, often on woodland pathsides and also in alpine areas. It appears to form mycorrhiza with a variety of trees. Records include *Abies*, *Betula*, *Carpinus*, *Dryas*, *Eucalyptus*, *Fagus*, *Helianthemum*, *Picea*, *Pinus*, *Populus*, *Quercus*, *Salix* and *Tilia*. We have one confirmed collection of *H. aanenii* with *Salix* sp. in New Zealand.

Additional specimens examined. BELGIUM, prov. Luxembourg, Barvaux (c. N50.34 E5.49, alt. c. 200 m) on wet soil in mixed woodland under *Salix* sp., 18 Oct. 2003, *E. Emmett*, HJB8896; prov. Luxembourg, Wilbauroche (N49.81335 E5.27330, alt. c. 312 m) on rotten litter in broadleaf woodland under *Corylus* sp., *Fagus* sp., 17 Sept. 2004, *H. Beker* HJB10607; prov. Luxembourg, Goutelle (N50.01500 E5.2291667, alt. c. 401 m) on grassy soil in mixed woodland under *Picea* sp., 3 Oct. 2004, *M. Ghyselinck* HJB10164; prov. Namur, Biron (c. N50.30 E5.11, alt. c. 250 m) on rotten litter in conifer woodland under various broadleaf trees, 7 Oct. 2004, *M. Lenne* HJB10282; prov. Brussels, Scheutbos (N50.8531667 E4.2950500, alt. c. 58 m) on grassy soil in broadleaf woodland under *Betula* sp., *Salix* sp., 28 Oct. 2007, *H. Beker* HJB12164. – CZECH REPUBLIC, Moravia, LPA Moravian Karst, NNR Vyvery Punkvy (N49.37290 E16.72823, alt. c. 487 m) on soil in mixed woodland under *Fagus sylvatica*, 10 Oct. 2008, *V. Antonin* HJB12717; Moravia, LPA Moravian Karst, NNR Vyvery Punkvy (N49.37245 E16.73003, alt. c. 487 m) on grassy soil in mixed woodland scrub under *Populus* sp., 10 Oct. 2008, *S. Kelly*

HJB12721. – DENMARK, Region EJ, Århus, Brabrand, Gellerupparken, Dortesvej (N56.16041 E10.13308, alt. c. 50 m) on clayey soil in urban habitat under *Populus tremula*, 27 Oct. 2000, *J. Vesterholt* HJB3733. – ENGLAND, Mid Lancashire, Gait Barrows (N54.19061 W2.801503, alt. c. 31 m) on rotten litter in woodland under *Betula*, 25 Sept. 2002, *H. Beker* HJB9329; Warwick, Bishopton (N52.19831 W1.74099, alt. c. 64 m) on grassy soil under *Tilia* sp., 5 Oct. 2004, *A. Brand* HJB11219; Buckinghamshire, Rushbeds (c. N51.830 W1.030, alt. c. 100 m) on rotten litter in woodland under *Quercus* sp., *Salix* sp., 20 Oct. 2004, *D. Schafer* HJB10441; Derby, Ladybower (N53.38768 W1.754891, alt. c. 208 m) on rotten litter in broadleaf woodland under *Betula* sp., 24 Oct. 2004, *P. Ardron* HJB10435; Derby, Ladybower (N53.38768 W1.754891, alt. c. 208 m) on rotten litter in broadleaf woodland under *Betula* sp., *Fagus* sp., *Pinus* sp., *Salix* sp., 25 Oct. 2004, *H. Beker* HJB10446; Derby, Ladybower (N53.38768 W1.754891, alt. c. 208 m) on rotten Litter in broadleaf woodland under *Betula* sp., *Fagus* sp., *Pinus* sp., *Salix* sp., 25 Oct. 2004, *H. Beker* HJB10450; Nottinghamshire, Clumber Park (N52.73547 W1.096525, alt. c. 64 m) on grassy soil in broadleaf woodland under *Salix* sp., 30 Oct. 2004, *C. Hobart* HJB10696; Warwick, Bishopton (N52.19831 W1.74099, alt. c. 81 m) under *Populus trichocarpa*, 1 Nov. 2004, *A. Brand* HJB11220; Nottinghamshire, Daneshill Energy Forest near Suttin Cum Lound SK6785 (N53.36553 W0.98410, alt. c. 11 m) on grassy, mossy, sandy soil in woodland plantation under *Eucalyptus* sp., 13 Nov. 2010, *H. Beker*, *C. Hobart* HJB13734; Derby, Ladybower (N53.38768 W1.754891, alt. c. 208 m) on rotten litter in broadleaf woodland under *Betula* sp., *Fagus* sp., *Pinus* sp., *Salix* sp., 25 Oct. 2004, *H. Beker* HJB10452. – FRANCE, Hautes-Pyrenees, las gabietons, Gavarnie (c. N42.695 W0.0320, alt. c. 2550 m) under *Salix herbacea*, *Salix retusa*, 14 Sept. 2005, *G. Corriol* GC05 09 14 06, HJB12954; Nord Pas de Calais, Abscon (N50.32365 E3.29990, alt. c. 60 m) on rotten litter in chalk quarry site under *Quercus* sp., 13 Nov. 2006, *C. Lecuru* HJB11784; Nord Pas de Calais, Abscon (N50.32365 E3.29990, alt. c. 60 m) on mossy soil in chalk quarry site under *Quercus* sp., 13 Nov. 2006, *C. Lecuru* HJB11785; Aude, Le Bois du Pinet (N42.85661 E1.97465, alt. c. 840 m) on soil in mixed woodland under *Salix* sp., 13 Oct. 2008, *P. Roux* HJB12729. – ITALY, Trentino, Goccadioro (c. N46.05540 E11.13720, alt. c. 245 m) under broadleaf trees, Nov. 1914, *G. Bresadola* S F14406, database record HJB13470. – NETHERLANDS, Flevoland, Lelystad, Oostvaarderplassen (c. N52.450 E5.3667, alt. c. 0 m) under *Salix* sp., 11 Oct. 1995, *D. Aanen* WBS 9570, database record HJB12805; Groningen, Eemshaven (c. N53.455 E6.806, alt. c. 0 m) under *Salix repens*, 3 Oct. 1996, *D. Aanen* WBS 9677, database record HJB12478; Groningen, Eemshaven (c. N53.455 E6.806, alt. c. 0 m) under *Salix repens*, 3 Oct. 1996, *D. Aanen* WBS 9671, database record HJB12806; Utrecht, Lunetten (c. N52.03453 E5.07562, alt. c. 0 m) under *Salix alba*, 13 Oct. 1996, *D. Aanen* WBS 9683, database record HJB12475; Utrecht, Lunetten (c. N52.03453 E5.07562, alt. c. 0 m) under *Salix alba*, 13 Oct. 1996, *D. Aanen* WBS 9684, database record HJB12476; Utrecht, Lunetten (c. N52.03453 E5.07620, alt. c. 0 m) under *Salix alba*, 13 Oct. 1996, *K. Wolfs*, *D. Aanen* WBS 9685, database record HJB12477. – NEW ZEALAND, Nelson, Stephens Bay (c. S41.050 E173.010, alt. c. 20 m) on soil in riverside scrub under *Salix* sp., 3 May 2004, *P. Leonard* PL13504, PDD 102994, HJB10692. – NORWAY, Tislet (c. N61.083 E6.500, alt. c. 240 m) in broadleaf woodland pathside under *Betula* sp., 5 Aug. 2004, *A. Andrews* HJB10763. – POLAND, Mt Kamiensk (the outer damping ground of the Belchatow Lignite Mine), forest distr. 297 (by the pond) (N51.22134 E19.43924, alt. c. 340 m) on sandy soil in mixed woodland plantation under *Picea abies*; *Salix* sp., 23 Sept. 2008, *I. Kałucka*; *H. Beker* LOD, HJB12676. – SWEDEN, Uppland, Nåsten (c. N59.04 E18.65600, alt. c. 0 m) on grassy soil in mixed woodland, 20 Sept. 2003, *A. Taylor* AT2003063, HJB10670. – SWITZERLAND, Schiahorn, Strelapass, Davos (c. N46.822574 E9.781488, alt. c. 2200 m) under *Dryas octopetala*, *Helianthemum* sp., 8 Sept. 1996, *D. Aanen* WBS 9620, database record HJB12508; Mollendruz, Vaud (c. N46.649202 E6.367389, alt. c. 1200 m) under *Abies* sp., *Fagus* sp., *Salix caprea*, 21 Sept. 1996, *D. Aanen* WBS 9626, database record HJB12511.

Notes — The dominant cheilocystidial shape, clavate- to spathulate-stipitate clearly defines *H. aanenii* as belonging to *H.* subsect. *Denudata*. *Hebeloma aanenii* is a constituent of the *H. crustuliniforme* complex and most likely corresponds to ICG2 of Aanen & Kuyper (1999). It is likely that many collections of this species have been recorded under the name *H. crustuliniforme* and exist worldwide in herbaria under this name. It is morphologically most similar to *H. crustuliniforme*, *H. eburneum*, *H. alpinum* and *H. geminatum.* But its spores, normally < 11 µm long and < 6 µm wide distinguish it from the first three species. It can be distinguished from other members of this subsection by the number of complete lamellae, which is always ≥ 60. Until now we have found no consistent morpho-
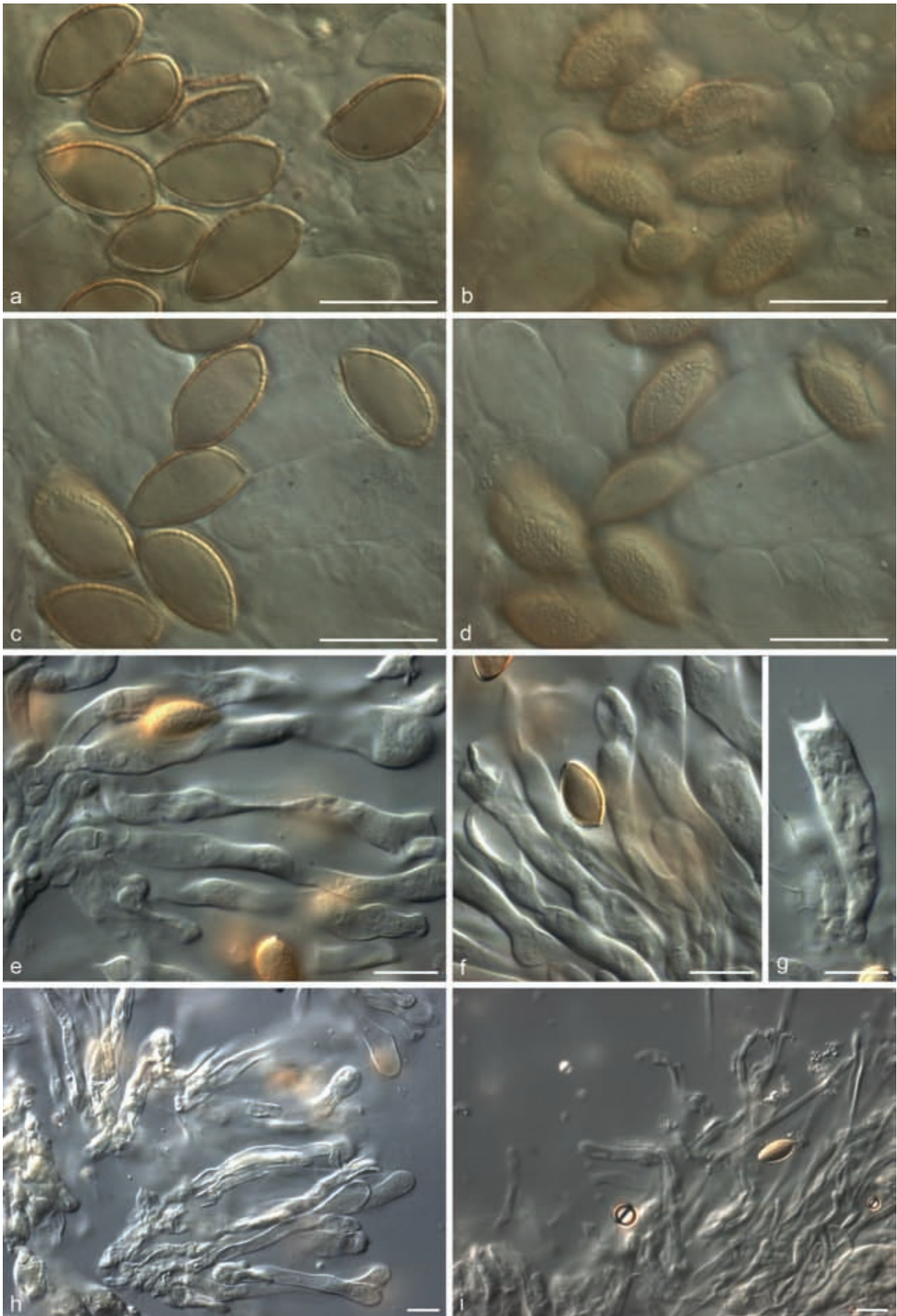
Fig. 8 *Hebeloma alpinum* (G GK13674, lectotype). a, b. Spores and spore ornamentation ×1 600 in 5 % Melzer's reagent; c, d. spores and spore ornamentation ×1 600 in 5 % KOH; e, f. cheilocystidia ×1 000 in 5 % KOH; g. basidium ×1 000 in 5 % KOH; h. cheilocystidia ×500 in 5 % KOH; i. epicutis hyphae ×500 in 5 % KOH. — Scale bars: 10 μm.

logical character to unambiguously separate *H. aanenii* and *H. geminatum*. However, we can often separate these two taxa. The cheilocystidium average apex width for *H. aanenii* is usually smaller than that for *H. geminatum*. From our records, if the average width of the apex of the cheilocystidium is < 8 μm then the collection is almost certainly *H. aanenii*. However, the average apex width can reach 9 μm. Average apex widths in this interval between 8–9 μm can be found in either taxon. This is responsible for the overlap of the ellipses of *H. aanenii* and *H. geminatum* in the PCA diagram in Fig. 4b.

In spite of the rather large intraspecific ITS variation it should normally be possible to recognize *H. aanenii* based on this locus. Only a single collection (WBS 9620, database record HJB12508) out of 33 is not included in the *H. aanenii* clade. Based on three or five loci, *H. aanenii* is monophyletic and weakly supported (Fig. 3), including WBS 9620. In none of the single locus phylogenies do all *H. aanenii* sequences form a monophylum. The combination of V6 and V9 also unambiguously identifies *H. aanenii*, though neither locus on its own suffices.

Hebeloma alpinum (J. Favre) Bruchet, Bull. Mens. Soc. Linn. Lyon 39, 6 (Suppl.): 68. 1970. — MycoBank MB314944; Fig. 8, 9

Type. SWITZERLAND, Val dal Botsch (c. N46.65 E10.10, alt. c. 2600 m) alpine scrub, on calcareous soil with *Dryas octopetala* and *Salix herbacea*, 27 Aug. 1949, *J. Favre*, lectotype G GK13674; database record HJB1000060, selected by Vesterholt in Symb. Bot. Upsal. 30 (no. 3): 134, 1995.

Basidiomes usually in scattered groups, sometimes solitary, rarely caespitose. *Pileus* 12–70 mm diam, convex often umbonate, tacky when moist but never hygrophanous; *cuticle colour* quite variable from cream through pinkish buff to Isabella and yellow brown, to clay buff, cinnamon or even sepia, often unicoloured but sometimes paler towards the margin which may be pinkish buff, clay buff or greyish buff through to cream or white; *pileus margin* often involute particularly in young basidiomes but often becoming serrate or crenulate in older basidiomes. *Lamellae* emarginate, usually moderately crowded (L = 40–72); maximum depth of 3–9 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, usually paler than lamella surface; droplets normally visible on the lamella edge usually by naked eye but sometimes absent; *lamellules* frequent. *Stipe* central, sometimes cylindrical but more often clavate, rarely bulbous, becoming hollow with age, 11–50 × 3–13 mm and up to 15 mm at the base with no (or very weak) discolouration towards the base of the stipe; *surface* dry, pruinose to floccose, especially towards the apex. *Cortina* not observed. *Flesh* thick, white to pale buff. *Smell* raphanoid, sometimes weak, sometimes absent and occasionally a hint of cocoa. *Taste* mild but sometimes a little bitter. *Spore deposit* brownish olive to clay-buff or Isabella. *Exsiccata* with no special features.

Spores amygdaloid or limoniform, with small apiculus and rounded at the end opposite the apiculus, with some thinning of the spore wall, and usually with a papilla, often very noticeable, sometimes guttulate with one or more oily drops, usually weakly ornamented but sometimes more distinctly ornamented, sometimes with slightly loosening perispore in a few spores and weakly but sometimes distinctly dextrinoid (O1,O2(O3); P0,P1; D0,D1,D2); *spore colour* under the microscope brown, sometimes with a yellow tinge; *spore size* based on n = 60 spores of the holotype, 5–95 % percentile range 11.2–13.3 × 6.6–8.0 μm, with median 12.3 × 7.3 μm and av 12.3 × 7.3 μm with SD length 0.65 μm and width 0.45 μm, Q value 5–95 % percentile range 1.50–1.86, with median 1.69 and av 1.69 with SD 0.11; *spore size* based on 34 collections medians 10.9–13.7 × 6.1–7.6 μm and av 11.0–13.7 × 6.1–7.7 μm with SD length

0.53–1.16 μm and width 0.25–0.57 μm, Qav 1.60–1.97. *Basidia* cylindrical to clavate and 4-spored, 25–45 × 7.1–11.7 μm, with av 28–40 × 8.0–11.1 μm and basidium Qav in the range 3.0–4.3. *Pleurocystidia* not found. *Cheilocystidia* clavate-stipitate or spathulate-stipitate, occasionally swollen towards the base (clavate-lageniform), sometimes with thickening of the apex or thickening of the median, sometimes septate, rarely bifurcate, sinuate or rostrate; *width of apex* holotype 5–95 % percentile range 6.4–9.7 μm, with median 7.8 μm and av 7.9 μm with SD 1.10 μm; across 34 collections median 6.8–9.8 μm and av 6.8–9.8 μm; with n ≥ 20 selected cheilocystidia of 34 collections the 5–95 % percentile ranges are 30–92 × 4.8–13.1 × 2.7–6.3 × 2.3–8.1 μm while the averages are 40–71 × 6.8–9.8 × 3.6–5.1 × 3.2–6.1 and 58 × 7.9 × 4.4 × 4.3 μm av for the holotype. The av cheilocystidia ratios for the 34 collections were: A/M = 1.61–2.74; A/B = 1.52–2.71; B/M = 0.87–1.24. *Caulocystidia* resemble cheilocystidia, up to 120 × 11 μm wide at the apex. *Pileipellis* is an ixocutis with an epicutis from relatively thin to medium thick, 60–160 μm, embedded hyphae up to 5–6 μm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Subcutis* yellow to orange and made up of cylindrical to isodiametric elements. *Trama below the subcutis* contains angular, ellipsoid, cylindrical, spherical and sausage-shaped elements up to 18 μm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — *Hebeloma alpinum* has been recorded with a number of species of *Salix* in both arctic and alpine environments. It has also been recorded with *Dryas octopetala* when *Salix* was not recorded as present. We strongly suspect that it can be mycorrhizally associated with *Dryas*. We have no records of this taxon outside of such habitats. Our database records of *H. alpinum* have the following *Salicaceae* associations: *Salix herbacea, S. polaris, S. reticulata* and *S. retusa.* We have records in both acid and calcareous soils, bare, grassy and sandy. As well as the 34 collections upon which our description has been based, we have a number of other confirmed records of *H. alpinum* including a number from outside of Europe. So far we have no records on our database from alpine areas outside Europe but we suspect it may well be present in these regions too.

Additional specimens examined. GREENLAND, Zackenberg, just south of Teltdammen (c. N74.30 W21.00, alt. c. 700 m) in scrub under *Dryas octopetala, Salix* sp., 20 July 1999, *T. Borgen* TB99.023, duplicate HJB12194; Zackenberg, 100 m west of Zackenberg River (c. N74.50 W21.00, alt. c. 700 m) on dry soil in scrub under *Dryas octopetala*, 3 Aug. 1999, *T. Borgen* TB99.199, duplicate HJB12204. – ICELAND, Valavatn (N64.86655 E23.5597167, alt. c. 301 m) on bare soil in scrub under *Salix herbacea*, 29 July 2005, *H. Beker, M.L. Beker* HJB11051. – ITALY, Lac Verney (N45.688183 E6.882441, alt. c. 2090 m) under *Salix reticulata*, 24 Aug. 2009, *G. Corriol* HJB13096. – NORWAY, Møre & Romsdal, Beiaren kommune: Sokumfjellet (N66.87940 E14.28040, alt. c. 800 m) under *Dryas octopetala, Salix polaris, Salix reticulata*, 4 Aug. 2008, *P. Larsen* Larsen 56-2008, HJB13008. – SVALBARD, Endalen (N78.1937333 E15.7891167, alt. c. 29 m) on soil in grazed scrub under *Salix polaris*, 13 Aug. 2007, *M.L. Beker* HJB11986; Ekmanfjorden (N78.61705 E14.837183, alt. c. 9 m) on soil in maritime coastal scrub under *Salix polaris*, 15 Aug. 2007, *H. Beker, M.L. Beker* HJB11997; Ekmanfjorden (N78.617033 E14.837683, alt. c. 12 m) on soil in maritime coastal scrub under *Salix polaris*, 15 Aug. 2007, *H. Beker, M.L. Beker* HJB12000; Ekmanfjorden (N78.617033 E14.837683, alt. c. 12 m) on soil in maritime coastal scrub under *Salix polaris*, 15 Aug. 2007, *H. Beker, M.L. Beker* HJB12001; Ekmanfjorden (N78.617233 E14.838083, alt. c. 14 m) on soil in maritime coastal scrub under *Salix polaris*, 15 Aug. 2007, *J. Sandmo* HJB12002; Dicksonfjorden (N78.6207667 E14.8823000, alt. c. 24 m) on soil in maritime coastal scrub under *Salix polaris*, 15 Aug. 2007, *H. Beker, M.L. Beker* HJB12004; Dicksonfjorden (N78.6210333 E14.8840500, alt. c. 25 m) on soil in maritime coastal scrub under *Salix polaris*, 15 Aug. 2007, *H. Beker, M.L. Beker* HJB12005. – SWITZERLAND, Graubünden Samnaun (c. N46.940 E10.360, alt. c. 1900 m) under *Salix reticulate, Salix retusa*, 28 Aug. 1984, *H. Knudsen* C HK36-84, HJB10642; Adelboden, Bern (c. N46.500 E7.550, alt. c. 1900 m) on calcareous soil under *Salix retusa*, 5 Sept. 1996, *D. Aanen* WBS 9605, database record HJB12498; Adelboden, Bern (c. N46.500 E7.550, alt. c. 1900 m) on calcareous soil under *Salix retusa*, 5 Sept. 1996,

D. Aanen WBS 9607, database record HJB12499; Adelboden, Bern (c. N46.500 E7.550, alt. c. 1900 m) on calcareous soil under *Dryas octopetala*, *Salix retusa*, 5 Sept. 1996, *D. Aanen* WBS 9609, database record HJB12500; Adelboden, Bern (c. N46.500 E7.550, alt. c. 1900 m) on calcareous soil under *Dryas octopetala*, *Salix retusa*, 5 Sept. 1996, *D. Aanen* WBS 9613, database record HJB12502; Adelboden, Bern (c. N46.500 E7.550, alt. c. 1900 m) on calcareous soil under *Salix retusa*, 5 Sept. 1996, *D. Aanen* WBS 9608, database record HJB12503; Adelboden, Bern (c. N46.500 E7.550, alt. c. 1900 m) on calcareous soil in mountain scrub under *Dryas octopetala*, *Salix retusa*, 5 Sept. 1996, *D. Aanen* WBS 9606, database record HJB12504; Adelboden, Bern (c. N46.500 E7.550, alt. c. 1900 m) on calcareous soil under *Dryas octopetala*, *Salix* sp., 5 Sept. 1996, *D. Aanen* WBS 9614, database record HJB12505; Adelboden, Bern (c. N46.500 E7.550, alt. c. 1900 m) on calcareous soil under *Salix retusa*, 5 Sept. 1996, *D. Aanen* WBS 9617, database record HJB12506; Adelboden, Bern (c. N46.500 E7.550, alt. c. 1900 m) on calcareous soil under *Salix retusa*, 5 Sept. 1996, *D. Aanen* WBS 9616, database record HJB12507; Adelboden, Bern (c. N46.500 E7.550, alt. c. 1900 m) on calcareous soil under *Dryas octopetala*, 5 Sept. 1996, *D. Aanen* WBS 9615, database record HJB12998; Spittelmatte (N46.440 E7.640, alt. c. 2000 m) on rotten litter in scrub under *Dryas octopetala*, 9 Aug. 2005, *H. Beker, M.L. Beker* HJB11085; Spittelmatte (N46.440 E7.640, alt. c. 1909 m) on herbaceous litter in scrub under *Dryas octopetala*, 9 Aug. 2005, *H. Beker, M.L. Beker* HJB11087; Spittelmatte (N46.4195 E7.62375, alt. c. 2220 m) on herbaceous litter in scrub under *Dryas octopetala*, 9 Aug. 2005, *H. Beker, M.L. Beker* HJB11088; Spittelmatte (N46.41050 E7.62220, alt. c. 2000 m) on bare soil in scrub under *Salix* sp., 9 Aug. 2005, *H. Beker, M.L. Beker* HJB11092; Spittelmatte (N46.41070 E7.62220, alt. c. 2000 m) on bare soil in scrub under *Salix* sp., 9 Aug. 2005, *H. Beker, M.L. Beker* HJB11094; Spittelmatte (N46.43953 E7.63781, alt. c. 2000 m) on rotten litter in scrub under *Dryas octopetala*; *Salix* sp., 9 Aug. 2005, *H. Beker, M.L. Beker* HJB11100; Corno Gries (N47.480 E8.500, alt. c. 2500 m) on grassy soil in scrub under *Salix* sp., 11 Aug. 2005, *H. Beker, M.L. Beker* HJB11117; Corno Gries (N46.4665833 E8.4069500, alt. c. 2500 m) on litter in scrub under *Salix herbacea*, 11 Aug. 2005, *H. Beker, M.L. Beker* HJB11123; Albulapass (N46.58200 E9.84300, alt. c. 2300 m) on bare soil in scrub under *Salix* sp., 12 Aug. 2005, *H. Beker, M.L. Beker* HJB11132; Morteratsch (N46.43340 E9.93623, alt. c. 2002 m) on sandy soil in scrub under *Salix* sp., 13 Aug. 2005, *H. Beker, M.L. Beker* HJB11133.

Notes — Given the shape of its cheilocystidia, *Hebeloma alpinum* clearly belongs to *H.* subsect. *Denudata. Hebeloma alpinum* most likely corresponds to ICG4 of Aanen & Kuyper (1999). As discussed in the Discussion in more detail, some members of this species might be intercompatible with *H. eburneum* (ICG3) or even with *H. aanenii* (ICG2) (Aanen & Kuyper 1999, Aanen et al. 2000). *Hebeloma alpinum* certainly appears to be confined to alpine or arctic habitats and can be readily separated from other alpine/arctic species in this section based on the number of lamellae, usually between 40 and 60 on average, and the size of the spores, on average ≥ 11 μm long and

Fig. 9 *Hebeloma alpinum* (G GK13674, lectotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 μm.

> 6 μm wide. It also has quite a robust stature. Microscopically it is closest to *H. minus* but it can normally be separated on macroscopic characters, since *H. minus* is smaller with darker coloured pileus and with fewer lamellae than *H. alpinum. Hebeloma alpinum* is the most common *Hebeloma* species we have collected in arctic/alpine areas and can usually be determined, with reasonably high confidence, in the field.

Among the loci applied in this study, not a single one can distinguish *H. alpinum* on its own. Even when combining a minimum of three out of five loci (Fig. 3), *H. alpinum* is not monophyletic, though, apart form HJB11051 and HJB11545 (discussed in detail above and under *H. geminatum*), *H. alpinum* does not form mixed clades with other taxa. Again, the combination of V6 and V9 is probably the most reliable combination of fewer loci for identifying *H. alpinum. Hebeloma alpinum* V6 sequences cluster with *H. geminatum* and V9 sequences with *H. eburneum*, whereas *H. geminatum* V9 sequences are much longer and the great majority forms a monophylum, except for the two deviant collections, and *H. eburneum* V6 sequences cluster with *H. aanenii*.

We have examined material of *Naucoria bellotiana* (K K(M) 165365). This collection from Bellot Island in Canada was collected by Capt. Feilden on 14 August 1876 and described by M.J. Berkeley as *Agaricus (Naucoria) bellotianus* in the Journal of the Linnean Society, vol. 17, 1878, p. 14. This species certainly belongs to the genus *Hebeloma* and we make the new combination here:

Hebeloma bellotianum (Berk.) Beker & U. Eberh. *comb. nov.* — MycoBank MB809913

Hebeloma bellotianum has cheilocystidia that clearly place it in *H.* sect. *Denudata* subsect. *Denudata.* Given the habitat at N81.68 it falls into the arctic/alpine group from this subsection. The number of lamellae (estimated from the exsiccata) and spore size would mean that it would key out, among known species from this subsection, as *H. alpinum* to which it is certainly similar and were it not for the very large spores we would be confident this was the same species. However the spores of *H. bellotiana* measured, on average, 14.7 × 7.1 μm and the largest average spore size we have measured for *H. alpinum* (across 71 collections) is 13.7 μm long (and 7.7 μm wide). We have not been able to obtain any molecular data from this collection and cannot rule out that this may be a species from this subsection that we have not yet encountered. Thus at this point we hesitate to synonymise these species and await further evidence one way or the other.

