

## *Hebelomina* (Agaricales) revisited and abandoned

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**Background and aims** – The genus *Hebelomina* was established in 1935 by Maire to accommodate the new species *Hebelomina domardiana*, a white-spored mushroom resembling a pale *Hebeloma* in all aspects other than its spores. Since that time a further five species have been ascribed to the genus and one similar species within the genus *Hebeloma*. In total, we have studied seventeen collections that have been assigned to these seven species of *Hebelomina*. We provide a synopsis of the available knowledge on *Hebelomina* species and *Hebelomina*-like collections and their taxonomic placement.

**Methods** – *Hebelomina*-like collections and type collections of *Hebelomina* species were examined morphologically and molecularly. Ribosomal RNA sequence data were used to clarify the taxonomic placement of species and collections.

**Key results** – *Hebelomina* is shown to be polyphyletic and members belong to four different genera (*Gymnopilus*, *Hebeloma*, *Tubaria* and incertae sedis), all members of different families and clades. All but one of the species are pigment-deviant forms of normally brown-spored taxa. The type of the genus had been transferred to *Hebeloma*, and Vesterholt and co-workers proposed that *Hebelomina* be given status as a subsection of *Hebeloma*. In the meantime, *Hebelomina*-like *Hebeloma*, belonging to seven different species in three different sections, have been found. We conclude that *Hebelomina* should be abandoned as a supraspecific taxon.

**Key words** – Agaricales, albinotic forms, basidiomycetes, *Gymnopilus*, *Hebeloma*, *Hebelomina*, *Hydropus*, *Mycopan*, *Rapacea*, *Tubaria*.

### INTRODUCTION

In 1933 Maire discovered a mushroom that appeared, on the face of it, to be a *Tricholoma* but which he judged to be a *Hebeloma* with hyaline spores; he erected a new genus for it, *Hebelomina* (Maire 1935). He described his collection as *Hebelomina domardiana*, which became the type for this genus (see fig. 1). The genus remained with just one species until 1946, when a second species was added, *Hebelomina microspora* (Huijsman 1946). In fact, the name of this second species was invalidly published due to the lack of a Latin diagnosis (Art 39.1, McNeill et al. 2012) and was not rectified until the name was replaced by *Hebelomina neerlandica* (Huijsman 1978). Singer (1986) in his study of the Agaricales accepted Maire's view that *Hebelomina* was closely related to *Hebeloma* and placed the genus with *Hebeloma* in the Cortinariaceae. He commented that the genus was “probably ectomycorrhizal”. Singer was only able to study original material of *Hebelomina neerlandica* as the

type of *Hebelomina domardiana* was ‘lost’ at that point in time. Moncalvo et al. (2002), also without access to original material of the type species, demonstrated that *Hebelomina neerlandica* was closely associated with *Gymnopilus* based on collection L0490460 in their tree. The authors concluded that *Hebelomina* is derived from *Gymnopilus*, another dark-spored genus, instead of *Hebeloma*. Because of the placement of their sequence of *Hebelomina neerlandica* in a non-ectomycorrhizal clade they concluded that *Hebelomina* was probably non-mycorrhizal.

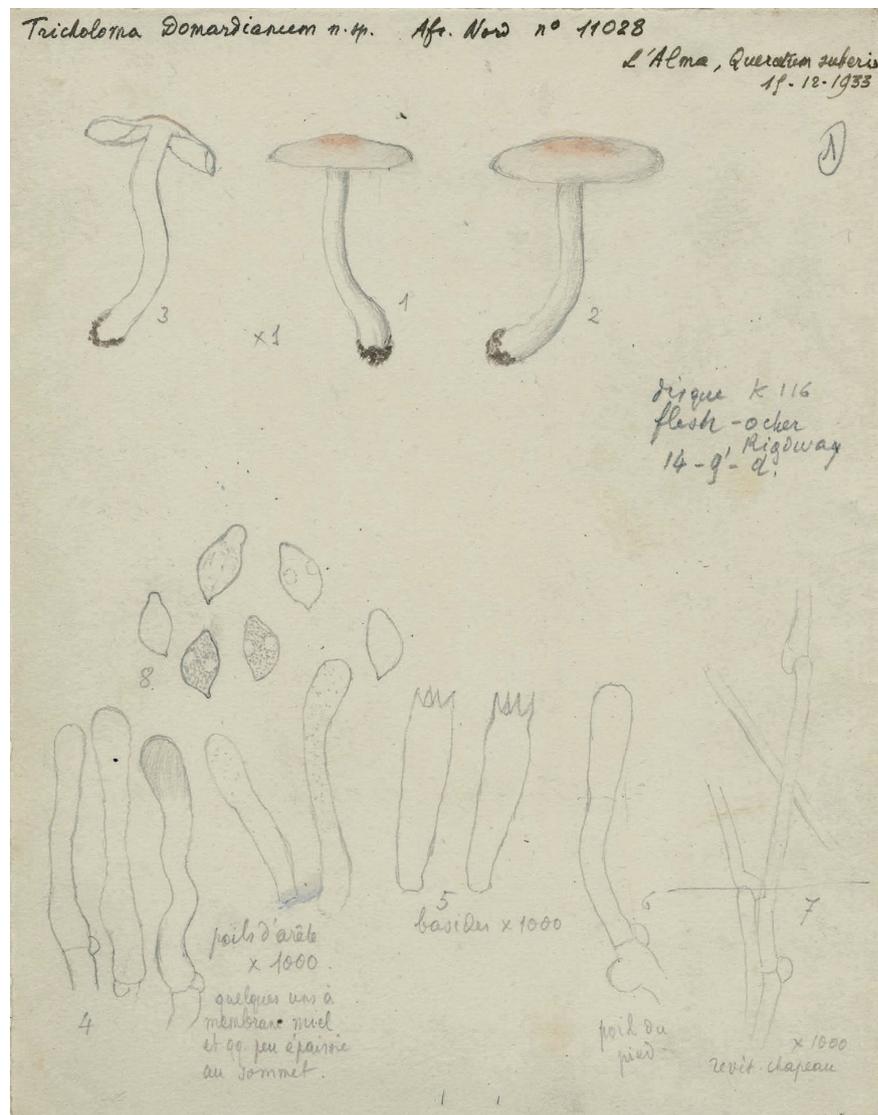
*Hebelomina domardiana* was transferred to *Hebeloma*, which made *Hebelomina* a synonym of *Hebeloma* (Vesterholt 2005). Without access to the original material of Maire – the material was apparently lost – the description of *Hebeloma domardianum* given by Vesterholt (2005) was based on an Estonian collection that he believed to be conspecific. This collection from Estonia gave rise to a partial ITS sequence that placed the collection within *Hebeloma* sect. *Denudata*.