Hebeloma aurantioumbrinum Beker, Vesterh. & U. Eberh., *sp. nov.* — MycoBank MB809906; Fig. 5b, 10, 11

Etymology. From *aurantio* - orange and *umbrinum* - umber.

Type. SVALBARD, Knudsenheia (N78.9373333 E11.8425333, alt. c. 9 m) on grazed scrub with *Salix polaris*, 19 Aug. 2007, *M.L. Beker, H. Beker*, holotype BR BR-MYCO 173985-64; isotypes C C-F-90148, HJB12058.

Diagnosis — *Hebeloma aurantioumbrinum* possesses the cheilocystidia typical of *H.* subsect. *Denudata.* It is a species typically occurring in alpine or arctic habitats where it can be recognized by the combination of an average spore width of < 7 μm and an average cheilocystidium apex width of < 8.5 μm. Outside these habitats it can be differentiated from other small species of the subsection (*H. luteicystidiatum, H. helodes* and *H. pusillum*) by its uniformly brownish orange pileus and by its cheilocystidium apex without abnormal wall thickening.

Basidiomes usually in scattered groups. *Pileus* up to 21 mm diam, umbonate, slightly tomentose at high magnification;
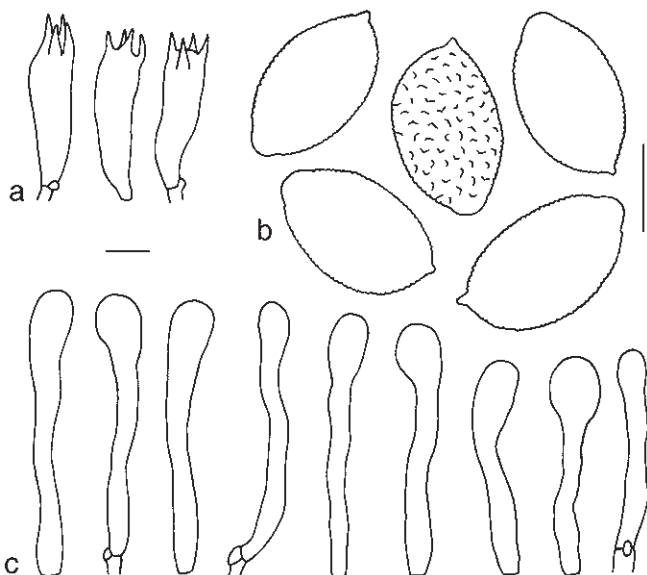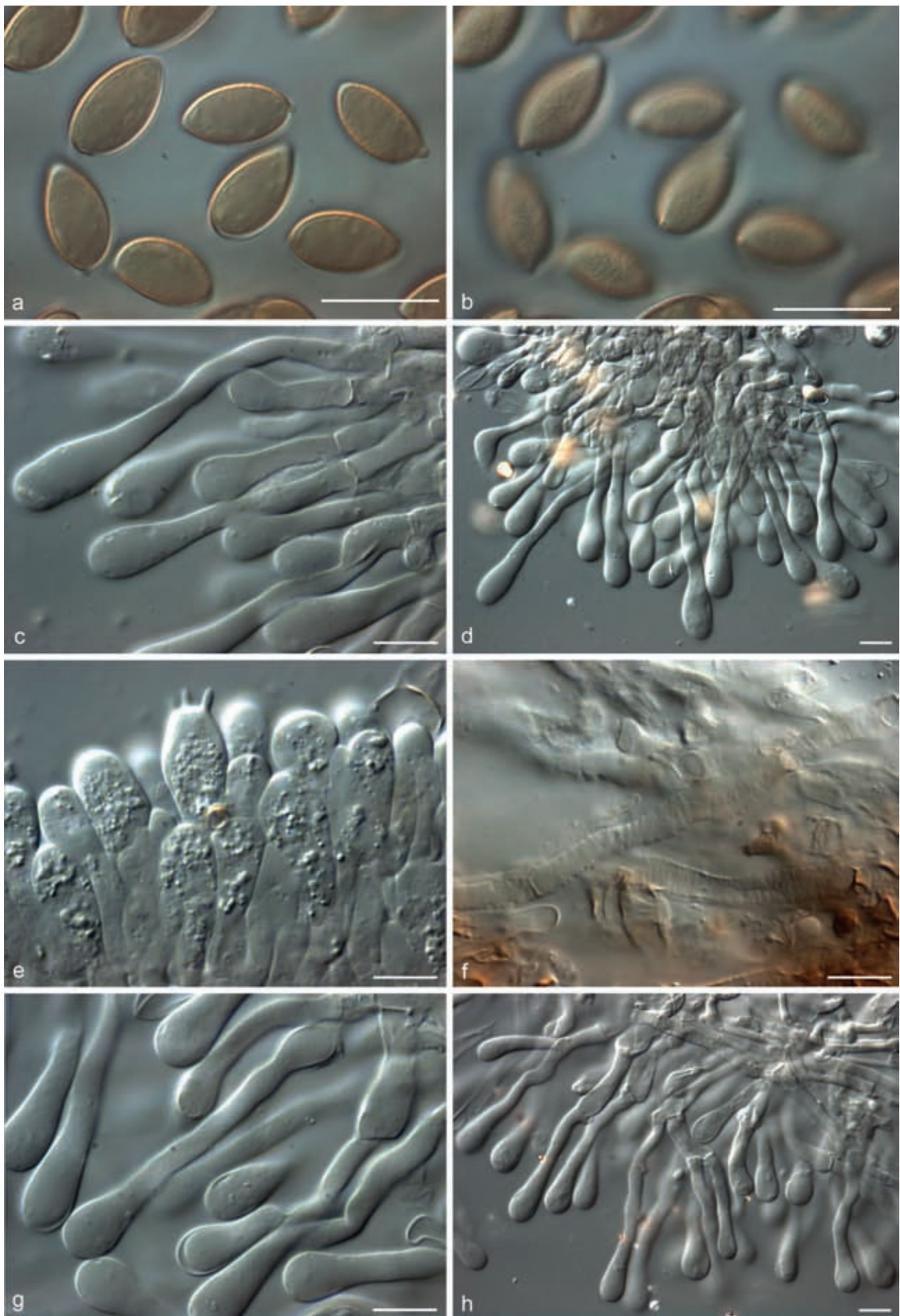
Fig. 10 *Hebeloma aurantioumbrinum* (BR-MYCO 173985-64, holotype). a, b. Spores and spore ornamentation ×1 600 in Melzer's reagent; c. cheilocystidia ×1 000 in 5 % KOH; d. cheilocystidia ×500 in 5 % KOH; e. basidium ×1 000 in 5 % KOH; f. epicutis hyphae ×1 000 in 5 % KOH; g. caulocystidia ×1 000 in 5 % KOH; h. caulocystidia ×500 in 5 % KOH. — Scale bars: 10 μm.

surface slightly viscid, tacky when moist rarely hygrophanous; *cuticle colour* from yellow brown to cinnamon to umber but with some orange, sometimes with a thin paler pinkish buff to clay buff margin; *pileus margin* usually straight, sometimes slightly scalloped. *Lamellae* emarginate, quite widely spaced (L = 26–39) with a maximum depth of 2.5 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, paler than lamella surface; droplets on the lamella edge are usually present and visible to the naked eye, however in dry conditions they may not be seen; *lamellules* sparse. *Stipe* central, cylindrical occasionally clavate, stuffed, (14–)15–28 × 2.5–3.1(–3.5) mm and up to 6 mm at the base; white or alutaceous, with no visible discolouring when handled; *surface* dry, pruinose particularly towards the apex. *Cortina* not observed. *Flesh* rather thin, cream or pale brown. *Smell* raphanoid, sometimes weakly. *Taste* not recorded. *Spore deposit* clay-buff.

Spores amygdaloid, with small apiculus and rounded at the end opposite the apiculus, with a distinct thinning of the spore wall but rarely with any papilla, guttulate with one or more oily drops, almost smooth to very weakly ornamented but occasional spores more distinctly ornamented, sometimes with some sign of loosening perispore in a few spores and weakly dextrinoid but sometimes distinctly so (O1,O2(O3); P0,P1; D1,D2); *spore colour* under the microscope pale brown to yellow brown to brown; *spore size* based on n = 96 spores of the holotype, 5–95 % percentile range 10.7–12.3 × 6.0–7.1 µm, with median 11.5 × 6.6 µm and av 11.5 × 6.5 µm with SD length 0.47 µm and width 0.33 µm, Q value 5–95 % percentile range 1.65–1.89, with median 1.76 and av 1.76 with SD 0.07; *spore size* based on 12 collections medians 10.1–11.7 × 6.2–6.8 µm and av 10.2–11.8 × 6.2–6.8 µm with SD length 0.47–0.97 µm and width 0.25–0.34 µm, Qav 1.60–1.85. *Basidia* cylindrical to clavate and 4-spored, 25–43 × 5.7–11.0 µm, with av 28–38 × 7.1–9.4 µm. *Pleurocystidia* not found. *Cheilocystidia* clavate, clavate-stipitate and sometimes spathulate-stipitate, occasionally slightly swollen towards the base (clavate-lageniform) and occasionally with septa, some median thickening or bent; *width of apex* holotype 5–95 % percentile range 6.1–10.1 µm, with median 8.1 µm and av 8.1 µm with SD 1.19 µm; across 12 collections median 7.1–8.4 µm and av 7.2–8.4 µm; with n ≥ 20 selected cheilocystidia of 12 collections the 5–95 % percentile ranges are 39–71 × 5.3–10.2 × 2.8–5.7 × 2.8–7.1 µm while the averages are 45–61 × 7.2–8.4 × 4.0–4.8 × 4.3–5.4 and 52 × 8.1 × 4.3 × 4.3 µm av for the holotype. The av cheilo-

cystidia ratios for the 12 collections were: A/M = 1.61–1.95; A/B = 1.62–1.98; B/M = 0.97–1.18. *Caulocystidia* resemble cheilocystidia, up to 75 µm long and 10 µm wide at the apex. *Pileipellis* is an ixocutis with a medium thick epicutis up to a maximum of 100 µm, embedded hyphae up to 6 µm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* orange brown and made up of cylindrical to isodiametric elements. *Trama below the subcutis* contains ellipsoid elements up to 6 µm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — As well as the 12 collections used in the above description, we also have additional non-European collections from Greenland, the Russian Federation and further collections from the United States. To date all our collections of *H. aurantioumbrinum* have been collected from alpine or arctic habitats with one collection from a boreal habitat. In every instance, apart from the boreal collection, *Salix* has been recorded as present. The boreal collection was recorded with *Betula* sp. and *Picea* sp. As *Salix* spp. are easily overlooked, we suspect that *Salix* was also present although we cannot confirm it. Furthermore, many of our collections have been recorded in wet or damp places. So, while this species has a clear preference for alpine or arctic environments it can also be present in boreal environments if the conditions are appropriate.

Additional specimens examined. Iceland, Egilsstadir (c. N65.17 W14.23, alt. c. 250 m) arctic, scattered near lakeside on wet clayey soil with *Salix* sp., 23 July 1987, *H. Hallgrimsson* HH11047, duplicate HJB11845. – Norway, Bollesteinseggi, W of Sogndal Valley, Sogndal (c. N61.22 E6.97, alt. c. 400 m) scattered in an alpine habitat with *Salix herbacea*, 10 Sept. 2000, *E. Bendiksen* JV00-291, duplicate HJB10906; Nesseby (c. N70.17 E28.53, alt. c. 120 m) arctic, scattered on boggy mossy ground with *Salix* sp., 25 Aug. 1998, *R. Pöder*, *B. Pernfuss* IB 19980462, database record HJB11835. – Svalbard, Ny Ålesund (N78.9164333 E11.9717000, alt. c. 12 m) on soil in grazed valley with *Salix polaris*, 16 Aug. 2007, *M.L. Beker*, *H. Beker* HJB12012; Longyearbyen (N78.2113500 E15.6216000, alt. c. 56 m) solitary on urban grazed scrub with *Salix polaris*, 9 Aug. 2007, *M.L. Beker*, *H. Beker* HJB11934. – Sweden, Medelpad, Sattna parish, Norrbacken (c. N59.73 E18.01, alt. c. 20 m) boreal, scattered in mixed woodland on wet mossy soil with *Betula* sp., *Picea* sp. and *Salix* sp., 22 Aug. 1995, *J. Vesterholt, J.H. Petersen* JV95-314, duplicate HJB12310. – USA, Wyoming, Beartooth Plateau, Wyoming Creek (N44.98715 W109.41104, alt. c. 3176 m) alpine, acid soil on scrubland with *Salix arctica* and *S. glauca*, 6 Aug. 2008, *C. Cripps, H. Beker* HJB12445; Wyoming, Beartooth Plateau, Wyoming Creek (N44.9870700 W109.4111100, alt. c. 3177 m) on soil in scrubland under *Salix arctica*, *S. glauca*, 6 Aug. 2008, *H. Beker* HJB12448; Wyoming, Beartooth Plateau, Wyoming Creek (N44.9870700 W109.4111100, alt. c. 3177 m) on mossy, wet soil in scrubland under *Salix arctica*, *S. glauca*, 6 Aug. 2008, *H. Beker* HJB12451; Wyoming, Beartooth Plateau, Wyoming Creek (N44.9871500 W109.4110400, alt. c. 3176 m) on litter and soil in scrubland under *Salix arctica*, *S. glauca*, 6 Aug. 2008, *C. Cripps* HJB12446; Wyoming, Beartooth Plateau, Upper Wyoming Creek (N44.9871500 W109.4110400, alt. c. 3176 m) on mossy, wet soil in scrubland under *Salix arctica*, 8 Aug. 2008, *J. Antibus* HJB12456.

Notes — Given the shape of its cheilocystidia, *H. aurantioumbrinum* clearly belongs to *H.* subsect. *Denudata*. It appears to be confined to boreal, alpine or arctic habitats. The species has not been tested for intercompatibility by Aanen & Kuyper (1999). In the past it has probably been overlooked or confused with *H. minus* or *H. subconcolor*. It can be distinguished from *H. minus* through the average width of the cheilocystidia apex which ≤ 8.5 µm for *H. aurantioumbrinum* while the average cheilocystidium apex for *H. minus* is always > 8.5 µm. With regard to *H. subconcolor*, this species is from *H.* sect. *Velutipes* and as such has cheilocystidia of the velutipes-type hence more gently clavate and with a lower average value for ratio A/M, rarely > 1.5. In determining *H. aurantioumbrinum* the combination of characters is important. As a small *Hebeloma* sp. in an alpine or arctic habitat with the distinctive subsect. *Denudata* shaped cheilocystidia there are few possibilities and the average spore width (< 7 µm) and the average cheilocystidium apex (< 8.5 µm) means it can only be *H. aurantioumbrinum*. In the

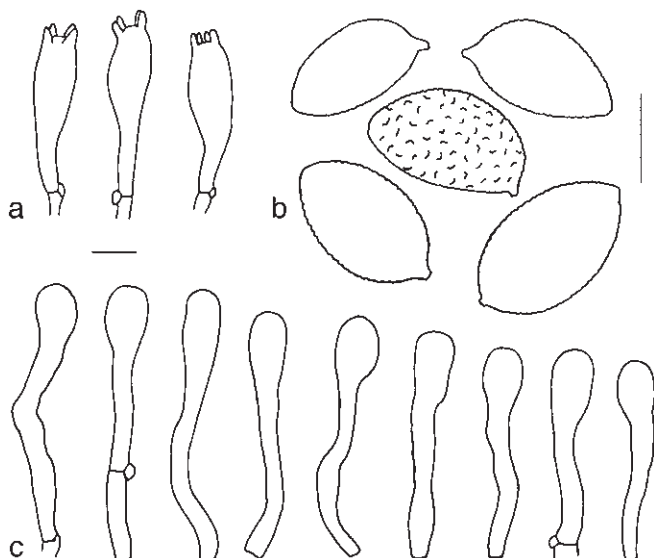**Fig. 11** *Hebeloma aurantioumbrinum* (BR-MYCO 173985-64, holotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 µm.

case when it might be collected in a boreal rather than alpine or arctic habitat (we have only seen one such collection), then the small size of mushroom, the apex of the cheilocystidia that does not show any abnormal thickening and the more or less unicoloured brownish orange pileus separates this species from the other small species of *H.* subsect. *Denudata*, namely: *H. luteicystidiatum*, *H. helodes* and *H. pusillum*.

Molecularly, *H. aurantioumbrinum* is sister species to *H. helodes* from which it can only be separated based on *RPB2* and *MCM7*. With either of these, *H. aurantioumbrinum* forms a well-supported species clade.

Hebeloma eburneum Malençon, Champignons Supérieurs du Maroc 1: 445. 1970. — MycoBank MB314954; Fig. 12, 13

= *Hebeloma perpallidum* M.M. Moser, Z. Pilzk. 36, 1-2: 72. 1970.
= *Hebeloma ochroalbidum* Bohus, Ann. Hist.-Nat. Mus. Natl. Hung. 64: 71. 1972.
= *Hebeloma albocolossum* M.M. Moser, Sydowia 38: 174. 1986 [1985].
= *Hebeloma crustuliniforme* var. *tiliae* Bres., Z. Mykol. 53, 2: 294. 1987.

Type. Morocco, Azrou (c. N33.417 W5.217, alt. c. 1500 m) with *Cedrus libanotica* ssp. *atlantica*, 8 Nov. 1941, *G. Malençon*, MPU GM1122, database record HJB1000095.

Basidiomes usually in scattered groups, sometimes solitary, sometimes caespitose. *Pileus* (8–)20–133 mm diam, convex often umbonate, surface often viscid, tacky when moist but never hygrophanous; *cuticle colour* always pale from pale cream to buff or buff yellow occasionally with the centre slightly yellow brown or light ochre or Isabella but then becoming paler towards the margin which is always pale cream or slightly yellowish; *pileus margin* often involute particularly in young basidiomes but then straightening in older basidiomes, rarely serrate. *Lamellae* emarginate or adnate, usually crowded with L = 70–110 but we do have some collections with L = 40–70, so unusually within the genus this character appears quite variable for this species; maximum depth up to 9 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, usually significantly paler than lamella surface; droplets normally very visible on the lamella edge; *lamellules* frequent. *Stipe* central, sometimes cylindrical but often clavate and rarely tapering, becoming hollow with age and very rarely with a superior wick, 20–106 × (3–)6–29(–36) mm, sometimes with slight yellowish discolouration towards the base of the stipe; *surface* dry, pruinose to distinctly floccose, especially towards the apex. *Cortina* not observed. *Flesh* thick, white to pale buff. *Smell* raphanoid, sometimes weak, sometimes absent and occasionally a hint of cocoa. *Taste* mild to weakly bitter with some raphanoid components. *Spore deposit* brownish olive to Isabella. *Exsiccata* with no special features but sometimes very pale.

Spores amygdaloid, sometimes weakly limoniform or fusoid, with small apiculus and rounded at the end opposite the apiculus, with some thinning of the spore wall, and rarely with a distinct papilla, sometimes guttulate with one or more oily drops, sometimes weakly ornamented but usually more distinctly ornamented, sometimes with slightly loosening perispore in a few to many spores and weakly but usually distinctly dextrinoid (O2,O3; (P0)P1(P2); D1,D2); *spore colour* under the microscope brown, sometimes with a yellow tinge; *spore size* based on n = 53 spores of the holotype, 5–95 % percentile range 10.4–12.8 × 6.0–7.0 μm, with median 11.7 × 6.5 μm and av 11.6 × 6.5 μm with SD length 0.69 μm and width 0.33 μm, Q value 5–95 % percentile range 1.65–1.98, with median 1.78 and av 1.80 with SD 0.11; *spore size* based on 38 collections medians (10.3–)10.9–13.7 × (5.5–)6.1–7.1 μm and av (10.3–) 10.9–13.7 × (5.5–)6.1–7.0 μm with SD length 0.49–0.94 μm and width 0.23–0.49 μm, Qav (1.60–)1.69–2.06. (It should be noted that among the collections examined was one collection with unusually small spores.) *Basidia* cylindrical to clavate and 4-spored, 23–42 × 6.5–11.7 μm, with av 24–37 × 7.1–10.4 μm and basidium Qav in the range 2.9–4.4. *Pleurocystidia* not found. *Cheilocystidia* capitate-stipitate, clavate-stipitate or occasionally spathulate-stipitate, sometimes swollen towards the base (capitate-lageniform or clavate-lageniform), often conglutinate, sometimes with thickening of the apex or thickening of the median, sometimes septate, occasionally sinuate, bifurcate or with yellowish contents; *width of apex* holotype 8–10 μm (according to Malençon as we were unable to find cheilocystidia when we examined the exsiccata); across 38 collections median 7.8–10.3 μm and av 8.0–10.4 μm; with n at least 20 selected cheilocystidia of 38 collections the 5–95 % percentile ranges are 35–93 × 6.1–13.2 × 2.8–6.8 × 2.6–7.7 μm while the averages are 45–71 × 8.0–10.4 × 3.6–4.9 × 3.7–5.1. The av cheilocystidia ratios for the 38 collections were: A/M = 1.78–2.71; A/B = 1.80–2.72; B/M = 0.90–1.19. *Caulocystidia* resemble cheilocystidia, up to 90 × 11 μm wide at the apex. *Pileipellis* is an ixocutis with an epicutis medium thick, 80–120 μm, embedded hyphae up to 6 μm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* cream to yellow and made up of cylindrical to isodiametric elements. *Trama below the subcutis* contains angular, cylindrical and sausage-shaped elements up to 18 μm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — *Hebeloma eburneum* has been recorded with a wide variety of trees, primarily broadleaf but occasionally also with conifers. In Malençon's original description he claims it is uniquely associated with *Cedrus* but we have numerous collections where no *Cedrus* was present. Trees recorded as associates include: *Betula* spp., *Carpinus betulus*, *Cedrus* spp., *Fagus* sp., *Larix* sp., *Picea* sp., *Pinus* sp., *Populus* sp., *Quercus* sp., *Salix* sp., *Tilia* sp. It has been recorded in various types of woodland, both broadleaf and conifer, parklands, churchyards, urban areas, dunes, *Salix* thickets, often close to paths. Habitats include grassy places as well as exposed and overgrazed alvar. We have no records of this species from arctic or alpine habitats. The species occurs in calcareous, chalky, sandy and clayey, both wet and dry soil conditions.

Additional specimens examined. Austria, Tirol, Silz, Forstgarten (c. N48.38 WE16.72, alt. c. 150 m) in plantation with *Picea* sp. and *Pinus sylvestris*, 18 Oct. 1962, *F. Gobl* IB 19620069, database record HJB1000071; this is the holotype of *H. perpallidum*. – Belgium, Brussels, Foret de Soignes (N50.7950333 E4.4332833, alt. c. 114 m) in broadleaf woodland on calcareous soil with *Fagus sylvatica*, 8 Sept. 2006, *H. Beker* HJB11687; Foret de Soignes (N50.79578333 E4.4297333, alt. c. 100 m) in broadleaf woodland on calcareous soil with *Fagus sylvatica*, 8 Sept. 2006, *H. Beker* HJB11690; Zaventem (c. N50.89 E4.46, alt c. 40 m) in grassland under *Betula* sp., 8 Oct. 2005, *D. Deschutyer* HJB11235; prov. Luxembourg, Reine (N50.30185 E5.4318333, alt. c. 180 m) in mixed woodland with *Picea* sp., 8 Oct. 2004, *M. Lenne* HJB10290. – Czech Republic, LPA Moravian Karst, NNR Vyvery Punkvy (N49.37245 E16.73003, alt. c. 490 m) in mixed woodland on calcareous grassy soil under *Populus* sp., 10 Oct. 2008, *S. Kelly* HJB12719; LPA Moravian Karst, NNR Vyvery Punkvy (N49.3724500 E16.7300300, alt. c. 487 m) on soil in mixed woodland scrub under *Populus* sp., 10 Oct. 2008, *S. Kelly* HJB12720. – Denmark, Brabrand W of Århus, Egebjergvej (c. N56.15 E10.10, alt. c. 30 m) on grassy soil with *Pinus* sp., 6 Oct. 1983, *J. Vesterholt* C He83-207, duplicate HJB10940; Vejle, Nordre Kirkegård (c. N55.719 E9.555, alt. c. 50 m) with *Tilia* sp., 12 Sept. 2004, *J. Vesterholt* C JV04-245; duplicate HJB10708; Vejle, Bredballe N, Solgave Alle (N55.72682 E9.5850860, alt. c. 70 m) on dry clayey soil in urban broadleaf scrub under *Salix* sp., 11 Oct. 1991, *J. Vesterholt* C JV91-586, duplicate HJB12359. – England, South Lancashire, Ainsdale (c. N53.59273 W3.054548, alt. c. 0 m) on sandy soil in dune with *Salix* sp. and *Populus* sp., 22 Sept. 2002, *M. Rotheroe* HJB9267. – Estonia, Saaremaa, Salme commune, Kaugatoma-Löo (N58.09321 E22.17693, alt. c. 5 m) on alvar soil in maritime scrub under *Betula* sp., *Pinus sylvestris*, 18 Sept. 2008, *J. Vesterholt* JV08-251, HJB12327; Hiiumaa, Pühalepa commune, Sarve peninsula, Soonlepa (N58.85049 E23.03069, alt. c. 10 m) in mixed woodland, on grassy calcareous soil with *Betula pubescens*, *Picea abies* and *Pinus sylvestris*, 25 Sept. 2008, *J. Vesterholt* C JV08-408; duplicate HJB12338;
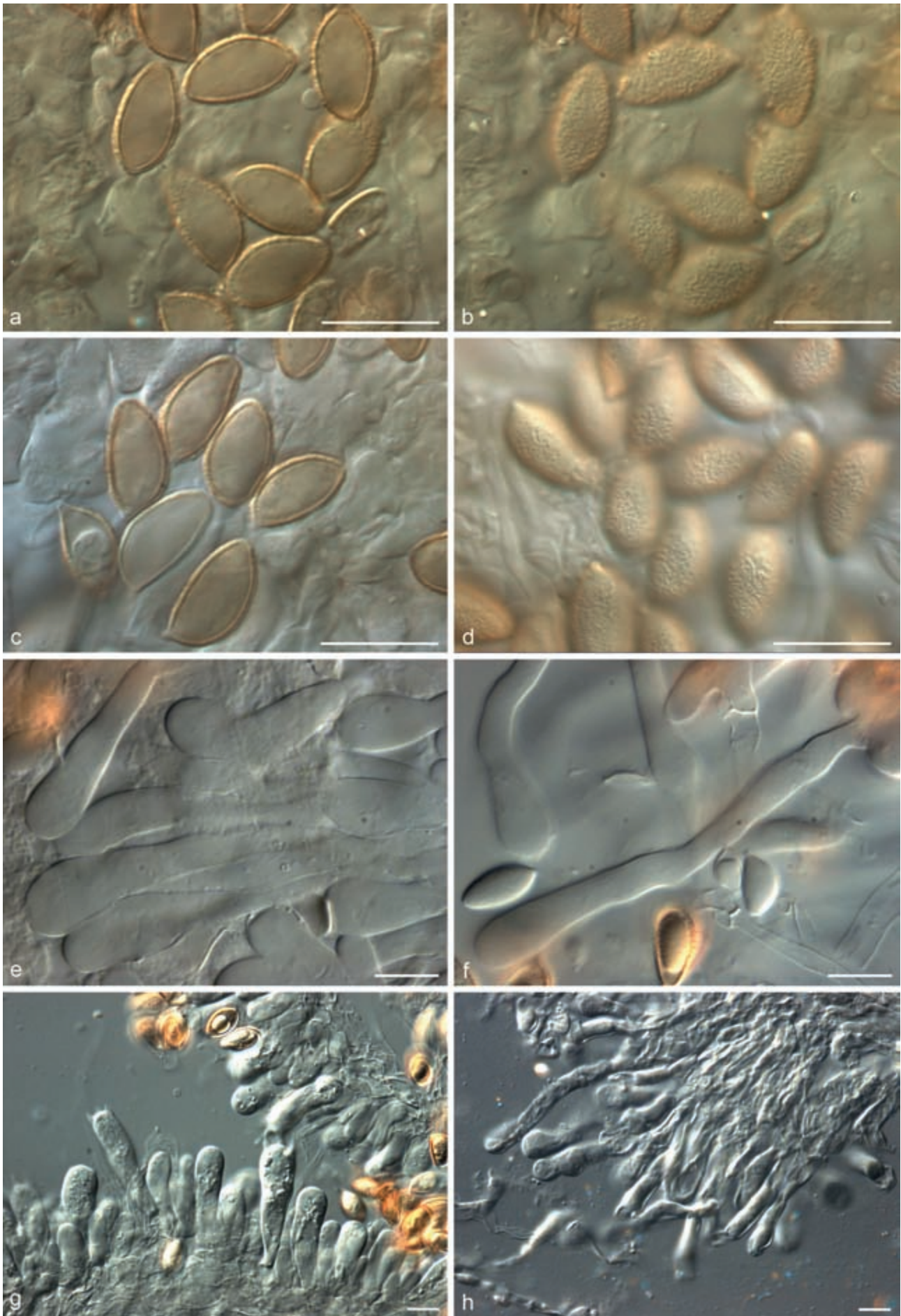
Fig. 12 *Hebeloma eburneum* (MPU GM1122, holotype). a, b. Spores and spore ornamentation ×1 600 in Melzer's reagent; c, d. spores and spore ornamentation ×1 600 in 5 % KOH. — *H. eburneum* (HJB12772). e, f. Cheilocystidia ×1 000 in 5 % KOH; g. basidia at gill edge ×500 in 5 % KOH; h. caulocystidia ×500 in 5 % KOH. — Scale bars: 10 µm.

Hiiumaa, Körgessare Commune, Reigi cemetery (N58.98308 E22.51068, alt. c. 10 m) in churchyard lawn on dry calcareous soil under *Betula pubescens* and *Larix* sp., 25 Sept. 2008, *J. Vesterholt* C JV08-405, duplicate HJB12343. – FINLAND, Turku town, Mäntymäki, near the cross of Vähä-Heikkiläntie and Luolavuorentie (c. N60.64505 E22.27442, alt. c. 40 m) on lawn under *Tilia* sp., 22 Sept. 2005, *J. Vauras* C TURA JV23655, duplicate HJB12399. – FRANCE, Vienne, Saint-Bermier (N46.4542667 W0.0174167, alt. c. 117 m) in parkland on grassy soil under *Populus* sp., 4 Nov. 2004, *H. Beker* HJB10525; Provence, Le Verdiere (c. N43.94 E4.877, alt. c. 30 m) with *Pinus halepensis* and *Quercus ilex*, 9 Nov. 1999, *P.-A. Moreau* C JV99-720, duplicate HJB10899. – GERMANY, Herrnhut, Herrschaftsgarten (c. N51.0110430 E14.7508300, alt. c. 330 m) under *Carpinus betulus*, 29 Oct. 1999, *G. Zschieschang* GLM GL40795, database record HJB10979; Lossa (c. N51.220 E11.410, alt. c. 310 m) under *Betula* sp., *Populus* sp., *Salix* sp., 24. Oct. 2004, *D. Penke* GLM: HBo79138, duplicate HJB12243; Parkplatz, Hilpoltstein, Bayern (c. N49.189 E11.184, alt. c. 380 m) with *Tilia* sp., 24 Sept. 1995, *D. Aanen* WBS 9511, database record HJB12501; Regensburg, Universitätsgelände (c. N49.00 E12.09, alt. c. 370 m) with *Tilia* sp., 4 Oct. 1978, *A. Bresinsky* M M5340, database record HJB13014. – HUNGARY, Fot Com. Pest (c. N47.50 E19.40, alt. c. 220 m) in broadleaf woodland on sandy soil under *Populus* sp., 20 Oct. 1971, *I. Schumeth* BP 48.427, database record HJB1000052, this is the holotype of *H. ochroalbidum*. – MACEDONIA, Ezerani near Asamati Village (N40.99356 E21.03927, alt. c. 850 m) in *Salix* thicket on calcareous soil with *Salix fragilis* and *S. amplexicaulis*, 10 Nov. 2008, *H. Beker* HJB12769, duplicate C JV08-451; Ezerani near Asamati village (N40.99359 E21.03931, alt. c. 855 m) in *Salix* thicket under *Salix fragilis*, *Salix* sp., 10 Nov. 2008, *H. Beker* HJB12771; Ezerani near Asamati village (N40.99320 E21.03889, alt. c. 854 m) in *Salix* thicket with *Salix fragilis*, *Salix* sp., 10 Nov. 2008, *J. Vesterholt* JV08-452, HJB12772. – MOROCCO, Azrou Clairicie de Boudmeme (c. N33.4167 W5.2157, alt. c. 1740 m) with *Cedrus* sp., 1 Nov. 1943, *G. Malençon* MPU GM1415, database record HJB12229. – NETHERLANDS, Limburg, Elsloo (c. N50.57 E5.46001, alt. c. 65 m) with *Populus* sp., 25 Oct. 1996, *D. Aanen* WBS 9699, database record HJB12537; Zuid-Holland, Hoornaar, Grootewaard (c. N51.8767 E4.9469, alt. c. 0 m) with *Populus* sp., 20 Oct. 1996, *D. Aanen* WBS 9693, database record HJB12536); Zuid-Holland, Hoornaar, Grootewaard (c. N51.8767 E4.9469, alt. c. 0 m) with *Populus* sp., 15 Oct. 1996, *D. Aanen* WBS 9680, database record HJB12480; Zuid-Holland, Hoornaar, Grootewaard (c. N51.8767 E4.9469, alt. c. 0 m) with *Populus* sp., 15 Oct. 1996, *D. Aanen* WBS 9679, database record HJB12804; Utrecht, Lunetten (c. N52.03453 E5.07562, alt. c. 4 m) with *Salix alba*, 13 Oct. 1996, *D. Aanen* WBS 9686, database record HJB12996. – POLAND, Mt Kamiensk (the outer damping ground of the Belchatow Lignite Mine), forest distr. 300b (near the cross, plot Z-5d, 12 year old plantation) (N51.21337 E19.44114, alt. c. 372 m) conifer woodland plantation with *Pinus sylvestris* and *Quercus* sp., 23 Sept. 2008, *I. Kałucka*, *H. Beker* HJB12667; Mt Kamiensk (the outer damping ground of the Bel-chatow Lignite Mine), forest distr. 300b (near the cross, plot Z-5d, 12 year old plantation) (N51.21322 E19.44148, alt. c. 370 m) conifer woodland plantation with *Pinus sylvestris*, *Betula* sp. and *Alnus* sp., 23 Sept. 2008, *I. Kałucka*, *H. Beker* HJB12670; Jelonka reserve (undisturbed), plot 16 (phase 8) (c. N52.596 E23.363, alt. c. 180 m) in naturally regenerated conifer woodland on abandoned fields with *Pinus sylvestris*, *Populus tremula* and *Salix* sp., 9 Oct. 1996, *I. Kałucka* LOD 19481, database record HJB13070. – SWEDEN, Hammarskog, Dalkarlskärret, Uppsala (c. N59.77 E17.55, alt. c. 20 m) in mixed woodland with *Populus* sp., 29 Sept. 2003, *A. Taylor* UPS AT2003093, duplicate HJB10667; north shore of Tornesträsk, Norbot-ten (c. N66.943 E19.81, alt. c. 420 m) with *Betula tortuosa*, 25 Aug. 1981, *M. Moser* IB 19810313, database record HJB1000069, this is the holotype of *H. albocolossum*. – SWITZERLAND, Bern, Gampelen (c. N47.01 E7.05, alt. c. 520 m) in mixed woodland on wet soil with *Populus* sp., 19 Sept. 1993, *J. Vesterholt* C JV93-943, duplicate HJB10840.

Notes — Given the shape of its cheilocystidia, *H. eburneum* clearly belongs to *H.* subsect. *Denudata*. The species most likely corresponds to ICG3 of Aanen & Kuyper (1999). It appears to have a wide range both geographically and ecologically. There is no morphological or molecular evidence to separate this species from *H. albocolossum*, *H. ochroalbidum* and *H. perpallidum*, which were all described as large and fleshy with a very pale coloured cap. Moser saw the primary differences as being the presence or absence of tears on the lamellae and the discolouration of the stipe. He regarded *H. eburneum* as a Mediterranean species and the others as more northern. He also believed spore size and the presence of a papilla on the spores, leading to a more limoniform shape, as significant (Moser 1970, 1985). The presence or absence of tears can be

affected by the weather and while it is a good character it is not a dependable character. The discolouration of the stipe is also an important character but again can be affected by local ecology; for this species the stipe does not usually discolour very much with age, however, when conditions are very damp the stipe can exhibit some discolouring which starts from the base of the stipe. This species is morphologically close to *H. aanenii* and to *H. geminatum* but usually has rather larger spores; we have had one collection of *H. eburneum* that has smaller spores than usual and if the spores are both short and narrow it may become impossible to separate these species purely on the basis of the spore size. *Hebeloma eburneum* is also morphologically close to *H. crustuliniforme* but can be distinguished through its cheilocystidia, which have on average a larger apex. *Hebeloma crustuliniforme* also tends to have a rather more coloured cap.

If species identification was attempted with a single locus only, then *RPB2* was probably the most reliable among the loci tested. The majority of *H. eburneum* ITS sequences form a *H. eburneum* clade (Fig. 1a). Most of the *H. eburneum* sequences placed outside this clade are phased copies from collections with length differences within their ITS. These sequences are in the unresolved part of the tree, together with *H. alpinum* and *H. geminatum* sequences. Typically, only one of the two phased alleles of a collection falls outside the *H. eburneum* clade. The only exception to this is the type of *H. albocolossum* where both alleles, if phased (results not shown as there are only ambiguities, no length difference in the direct ITS reads), are in the unresolved part of the tree. We did not obtain many *RPB2* sequences, but the results obtained so far argue against hybridization and suggest that the presence of unspecific ITS alleles in *H. eburneum* is more likely a consequence of incomplete lineage sorting than of frequent hybridization events.

As in *H. alpinum*, the combination of V6 and V9 is another option for separating *H. eburneum* from other members of the *H. crustuliniforme* complex, because *H. eburneum* V6 sequences form mixed clades with *H. aanenii* and V9 sequences with *H. alpinum*, and the *H. alpinum* V6 sequences or the *H. aanenii* V9 sequences, respectively, are clearly different from *H. eburneum* based on presence/absence patterns of indels.

In deciding on the priority of the name *H. eburneum* a number of factors have been taken into account:
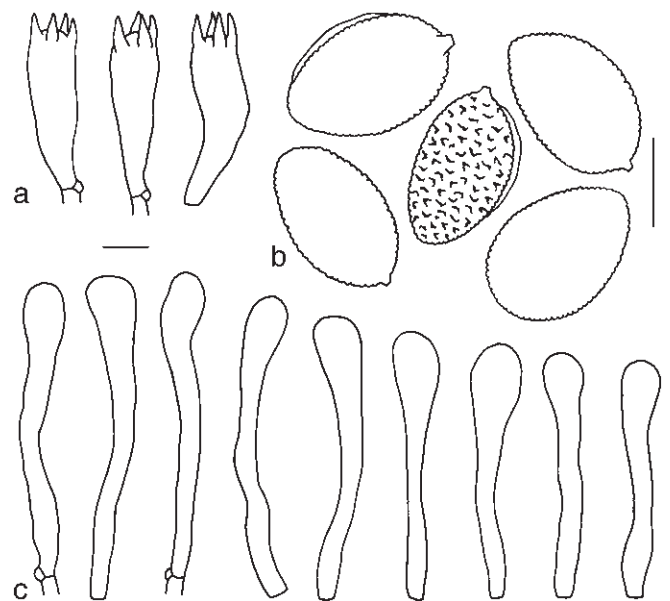

Fig. 13 *Hebeloma eburneum* (MPU GM1122, holotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 μm.

Hebeloma eburneum and *H. perpallidum* both have publication dates of 1970 (Malençon & Bertault 1970, Moser 1970). *Hebeloma ochroalbidum* has an effective publication date of 1972 (Bohus 1972) and *H. albocolossum* has an effective publication date of 1986 (Moser 1985).

Hebeloma perpallidum was published in Z. Pilzk. vol. 36, Parts 1 & 2. We have been informed by the publishers that this was published in December 1970.

Hebeloma eburneum was published in the Flore des Champignons Superieurs du Maroc Vol. 1 which is Volume 32 of Trave. Inst. Sci. Cherifien de la Fac. Sci. Rabat. We have not been able to establish a precise date of publication for this volume but:

Hebeloma eburneum was listed in Index of Fungi 4, 3: 65 (early 1972); but *perpallidum* was not listed until a year later, in Index of Fungi 4, 5: 133 (early 1973).

The book by Malençon & Bertault was reviewed in Bull. Soc. Mycol. France 86, 3: 793 on 7 May 1971 and most other publications reviewed in that issue of the journal have a publication date of 1969, or even 1968. This suggests that the book was published relatively early in 1970 and almost certainly not as late as December 1970.

The holotype of *H. crustuliniforme* var. *tiliae* is a mixed collection. The part of the collection that corresponds best with the species description is designated here as lectotype of the species (M M-0151680, database record HJB13014, MycoBank MBT198154).

Hebeloma geminatum Beker, Vesterh. & U. Eberh., *sp. nov.* — MycoBank MB809907; Fig. 5c, 14, 15

Etymology. From the base *geminus* meaning a double or twin and to emphasise that this is one of two taxa that can be differentiated molecularly and biologically but for which we have found no unambiguous morphological character to separate them.

Type. DENMARK, Nystrup Klitplantage, S of Kridtstien (N57.00 E8.52, alt. c. 42 m) with *Abies* sp., 10 Oct. 1996, *J. Vesterholt* holotype C JV96-341; isotype BR BR-MYCO 173983-62, database record HJB10833.

Diagnosis — *Hebeloma geminatum* with primarily capitate-, clavate- or spathulate-stipitate cheilocystidia belongs to *H.* subsect. *Denudata*. It can be distinguished from other taxa of the section by its average number of lamellae, which is ≥ 60, its spores, which are on average between 6 and 6.4 µm wide and < 10.75 µm long, and the cheilocystidia apex, which is always on average > 8 µm and often > 9 µm. The species is morphologically most similar to *H. aanenii* from which it can be distinguished by comparison of the sequence of the internal transcribed spacer region of the nuclear ribosomal RNA genes.

Basidiomes usually in scattered groups, sometimes solitary, sometimes caespitose. *Pileus* up to 120 mm diam, convex, sometimes umbonate or applanate; *surface* slightly viscid, tacky when moist never hygrophanous, sometimes rugulose; *cuticle colour* usually from white to cream to buff, sometimes yellowish, becoming paler towards the margin which is always very pale; *pileus margin* usually straight, but occasionally involute or crenulate, upturned with age. *Lamellae* emarginate, adnexed or adnate, crowded (L = 65–100) with a maximum depth of 4–8 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, paler than lamella surface; droplets on the lamella edge are usually present and visible to the naked eye; *lamellules* frequent. *Stipe* central, cylindrical, often clavate, (15–)27–110 × 6.5–13 mm and up to 16 mm at the base; white or alutaceous, sometimes but not always discolouring from the base when handled or with age; *surface* dry, strongly floccose particularly towards the apex; *interior* stuffed when young but sometimes becoming hollow with age. *Cortina* not observed. *Flesh* rather thick, cream or

pale brown. *Smell* raphanoid. *Taste* raphanoid, usually mild. *Spore deposit* greyish brown to brownish olive.

Spores amygdaloid, with small apiculus and rounded at the end opposite the apiculus, with a distinct thinning of the spore wall but rarely with any papilla, guttulate with one or more oily drops, weakly ornamented to distinctly ornamented, sometimes with some sign of loosening perispore in a few spores and weakly dextrinoid (O2,O3; (P0)P1(P2); D0,D1); *spore colour* under the microscope yellow- or grey-brown to brown; *spore size* based on n = 63 spores of the holotype, 5–95 % percentile range 9.2–11.7 × 5.4–6.9 µm, with median 10.3 × 6.0 µm and av 10.4 × 6.0 µm with SD length 0.85 µm and width 0.51 µm, Q value 5–95 % percentile range 1.58–1.89, with median 1.74 and av 1.74 with SD 0.1; *spore size* based on 25 collections medians 9.8–10.8(–11.6) × 5.4–6.4 µm and av 9.8–10.8(–11.6) × 5.4–6.3 µm with SD length 0.38–1.02 µm and width 0.19–0.51 µm, Qav 1.65–1.93. *Basidia* cylindrical to clavate and 4-spored, 22–38 × 6.6–9.9 µm, with av 26–35 × 7.1–9.0 µm. *Pleurocystidia* not found. *Cheilocystidia* capitate-, clavate- and sometimes spathulate-stipitate, occasionally slightly swollen towards the base (clavate-lageniform) and occasionally with some median thickening, sinuate, septate or bifurcate; *width of apex* holotype 5–95 % percentile range 6.8–12.2 µm, with median 9.4 µm and av 9.4 µm with SD 1.74 µm; across 25 collections median 8.0–10.4 µm and av 8.0–10.4 µm (of the 25 collections 10 have the cheilocystidium apex av ≥ 9 µm); with n ≥ 20 selected cheilocystidia of 25 collections the 5–95 % percentile ranges are 36–91 × 6.2–13.2 × 2.8–6.2 × 2.4–7.2 µm while the averages are 50–72 × 8.0–10.4 × 4.0–4.7 × 3.7–5.0 and 55 × 9.4 × 4.2 × 5.0 µm av for the holotype. The av cheilocystidia ratios for the 19 collections were: A/M = 1.76–2.57; A/B = 1.68–2.85; B/M = 0.81–1.19. *Caulocystidia* resemble cheilocystidia, up to 70 µm long and 12 µm wide at the apex. *Pileipellis* is an ixocutis with a medium thick epicutis 110–200 µm, embedded hyphae up to 5–8 µm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* yellowish and made up of cylindrical to isodiametric elements. *Trama below the subcutis* contains cylindrical, ellipsoid, spherical and thick sausage shaped elements up to 16 µm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — *Hebeloma geminatum* has been recorded with a variety of trees including: *Abies*, *Betula*, *Corylus*, *Fagus*, *Picea*, *Pinus*, *Populus*, *Quercus*, *Salix*, *Tilia*, on various acid and neutral soils, often sandy or mossy and in rotten litter, in a range of woodlands and plantations, often on roadsides or pathsides, as well as in gardens and parklands and also on slagheaps.

Additional specimens examined. BELGIUM, prov. Brussels, Foret de Soignes (N50.790 E4.430, alt. c. 114 m) on rotten litter in broadleaf woodland under *Fagus* sp., 16 Sept. 2003, *H. Beker* HJB8633; prov. Antwerp, Geel, Dekshoevevijver IFBL: C6.21.34 (c. N51.1667 E5.000, alt. c. 20 m) under *Populus* sp., 19 Oct. 2003, *J. Volders* VJ03073, duplicate HJB10969; prov. Luxembourg, Ste-Cecile (N49.7632167 E5.2690500, alt. c. 257 m) on rotten litter in broadleaf woodland under *Fagus* sp., 17 Sept. 2004, *M. Lenne* HJB10603; prov. Hainaut, Maubray (N50.5302833 E3.4948667, alt. c. 52 m) on rotten litter in broadleaf woodland on slagheap under *Betula* sp., *Populus* sp., *Salix* sp., 10 Nov. 2006, *P.-A. Moreau* HJB11736. – DENMARK, region NEZ, Tisvilde Hegn, East end (c. N56.020 E12.030, alt. c. 15 m) under *Betula* sp., *Picea* sp., 24 Sept. 2003, *T. Læssøe* TL-11137, HJB10834; region EJ, Als Odde, Sommerland (N56.71199 E10.32148, alt. c. 10 m) on sandy mossy soil in roadside woodland under *Betula* sp., *Larix* sp., *Picea* sp., *Pinus* sp., *Populus tremula*, *Quercus* sp., 30 Aug. 2008, *J. Vesterholt* JV08-101, HJB12319. – ENGLAND, East Kent, Bedgebury Pinetum (c. N51.280 E0.540, alt. c. 55 m) on soil, 17 Oct. 1971, *D.A. Reid* K K(M)106232, database record HJB11604; Berkshire, California Park (N51.3813000 W0.8762839, alt. c. 55 m) on wet soil in mixed woodland under *Salix* sp., 5 Oct. 1997, *H. Beker* HJB1889; Surrey, Whitley (N51.1570200 W0.6686763, alt. c. 66 m) on rotten litter in mixed woodland under *Salix* sp., 4 Nov. 2000, *H. Beker* HJB3808; West Sussex, Graffham (N50.9655900 W0.6798483, alt. c. 52 m) in conifer woodland under *Betula* sp., 17 Sept. 2002, *M. Storey* HJB10766; Surrey, La
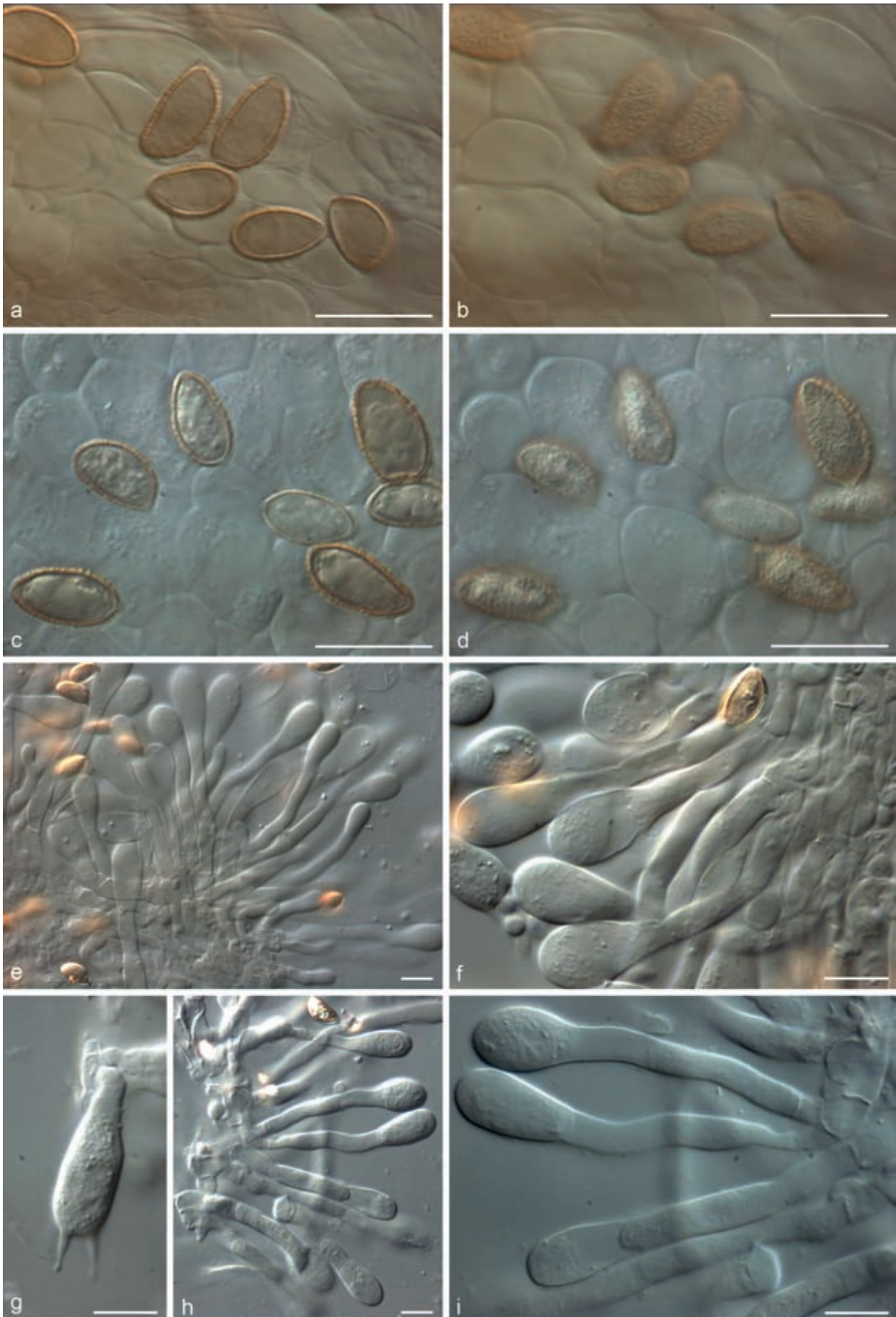
Fig. 14   *Hebeloma geminatum* (C-F-90152 (JV96-341, holotype)). a, b. Spores and spore ornamentation ×1 600 in Melzer's reagent; c, d. spores and spore ornamentation ×1 600 in 5 % KOH; e. cheilocystidia ×500 in 5 % KOH; f. cheilocystidia ×1 000 in 5 % KOH; g. basidia ×1 000 in 5 % KOH; h. caulocystidia ×500 in 5 % KOH; i. caulocystidia ×1 000 in 5 % KOH. — Scale bars: 10 μm.

Baraka, Gorse Hill Road (N51.4093800 W0.5650113, alt. c. 70 m) on rotten litter in urban garden under *Betula* sp., 31 Oct. 2004, *H. Beker* HJB10384; West Kent, Tudeley Wood (c. N51.1660700 E0.3099706, alt. c. 88 m) on sandy soil in broadleaf woodland under *Betula* sp., *Quercus* sp., 22 Oct. 2005, *A. Andrews* HJB11545; Surrey, La Baraka, Gorse Hill Road (N51.4088400 E0.5650200, alt. c. 51 m) on mossy soil in urban garden under *Betula pendula*, 28 Oct. 2009, *H. Beker* HJB13309. – Estonia, Hiiumaa district, Puhalepa commune, Sarve (c. N58.180 E22.060, alt. c. 0 m) on alvar soil in woodland path under *Betula* sp., *Corylus avellana*, *Juniperus* sp., *Pinus sylvestris*, 16 Sept. 2001, *J. Vauras* 17928F, HJB10961. – France, Yvelines, St-Leger-en-Yvelines, Foret domaniale de Rambouillet (c. N48.6703 E1.7797, alt. c. 160 m) on sandy soil in conifer woodland plantation under *Pinus* sp., 3 Nov. 1998, *G. Corriol* GC98 11 03 02, HJB12934; Nord Pas de Calais, Auberchicourt (N50.3475667 E3.2351667, alt. c. 23 m) on grassy soil in broadleaf woodland slagheap under *Betula* sp., *Salix* sp., 13 Nov. 2006, *C. Lecuru* HJB11801. – Netherlands, Groningen, Eemshaven (c. N53.455 E6.806, alt. c. 0 m) under *Salix alba*, *S. caprea*, *S. repens*, 3 Oct. 1996, *D. Aanen* WBS 9675, database record HJB12469. – Norway, Skibotndalen fieldstation Tromsø (c. N69.260 E20.510, alt. c. 280 m) under *Betula pubescens*, 6 Aug. 1995, *M. Moser* (as *H. albocolossum*) IB 19950057, HJB11829. – Poland, Mt Kamiensk (N51.2245833 E19.4003611, alt. c. 220 m) on calcareous, clayey, sandy soil in conifer woodland plantation and quarry site under *Pinus sylvestris*, *Populus* sp., *Salix* sp., 2 Nov. 2004, *I. Kałucka* LOD IK-H0004, HJB13188; Wolka Lekawska, forest distr. 8C k (plot no. P-2), 9 year old pine plantation (75 % pine; 25 % birch) on former arable land (N51.3001500 E19.3972700, alt. c. 200 m) on mossy, sandy soil in mixed woodland plantation under *Betula* sp., *Pinus sylvestris*, 22 Sept. 2008, *I. Kałucka, H. Beker* HJB12655; Bialowieski Park Narodowy (c. N52.72111 E23.90560, alt. c. 150 m) on soil in mixed woodland under *Betula* sp., 19 Sept. 2008, *D. Karasinski, A. Szczepkouski* HJB12639. – Sweden, Medelpad, Borgsjö (c. N62.560 E15.870, alt. c. 200 m) under *Betula* sp., 19 Sept. 1995, *E. Arnolds* WBS 9503, database record HJB12809; Stradssbergen (c. N59.850 E17.610, alt. c. 40 m) on mossy litter in mixed woodland, 24 June 2004, *A. Taylor* AT2004020, HJB10770; Uppsala, Uppsala Hospital (c. N59.600 E16.540, alt. c. 49 m) on grassy soil in mixed parkland under *Picea* sp., *Pinus* sp., *Tilia* sp., 5 July 2004, *A. Taylor* AT2004061, HJB10776.

Notes — Given the shape of its cheilocystidia, *H. geminatum* clearly belongs to *H.* subsect. *Denudata*. Hebeloma geminatum most likely corresponds to ICG1 of Aanen & Kuyper (1999) and is a constituent of the 'Hebeloma crustuliniforme complex'. It is likely that many collections of this species have been recorded under the name *H. crustuliniforme* and exist worldwide in herbaria under this name. It is morphologically similar to *H. aanenii*, *H. alpinum*, *H. crustuliniforme* and *H. eburneum*. But its spores, normally < 11 μm long and < 6 μm wide (rarely longer or wider) distinguish it from the first three species. It can be distinguished from other members of this subsection by the number of complete lamellae, which is always ≥ 60.
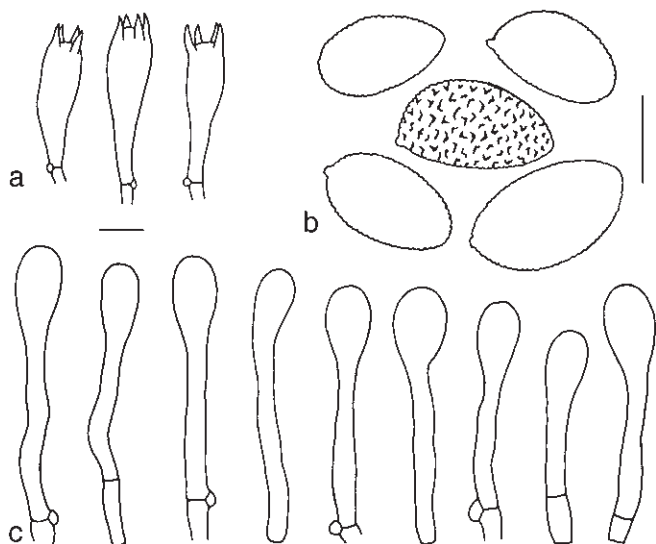

Fig. 15 *Hebeloma geminatum* (C-F-90152 (JV96-341, holotype; database record HJB HJB10833)).

Until now we have found no consistent morphological character to separate *H. aanenii* and *H. geminatum*. However, we can often separate these two taxa through the use of a mixture of characters, although none appears fool proof. The best character appears to be the cheilocystidium apex width; for *H. geminatum* this is usually larger than that for *H. aanenii*. From our records, if the average width of the apex of the cheilocystidium is more than 9 μm then the collection is almost certainly *H. geminatum*. However, the average apex width can be as small as 8 μm and widths in this interval between 8–9 μm can be from either taxon. This is illustrated in the scatter diagram (Fig. 4b).

Of course one can combine characters, so, for instance a collection with large basidiomes exhibiting a thick epicutis in excess of 200 μm and a cheilocystidium apex width of < 8.5 μm will almost certainly be *H. aanenii*. Similarly, a collection with small basidiomes, a relatively thin epicutis and cheilocystidium apex width of > 8.5 μm will almost certainly be *H. geminatum*. A synoptic key will be far more powerful as a tool based on morphological characters; but we do not yet feel we have examined sufficient collections to build such a key with confidence.

It is worth noting that we do not have any confirmed records from southern Europe. Other than two Swiss alpine collections we have not seen (and therefore are not cited in the species description, WBS 9618, WBS 9621, corresponding to ICG1, Aanen & Kuyper 1999), our most southerly collection is from France at a latitude of more than N48.67.

Molecularly, *H. geminatum* and *H. alpinum* are very close and sequences of both species are paraphyletic in four out of the five loci tested, though, in *MCM7* *H. geminatum* forms clades not including *H. alpinum* (apart from collection HJB11051 discussed elsewhere). The only locus that normally clearly separates *H. geminatum* from *H. alpinum* is V9. *Hebeloma alpinum* lacks an indel present in *H. geminatum* and some other members of *H.* subsect. *Denudata*. In fact, there is only a single bp difference between some *H. aanenii* and *H. geminatum* V9 sequences, but all other loci, including the ITS, can separate those two taxa.

Collection HJB11051 (see also in the Discussion) is genetically closer to *H. geminatum* in all loci tested than to *H. alpinum*, but corresponds morphologically with *H. alpinum* and, being an alpine collection, is also ecologically more typical for the latter species. One could argue that the genetic assignment is more meaningful in terms of ancestry and call the collection *H. geminatum*. However, as it is morphologically clearly different from typical *H. geminatum*, we decided not to include it here.

The V9 sequence of *H. geminatum* HJB11545, in spite of possessing the indel, differs quite strikingly in a number of positions from the 'normal' V9 of *H. geminatum* and in fact from all other V9 sequences obtained from members of its subsection. The placement of HJB11545 in the concatenated analyses has to be interpreted as being outside the *H. geminatum* clade as opposed to being a member of *H. alpinum*. Morphologically and ecologically, HJB11545 fits well into *H. geminatum*, only the spore width with an average of 5.4 μm is an outlier within this taxon.

Hebeloma helodes J. Favre, Beitr. Kryptogamenfl. Schweiz 10, 3: 214. 1948. — MycoBank MB286871; Fig. 16, 17

Type. Switzerland, Vaud, Jura, Tourbiere du sentier, Vallee de Joux (c. N48.6122 E6.2358, alt. c. 1000 m) in wet soil with *Filipendula ulmaria* in a bog with *Betula* sp. and *Pinus* sp., 30 Aug. 1939, *G. Favre 9139*, lectotype G 00053920, database record HJB1000054, selected by F. Gröger in Myk. Mittbl. 30, 2: 46, 1987.

Basidiomes usually in scattered groups or sometimes solitary. *Pileus* 13–38 mm diam, convex, sometimes weakly umbonate,
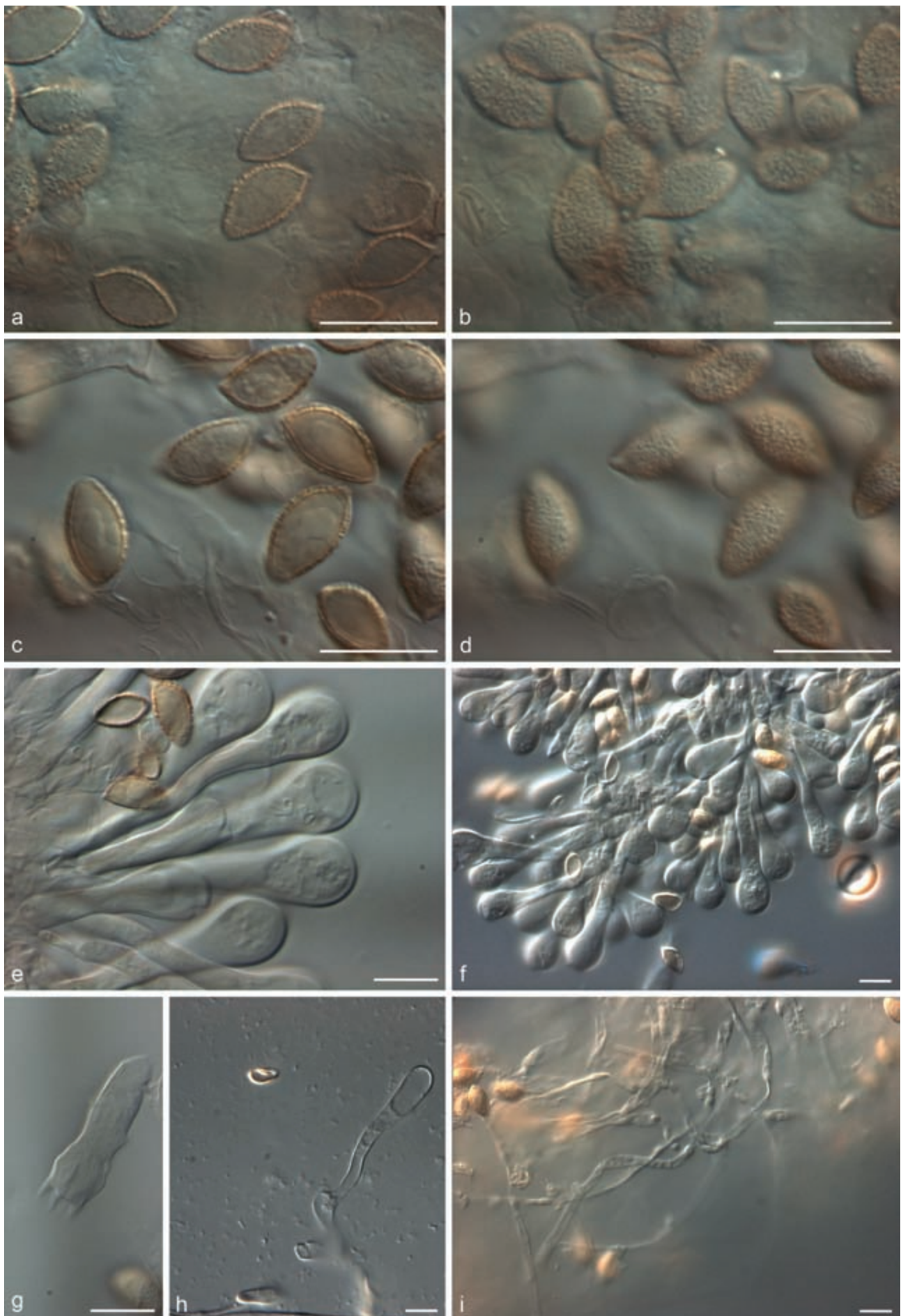
Fig. 16 *Hebeloma helodes* (G 00053920, lectotype). a, b. Spores and spore ornamentation ×1 600 in Melzer's reagent; c, d. spores and spore ornamentation ×1 600 in 5 % KOH; e. cheilocystidia ×1 000 in 5 % KOH; f. cheilocystidia ×500 in 5 % KOH; g. basidium ×1 000 in 5 % KOH; h. caulocystidium ×500 in 5 % KOH; i. epicutis hyphae ×500 in 5 % KOH. — Scale bars: 10 µm.

sometimes slightly depressed in the centre especially when older, often viscid, tacky when moist but never hygrophanous; *cuticle colour* quite pale and cream or white towards the margin with the centre sometimes darker from light ochraceous to dark beige or yellowish brown; *pileus margin* usually involute although this feature sometimes disappears in older basidiomes. *Lamellae* emarginate, moderately spaced (L = 37–54) with a maximum depth of 3–5 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, significantly paler than lamella surface; droplets normally visible on the lamella edge even with the naked eye; *lamellules* frequent. *Stipe* central, usually cylindrical but sometimes slightly to distinctly clavate, becoming hollow with age, 15–60 × 3–4.5 mm and up to 7 mm at the base; white or alutaceous, occasionally with some slight brown discolouration at the base of the stipe; *surface* dry, floccose particularly towards the apex. *Cortina* not observed. *Flesh* rather thin, whitish but slightly more coloured in the base of the stipe. The whole basidiome has a very slender appearance with the length of the stipe normally at least twice the width of the pileus. *Smell* raphanoid, rarely absent. *Taste* raphanoid, not bitter. *Spore deposit* Isabella to brownish olive.

Spores amygdaloid, with small apiculus and rounded at the end opposite the apiculus, with a distinct thinning of the spore wall, rarely with any papilla, guttulate with one or more oily drops, from weakly to distinctly ornamented, usually with some sign of loosening perispore in at least a few spores and often in many spores and at most weakly dextrinoid (O2,O3; (P0)P1,P2; DO,D1(D2)); *spore colour* under the microscope yellow, occasionally with a brown tinge; *spore size* based on n = 97 spores of the holotype, 5–95 % percentile range 9.0–10.7 × 5.1–6.0 μm, with median 9.8 × 5.6 μm and av 9.9 × 5.6 μm with SD length 0.58 μm and width 0.26 μm, Q value 5–95 % percentile range 1.63–1.93, with median 1.78 and av 1.78 with SD 0.09; *spore size* based on 22 collections medians 9.0–10.8 × 4.9–6.0 μm and av 9.1–10.8 × 4.9–6.0 μm with SD length 0.40–0.99 μm and width 0.18–0.55 μm, Qav 1.61–2.02. *Basidia* cylindrical to clavate and 4-spored, 21–30 × 5.5–9.1 μm, with av 22–27 × 6.6–8.2 μm and basidium Qav in the range 2.8–4.2. *Pleurocystidia* not found, although cheilocystidia sometimes found behind the lamella edge. *Cheilocystidia* capitate-stipitate or clavate-stipitate, occasionally slightly swollen towards the base (capitate-lageniform or clavate-lageniform) and almost always with apical thickening, occasionally septate and rarely with median thickening; *width of apex* holotype 5–95 % percentile range 7.5–11.9 μm, with median 9.7 μm and av 9.6 μm with SD 1.25 μm; across 22 collections median 8.2–11.4 μm and

av 8.3–11.4 μm; with n ≥ 20 selected cheilocystidia of 22 collections the 5–95% percentile ranges are 35–76 × 6.5–14.1 × 3.1–6.0 × 2.4–6.6 μm while the averages are 44–63 × 8.3–11.4 × 4.0–4.9 × 3.3–5.4 and 47 × 9.6 × 4.3 × 4.4 μm av for the holotype. The av cheilocystidia ratios for the 22 collections were: A/M = 1.90–2.86; A/B = 2.02–3.38; B/M = 0.77–1.17. *Caulocystidia* resemble cheilocystidia, up to 11 μm wide at the apex but on average shorter than the cheilocystidia. *Pileipellis* is an ixocutis with a relatively thick epicutis 100–135 μm, embedded hyphae up to 5–6 μm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* pale yellow and made up of cylindrical to isodiametric elements. *Trama below the subcutis* contains thick sausage shaped elements up to 15 μm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — *Hebeloma helodes* is widespread across northern and central Europe, but as yet we have no confirmed records of this taxon in southern Europe. Also, we have not yet seen any confirmed records from outside of Europe. It has been recorded with a variety of deciduous trees including *Alnus*, *Betula*, *Corylus*, *Fagus*, *Populus*, *Quercus* and *Salix* spp. However, we suspect that it is not mycorrhizal with *Alnus* as we have no records of it growing with *Alnus* when no other trees were present, nor has it, to our knowledge, ever been found in studies of mycorrhiza on *Alnus* roots. Similarly, although some records include *Picea* and *Pinus*, again all of these records also record a deciduous tree close by and we suspect that the mycorrhizal association is with the deciduous tree. The species is found on both calcareous and acid ground, often in sandy or wet places. Habitats are often described as grassy and include deciduous and mixed woodland, often on the side of a path or road.

Additional specimens examined. Belgium, prov. Namur, on the road between Voneche and Ave-et-Auffe, Hainaut (c. N50.10 E5.14, alt. c. 180 m) association not recorded, 4 Oct. 1982, *J. Boekhout* L 0490428, database record HJB12905; prov. Brabant-Wallonia, Bois de Lauzelles, Ottignies (c. N50.6784 E4.5999, alt. c. 110 m) scattered on wet soil in broadleaf woodland with *Alnus* sp. and *Betula* sp., 13 Sept. 2003, *D. Ghyselinck* HJB8816; prov. Luxembourg, Wilbauroche (N49.8133500 E5.2733000, alt. c. 310 m) in litter in broadleaf woodland with *Corylus avellana* and *Fagus sylvatica*, 17 Sept. 2004, *H. Beker* HJB10606. – England, South Lancashire, Ainsdale (N53.59273 W3.054548, alt. c. 0 m) scattered in sand on dune with *Salix repens*, 22 Sept. 2002, *H. Beker* HJB9266; Shropshire, Poles Coppice (N52.63748 W2.90287, alt. c. 205 m) on grassy soil in broadleaf woodland under *Salix* sp., 17. Oct. 2002, *T. Kirk* HJB8181; East Kent, Ashdown Forest (c. N50.8852 E0.033, alt. c. 160 m) on grassy soil, association not recorded, 18 Sept. 2004, *A. Andrews* HJB10680; South West Yorkshire, Burnt Stones Pasture (c. N53.3772 W1.5505110, alt. c. 265 m) in litter with *Salix cinerea*, 18 Oct. 2004, *C. Hobart*, *P. Ardron* HJB10731. – Faroe Islands, Streymoy, Torshavn, at Foroya Natturugripasavn (c. N62.0167 W6.783, alt. c. 60 m) with *Salix phylicifolia*, 3 Aug. 1988, *J. Vesterholt* F560, duplicate HJB10726. – Finland, Etelä-Häme, Tampere, Peltolammi (c. N61.44 E23.74, alt. c. 100 m) in mixed woodland with *Alnus* sp., *Betula* sp., *Picea* sp. and *Salix* sp., 20 Aug. 1992, *U. Söderholm* US1993, duplicate HJB10727. – France, Normandy, Foret d'Ecouves (N48.55745 W0.0832667, alt. c. 350 m) in damp litter in a mixed woodland on calcareous soil with *Picea* sp., *Pinus* sp. and *Quercus* sp., 6 Oct. 2006, *M. Beker* HJB11698; Jura, Lac des Rouges Truites (c. N43.36252 E5.59531, alt. c. 940 m) in mixed woodland with *Salix* sp., 26 Sept. 1996, *D. Aanen* WBS 9655, database record HJB12520; Puy-de-Dome, lower lake at La Godivelle (N45.382653 W2.92516, alt. c. 1200 m) with *Salix cinerea* and *S. pentandra*, 18 Sept. 1998, *G. Corriol*, GC98091808, duplicate HJB12930. – Netherlands, Drenthe, Beilen, Holthe, Wilgen Bosje (c. N52.84 E6.56, alt. c. 20 m) in wet *Sphagnum* with *Salix aurita* and *S. cinerea*, 1 Oct. 1996, *D. Aanen* WBS 9660, database record HJB12521; Drenthe, Beilen, Holthe, Griendje (c. N52.50267 E6.32319, alt. c. 15 m) collected with *Salix aurita* and *S. cinerea*, 1 Oct. 1996, *D. Aanen* WBS 9661, database record HJB12524; Drenthe, Beilen, lieving (c. N52.5124 E6.3040, alt. c. 10 m) on wet soil under *Salix aurita* and *S. cinerea*, 1 Oct. 1996, *D. Aanen* WBS 9664, database record HJB12525; Groningen, Drachten, Boerakker (c. N53.187 E6.329, alt. c. 0 m) with *Populus* sp. 18 Oct. 1996, *D. Aanen* WBS 9696, database record HJB12539. – Norway, Luster, S. of Fortun (c. N61.44 W7.45, alt. c. 50 m) on soil with *Picea* sp. and *Salix* sp., 8 Sept. 2000, *J. Vesterholt* JV00-277, duplicate HJB10725. – Poland, open ground between Bialowieza Park and
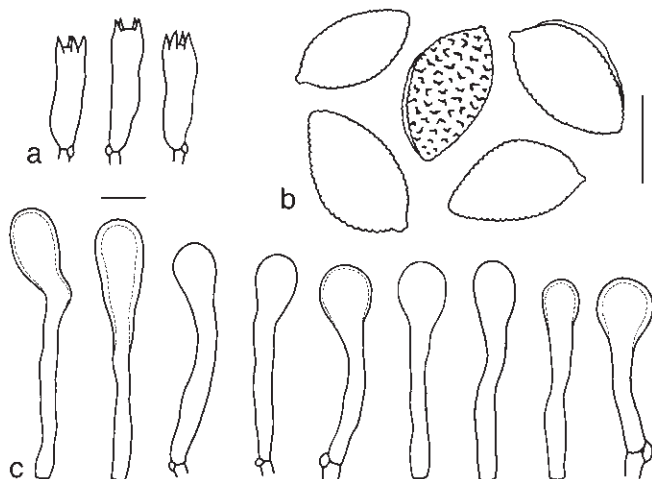
Fig. 17 *Hebeloma helodes* (G 00053920, lectotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 μm.

Bialowieski Park Narodowy (N52.7100 W23.84479, alt. c. 150 m) on grassy wet acid soil in broadleaf woodland under *Betula* sp., 20 Sept. 2008, *I. Kałucka*, *H. Beker* HJB12634; Jelonka Reserve Plot 67 (N52.595 E23.359, alt. c. 180 m) on soil in mixed woodland under *Pinus sylvestris*, *Populus tremula* and *Salix* sp., 4 Oct. 1995, *I. Kałucka* LOD 19484, database record HJB13151. – Scotland, Orkney, Ravie Hill Plantation (c. N59.1056 W3.2867, alt. c. 30 m) in litter in conifer woodland with *Pinus contorta*, 22 Sept. 1990, *T. Eggeling* E 00159158, database record HJB11906. – Wales, Denbigh, Erddig (N53.01608 W3.000195, alt. c. 80 m) in litter in broadleaf woodland under *Fagus sylvatica*, 5 Oct. 2002, *H. Beker* HJB8115.

Notes — Given the shape of its cheilocystidia, *H. helodes* clearly belongs to *H.* subsect. *Denudata*. The species most likely corresponds to ICG12 of Aanen & Kuyper (1999). We have no confirmed records of this taxon in arctic or alpine habitats although it appears closely related to *H. aurantioumbrinum*, which does exist in these habitats. It can be readily distinguished from the other members of this subsection that grow in lowland areas based on the number of lamellae, 30–60, the small spore length, < 11 μm, the large average width of the cheilocystidium apex, > 8 μm, and the regular apical thickening of the cheilocystidium. It has probably often been confused with *H. pusillum*, which is also a small *Hebeloma* sp., but *H. pusillum* is confined to *Salix*, often has < 30 full length lamellae, has a more fragile stature and usually a rather darker centre to the pileus. It also has significantly longer spores, on average. *Hebeloma luteicystidiatum* also has fewer lamellae and longer spores and is usually somewhat smaller. *Hebeloma aurantioumbrinum* is rarely found in non alpine/arctic habitats, but in any case can be distinguished microscopically because its cheilocystidia very rarely have any sign of apical thickening. It also usually has a much more brightly coloured pileus.

As shown in Fig. 1 and 2, all loci tested are suitable for distinguishing *H. helodes* from species other than *H. aurantioumbrinum*. *Hebeloma helodes* cannot be distinguished molecularly from *H. aurantioumbrinum* based on ITS, V6 or V9, but either of the coding genes *RPB2* or *MCM7* will be suitable for the identification of *H. helodes*.

Hebeloma louiseae Beker, Vesterh. & U. Eberh., *sp. nov.* — MycoBank MB809908; Fig. 5d, 18, 19

Etymology. To mark the support Louise Beker has provided to this entire project not only with her time but also travelling to remote places in search of *Hebeloma* spp.

Type. Svalbard, Ossian near Ny Ålesund (N78.9260500 E12.4542667, alt. c. 3 m) on mossy soil with *Salix polaris*, 17 Aug. 2007, *M.L. Beker*, *H. Beker* holotype BR BR-MYCO 173982-61; isotypes C C-F-90149, HJB12019.

Diagnosis — *Hebeloma louiseae* was found in arctic conditions in Svalbard and is most similar to *H. minus*, from which it differs by the less prominent spore ornamentation - O1 or O2 and at most a few spores O3. It differs from other taxa of *H.* subsect. *Denudata* occurring in arctic conditions by its small number of complete lamellae (< 40) in combination with an average cheilocystidium apex width of ≥ 9 μm.

Basidiomes usually in scattered groups. *Pileus* up to 15 mm diam, convex or plano-convex to broadly umbonate; *surface* dry or slightly viscid, neither hygrophanous nor striate, sometimes with a slight pruinose layer; *cuticle colour* clay buff to Isabella sometimes with a thin paler margin; *pileus margin* straight, sometimes crenulate and slightly involute even in fully grown basidiomes. *Lamellae* emarginate, quite widely spaced (L = 30–38); *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, paler than lamella surface; droplets on the lamellae edge were not seen; *lamellules* sparse. *Stipe* central, cylindrical sometimes slightly clavate or tapering towards the base, (8–)9.5–21.5(–25) × 2–3(–3.5) mm; white or alutaceous,

sometimes discolouring brown near the base when handled; *surface* dry, with fine fibrils and pruina over the length of the stipe. *Cortina* not observed. *Flesh* rather thin, cream or pale brown, discolouring slightly when bruised. *Smell* raphanoid or absent. *Taste* not recorded. *Spore deposit* greyish brown.

Spores amygdaloid to limoniform, with small apiculus and rounded at the end opposite the apiculus, with a distinct thinning of the spore wall and often with a pronounced papilla, guttulate with one or more oily drops, almost smooth to very weakly ornamented, with no sign of loosening perispore and dextrinoidity ranging from completely indextrinoid to weakly dextrinoid (O1,O2; P0; D0,D1); *spore colour* under the microscope yellow brown to brown; *spore size* based on n = 69 spores of the holotype, 5–95 % percentile range 11.6–14.4 × 6.9–8.6 μm, with median 12.7 × 7.7 μm and av 12.8 × 7.7 μm with SD length 0.82 μm and width 0.53 μm, Q value 5–95 % percentile range 1.50–1.80, with median 1.67 and av 1.66 with SD 0.1; *spore size* based on 3 collections medians 12.2–12.7 × 7.5–7.7 μm and av 12.3–12.8 × 7.5–7.7 μm with SD length 0.53–0.82 μm and width 0.36–0.53 μm, Qav 1.63–1.66. *Basidia* cylindrical to clavate and 4-spored, 28–56 × 8.6–11.6 μm, with av 33–48 × 9.5–10.5 μm. *Pleurocystidia* not found. *Cheilocystidia* clavate-stipitate to subcapitate-stipitate, occasionally slightly swollen towards the base and occasionally septate, some apical thickening, sinuate or bifurcate; *width of apex* holotype 5–95 % percentile range 7.9–12.3 μm, with median 9.7 μm and av 9.9 μm with SD 1.48 μm; across 3 collections median 9.0–9.8 μm and av 9.0–9.9 μm; with n ≥ 20 selected cheilocystidia of 3 collections the 5–95 % percentile ranges are 37–76 × 7.1–12.7 × 3.5–6.5 × 4.0–6.8 μm while the averages are 49–59 × 9.0–9.9 × 4.4–5.4 × 4.8–5.6 and 57 × 9.9 × 5.4 × 4.9 μm av for the holotype. The av cheilocystidia ratios for the 3 collections were: A/M = 2.01–2.42; A/B = 1.99–2.25; B/M = 0.92–1.24. *Caulocystidia* resemble cheilocystidia, up to 75 μm long and 12 μm wide at the apex. *Pileipellis* is an ixocutis with a medium thick epicutis up to a maximum of 100 μm and embedded hyphae up to 6 μm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* orange brown and made up of cylindrical to isodiametric elements. *Trama below subcutis* contains larger thick sausage shaped elements up to 15 μm broad. *Clamp connections* present throughout the basidiome.
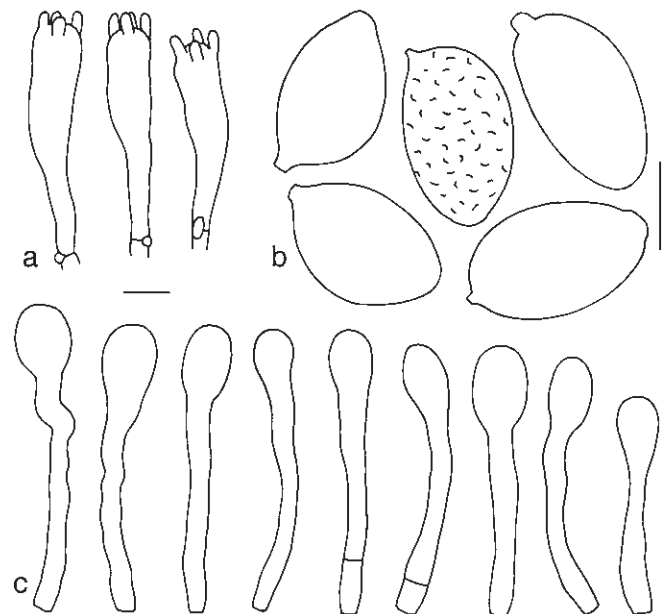
Fig. 18   *Hebeloma louiseae* (BR-MYCO 173982-61, holotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 μm.
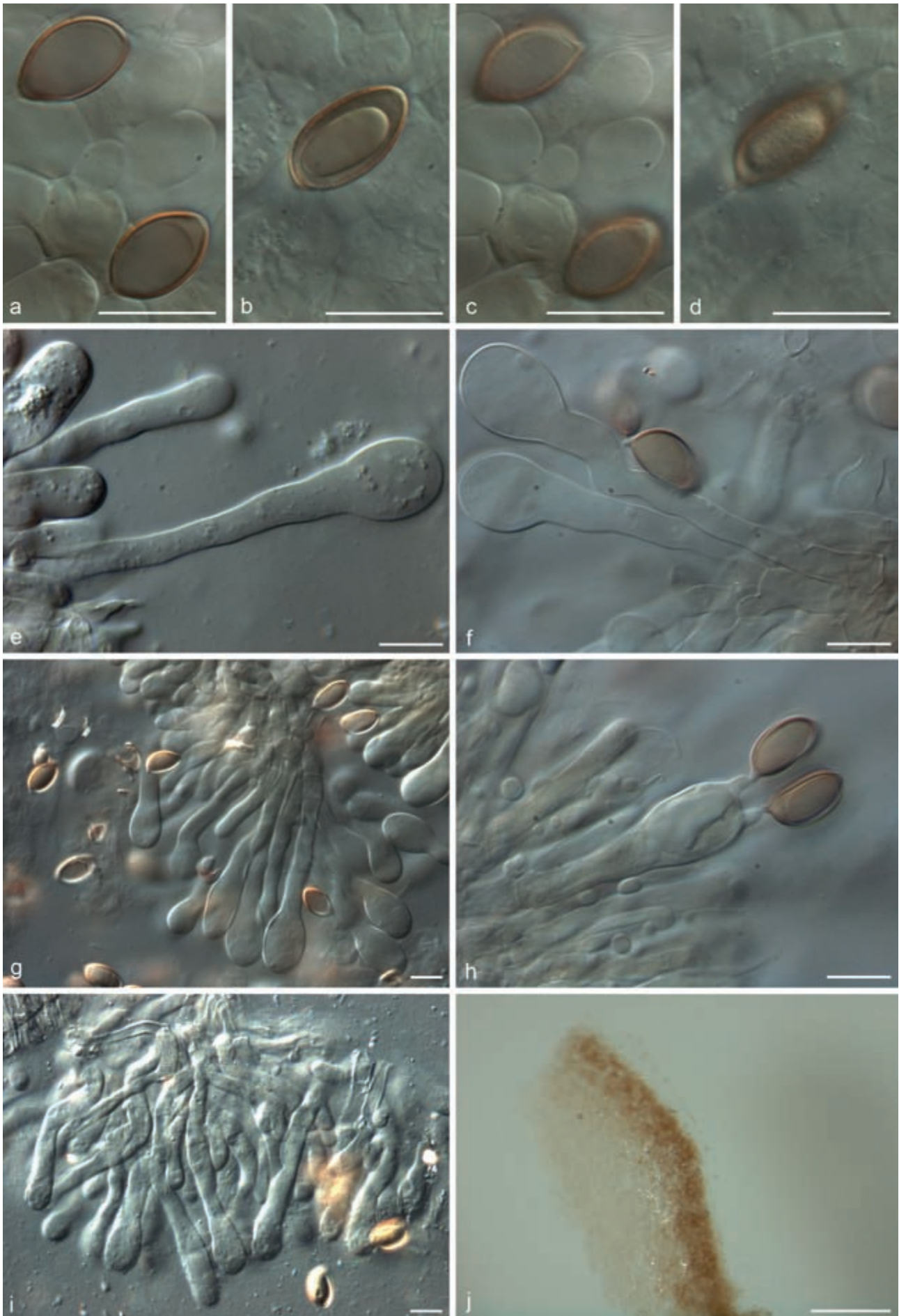
Fig. 19 *Hebeloma louiseae* (BR-MYCO 173982-61, holotype). a, b. Spores ×1 600 in Melzer's reagent or 5 % KOH, respectively; c, d. spore ornamentation ×1 600 in Melzer's reagent or 5 % KOH, respectively; e, f. cheilocystidia ×1 000 in 5 % KOH; g. cheilocystidia ×500 in 5 % KOH; h. basidium ×1 000 in 5 % KOH; i. caulocystidia ×500 in 5 % KOH; j. cutis ×80 in 5 % KOH. — Scale bars: 10 μm, in j. 100 μm.

Habitat & Distribution — All 3 collections of *H. louiseae* have been collected in Svalbard in association with *Salix polaris*. Two of the collections have been on coastal shingle, not far from the water's edge but the third collection was from a grazed scrub area 4–5 km from the sea.

Additional specimens examined. Svalbard, Endalen near Longyearbyen (N78.1940667 E15.7892500, alt. c. 28 m) on soil in grazed valley with *Salix polaris*, 13 Aug. 2007, *J. Sandmo* HJB11984; Ossian near Ny Ålesund (N78.9259500 E12.4541167, alt. c. 0 m) on grazed scrub with *Salix polaris*, 17 Aug. 2007, *M.L. Beker, H. Beker* HJB12023.

Notes — *Hebeloma louiseae* has most likely not been included in the intercompatibility tests of (Aanen & Kuyper 1999) and is currently only known from Svalbard, but it has been collected in two sites some 110 km apart. It is likely that it is *Salix*-specific. The cheilocystidia place this species within *H.* subsect. *Denudata*. Given its arctic habitat, small size and very wide weakly ornamented spores this species is easily distinguished from other members of *H.* subsect. *Denudata*. While it is possible that this species only exists on Svalbard it is likely that it could be found in other arctic habitats, but its size and camouflaged appearance may mean that it is often overlooked. Also it may in the past have been confused with other small arctic/alpine *Hebeloma* spp.

Hebeloma louiseae is not only monophyletic, but also receives (high) bootstrap support in four out of five tested loci. Only V9 cannot distinguish it from *H. minus*. Although the name *H. crustuliniforme* has traditionally been applied to collections of medium and large sporocarps (Vesterholt et al. 2014), typically growing outside the arctic and alpine habitats, in evolutionary terms, the *H. crustuliniforme* complex also includes small, arctic/alpine taxa. The analyses of V6, V9 and *RPB2* suggest that *H. louiseae* belongs to the *H. crustuliniforme* complex. This is contradicted by its placement in the ITS phylogram.

Hebeloma luteicystidiatum Beker, Vesterh. & U. Eberh., *sp. nov.* — MycoBank MB809909; Fig. 5e, 20, 21

Etymology. From *luteus* - yellow and *cystidiatus* – having cystidia, to emphasise the thick apical wall that sometimes looks yellow under the microscope.

Type. Belgium, prov. Limburg, Houthalen (N51.0154833 E5.3518667, alt. c. 45 m) in wet boggy ground next to slagheap with *Salix* sp., 22 Oct. 2006, *J. Volders* holotype BR BR-MYCO 166233-72 (VJ06095); isotypes C C-F-90150, HJB11837.

Diagnosis — Based on its cheilocystidium shape, *H. luteicystidiatum* is a member of *H.* subsect. *Denudata*. The most distinctive and constant character of the species are the thick walls of the cheilocystidium apices. With its small stature and 2-coloured pileus, *H. luteicystidiatum* is similar to *H. pusillum*. From the latter it can be separated based on the pileus colour, which may be dark, but not dark brick, and the cystidia of *H. pusillum* do not have cheilocystidia with wall thickening at the apex. Macroscopically, *H. helodes* is similar in terms of coloration, but is larger, has more crowded lamellae and shorter spores.

Basidiomes solitary or in scattered groups. *Pileus* 6–15 mm diam, convex, slightly tacky when moist but never hygrophanous, at high magnification the pileus has a slightly felty look; *cuticle colour* in the central region ochre to honey or rusty-coloured to dark brown but becoming paler towards the margin which may be anywhere from buff to cream to white; *pileus margin* usually straight, occasionally involute or eroded with age. *Lamellae* emarginate, almost free, distant (L = 21–26) with a maximum depth of 2.5 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, significantly paler than lamella surface; droplets normally visible on the lamella edge usually by the naked eye but

certainly with a ×10 lens; *lamellules* occasional. *Stipe* central, cylindrical usually stuffed, rarely hollow, 12–30 × 1.0–2.5 mm usually with strong brown discolouration towards the base of the stipe; *surface* dry, pruinose to floccose. *Cortina* not observed. *Flesh* rather thin, whitish but slightly more coloured in the base of the stipe. The whole basidiome has a very slender and fragile appearance with the stipe Q (ratio of stipe length to stipe width) in excess of 12. *Smell* raphanoid, sometimes absent. *Taste* not recorded. *Spore deposit* colour not recorded. *Exsiccata* fragile and brittle often dark, sometimes blackening.

Spores amygdaloid, with small apiculus and rounded at the end opposite the apiculus, with some thinning of the spore wall, sometimes with a papilla, sometimes guttulate with one or more oily drops, from almost smooth to normally weakly ornamented, sometimes with slightly loosening perispore in a few spores and weakly but sometimes distinctly dextrinoid (O1,O2; P0,P1(P2); D1,D2); *spore colour* under the microscope yellow brown to brown; *spore size* based on n = 53 spores of the holotype, 5–95 % percentile range 10.3–13.0 × 5.8–6.9 µm, with median 11.6 × 6.4 µm and av 11.6 × 6.4 µm with SD length 0.80 µm and width 0.32 µm, Q value 5–95 % percentile range 1.63–2.01, with median 1.85 and av 1.84 with SD 0.12; *spore size* based on 4 collections medians 11.6–11.9 × 6.1–6.4 µm and av 11.6–11.9 × 6.1–6.5 µm with SD length 0.59–0.80 µm and width 0.31–0.36 µm, Qav 1.80–1.95. *Basidia* cylindrical to clavate and 4-spored, 25–39 × 6.4–10.1 µm, with av 28–34 × 7.1–9.4 µm and basidium Q av in the range 3.3–4.7. *Pleurocystidia* not found. *Cheilocystidia*, clavate-stipitate or spathulate-stipitate, occasionally subcapitate-stipitate or slightly swollen towards the base (subcapitate-lageniform or clavate-lageniform), always with distinctive thickening of the apex, so much so that the apex sometimes appears yellow under the microscope, occasionally septate and rarely with median thickening; *width of apex* holotype 5–95 % percentile range 7.2–11.8 µm, with median 9.1 µm and av 9.3 µm with SD 1.45 µm; across 4 collections median 8.6–9.7 µm and av 8.8–9.9 µm; with n at least 20 selected cheilocystidia of 4 collections the 5–95 % percentile ranges are 37–77 × 6.7–12.6 × 3.0–5.7 × 2.7–6.1 µm while the averages are 50–62 × 8.8–9.9 × 4.0–4.3 × 4.0–4.9 and 50 × 9.3 × 4.0 × 4.9 µm av for the holotype. The av cheilocystidia ratios for the 4 collections were: A/M = 2.27–2.77; A/B = 2.21–2.68; B/M = 0.98–1.22. *Caulocystidia* resemble cheilocystidia, up to 90 × 10 µm wide at the apex. *Pileipellis* is an ixocutis with a thin epicutis 50–60 µm, embedded hyphae up to 5 µm broad, smooth or sometimes encrusted, hyaline
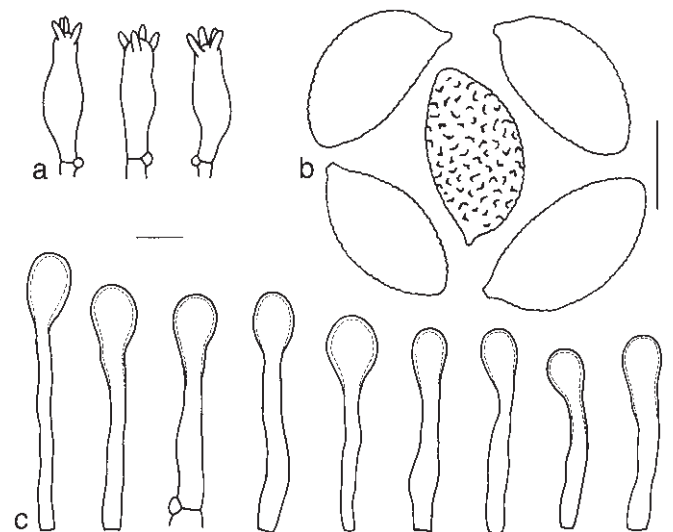
Fig. 20 *Hebeloma luteicystidiatum* (BR-MYCO 166233-72, holotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 µm.
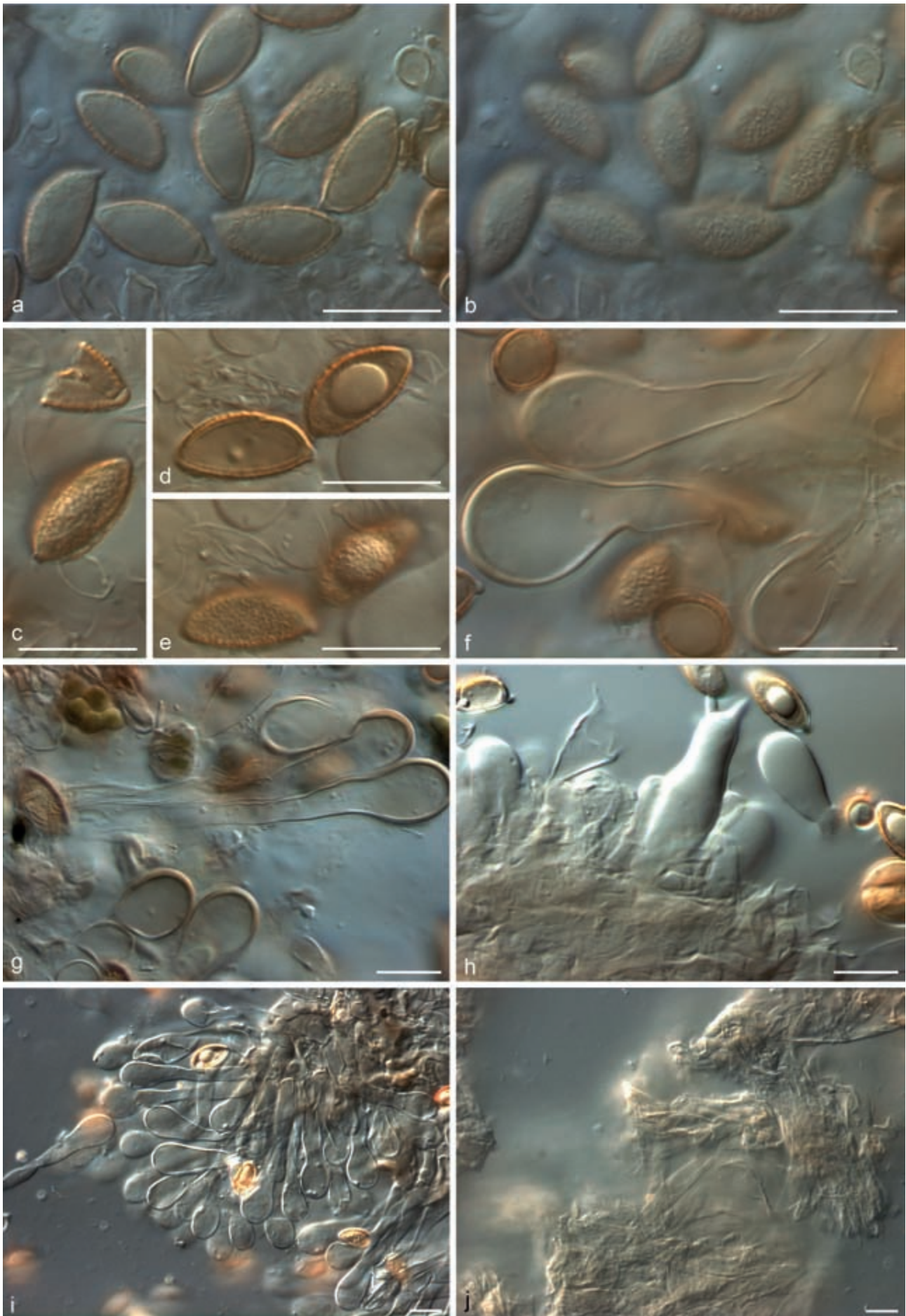
Fig. 21 *Hebeloma luteicystidiatum* (BR-MYCO 166233-72, holotype). a, b. Spores and spore ornamentation ×1 600 in Melzer's reagent; c. spore with loosening perispore ×1 600 in 5 % KOH; d, e. spores and spore ornamentation ×1 600 in 5 % KOH; f. cheilocystidia ×1 600 in Melzer's reagent; g. cheilocystidia ×1 000 in Melzer's reagent; h. basidium ×1 000 in 5 % KOH; i. cheilocystidia at gill edge ×500 in 5 % KOH; j. trama below cutis ×500 in 5 % KOH. — Scale bars: 10 μm.

or occasionally pigmented. *Cutis* orange brown and made up of cylindrical to isodiametric elements. *Trama below subcutis* contains ellipsoid, cylindrical and angular elements up to 20 μm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — All records of *H. luteicystidiatum* are in association with *Salix* with which it clearly has a mycorrhizal relationship. Furthermore, all collections are from wet boggy areas, usually in *Salix* thickets in woodland.

Additional specimens examined. BELGIUM, prov. Limburg, Houthalen (N51.0154833 E5.3518667, alt. c. 45 m) in wet boggy ground next to slagheap with *Salix* sp., 31 Oct. 2007, *H. Beker* HJB121740. – FRANCE, Yvelines, St-Remy-les-Chevreuse, Bois de Champfailly (N48.72208 E2.0650130, alt. c. 100 m) on boggy wet ground under *Alnus* sp. and *Salix* sp., 12 Sept. 1999, *G. Corriol* GC99081202, duplicate HJB12936. – NETHERLANDS, Amsterdam (c. N52.22 E4.53, alt. c. 30 m) collected with *Salix* sp., 9 Sept. 1995, *D. Aanen* WBS 9501, database record HJB12462.

Notes — Given the shape of its cheilocystidia, *H. luteicystidiatum* clearly belongs to *H.* subsect. *Denudata*. The species most likely corresponds to ICG6 of Aanen & Kuyper (1999). It certainly appears to be restricted to *Salix* and occurs on wet soil, usually in *Salix* thickets. The basidiomes are very small and we suspect it has either tended to be overlooked or confused with *H. pusillum* on account of its small slender appearance and 2-coloured cap. However, it can easily be separated from *H. pusillum*, macroscopically because of the centre which while quite dark is not the distinctive dark brick colour of *H. pusillum* and microscopically because *H. pusillum* never has a consistently thickening apex to its cheilocystidia. *Hebeloma helodes* has pileus colours more like *H. luteicystidiatum* but is a larger mushroom and while its cheilocystidia also have a thickening apex, its spores are significantly shorter and *H. helodes* also has rather more crowded lamellae.

Hebeloma luteicystidiatum is molecularly distinct and its clade receives high bootstrap support in all loci apart from *RPB2* for which only a single sequence could be obtained. The species is not part of the *H. crustuliniforme* complex.

Hebeloma lutense Romagn., Bull. Trimestriel Soc. Mycol. France 81: 342. 1965. — MycoBank MB331750; Fig. 22, 23

Type. FRANCE, Yvelines, Forêt de Rambouillet (S.-et.O.), étang de la Tour (c. N48.65 E1.88, alt. c. 175 m) at the edge of a lake amongst *Phragmites*, *Carex*, *Hydrocotyle* under mixed *Salix* sp. and *Betula* sp., 11 Oct. 1959, H. Romagnesi (holotype PC 59.232, database record HJB1000253; isotype L 0054088, database record HJB1000011).

Basidiomes usually in scattered groups or sometimes caespitose. *Pileus* 15–58 mm diam, convex, sometimes umbonate, slightly viscid, tacky when moist but never hygrophanous; *cuticle colour* often almost zonate with the centre from yellow brown to cinnamon to chestnut or even dark brick, sometimes then with a paler but still strongly coloured zone and finally pinkish buff to cream to almost white near the margin; *pileus margin* usually straight, sometimes involute and occasionally slightly scalloped. *Lamellae* emarginate, moderately spaced (L = 32–58) with a maximum depth of 5–10 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, paler than lamella surface; droplets normally visible on the lamella edge even with the naked eye; *lamellules* frequent. *Stipe* central, sometimes cylindrical but more often clavate and occasionally even subbulbous, (15–)22.5–90 × 3–11 mm and up to 18 mm at the base, stuffed when young but later hollow and sometimes with a superior wick; white or alutaceous, often with some brown discolouration in older basidiomes; *surface* dry, pruinose to floccose particularly towards the apex. *Cortina* not observed. *Flesh* rather thick, whitish but slightly more coloured in the base of the stipe. *Smell* raphanoid, sometimes with hint of cocoa,

rarely absent. *Taste* raphanoid to bitter. *Spore deposit* brownish olive to umber.

Spores amygdaloid, with small apiculus and rounded at the end opposite the apiculus, with a distinct thinning of the spore wall, occasionally with a weak papilla, guttulate with one or more oily drops, from almost smooth to weakly ornamented but more usually distinctly ornamented, usually with some sign of loosening perispore in a few spores and often in many spores and weakly but distinctly dextrinoid ((O1)O2,O3; (P0)P1,P2; D1,D2); *spore colour* under the microscope yellow brown to brown; *spore size* based on n = 57 spores of the holotype, 5–95 % percentile range 9.2–11.7 × 5.5–6.6 μm, with median 10.6 × 6.0 μm and av 10.6 × 6.1 μm with SD length 0.73 μm and width 0.34 μm, Q value 5–95 % percentile range 1.62–1.88, with median 1.74 and av 1.74 with SD 0.9; *spore size* based on 22 collections medians 9.4–11.7 × 5.2–6.3 μm and av 9.4–11.7 × 5.4–6.4 μm with SD length 0.46–1.08 μm and width 0.24–0.57 μm, Qav 1.63–1.91. *Basidia* cylindrical to clavate and 4-spored, 27–40 × 5.3–8.9 μm, with av 29–38 × 6.5–8.0 μm and basidium Qav unusually high in the range 4.0–5.7. *Pleurocystidia* not found. *Cheilocystidia* clavate or clavate-stipitate, occasionally slightly swollen towards the base (clavate-lageniform) and occasionally with septa, sometimes clamped, or median thickening and almost always with a large number of sinuate cheilocystidia; *width of apex* holotype 5–95 % percentile range 5.8–9.6 μm, with median 7.7 μm and av 7.7 μm with SD 1.22 μm; across 22 collections median 6.6–7.8 μm and av 6.7–7.9 μm; with n ≥ 20 selected cheilocystidia of 22 collections the 5–95 % percentile ranges are 28–71 × 5.2–10.4 × 2.7–5.7 × 2.4–7.4 μm while the averages are 42–56 × 6.7–7.9 × 3.4–4.5 × 3.5–4.8 and 47 × 7.7 × 4.2 × 4.3 μm av for the holotype. The av cheilocystidia ratios for the 22 collections were: A/M = 1.63–2.39; A/B = 1.58–2.34; B/M = 0.95–1.22. *Caulocystidia* resemble cheilocystidia, up to 95 μm long and 9 μm wide at the apex. *Pileipellis* is an ixocutis with a relatively thick epicutis 100–180 μm, embedded hyphae up to 5 μm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* orange brown and made up of cylindrical to isodiametric elements. *Trama below subcutis* contains ellipsoid or thick sausage shaped elements up to 15 μm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — All our records of *H. lutense* have been collected in the presence of *Salix* spp. and it would appear likely that this species is confined to *Salix*. Many of the collections have been from wet or damp environments on acid soil. It is interesting to note that while our description is based on 22 collections of *H. lutense*, on our database we have 53 records. All of these are from Western Europe (highest longitude is < E11°).

Additional specimens examined. BELGIUM, prov. Hainaut, Maubray (N50.5306167 E3.4941000, alt. c. 30 m) slagheap, on mossy soil, scattered with *Salix* sp. and *Betula* sp., 10 Nov. 2006, *P.-A. Moreau* HJB11719; prov. Limbourg, Tiewinkel (c. N50.967 E5.233, alt. c. 25 m) scattered on wet acid soil with *Salix cinerea*, 12 Sept. 2004, *A. de Haan* AdH04059, duplicate HJB10523; prov. Hainaut, Maubray (N50.5306167 E3.4941000, alt. c. 29 m) on rotten litter in broadleaf woodland on slagheap under *Betula* sp., *Salix* sp., 10. Nov. 2006, *P.-A. Moreau* HJB11726. – DENMARK, WJ, Marbaek plantation north of Esbjerg UTM MG5757 TBU 27 (c. N55.550 E8.310, alt. c. 0 m) on wet soil under *Salix* sp., 17 Sept. 1995, *J. Vesterholt* JV95-357, duplicate HJB10876; Naun Sø (c. N56.8 E9.5, alt. c. 40 m) scattered at lakeside with *Salix* sp., 24 Oct. 1996, *T. Læssøe* TL4413, duplicate HJB10905. – ENGLAND, Surrey, Bookham Common (c. N51.27 W0.37, alt. c. 100 m) in mixed woodland under *Betula* sp. and *Salix* sp., 15 Oct. 1955, *P.D. Orton* E 00076300, database record HJB12917: this forms part of a collection labelled as *H. leucosarx* which was mixed and the part that does not represent *H. leucosarx* as recently selected by Grilli (2007); Surrey, Boldermere (N51.3144100 W0.4517496, alt. c. 30 m) on wet soil in mixed woodland under *Salix* sp., 28 Sept. 2002, *H. Beker* HJB8098. – FRANCE, Landes, Mios (N44.5993667 W0.9407333, alt. c. 0 m) in damp litter in
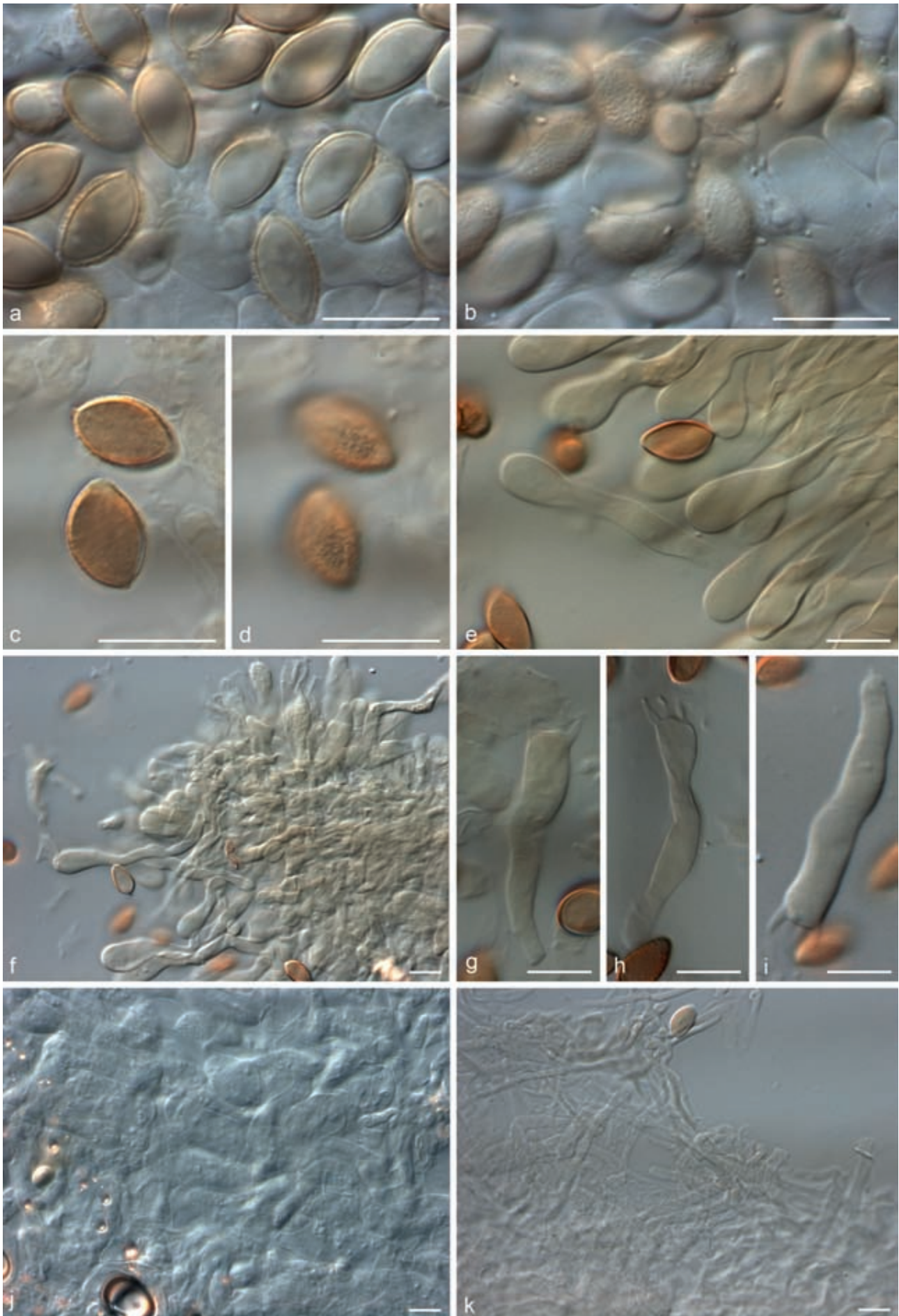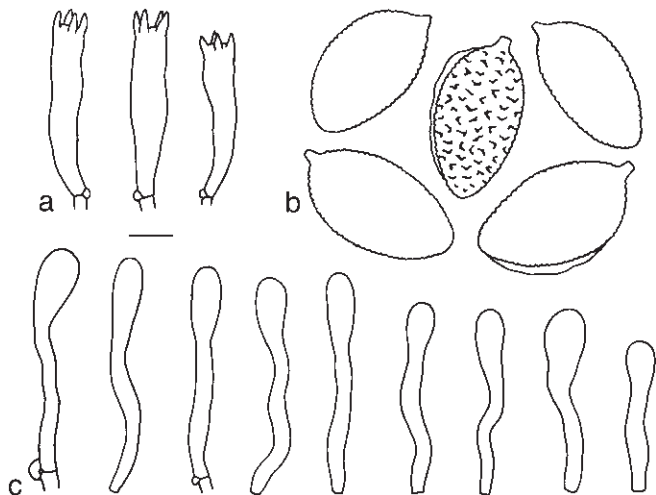
Fig. 22 *Hebeloma lutense* (P 59.232, holotype). a, b. Spores and spore ornamentation ×1 600 in 5 % KOH; c, d. spores and spore ornamentation ×1 600 in Melzer's reagent; e. cheilocystidia ×1 000 in Melzer's reagent; f. cheilocystidia ×500 in Melzer's reagent; g–i. basidia ×1 000 in Melzer's reagent; i. subcutis ×500 in 5 % KOH; j. epicutis hyphae ×500 in 5 % KOH. — Scale bars: 10 μm.

a broadleaf woodland with *Salix* sp., 17 Oct. 2005, *H. Beker* HJB11328; Alpes-Maritimes, Les Espagnols (N43.5090667 E6.7947833, alt. c. 186 m) on lakeside amongst wet litter in mixed woodland, under *Populus* sp. and *Salix* sp., 16 Oct. 2007, *H. Beker* HJB12122; Nord Pas de Calais, Saint Amand (N50.3976000 E3.4439833, alt. c. 20 m) on wet soil in broadleaf woodland scrub under *Salix* sp., 10 Nov. 2006, *P.-A. Moreau* HJB11755; Alpes-Maritimes, Les Espagnols (N43.5090333 E6.7947667, alt. c. 185 m) on litter in mixed woodland under *Populus* sp., *Salix* sp., 16 Oct. 2007, *P. Cavanagh* HJB12126. – Netherlands, Drenthe, Beilen, Wijster, IJsbaantje (c. N52.82 E6.52, alt. c. 10 m) collected in wet *Sphagnum* with *Salix aurita*, *Salix cinerea* and *Salix repens*, 1 Oct. 1996, *D. Aanen* WBS 9662, database record HJB12522; Drenthe, Eemsterveld, langs de Drentse Aa (c. N53.15 E6.60, alt. c. 2 m) under *Salix* sp., 10 Oct. 1995, *D. Aanen* WBS 9571, database record HJB12808; Drenthe, Beilen, Wijster ijsbaantje (c. N52.82 E6.52, alt. c. 10 m) collected in acid wet soil with *Sphagnum* and *Salix repens*, 1 Oct. 1996, *D. Aanen* WBS 9663, database record HJB12523. – Scotland, Orkney (c. N59.64959 W3.0094460, alt. c. 0 m) in dune in sandy soil with *Salix repens*, 21 Aug. 2002, *A. Andrews* HJB9819; Loch Loy (c. N57.58 W3.85, alt. c. 10 m) in wet mixed woodland under *Betula* sp. and *Salix* sp., 25 Sept. 1955, *P.D. Orton* K K(M)52712, database record HJB1000001: this forms part of the holotype collection of *H. leucosarx* which was mixed and the part not selected as typus for *H. leucosarx* by Grilli (2007); Easterness, Bogach (N57.1659300 W3.8482160, alt. c. 235 m) in bog on pathside with *Salix* sp., 22 Aug. 2005, *S. Huhtinen* SH05/44, duplicate HJB11168. – Spain, Castilla y Leon, Rio Cerneja (N43.1177667 W3.4608833, alt. c. 835 m) in acid litter with *Alnus glutinosa*, *Quercus pyrenaica* and *Salix atrocinerea*, 21 Oct. 2005, *I. Olariaga Ibarguren* HJB11344, duplicate JV05-602; Castilla y Leon, Rio Cerneja (N43.1226167 W3.4653500, alt. c. 825 m) caespitose in acid grassy soil with *Alnus glutinosa*, *Quercus pyrenaica* and *Salix atrocinerea*, 21 Oct. 2005, *I. Olariaga Ibarguren* HJB11365, duplicate JV05-634: note this collection was almost sterile; Castilla y Leon, Rio Cerneja (N43.1226167 W3.4653500, alt. c. 827 m) on grassy soil in mixed woodland under *Pinus sylvestris*, *Salix atrocinerea*, 21. Oct. 2005, *I. Olariaga Ibarguren* JV05-621, HJB11356; Castilla y Leon, Rio Cerneja (N43.1226167 W3.4653500, alt. c. 827 m) in mixed woodland under *Alnus glutinosa*, *Quercus pyrenaica*, 21 Oct. 2005, *H. Beker* HJB11363, duplicate JV05-631.

Notes — Given the shape of its cheilocystidia, *H. lutense* clearly belongs to *H.* subsect. *Denudata*. The species most likely corresponds to ICG9 of Aanen & Kuyper (1999). Its sinuate cheilocystidia and its consistently long thin basidia distinguish it from the other members of this subsection. Sinuate cheilocystidia do occur in other species, for example *H. eburneum*, but in our experience there is no other species where sinuate cheilocystidia occur so frequently and is such a consistent character. Similarly other species in this subsection can have quite long narrow basidia but again this taxon has them consistently. The basidium Q for this taxon ranges from 4.0–5.7. The combination of these sinuate cheilocystidia and the high average Q of the basidia unambiguously define this taxon. Additionally, the number of complete lamellae < 60 and the average cheilocystidium apex width of < 8 µm, means it is highly unlikely to miss-determine this taxon.

Fig. 23   *Hebeloma lutense* (P 59.232, holotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 µm.

The records on our database for *H. lutense* are confined to *Salicaceae* and to Western Europe, i.e. the most easterly collection is from Denmark. We suspect that an exclusive mycorrhizal association with *Salix* is correct. With regard to the geographical distribution we must await more confirmed records. While we do not have sufficient data to suggest that this species is restricted to Western Europe, it certainly appears more common in this area.

Hebeloma lutense is monophyletic and receives high bootstrap support in all tested loci apart from the ITS. The placement of the incomplete sequence of the isotype of *H. lutense* outside the *H. lutense* clade of the ITS result can be explained by missing data. The placement of a single *H. alpinum* collection (HJB11997; its ITS sequence has been confirmed by repetition and its V6 sequence is clearly not *H. lutense*) in the clade that otherwise only contains sequences from *H. lutense* collections only shows how similar the ITS is in this subsection. However, normally an ITS2 sequence of *H. lutense* should be sufficient to identify this species, too.

Hebeloma minus Bruchet, Bull. Mens. Soc. Linn. Lyon 39, 6 (Suppl.): 126. 1970. — MycoBank MB314960; Fig. 24, 25

Type. France, Savoie, Lac des Assiettes, Col de la Vanoise (c. N45.389 E6.792, alt. c. 2500 m) on alpine scrub, in calcareous dry lake bed with *Salix herbacea*, 11 Sept. 1969, *G. Bruchet*, LY BR69-15, database record HJB1000065.

Basidiomes usually in scattered groups. *Pileus* 9–31 mm diam, convex to umbonate, slightly tacky when moist and sometimes hygrophanous; *cuticle colour* from dark pinkish buff or Isabella to brownish olive, greyish brown or umber sometimes unicoloured but sometimes paler towards the margin which may be pinkish buff, occasionally pruinose (givré) especially after frosting; *pileus margin* usually straight, sometimes involute particularly in young basidiomes. *Lamellae* emarginate to adnate, relatively distant (L = 30–34) with a maximum depth of 4–5 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, significantly paler than lamella surface; droplets normally visible on the lamella edge usually by naked eye but certainly with a ×10 lens, rarely absent; *lamellules* occasional. *Stipe* central, cylindrical or slightly clavate, rarely bulbous, becoming hollow with age, 10–40 × 1–8 mm and up to 10 mm at the base rarely with some weak discolouration towards the base of the stipe; *surface* dry, pruinose to floccose, especially towards the apex. *Cortina* not observed. *Flesh* medium thick, pale buff. *Smell* raphanoid, sometimes weak. *Taste* mild, occasionally weakly bitter or weakly raphanoid. *Spore deposit* brownish olive. *Exsiccata* fragile and brittle.

Spores amygdaloid or limoniform, with small apiculus and rounded at the end opposite the apiculus, with some thinning of the spore wall, and usually with a papilla, sometimes guttulate with one or more oily drops, from weakly to distinctly ornamented, sometimes with slightly loosening perispore in a few to many spores and weakly but sometimes distinctly dextrinoid (O2,O3; P0,P1,P2; D1(D2)); *spore colour* under the microscope yellow to pale brown; *spore size* based on n = 64 spores of the holotype, 5–95 % percentile range 11.0–13.9 × 6.1–7.3 µm, with median 12.4 × 6.7 µm and av 12.4 × 6.7 µm with SD length 0.96 µm and width 0.40 µm, Q value 5–95 % percentile range 1.68–2.07, with median 1.84 and av 1.86 with SD 0.12; *spore size* based on 10 collections medians 11.2–13.1 × 6.3–7.6 µm and av 11.2–13.1 × 6.2–7.7 µm with SD length 0.62–1.12 µm and width 0.32–0.54 µm, Qav 1.61–1.87. *Basidia* cylindrical to clavate and 4-spored, 27–39 × 8.2–11.5 µm, with av 27–35 × 8.9–10.9 µm and basidium Qav in the range 2.8–3.8. *Pleurocystidia* not found. *Cheilocystidia* capitate-stipitate, clavate-stipitate or
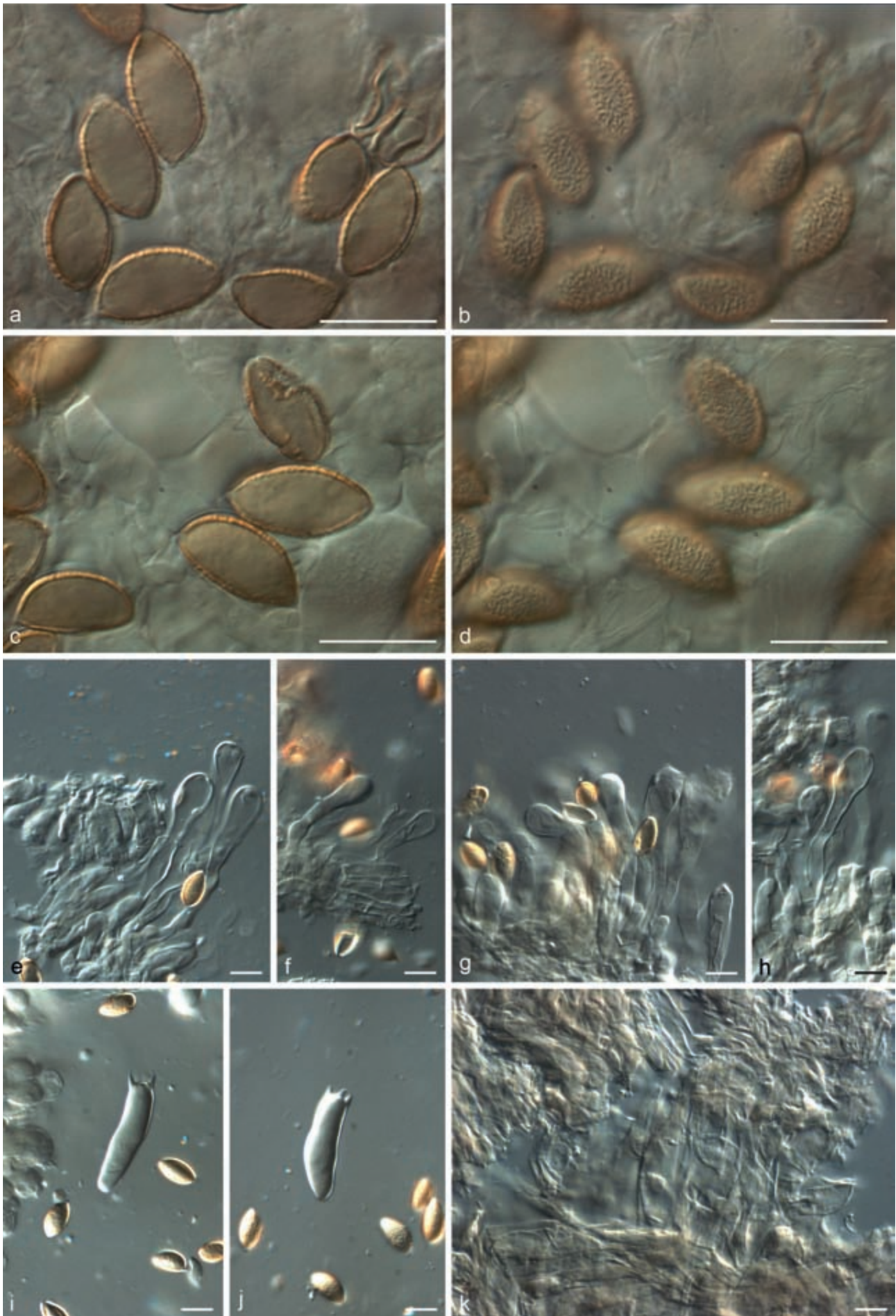
Fig. 24 *Hebeloma minus* (LY BR69-15, holotype). a, b. Spores and spore ornamentation ×1 600 in Melzer's reagent; c, d. spores and spore ornamentation ×1 600 in 5 % KOH; e–h. cheilocystidia ×500 in 5 % KOH; i, j. basidia ×500 in 5 % KOH; k. trama below cutis ×500 in 5 % KOH. — Scale bars: 10 µm.
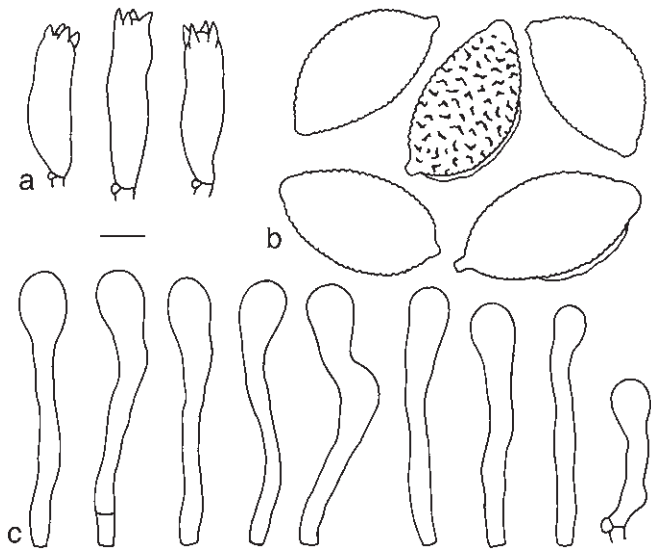
Fig. 25 *Hebeloma minus* (LY BR69-15, holotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 µm.

spathulate-stipitate, occasionally swollen towards the base (capitate-lageniform or clavate-lageniform), sometimes with thickening of the apex, and often appearing bent in the centre (kneeling), occasionally septate; *width of apex* holotype 5−95 % percentile range 6.7–10.6 µm, with median 9.0 µm and av 8.8 µm with SD 1.40 µm; across 10 collections median 8.9–10.5 µm and av 8.8–10.4 µm; with n ≥ 20 selected cheilocystidia of 10 collections the 5−95 % percentile ranges are 35−67 × 6.3–12.7 × 2.9−6.2 × 2.7–8.6 µm while the averages are 40−55 × 8.8–10.4 × (3.7−)4.2−5.4 × (3−)4.3−5.9 and 55 × 8.8 × 4.2 × 4.6 µm av for the holotype. The av cheilocystidia ratios for the 5 collections were: A/M = 1.99−2.44; A/B = 1.82−3.02; B/M = 0.84−1.24. *Caulocystidia* resemble cheilocystidia often gregarious, up to 70 × 12 µm wide at the apex. *Pileipellis* is an ixocutis with an epicutis from thin to medium thick, 40−100 µm, embedded hyphae up to 6.5 µm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* orange brown and made up of cylindrical to isodiametric elements. *Trama below subcutis* contains ellipsoid, cylindrical, spherical and sausage-shaped elements up to 30 µm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — We have records of *H. minus* both in arctic and alpine locations. In these locations it has been recorded with a variety of *Salix* shrubs and also with *Dryas*, specifically *Salix herbacea*, *S. polaris*, *S. reticulata*, *S. retusa* and *Dryas octopetala*. We also have one record of this species in a subalpine habitat with *Salix caprea*. The descriptions include acid, calcareous soil conditions and mossy, wet and exposed ground. As well as the ten European collections of *H. minus*, on which our description is based, we have also studied one collection from Canada.

Additional specimens examined. France, Jura, Lac des Rouges Truites (c. N46.36252 E5.59531, alt. c. 940 m) under *Salix caprea*, 22 Sept. 1996, *D. Aanen* WBS 9630, database record HJB12512. – Iceland, Nordur-Mulasysla, Hamborg, road to Jokladalur (c. N65.050 W14.917, alt. c. 400 m) in mountain heathland under *Salix herbacea*, 6 Aug. 1993, *J. Vesterholt* JV93-503, duplicate HJB10865; Nordur-Mulasysla, Hamborg, road to Jokladalur (c. N65.05 W14.917, alt. c. 400 m) in mountain heathland under *Salix herbacea*, 6 Aug. 1993, *J. Vesterholt* JV93-506, duplicate HJB10866; Valavatn (N64.8665500 W23.5597167, alt. c. 301 m) on rotten litter in scrub under *Salix herbacea*, 29 July 2005, *H. Beker, M.L. Beker* HJB11079. – Svalbard, Vestspitsbergen, Van Mijenfjorden, Sveagruva, Kylan W-puolella, Tuore sammaleinen tunturiniitty (N77.8848340 E16.9745880, alt. c. 300 m) on mossy, wet soil under *Salix* sp., 20 July 1969, *S. Eurola, A. Hakala* OULU EO20.7.69; F067388, database record HJB13577; Colesdalen (N78.1153333 E15.0278667, alt. c. 30 m) on soil in grazed grass-

land under *Salix polaris*, 10 Aug. 2007, *H. Beker, M.L. Beker* HJB11945; Ekmanfjorden (N78.6240500 E14.8289167, alt. c. 8 m) on exposed soil in maritime coastal scrub under *Salix polaris*, 15 Aug. 2007, *H. Beker, M.L. Beker* HJB12007. – Switzerland, Tessin, Val Bedretto, Col de Gries, TI (c. N46.4667 E8.3740, alt. c. 2190 m) Schneetälchen, Fleckenmergel, under *Dryas octopetala*, *Salix herbacea*, *Salix reticulata*, *Salix retusa*, 28 Aug. 1988, *E. Horak* ZT 4113, duplicate HJB12568; Oberaar (N46.5485667 E8.2768333, alt. c. 2312 m) on soil in wasteland under *Salix* sp., 10 Aug. 2005, *H. Beker, M.L. Beker* HJB11107.

Notes — Given the shape of its cheilocystidia, *H. minus* clearly belongs to *H.* subsect. *Denudata*. The species most likely corresponds to ICG7 of Aanen & Kuyper (1999). It certainly appears to be restricted to *Salix* (and possibly *Dryas*) and while it appears to be predominantly an arctic/alpine species it can occur in subalpine habitats and presumably subarctic habitats. While at present we only have 11 recorded collections of *H. minus* we would suspect that it is widely distributed throughout the arctic and alpine regions, appearing occasionally in the boreal zone. When we look at the distribution of our collections they are clustered in Iceland, Svalbard and the French/Swiss Alps, plus we have one collection from Canada (not included in our description). *Hebeloma minus* appears morphologically close to *H. alpinum* and *H. pallidolabiatum*. It can be difficult to separate from *H. alpinum* microscopically but can be separated on macroscopic characters, since *H. minus* is smaller with a darker coloured pileus and with fewer lamellae than *H. alpinum*. *Hebeloma minus* is macroscopically very similar to *H. pallidolabiatum* but can be separated microscopically using the cheilocystidium ratio A/B which is always > 1.8 for *H. minus* but < 1.8 for *H. pallidolabiatum*. With regard to the other alpine/arctic species, it can be distinguished from *H. aurantioumbrinum* through the average width of the cheilocystidia apex which ≤ 8.5 µm for *H. aurantioumbrinum* while the average cheilocystidium apex for *H. minus* is always > 8.5 µm. It can be separated from *H. louiseae* which has spores O1 or O2 and very rarely O3, while *H. minus* has many spores O3. In subalpine areas it is most similar to *H. salicicola* and *H. pusillum*. But *H. pusillum* has av spore Q > 1.9 while *H. minus* av spore Q ≤ 1.9 and *H. salicicola* has spores D2 or even D3 while *H. minus* spores are usually D1 and rarely even D2.

As *H. alpinum*, *H. minus* is a rather diverse species molecularly. The only single locus in which all available *H. minus* sequences form a supported monophyletic clade is *RPB2*. In other single locus analyses, *H. minus* forms mixed clades with either *H. louiseae* or *H. pallidolabiatum* or some of the *H. minus* sequences are included in the unresolved *H. crustuliniforme* complex part of the tree.

Hebeloma pallidolabiatum Beker & U. Eberh., *sp. nov.* — MycoBank MB809910; Fig. 5f, 26, 27

Etymology. From *pallidus* meaning pale and *labiatus* of the lip, to emphasise the thin pale margin that appears to be a consistent character of this taxon.

Type. Svalbard, Skansbukta (N78.5156167 E16.0139500, alt. c. 34 m) on soil in coastal scrub under *Salix polaris*, 14 Aug. 2007, *M.L. Beker, H. Beker* holotype BR BR-MYCO 174908-17; isotypes C C-F-92312, HJB11992).

Diagnosis — *Hebeloma pallidolabiatum* belongs, based on its cheilocystidium shape to *H.* subsect. *Denudata*. It can be separated from the other small arctic species of this section by the cheilocystidium ratio apex : base (A/B) which is always < 1.8 and the spores, most of which are always quite distinctly ornamented and > 12 µm in length.

Basidiomes in a scattered group. *Pileus* 12−21 mm diam, convex to broadly umbonate, slightly tacky when moist; *cuticle colour* 2-coloured, sepia to dark brick in the centre with a thin paler margin; *pileus margin* straight. *Lamellae* emarginate, quite
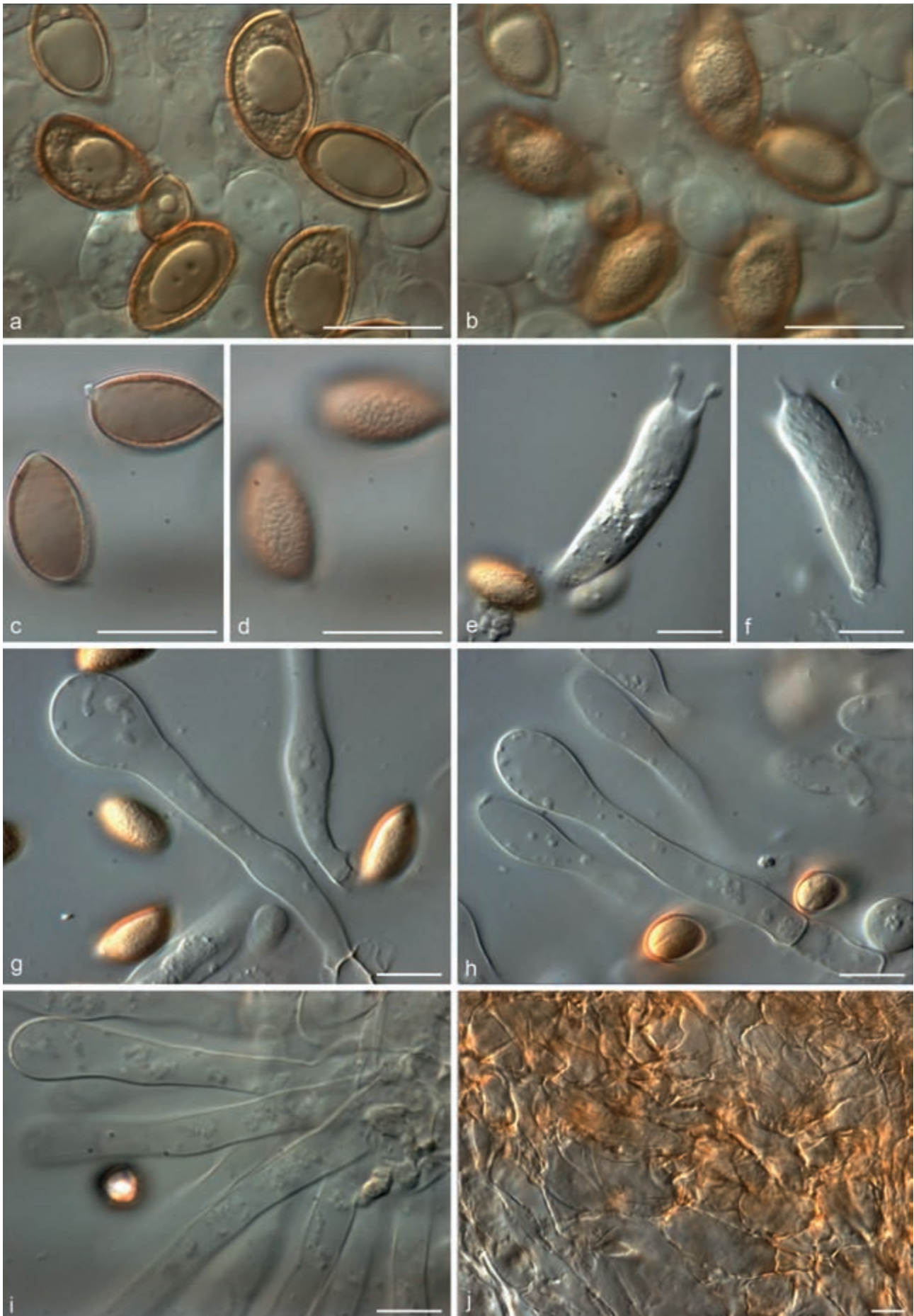
Fig. 26 *Hebeloma pallidolabiatum* (BR-MYCO 174908-17, holotype). a, b. Spores and spore ornamentation ×1 600 in 5 % KOH; c, d. spores and spore ornamentation ×1 600 in Melzer's reagent; e, f. basidia ×1 000 in 5 % KOH; g, h. cheilocystidia ×1 000 in 5 % KOH; i. caulocystidia ×1 000 in 5 % KOH; j. trama below cutis ×500 in 5 % KOH. — Scale bars: 10 μm.
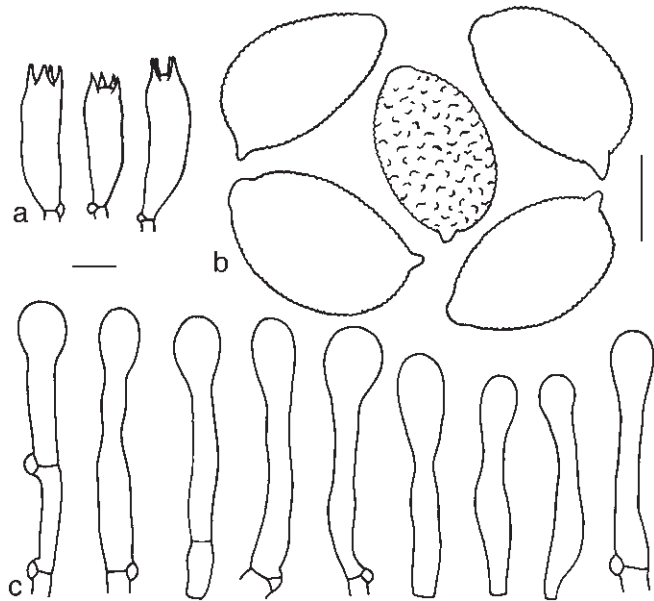
Fig. 27 *Hebeloma pallidolabiatum* (BR-MYCO 174908-17, holotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 μm.

distant (L = 30–33); *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, significantly paler than lamella surface droplets usually visible by naked eye; *lamellules* occasional. *Stipe* central, cylindrical, 14–24 × 2.0–3.5 mm with some brown discolouration towards the base of the stipe; *surface* dry, pruinose. *Cortina* not observed. *Flesh* rather thin, whitish but slightly more coloured in the base of the stipe. *Smell* raphanoid. *Taste* not recorded. *Spore deposit* Isabella to brownish olive.

Spores amygdaloid, with small apiculus and rounded at the end opposite the apiculus, with some thinning of the spore wall, with a papilla and guttulate, weakly but distinctly ornamented, at least under immersion, with no sign of loosening perispore and at most weakly dextrinoid (O2; P0; (D0)D1,D2); *spore colour* under the microscope brownish yellow; *spore size* based on n = 58 spores of the holotype, 5–95 % percentile range 12.0–14.1 × 7.0–8.5 μm, with median 12.8 × 7.5 μm and av 12.8 × 7.6 μm with SD length 0.65 μm and width 0.44 μm, Q value 5–95 % percentile range 1.57–1.80, with median 1.69 and av 1.69 with SD 0.07; *spore size* based on 2 collections medians 12.8–13.5 × 7.2–7.5 μm and av 12.8–13.5 × 7.2–7.6 μm with SD length 0.65–0.89 μm and width 0.33–0.44 μm, Qav 1.69–1.88. *Basidia* cylindrical to clavate and 4-spored, 26–40 × 6.6–10.6 μm, with av 27–37 × 7.9–9.8 μm and basidium Qav 3.6–3.9. *Pleurocystidia* not found. *Cheilocystidia* clavate-stipitate sometimes slightly swollen towards the base giving an hourglass appearance clavate-lageniform, occasionally with septa (sometimes clamped); *width of apex* holotype 5–95 % percentile range 6.8–11.5 μm, with median 8.8 μm and av 9.0 μm with SD 1.66 μm; across 2 collections median 8.5–8.8 μm and av 8.6–9.0 μm; with n ≥ 20 selected cheilocystidia of 2 collections the 5–95 % percentile ranges are 48–73 × 6.8–11.5 × 4.1–6.4 × 3.6–7.9 μm while the averages are 58–59 × 8.6–9.0 × 5.1–5.4 × 5.9–6.3 and 59 × 9.0 × 5.1 × 6.3 μm av for the holotype. The av cheilocystidia ratios across the 2 collections were: A/M = 1.61–2.05; A/B = 1.57–1.69; B/M = 1.09–1.24. *Caulocystidia* resemble cheilocystidia, up to 90 μm long and 11 μm wide at the apex. *Pileipellis* is an ixocutis with a thin to medium thickness epicutis up to 80 μm, embedded hyphae up to 5.5 μm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* orange brown and made up of cylindrical to isodiametric elements. *Trama below subcutis* contains angular elements, sometimes shaped like thick sausages

up to 20 μm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — We only have two collections of this species, both from Svalbard in arctic conditions with dwarf *Salix* but over 100 km apart. Consequently its habitat is not yet well understood.

Additional specimens examined. Svalbard, Knudsenheia (N78.9375333 E11.8438500, alt. c. 8 m) on soil in grazed scrubland under *Salix polaris*, 19 Aug. 2007, *M.L. Beker, H. Beker* HJB12059.

Notes — Given the shape of its cheilocystidia, *H. pallidolabiatum* clearly belongs to *H.* subsect. *Denudata.* The species has most likely not been included in the intercompatibility tests of Aanen & Kuyper (1999). Of the members of *H.* subsect. *Denudata* it is most likely to be confused with the other small arctic/alpine species: *H. louiseae*, *H. minus* and *H. perexiguum*. It can be readily separated from the first two of these on the basis of the cheilocystidium ratio A/B which for this taxon is always < 1.8 whereas it is > 1.8 for both *H. louiseae* and *H. minus*. The separation from *H. perexiguum* is straightforward as the spores for *H. pallidolabiatum* are more ornamented and longer. Given the small number of collections on which our description is based it is possible that our description is too narrow but until more collections of this taxon are recorded we cannot be sure.

Hebeloma pallidolabiatum is monophyletic in four out of five loci and supported by bootstrap in three of them. Two ITS sequences were obtained from the type collection, of which one is included in a (the) *H. pallidolabiatum* clade and the other is part of the unresolved *H. crustuliniforme* complex part of the tree. This provides further evidence that the ITS is less suited for species identification than any of the other loci.

Hebeloma perexiguum Beker, Vesterh. & U. Eberh., *sp. nov.* — MycoBank MB809911; Fig. 5g, 28, 29

Etymology. From *per* – very and *exiguus* – small, to emphasise the small size of this mushroom.

Type. Svalbard, London near Ny Alesund (N78.9631 E12.05035, alt. c. 5 m) in scrub on site of deserted settlement with *Salix polaris*, 18 Aug. 2007, *M.L. Beker, H. Beker* holotype BR BR-MYCO 173979-58; isotype HJB12038.

Diagnosis — *Hebeloma perexiguum* belongs based on its cheilocystidium shape to *H.* subsect. *Denudata*. It can be recognized by the swollen basal part of the cheilocystidia and its small size. It can be recognized from other species of the subsection that are known to occur in arctic/alpine habitats and form small basidiomes, such as *H. salicicola* by its small number of full length lamellae, which is < 30, from *H. minus* and *H. pallidolabiatum* by its low spore ornamentation (O1), from *H. aurantioumbrinum* by its spore width being > 7 μm and from *H. louiseae* by its average cheilocystidium apex width of < 9 μm.

Basidiomes in a scattered group. *Pileus* 7–12 mm diam, convex, slightly tacky when moist; *cuticle colour* almost unicolour, greyish brown with a thin paler margin; *pileus margin* straight. *Lamellae* emarginate, quite distant (L = 24–26); *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, significantly paler than lamella surface droplets not seen on the lamella edge; *lamellules* occasional. *Stipe* central, cylindrical, 10–15 × 2.0 mm with some weak brown discolouration towards the base of the stipe; *surface* dry, pruinose. *Cortina* not observed. *Flesh* rather thin, whitish but slightly more coloured in the base of the stipe. *Smell* absent. *Taste* not recorded. *Spore deposit* not recorded. *Exsiccata* fragile and brittle and pileus blackening.

Spores amygdaloid, with small apiculus and rounded at the end opposite the apiculus, with some thinning of the spore wall, sometimes with a papilla, not guttulate, almost smooth, with
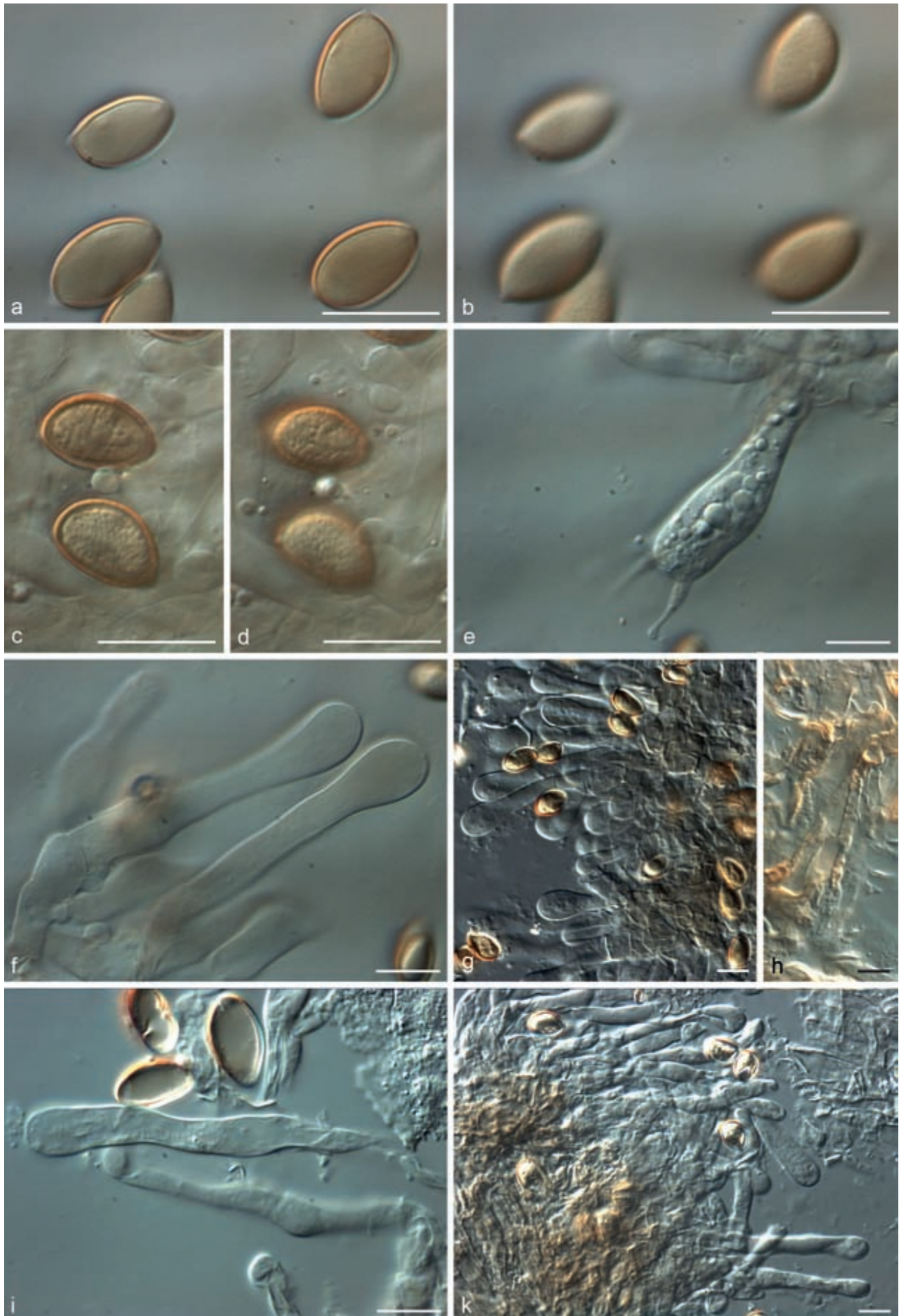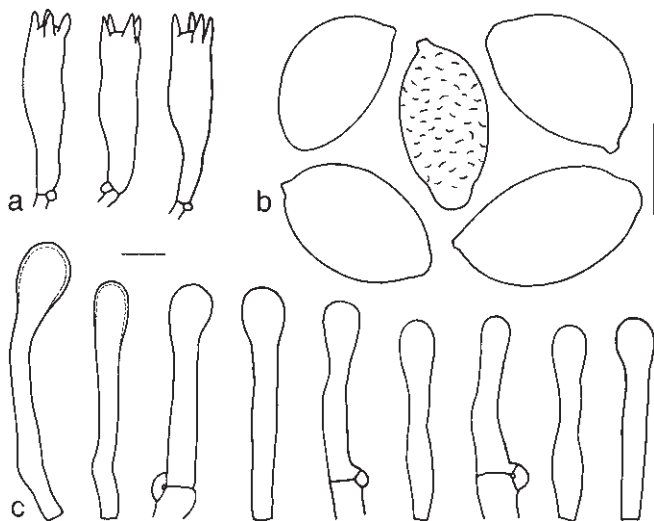
Fig. 28 *Hebeloma perexiguum* (BR-MYCO 173979-58, holotype). a, b. Spores and spore ornamentation ×1 600 in Melzer's reagent; c, d. spores and spore ornamentation ×1 600 in 5 % KOH; e. basidium ×1 000 in 5 % KOH; f. cheilocystidia ×1 000 in 5 % KOH; g. cheilocystidia ×500 in 5 % KOH; h. epicutis hyphae ×1 000 in 5 % KOH; i. caulocystidia ×1 000 in 5 % KOH; j. caulocystidia ×500 in 5 % KOH. — Scale bars: 10 μm.

ornamentation hardly visible, with no sign of loosening peri-spore and weakly dextrinoid (O1; P0; D1); *spore colour* under the microscope brownish yellow; *spore size* based on n = 56 spores of the holotype, 5−95 % percentile range 9.9−13.4 × 6.4−8.1 µm, with median 11.7 × 7.2 µm and av 11.7 × 7.2 µm with SD length 1.15 µm and width 0.56 µm, Q value 5−95 % percentile range 1.43−1.86, with median 1.64 and av 1.63 with SD 0.12. *Basidia* cylindrical to clavate and 4-spored, 31−43 × 8.9−10.1 µm, with av 38 × 9.6 µm and basidium Qav 3.9. *Pleurocystidia* not found. *Cheilocystidia* spathulate-stipitate or clavate sometimes slightly swollen towards the base giving an hourglass appearance or even appearing lageniform, with some thickening of the apex, occasionally with septa; *width of apex* holotype 5−95 % percentile range 6.7–10.6 µm, with median 8.2 µm and av 8.5 µm with SD 1.56 µm and overall av dimensions 54 × 8.5 × 4.8 × 6.4 µm av for the holotype. The av cheilocystidia ratios were: A/M = 1.75; A/B = 1.45; B/M = 1.33. *Caulocystidia* resemble cheilocystidia, up to 75 µm long and 9 µm wide at the apex. *Pileipellis* is an ixocutis with a very thin epicutis up to 30 µm, embedded hyphae up to 6 µm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* orange brown and made up of cylindrical to isodiametric elements. *Trama below subcutis* contains angular elements, sometimes shaped like thick sausages up to 16 µm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — We only have one collection of this species, growing in arctic conditions with dwarf *Salix*. Consequently its habitat is not yet well understood.

Notes — Given the shape of its cheilocystidia, *H. perexiguum* clearly belongs to *H.* subsect. *Denudata.* Of the members of *H.* subsect. *Denudata* it is the species with the most swollen basal part of the cheilocystidium and may be confused with species from other subsections of *H.* sect. *Denudata*, however there is no other arctic/alpine species in *H.* sect. *Denudata*, outside *H.* subsect. *Denudata* that is so small. Based on just one collection, this species appears to be readily distinguishable from other species in *H.* subsect. *Denudata* with which it might be confused. These would most likely be *H. louiseae*, *H. minus*, *H. pallidolabiatum* or small examples of *H. aurantioumbrinum* or *H. salicicola*. Based on its small number of full length lamellae, < 30, it is distinguished from alpine forms of *H. salicicola*. The low ornamentation of the spores will distinguish it from *H. minus* and *H. pallidolabiatum*. The wide spores, > 7 µm distinguish it from *H. aurantioumbrinum* and the cheilocystidium average apex width of < 9 µm distinguishes it from *H. louiseae*. Given that our description is based on a single collection it is possible

Fig. 29 *Hebeloma perexiguum* (BR-MYCO 173979-58, holotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 µm.

that our description is too narrow but until more collections of this taxon are recorded we cannot be sure.

The single *H. perexiguum* sequence is not included in any species clade for any of the tested loci. Based on the available data it is likely that the species can be recognized by any of the loci used in ML analyses, but its placement among the included taxa varies. In the result of the V9 analysis it is included in a supported clade with *H. pusillum* (which is highly supported as a species, too), but a sister species relationship with *H. pusillum* is not indicated by any of the other loci phylograms.

Hebeloma pusillum J.E. Lange, Fl. Agaric Danic. 5 (Taxon. Consp.): iv. 1940. — MycoBank MB275806; Fig. 30, 31

= *Hebeloma pusillum* var. *longisporum* Bruchet, Bull. Mens. Soc. Linn. Lyon 39, 6 (Suppl.): 126. 1970.

= *Hebeloma vaccinum* var. *cephalotum* Enderle & Vesterh. in Die Pilzflora des Ulmer Raumes (Ulm): 379. 2004.

Type. Denmark, Fyn, Langesøskovene S. of Morud (c. N55.45 E10.19, alt. c. 30 m) with *Salix* sp., Danske Agaricacéer, pl. 460 (aquarelle, C), reproduced in Lange 1938 as pl. 120C; same locality, 16 Oct. 1991, *J. Vesterholt*, epitypus C JV91-685, database record HJB1000128, selected by J. Vesterholt in Fungi of Northern Europe 3: 82. 2005.

Basidiomes usually in scattered groups. *Pileus* 5−40 mm diam, convex or applanate, sometimes with a small umbo, often viscid, slightly tacky when moist but never hygrophanous; *cuticle colour* cinnamon to sepia to dark brick in the central region and becoming paler towards the margin which may be anywhere from cream to clay coloured, distinctly 2-coloured in older specimens; *pileus margin* usually straight, occasionally involute when young and sometimes upturned with age. *Lamellae* emarginate, quite widely spaced (L = 20−38) with a maximum depth of 3−4 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, significantly paler than lamella surface; droplets normally visible on the lamella edge even with the naked eye; *lamellules* occasional. *Stipe* central, cylindrical usually stuffed, rarely hollow, 14−58 × 1.5−2.5(−3.5) mm usually with some brown discolouration towards the base of the stipe; *surface* dry, pruinose. *Cortina* not observed. *Flesh* rather thin, whitish but slightly more coloured in the base of the stipe. The whole basidiome has a very slender and fragile appearance with the av stipe Q (ratio of stipe length to stipe width) usually well in excess of 11. *Smell* raphanoid, sometimes absent. *Taste* raphanoid. *Spore deposit* brownish olive to umber.

Spores amygdaloid or fusoid, with small apiculus and rounded at the end opposite the apiculus, with some thinning of the spore wall, rarely with any papilla, sometimes guttulate with one or more oily drops, from weakly to distinctly ornamented, usually with some sign of loosening perispore in at least a few spores and often in many spores and weakly but sometimes distinctly dextrinoid ((O1)O2,O3; (P0)P1,P2; (DO)D1,D2); *spore colour* under the microscope yellow brown to brown; *spore size* based on n = 55 spores of the epitype, 5−95 % percentile range 11.1−13.7 × 5.8−7.0 µm, with median 12.3 × 6.4 µm and av 12.3 × 6.4 µm with SD length 0.87 µm and width 0.48 µm, Q value 5−95 % percentile range 1.79−2.11, with median 1.92 and av 1.93 with SD 0.13; *spore size* based on 20 collections medians 11.3−13.6 × 5.6−6.7 µm and av 11.4−13.6 × 5.6−6.7 µm with SD length 0.64−1.04 µm and width 0.22−0.55 µm, Qav 1.91−2.22. *Basidia* cylindrical to clavate and 4-spored, 23−40 × 5.7−10.7 µm, with av 25−35 × 6.8−9.6 µm and basidium Qav in the range 3.0−4.4. *Pleurocystidia* not found. *Cheilocystidia* capitate-stipitate, clavate-stipitate or spathulate-stipitate, occasionally slightly swollen towards the base (capitate-lageniform or clavate-lageniform), occasionally with septa and rarely with median thickening, sometimes the cheilocystidia appear con-
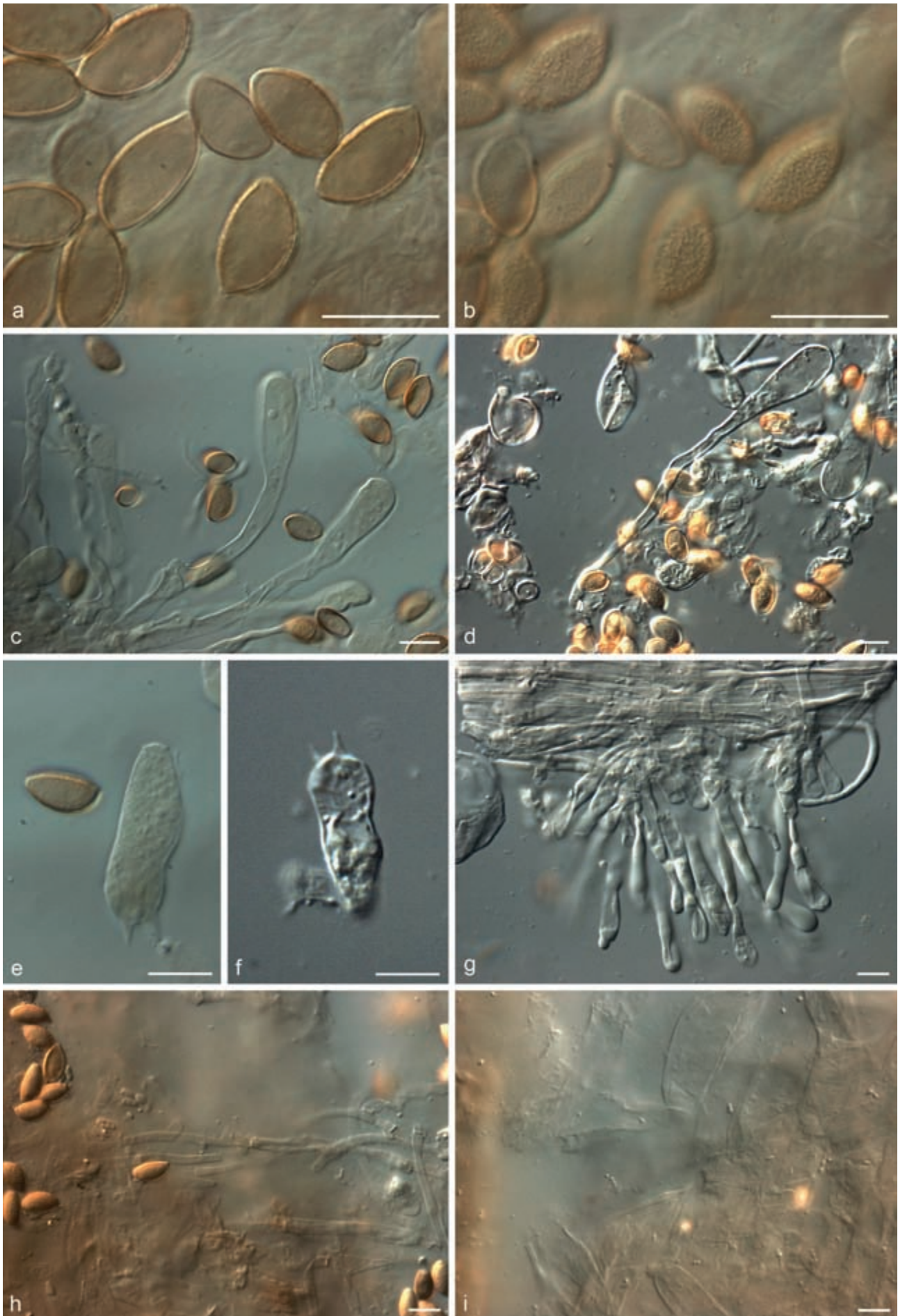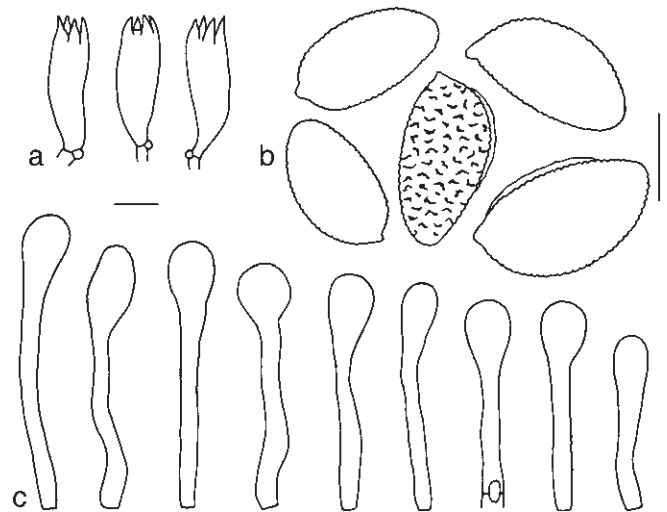
Fig. 30 *Hebeloma pusillum* (C JV91-685, epitype). a, b. Spores and spore ornamentation ×1 600 in Melzer's reagent; c. cheilocystidia x 630 in Melzer's reagent; d. cheilocystidia ×500 in Melzer's reagent; e, f. basidia ×1 000 in Melzer's reagent; g. caulocystidia ×500 in 5 % KOH; h. epicutis hyphae ×500 in 5 % KOH; i. trama below cutis ×500 in 5 % KOH. — Scale bars: 10 µm.

glutinate and tend to break rather than separate; *width of apex* epitype 5–95 % percentile range 6.1–12.4 µm, with median 8.7 µm and av 9.0 µm with SD 1.96 µm; across 20 collections median 7.9–9.9 µm and av 8.0–10.0 µm; with n ≥ 20 selected cheilocystidia of 20 collections the 5–95 % percentile ranges are 32–97 × 5.6–12.8 × 2.7–6.1 × 2.7–6.8 µm while the averages are 41–70 × 8.0–10.0 × 3.8–4.8 × 3.6–4.9 and 70 × 9.0 × 4.3 × 4.4 µm av for the epitype. The av cheilocystidia ratios for the 15 collections were: A/M = 1.71–2.71; A/B = 1.68–2.52; B/M = 0.94–1.20. *Caulocystidia* resemble cheilocystidia, up to 75 × 12 µm wide at the apex. *Pileipellis* is an ixocutis with a thin epicutis 40–80 µm, embedded hyphae up to 6 µm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* red brown and made up of cylindrical to isodiametric elements. *Trama below subcutis* contains ellipsoid, cylindrical and thick sausage shaped elements up to 18 µm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — All our records of *H. pusillum* record *Salix* as present. Thus we believe that this species is confined in its mycorrhizal associations to *Salix* spp. All our records also indicate moist or wet ground, sometimes moss-covered, including records where it has been collected in *Sphagnum.* The habitat is often described as a *Salix* thicket but it also occurs on slagheaps or in scrubland. Based on our records *H. pusillum* is widespread across Central and Western Europe, but we suspect that it is widespread across all of Europe. Although generally not common it can be locally common.

Additional specimens examined. BELGIUM, prov. Hainaut, Maubray (N50. 5306167 E3.4941000; alt. c. 30 m) slagheap, on mossy soil, scattered with *Salix* sp. and *Betula* sp., 10 Nov. 2006, *P.-A. Moreau* HJB11723; prov. Brussels, Hof Musschen (N50.8538167 E4.4458333, alt. c. 53 m) on wet litter in broadleaf woodland scrub under *Salix* sp., 20 Oct. 2006, *H. Beker* HJB11716; prov. Hainaut, Maubray (N50.5308500 E3.4940333, alt. c. 29 m) on rotten litter in broadleaf woodland on slagheap under *Betula* sp., *Salix* sp., 10 Nov. 2006, *P.-A. Moreau* HJB11728. – DENMARK, Kogsbøl Mose N. of Højer (c. N56.01 E8.72, alt. c. 15 m) with *Salix* sp., 23 Sept. 1991, *T. Læssøe* TL2542, duplicate HJB10941; Snarup Mose SW of Kværndrup (c. N56.16 E10.44, alt. c. 65 m) with *Salix* sp., 28 Aug. 1993, *J. Vesterholt* JV93-758, duplicate HJB10715; Søgårds Mose, Fløjstrup Skov S. of Århus (c. N56.08 E10.24, alt. c. 25 m) in boggy soil with *Salix* sp., 6 Oct. 1991, *J. Petersen* JV91-525, duplicate HJB10880; region NWJ, Stokholm Mose, north side of Skalleso, NE of Vinderup UTM MH9162 TBU (c. N56.500 E8.840, alt. c. 5 m) under *Salix* sp., 1 Oct. 2002, *P. Boisen Hansen* JV02-632, duplicate HJB10879. – FRANCE, Ain, Saint-Etienne-du-bois, Bourg (c. N46.26 W5.28; alt. c. 250 m) on wet ground with *Sphagnum* under *Alnus glutinosa* and *Salix aurita*, 19 Oct. 1964, *G. Bruchet* LY BR64-36, database record HJB1000067, this is the holotype of *H. pusillum* var. *longisporum*; Jura, Lac des Rouges Truites (c. N46.36252 E5.59531, alt. c. 940 m) in mixed woodland under *Salix aurita*, *S. cinerea* and *S. caprea*, 24 Sept. 1996, *D. Aanen* WBS 9644, database record HJB12515; Jura, Lac des Rouges Truites (c. N46.36252 E5.59531, alt. c. 940 m) in mixed woodland under *Salix* sp., 24 Sept. 1996, *D. Aanen* WBS 9648, database record HJB12518; Aude, Roquefeuil, Tour-biere du Pinet (N42.86421 E1.9775, alt. c. 880 m) in wet, boggy mixed woodland with *Salix atrocinerea*, 14 Oct. 2008, *J.-P. Priou* HJB12730; Ariege, Freychinede (N42.8031167 E1.4225500, alt. c. 1350 m) on wet boggy soil in woodland under *Salix atrocinerea*, 29 Sept. 2007, *G. Corriol* GC 07 09 29 03, duplicate HJB12107. – GERMANY, Bavaria, near Riedheim, Gunzberg, MTB7527/1 (c. N48.462 E10.189, alt. c. 456 m) under *Betula* sp., *Salix* sp., 9 Sept. 1994, *M. Enderle* M 0155166, database record HJB1000137, this is part of the holotype of *H. vaccinum* var. *cephalotum*; Berlin-Altglienicke, Grünauer Railway Junction, Flat Gk 1 (c. N52.4167 E13.55, alt. c. 35 m) on moist ground under *Alnus* sp. and *Salix* sp., 4 Oct. 1999, *F. Gröger* GLM GL42941, database record HJB10993. – NETHERLANDS, Drenthe, Vledder, Wagserveense (c. N52.84 E6.22, alt. c. 0 m) with *Salix* sp., 20 Sept. 1995, *D. Aanen* WBS 9507, database record HJB12810; Drenthe, Vledder, Wagserveense (c. N52.84 E6.22, alt. c. 0 m) collected with *Salix* sp., 20 Sept. 1995, *D. Aanen* WBS 9508, database record HJB12460; Drenthe, Vledder (c. N52.512692 E6.123788, alt. c. 5 m) collected with *Salix* sp., 20 Sept. 1995, *D. Aanen* WBS 9509, database record HJB12461; Zouweboezem, Meerkerk (c. N51.9539 E4.9858, alt. c. 0 m) under *Salix aurita* and *S. cinerea*, 20 Oct. 1996, *D. Aanen* WBS 9690, database record HJB12801. – WALES, Brecon, Illkyd Pools (c. N51.92107 W3.503536, alt. c. 320 m) on wet soil under *Salix* sp., 17 Oct. 2003, *A. Andrews* HJB9494.


Fig. 31 *Hebeloma pusillum* (C JV91-685, epitype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 µm.

Notes — Given the shape of its cheilocystidia, *H. pusillum* clearly belongs to *H.* subsect. *Denudata*. The species most likely corresponds to ICG8 of Aanen & Kuyper (1999). The strongly 2-coloured cap, somewhat reminiscent of *H. mesophaeum* but with much more slender stature and without cortina leaves very few possibilities. Other small *Hebeloma* spp. have not such strongly 2-coloured caps, nor are they so slender. We have no confirmed records of this taxon in arctic or alpine habitats. It can be readily distinguished from the other members of this subsection that grow in lowland areas based on the distinctly 2-coloured cap, the number of lamellae 20–40, the slender basidiomes with stipe width ≤ 3.5 mm and stipe Q normally > 10, the spore length, > 11 µm, the large average width of the cheilocystidium apex ≥ 8 µm, and with no regular apical thickening of the cheilocystidium. It has probably often been confused with *H. helodes*, which is also a small *Hebeloma* sp., but *H. pusillum* is confined to *Salix*, has a more fragile stature and usually a rather darker centre to the pileus and significantly longer spores, on average. *Hebeloma luteicystidiatum* also has long spores but the very distinct apical thickening of the cheilocystidium distinguishes this taxon from *H. pusillum*, which rarely has any apical thickening of the cheilocystidium. *Hebeloma aurantioumbrinum*, is rare in non-arctic/alpine environments but also has shorter spores on average. *Hebeloma minus* is also rare in non arctic/alpine environments but in any case this taxon has a smaller spore Q from that of *H. pusillum*. *Hebeloma salicicola* could be confused with *H. pusillum* but normally it has a more robust stature with a wider stipe, a smaller stipe Q and the spores of *H. salicicola* are on average more dextrinoid.

Hebeloma pusillum forms species clades in all of the loci tested, and receives bootstrap support in all single locus results apart from ITS.

Having studied the description and holotype material of *H. vaccinum* var. *cephalotum* we are convinced this was a mixed collection of *H. salicicola*, *H. vaccinum* and *H. pusillum*. We have extracted DNA several times and every sequence we have generated is of *H. pusillum*, similarly the material we have examined is *H. pusillum*. However, the macroscopic description given for this taxon very much more resembles *H. salicicola*. We have also examined the isotype of this material, but that is *H. vaccinum*. So we conclude that we should synonymise it with *H. pusillum* but point out that the macroscopic description does not really match *H. pusillum*. See also the discussion following the description of *H. salicicola*.

We have examined the description and holotype material of *H. pusillum* var. *longisporum* both morphologically and molecu-
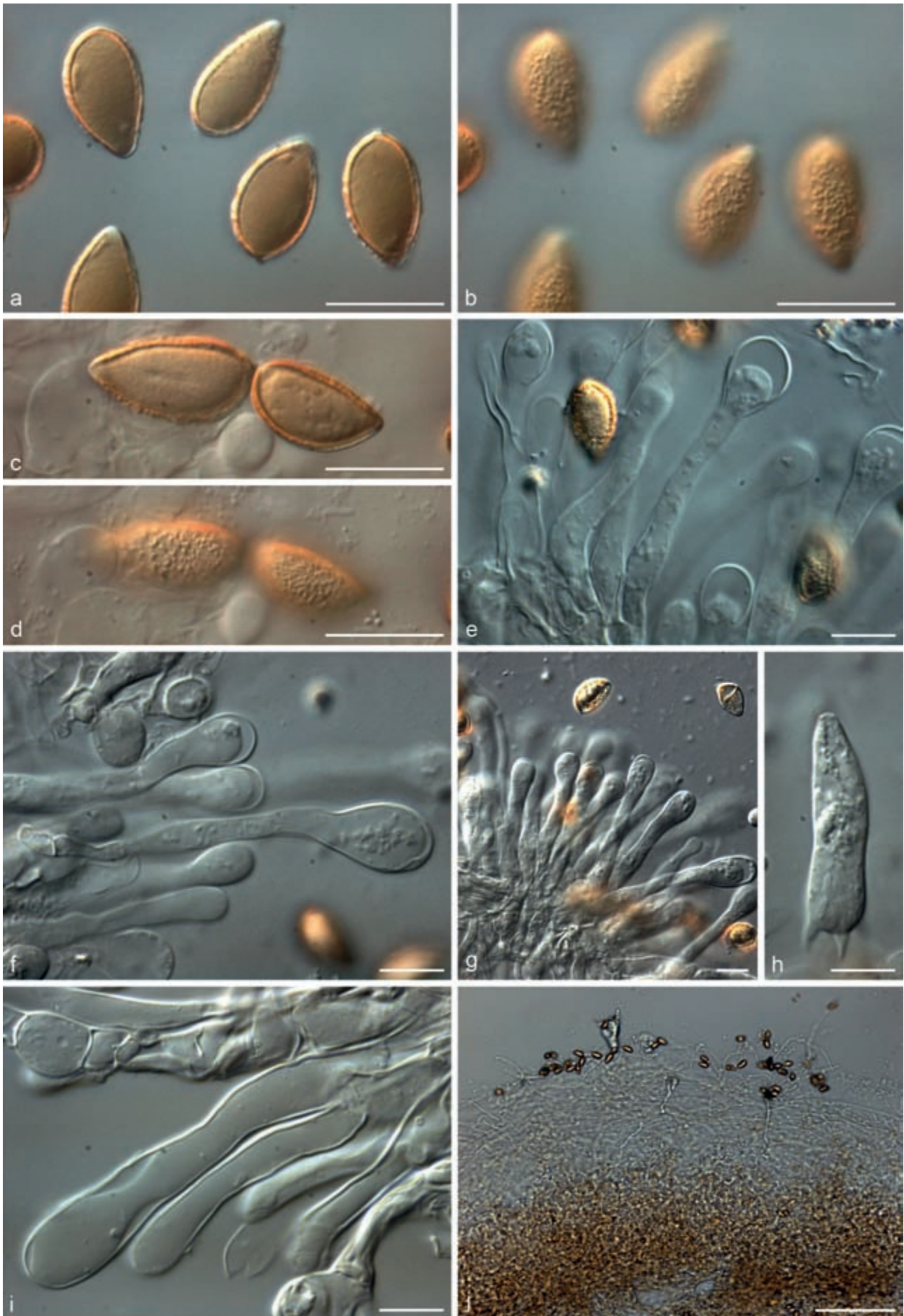
Fig. 32 *Hebeloma salicicola* (BR-MYCO 173977-56, holotype). a, b. Spores and spore ornamentation ×1 600 in Melzer's reagent; c, d. spores and spore ornamentation ×1 600 in 5 % KOH; e, f. cheilocystidia ×1 000 in 5 % KOH; g. cheilocystidia ×500 in 5 % KOH; h. basidium ×1 000 in 5 % KOH; i. caulocystidia ×1 000 in 5 % KOH; j. cutis ×125 in 5 % KOH. — Scale bars: 10 μm, in j. 100 μm.

larly and have concluded that there are no grounds for separating this variety. This is in agreement with Gröger (1987). The molecular sequences we have generated are identical to *H. pusillum* and our measurements of the spore length show it to be in the middle of the range for this species; we have included Bruchet's collection within the set of collections upon which our overall species description is based.

The original iconotype of Lange is an excellent representation of this taxon. The epitype selected by Vesterholt is also representative.

Hebeloma salicicola Beker, Vesterh. & U. Eberh., *sp. nov.* — MycoBank MB809912; Fig. 5h, 32, 33

Etymology. Meaning lover of *Salix*, being exclusively mycorrhizal with *Salicaceae*.

Type. Belgium, De Panne, Westhoek, West Flanders (N51.08793 E2.57568, alt. c. 3 m) on sand in calcareous dune slack with *Salix repens*, 12 Oct. 2009, *H. Beker, L. Davies* holotype BR BR-MYCO 173977-56; isotype C C-F-90151, HJB13302.

Diagnosis — *Hebeloma salicicola* is a member of *H.* subsect. *Denudata* based on cheilocystidium shape, though the cystidia can be rather broad at the base. Macroscopically it is similar to *H. vaccinum*, but in contrast to *H. vaccinum*, mature specimens nearly always have a 2-coloured pileus with a darker centre. Microscopically *H. salicicola* differs from other members of its subsection by a combination of characters, i.e. its small stature, the low number of full length lamellae (< 50), the rather strong dextrinoidity (D2,D3) and ornamentation of the spores (O2,O3), which are on average > 11 μm.

Basidiomes usually in scattered groups, rarely solitary, sometimes gregarious. *Pileus* 10–48 mm diam, convex often umbonate, surface often viscid, tacky when moist but never hygrophanous; *cuticle colour* mature basidiomes are almost always 2-coloured with the centre from ochre to a rich red brown, dark brick or sepia and the margin from cream to clay pink or buff or Isabella; *pileus margin* usually straight but sometimes scalloped. *Lamellae* adnate or emarginated, sometimes almost free, usually quite distant with L = 30–49; maximum depth 2–9 mm; *colour* cream, alutaceous or brown when young, later umber to sepia following spore maturity; *edge* fimbriate, usually significantly paler than lamella surface; droplets sometimes visible on the lamella edge, but often absent; *lamellules* frequent. *Stipe* central, sometimes cylindrical but more often clavate or even appearing bulbous, particularly when collected in a sand dune with a bulb formed from sand, rarely tapering, becoming hollow with age, (5–)9–48(–56) × (1.5–)2–7 mm, and up to 11 mm at the base with stipe Q (5–95 %) ranging from 3.5–11.1, sometimes with slight discolouration towards the base of the stipe; *surface* dry, pruinose to floccose, especially towards the apex. *Cortina* not observed. *Flesh* thick, white to pale buff. *Smell* raphanoid, often with a cocoa smell, sometimes weak, sometimes absent. *Taste* usually bitter. *Spore deposit* brownish olive to umber. *Exsiccata* sometimes, but not always, dark coloured with blackening lamellae.

Spores amygdaloid or limoniform, sometimes fusoid, with small apiculus and rounded at the end opposite the apiculus, with some thinning of the spore wall, and often with a papilla, sometimes guttulate with one or more oily drops, sometimes weakly ornamented but usually more distinctly ornamented, sometimes with slightly loosening perispore in a few to many spores and distinctly to rather strongly dextrinoid with spores becoming orange brown or light brick in Melzer's reagent (O2,O3; (P0)P1,P2; D2,D3); *spore colour* under the microscope from yellow through yellow brown to brown; *spore size* based on n = 54 spores of the holotype, 5–95 % percentile range
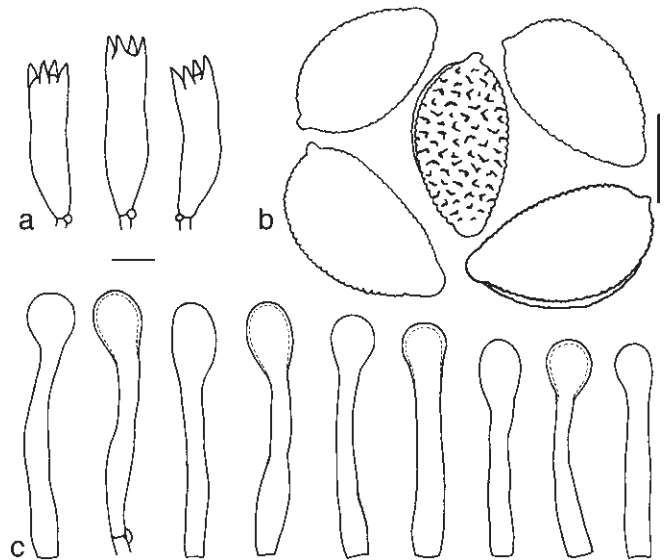
Fig. 33 *Hebeloma salicicola* (BR-MYCO 173977-56, holotype). a. Basidia; b. spores; c. cheilocystidia. — Scale bars: 5 μm.

11.6–13.9 × 6.4–7.8 μm, with median 12.7 × 7.2 μm and av 12.7 × 7.1 μm with SD length 0.67 μm and width 0.46 μm, Q value 5–95 % percentile range 1.67–1.92, with median 1.78 and av 1.78 with SD 0.08; *spore size* based on 21 collections medians 11.2–13.3 × 6.0–7.6 μm and av 11.2–13.3 × 6.1–7.5 μm with SD length 0.50–1.24 μm and width 0.25–0.51 μm, Qav 1.64–2.00. *Basidia* cylindrical to clavate and 4-spored, 22–38 × 7.2–10.2 μm, with av 24–37 × 8.0–9.9 μm and basidium Qav in the range 3.0–4.1. *Pleurocystidia* not found. *Cheilocystidia* capitate-stipitate or clavate-stipitate, sometimes swollen towards the base (capitate-lageniform or clavate-lageniform), usually with some thickening of the apex, occasionally with septa and occasionally bifurcate; *width of apex* holotype 5–95 % percentile range 7.5–10.8 μm, with median 8.9 μm and av 8.9 μm with SD 1.01 μm; across 21 collections median 7.8–10.6 μm and av 7.9–10.7 μm; with n ≥ 20 selected cheilocystidia of 21 collections the 5–95 % percentile ranges are 37–77 × 6.1–15.5 × 3.0–5.7 × 2.5–8.9 μm while the averages are 46–63 × 7.9–10.7 × 3.8–5.0 × 3.6–5.9 while the av for the holotype was 54 × 8.9 × 4.3 × 4.9. The av cheilocystidia ratios for the 17 collections were: A/M = 1.83–2.63; A/B = 1.60–2.82; B/M = 0.96–1.27. *Caulocystidia* resemble cheilocystidia but with a more swollen base, up to 85 × 13 μm wide at the apex. *Pileipellis* is an ixocutis with an epicutis medium thick, 80–150 μm, embedded hyphae up to 10 μm broad, smooth or sometimes encrusted, hyaline or occasionally pigmented. *Cutis* orange brown and made up of cylindrical to isodiametric elements. *Trama below subcutis* contains cylindrical, ellipsoid, ovate and sausage-shaped elements up to 16 μm broad. *Clamp connections* present throughout the basidiome.

Habitat & Distribution — *Hebeloma salicicola* appears to be confined in its mycorrhizal association to *Salix* and *Populus*. It is common and often gregarious in calcareous dune slacks growing with *Salix repens*, where it appears to have two fruiting periods per year, in the spring and in the autumn. We also have one alpine record of *H. salicicola* with *Salix herbacea* and one arctic record where it was growing in association with *Salix polaris*. Other records (not from dunes or alpine or arctic) are from grassy or mossy, often sandy ground with *Populus × alba* or *Salix* sp. in scrub, gardens, grassland or woodland plantations, on both acid and calcareous soils.

Additional specimens examined. Belgium, prov. West Flanders, Westhoek (c. N51.04 E3.56, alt. c. 0 m) in dune on sandy, calcareous soil with *Salix repens*, 26 Apr. 2004, *H. Beker* HJB9911; prov. West Flanders, Westhoek

(c. N51.04 E3.56, alt. c. 0 m) in dune on sandy, calcareous soil with *Salix repens*, 26 Apr. 2004, *H. Beker* HJB9913; prov. West Flanders, Westhoek (N51.08750 E2.5754833, alt. c. 0 m) in dune on sandy, calcareous soil with *Salix repens*, 6 Oct. 2004, *H. Beker* HJB10260; prov. West Flanders, Ter Yde (N51.1379 E2.69635, alt. c. 0 m) in dune on sandy, calcareous soil with *Salix repens*, 22 Oct. 2004, *H. Beker* HJB10422; prov. West Flanders, Westhoek (N51.08750 E2.5754833, alt. c. 0 m) in dune on sandy, calcareous soil with *Salix repens*, 22 Apr. 2005, *H. Beker* HJB10923; prov. Brabant-Flanders, Meise, Botanical Gardens (c. N50.92 E4.32, alt. c. 35 m) in rural gardens on mossy, calcareous soil with *Salix* sp., 1 May 2005, *H. Beker* HJB10926; prov. Antwerp, Linker oever (c. N51.216667 E4.416667, alt. c. 10 m) on calcareous soil with *Salix* sp., 16 Apr. 2000, *J. Volders* VJ00012, duplicate HJB11501; prov. West Flanders, Westhoek (N51.0875000 E2.5754833, alt. c. 0 m) on sandy soil in maritime dune under *Salix repens*, 6. Oct.10. 2004, *H. Beker* (HJB10254); prov. West Flanders, Westhoek (N51.0875000 E2.5754833, alt. c. -6 m) on sandy soil in maritime dune under *Salix repens*, 6 Oct. 2004, *H. Beker* HJB10261; prov. West Flanders, Ter Yde (N51.13790 E2.69635, alt. c. 8 m) on grassy soil in dune under *Salix repens*, 22 Oct. 2004, *H. Beker* HJB10427. – Estonia, Saaremaa, Kaarma Community, Mändjala, near Hotel Saaremaa (N58.21198 E22.31861, alt. c. 5 m) on sandy, calcareous soil with *Pinus sylvestris* and *Salix* sp., 19 Sept. 2008, *J. Vauras* C TURA JV08-278, duplicate HJB12323. – Finland, Uusimaa, Hanko, Tvärminne, Tvärminneby (c. N59.84 E23.2, alt. c. 10 m) on calcareous soil under *Salix* sp., 30 June 1998, *J. Vauras* C TURA JV13610, duplicate HJB10930. – France, Haute Savoie, Lac des assiettes (N45.39001 E6.78529, alt. c. 2478 m) on bare soil in mountain scrub under *Salix herbacea*, 23 Aug. 2009, *L. Davies* HJB13087. – Netherlands, Groningen, Eemshaven (c. N53.448 E6.831, alt. c. 0 m) with *Salix repens*, 3 Oct. 1996, *D. Aanen* WBS 9670, database record HJB12473; Groningen, Eemshaven (c. N53.45 E6.83, alt. c. 0 m) with *Salix repens*, 3 Oct. 1996, *D. Aanen* WBS 9678, database record HJB12479; Lelystad, Oostvaardersplassen (Flevoland) (c. N52.45 E5.37, alt. c. 0 m) in dune with *Salix repens*, 11 Oct. 1995, *D. Aanen* WBS 9567, database record HJB12533. – Poland, Mt Kamiensk (the outer damping ground of the Belchatow Lignite Mine) forest distr. 297 (by the pond) (N51.22136 E19.43898, alt. c. 340 m) conifer woodland plantation with *Salix* sp., 23 Sept. 2008, *I. Kałucka*, *H. Beker* HJB12677. – Spain, Madrid, Colmenarejo (c. N40.56 W4.01, alt. c. 890 m) in broadleaf plantation with *Populus × alba*, 17 Apr. 2001, *F. Prieto* HJB9072. – Svalbard, Ossian (N78.9257000 E12.4542167, alt. c. 2 m) on grassy soil in maritime coastal scrub under *Salix polaris*, 17 Aug. 2007, *H. Beker*, *M.L. Beker* HJB12020. – Wales, Anglesey, Newborough (N53.1483800 W4.0425270, alt. c. 0 m) on sand in dune under *Salix* sp., 24 Sept. 2001, *H. Beker* HJB5117.

Notes — Given the shape of its cheilocystidia, *H. salicicola* clearly belongs to *H.* sect. *Denudata* and, although its cheilocystidia are perhaps more swollen in their lower half than those of many other species of *H.* subsect. *Denudata*, this taxon still falls within the subsection parameters. The species most likely corresponds to ICG14 of Aanen & Kuyper (1999). It appears restricted to *Salix* and *Populus* and can be common, even gregarious, in calcareous dunes where it is often growing alongside *H. vaccinum* with which, macroscopically, it can be confused particularly when young and still appearing almost unicoloured. In the key to this subsection we key it out in both subkeys. It can be distinguished from other arctic/alpine species of this subsection through the number of lamellae, < 60, and the spores more ornamented or more dextrinoid than *H. aurantioumbrinum*, *H. alpinum*, *H. louiseae*, *H. minus*, *H. pallidolabiatum* and *H. perexiguum* and usually without a very strong distinct papilla, unlike *H. alpinum*. It can be separated from other lowland species in this section through the number of full length lamellae 30–60, the spore length > 11 µm, the smallish stature and the dextrinoidity of the spores. In the past this species has probably been confused with *H. vaccinum* and perhaps *H. pusillum* in dunes and lowland areas and with *H. minus* in alpine and arctic habitats. Both ITS and *RPB2* distinguish this species.

Originally, we referred to this taxon as 'Hebeloma cephalotum' as it matched closely with the description of *H. vaccinum* var. *cephalotum* Enderle & Vesterh. in Enderle (2004). However, as mentioned above, we have examined the holotype of this species (M M-0155166) and it appears to be a mixed collection. While some of the fragments we have examined may

belong to *H. salicicola*, all fragments we have sequenced are of *H. pusillum*, which is certainly present, from a morphological perspective, in the material deposited. Similarly the microscopic morphological analysis we have carried out also corresponds to *H. pusillum*. Trying to resolve this, we also examined an isotype (C C43996) but this collection, based on both molecular and morphological study is *H. vaccinum*. We do believe that the material of *H. vaccinum* var. *cephalotum* studied by J. Vesterholt corresponded to the taxon we have called *H. salicicola*, however, given the mixed nature of both the holotype and the isotype of *H. vaccinum* var. *cephalotum* we conclude that it is safer to describe this taxon as new.

DISCUSSION

The evolutionary distance, on the whole small, between all members of *H.* subsect. *Denudata* and particularly between some members of the *H. crustuliniforme* complex, suggest that, in spite of the demonstrated differentiation between clades and morphotypes, their presumably short evolutionary history may not have been sufficient for species to be fully differentiated in all characters. The analyses presented here give an impression of how well the species characterized above are supported by different analyses. With a full dataset of five genes, all species, apart from *H. alpinum*, are monophyletic and all, apart from *H. minus*, receive bootstrap support. Missing data introduce uncertainty in the results, which could not be avoided, as we were aiming for the best possible geographical, morphological and ecological representation for every species on the basis of the available material. Confronted with probable coalescence and possible hybridization, leading to an increased probability of recombination, phylogenetic analysis methods are not the most appropriate analysis methods. Both coalescence-based species tree methods or population genetic methods might be more appropriate. These kinds of analyses are geared towards haploid and unlinked markers and call for knowledge of population parameters; requirements that the available data do not readily fulfil. While we are still in the process of exploring the applicability of these methods, we do not expect the results will be very different from the results presented here with regard to species delimitation.

The data presented above show that the DNA barcode (ITS) is, among the loci tested, perhaps the least well suited for discriminating between taxa of *H.* subsect. *Denudata*. A cut-off value of 3 % allows the separation of some *H. pusillum* and some *H. eburneum* sequences from the rest of the sequences, but the overwhelming majority of ITS sequences are more similar than 97 % and defied species identification with a 3 % cut-off. It is obvious from Table 1 that a blast search based identification based on any cut-off values of ITS similarity is bound to fail, if requiring all matches below a certain cut-off value to be assigned to the same species. In spite of this, complete ITS sequences can usually be correctly assigned to a species, because normally the great majority of very good matches belong to a single taxon and the great majority of sequences belonging to other species have noticeably worse scores. Furthermore, once the ITS data will be entered into the species hypotheses clustering of UNITE (Kõljalg et al. 2013), we will be able to annotate the sequences in a way, so that the users of this database will be aware of the identification caveats within this group of species.

The ML results suggest that the *RPB2* is the most powerful single locus for recognizing species, but *H. aanenii*, *H. alpinum* and *H. geminatum* do not form monophyla. Obviously, this result may be biased due to the smaller number of sequences in the *RPB2* dataset as opposed to some others, namely ITS.

In our analyses, we found eight new species within *H.* subsect. *Denudata*, for which old names were not available. They are

described above as *Hebeloma aanenii*, *H. aurantioumbrinum*, *H. geminatum*, *H. louiseae*, *H. luteicystidiatum*, *H. pallidolabiatum*, *H. perexiguum* and *H. salicicola*, alongside descriptions of our concepts of known species (*H. alpinum*, *H. eburneum*, *H. helodes*, *H. lutense*, *H. minus* and *H. pusillum*). For all of these taxa, type material was studied. For the concept adopted for *H. crustuliniforme* (*H. crustuliniforme* (Bull.) Quél. emend. Vesterh., U. Eberh. & Beker) see Vesterholt et al. (2014). Molecular results suggest that the *H. crustuliniforme* complex includes nine taxa in Europe (*H. aanenii*, *H. alpinum*, *H. crustuliniforme*, *H. eburneum*, *H. geminatum*, *H. louiseae*, *H. minus*, *H. pallidolabiatum* and *H. salicicola*), of which *H. alpinum* is the least distinctive in molecular terms (followed by *H. minus* and *H. geminatum*), and *H. aanenii* and *H. geminatum* in morphological terms. Above, in the species comments of the taxonomy part of the paper, we discuss the lines of evidence leading to the acceptance of the respective species and how the species can be recognized.

The species classification adopted here is superficially in stark contrast to the taxonomical conclusions of Aanen & Kuyper (2004) who, also with regard to the determination of species by morphology alone, included *H. aanenii*, *H. alpinum*, *H. crustuliniforme*, *H eburneum*, *H. geminatum* and *H. salicicola* as adopted here in *H. crustuliniforme*. *Hebeloma helodes*, *H. luteicystidatum*, *H. lutense*, *H. minus*, *H. pusillum* and some other taxa outside of *H.* subsect. *Denudata* as defined here were merged in *H. helodes*. The latter species (*H. helodes* sensu Aanen & Kuyper 2004) was entirely based on morphology, not on intercompatibility test results, adopting a wide morphological concept. This concept is also not supported by the results of molecular analyses presented here, clearly showing a number of well-supported taxon clades, matching with morphological and ICG data.

Another important reason for the different morphological conclusions between this work and that of Aanen & Kuyper (2004) is that they used cheilocystidia length and width where here width ratios between different parts of the cheilocystidia were used to better capture cheilocystidia shapes. This does also explain why their concept of *H. helodes* does not fit into our concept of *H.* subsect. *Denudata*, which is strongly based on cheilocystidium shape. In addition, Aanen & Kuyper (2004) appear to have used size classes for spore measure means rather than the means of the measures themselves.

In the case of *H. crustuliniforme* sensu Aanen & Kuyper the species delimitation of Aanen & Kuyper (2004) was also related to intercompatibility between some members of different ICGs and the observation of a strain of ambiguous ICG membership. Their (Aanen & Kuyper 2004) reluctance to split *H. crustuliniforme* and *H. helodes* sensu auct. was further fed by molecular results based on ITS and IGS (intergenic spacer of the nuclear ribosomal RNA genes) data that – analoguous to some results presented here – show that neither all ICGs nor all morphospecies readily form monophyletic clades in gene trees.

However, taking a different view on the intercompatibility test results, one could also argue as we are doing here: If indeed the great majority of basidiomes can unambiguously be assigned to a single ICG (Aanen & Kuyper 1999), it stands to reason that at least some ICGs do represent biological species, which are then likely to have evolved a distinct morphology. We did not use ICG membership as a criterion for species delimitation. In spite of occasional intercompatibility between different ICGs (Aanen & Kuyper 1999) in the core of the *H. crustuliniforme* complex (*H. aanenii*, *H. alpinum*, *H. eburneum*, *H. geminatum*), there is good correspondence between ICG data and the species limits used here, in that all collections belonging to the same ICG are assigned to the same species, none of

the species includes more than one ICG. (The special case of collection WBS 9605, database record HJB12498, compatible ICG3 and ICG4 and included in the same clade as other ICG4 members, is discussed below in more detail.) Eleven of the species recognized by us here appear to correspond to ICGs of Aanen & Kuyper (1999) and should accordingly be biological species. Apart from *H. aanenii* and *H. geminatum* all of these species can also be unambiguously separated based on morphology. This could be taken as an indication that hybridization, i.e. crosses between different ICGs, does not play a major role in nature. A contributing factor could well be that the two species corresponding to the most promiscuous ICGs according to Aanen & Kuyper's (1999) results, *H. alpinum* and *H. eburneum*, though widespread and common, are separated by their respective ecologies, in that the first is restricted to arctic and alpine areas where the latter does not occur. This is rather suggestive of speciation by isolation in progress, with residual intercompatibility in some genotypes (Aaenen et al. 2000). The intercompatibility results (Aanen & Kuyper 1999) indicated possible, but less clear, intercompatibility of representatives of *H. geminatum* and *H. aanenii* and *H. alpinum* and *H. aanenii*. Both hybridisation and coalescence might be responsible for the lack of monophyly in some taxa and species clades in the shape of badly supported short-stemmed monophyla. The example of *H. alpinum* WBS 9605 (ICG 3/4) shows that on the basis of the molecular and morphological data we obtained, genotypes with exceptional biological intercompatibility cannot be detected. We do not know whether WBS 9605 could have produced viable offspring with a member of ICG3 and how the progeny might look. However, if viable offspring resulted, one would expect contradictions between morphology and genotype as in HJB11051, which is morphologically *H. alpinum* (ICG4) and genetically, based on five markers, *H. geminatum* (ICG1). Further, if HJB11051 was the direct product of hybridization, one would expect phased nuclear markers to belong to different taxon clades. This is not the case (results not shown). It is the only collection of *H. alpinum* we have from Iceland, and, given the relative vicinity of Iceland with Greenland, and given that we know that *H. alpinum* as delimited in Europe exists in Greenland, this might be an indication that the species delimitation between *H. geminatum* and *H. alpinum* as it works in Europe, might not do so with American material. In all of the 273 collections we examined molecularly, HJB11051 was the only one where a clear contradiction between genotype and morphology occurred.

It is tempting to see a key property of the *H. crustuliniforme* complex, actually of all species of *H.* subsect. *Denudata*, in their association to *Salix* ssp. While all the taxa of this subsection have been recorded with *Salix*, some of the taxa seem to only associate with this host genus (or with *Salicaceae*), see Table 3. Though the results reported by Tedersoo et al. (2013) implicitly caution against assuming that ectomycorrhizal taxa associating with one species of *Salix* would automatically form associations easily with other species of *Salix*, association with *Salix* could be considered an advantage to thrive during the climatic changes that took place in the northern hemisphere in the Pleistocene, and also to acquiring a Palearctic distribution.

Hebeloma aurantioumbrinum, one of the less common species in Europe, has been found in North America. *Hebeloma alpinum* is known from Greenland. It is likely that at least the cold-adapted taxa like *H. alpinum*, *H. minus* and possibly also *H. aanenii*, *H. geminatum* and *H. salicicola* are circumpolar species. Sequence data from the US and Canada is publicly available, but as the results presented here show, ITS diversity is not a reliable predictor for species diversity in this group of fungi. Reviewing a number of environmental sequencing studies of ectomycorrhizal fungi from arctic northern hemisphere

environments, Timling & Taylor (2012) reported that *Hebeloma* spp. are among the fungal lineages that were recovered in all studies with at least moderate frequencies. Based on a 97 % cut-off value they concluded, that almost 3/4 of the arctic phylotypes of ectomycorrhizal agarics can also be found outside the arctic. The results presented here for *H.* subsect. *Denudata* cast serious doubt on the appropriateness of such a statement, firstly with view to methodology – a 97 % cut-off value is far too crude to capture spatial genetic structure in the genus *Hebeloma*; and secondly with regard to conclusions. There is a species overlap between arctic and alpine places, but the species overlap between arctic and temperate or boreal areas is small, if frequencies are also considered. Taxa that allegedly occur in both biomes (i.e., *H. aanenii*, *H. aurantioumbrinum*, *H. geminatum*, *H. minus*, *H. salicicola*), have a strong preference either for the arctic/alpine areas or lesser latitudes and altitudes, and must, according to our database, be considered rare in their less favoured habitats. It is of course possible that the taxa that were so far only collected in Svalbard (*H. louiseae*, *H. pallidolabiatum* and *H. perexiguum*) are North American taxa and perhaps not restricted to arctic or alpine habitats. Given the low level of interspecific variation in *H.* subsect. *Denudata*, and the probability of intercompatibility of at least some members of some species to mate with members of other taxa, it appears unlikely, that putative North American taxa have persisted unchanged in Svalbard since the islands' isolation, given the geological and vegetation history of the islands (summarized by Geml et al. 2012). Long-distance dispersal may or may not be frequent from boreal or temperate regions to northern arctic environments (Geml et al. 2012), but one could argue that not dispersal but climatic selection does play a key role in the arctic *Hebeloma* flora.

Dispersal in the other direction, from the arctic to boreal and temperate zones, might be a lot more successful, when looking at the example of *H. alpinum*. This strictly arctic/alpine taxon is a rather common species (around 80 records on the database) and associates with *Salix* or *Dryas*. It is most difficult to distinguish molecularly and could be confused with *H. aanenii*, *H. eburneum* and *H. geminatum*, which have wide host spectra and do not (typically) occur under arctic/alpine conditions. The situation is characterised by shared alleles and there is little evidence of shared divergence within *H. alpinum* compared to its temperate sistertaxa which all show specific differentiation in a subset of the markers used. Incidentally, *H. alpinum* very likely corresponds to the most promiscuous ICG (Aanen & Kuyper 1999).

Compatibility is a driver of speciation (Aanen et al. 2000). According to the results of Aanen and co-workers (Aanen & Kuyper 1999, Aanen et al. 2000) it is a quantitative rather than purely qualitative trait. This is true for pairings within the same ICG as well as between members of different ICGs. Loss of compatibility may be precluded or followed by differentiation in morphology and genetic divergence in parts of the genome not directly involved in intercompatibility. While speciation and divergence are still in progress, every individual is likely to be a mosaic of genes and traits with different evolutionary histories. It appears likely that in the ancestral population of *H.* subsect. *Denudata* and in particular the ancestor of the *H. crustuliniforme* complex (with the possible exception of *H. crustuliniforme* itself) loss of compatibility and divergence in other characters did not always follow the same pattern. Possibly *H. alpinum* has maintained most of the traits of this ancestral population, retaining more ancestral variation, staying faithful to arctic/alpine habitats and associating with *Dryas* and *Salix*, but not with conifers or other broadleaves (non-arctic/alpine *Salix*) and preserving the highest level of intercompatibility (Aanen & Kuyper 1999). Based on the data we have it is impossible to unambiguously trace

the evolutionary history of the species of *H.* subsect. *Denudata*. The climatic oscillations during the Quaternary might even have arrested the divergence of *H. alpinum* and intercompatible taxa, potentially bringing intercompatible members of different taxa in touch that normally would live in separate habitats or geographically distant areas, i.e. Europe and America. On a side note, it is remarkable that the closest relative of *H.* sect. *Denudata*, *H. mediorufum* (Rees et al. 2013) associates with *Nothofagus* and seems restricted to New Zealand, where *Salix* is not endogeneous.

On an evolutionary timescale, species are transient. In cases like the *H. crustuliniforme* complex and related taxa it is to an extent subjective whether to consider divergence and non-compatibility as sufficiently advanced to separate groups of organisms into species. One might argue that it does not make sense to recognize or even describe species that are likely to be unidentifiable without huge effort and using identification tools that may not be widely used today. It may be argued that a consequence is that misnamed sequences and collections might crowd databases and be misleading rather than elucidating. Indeed, it is also possible that what we describe here as species may turn out to be somewhat differentiated sub-populations of to-date unstudied larger entities that are better suited to represent species. However, we believe that the dataset that forms the basis of this study is sufficiently extensive and sufficiently consistent to recognize entities, here described as species, that have diverged in the context of the climatic, geological and biological history of Europe.

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