Since this taxon is the type species of the genus *Hebelomina*, Vesterholt and others (in Vesterholt 2005) proposed that *Hebelomina* be given status as a subsection of *Hebeloma* sect. *Denudata*. Vesterholt (2005) was well aware that at least one other species of this genus *Hebelomina* was not a *Hebeloma*, acknowledging that *Hebelomina neerlandica* is more likely to be an albinotic *Gymnopilus*. Indeed, this latter taxon was recombined as *Gymnopilus neerlandicus* (Huijsman) Contu (Cittadini et al. 2008). With regard to his collection from Estonia, Vesterholt was at the time not aware that the resulting ITS sequence actually placed his collection within the *Hebeloma hiemale* clade (Beker et al. 2016).

Meanwhile Fraiture & Hayova (2006) recognised that the genus *Hebelomina* is heterogenous, reviewing the conclusions of Moncalvo et al. (2002) and Vesterholt (2005). They noted that, although the genus *Hebelomina* had been included in *Hebeloma*, it would not be possible to transfer all of the *Hebelomina* species to *Hebeloma*. Reviewing further *He-*

*beloma domardianum* collections from Lithuania and Latvia (Urbonas et al. 1986), Fraiture & Hayova (2006) reasoned that it appeared likely that different collections from the three Baltic states may well belong to the same species, but that it was unlikely to be conspecific with the type of *Hebelomina domardiana*, a collection from a *Quercus suber* wood in Algeria.

Fortunately, the holotype for *Hebelomina domardiana* has recently been found. During our visit to MPU we were able to locate the original holotype material that had been placed within the *Tricholoma* section of the herbarium (see fig. 1). We made a morphological examination of the holotype, but, unfortunately, we have not been able to amplify DNA and generate an ITS sequence. However, we have no doubt that this taxon lies within *Hebeloma* subsect. *Clepsydroidea* and corresponds to *Hebeloma fragilipes* (Beker et al. 2016).



**Figure 1** – Université de Montpellier, Herbar MPU (SPH) drawing of the holotype of *Hebelomina domardiana* Maire (*Hebeloma domardianum* (Maire) Beker, U.Eberh. & Vesterh.) (MPU310735) by R. Maire. Reproduction kindly supplied by the herbarium of the Université de Montpellier.

In this paper, we aim at assembling all available knowledge on taxa that have at some time been part of *Hebelomina*. We are aware of six legitimately published *Hebelomina* species plus one more published post 2005 as a *Hebeloma*, *Hebeloma pamphiliense*. We have examined the types of all these species other than *Hebelomina maderaspatana* and *Hebelomina pallida*, for which we have only studied the protologues. We have also examined a further 12 collections of *Hebelomina*-like mushrooms (for examples see fig. 2). In all, therefore, we have studied 17 such collections. Of these, ten are *Hebeloma* species, representing seven different *Hebeloma* taxa; five are *Gymnopilus* species representing at least two different taxa; one is likely to be a *Tubaria* sp.; one is *incertae sedis* and undetermined to generic level.

It is clear that *Hebelomina* is polyphyletic. The type species is placed in the genus *Hebeloma*, and thus we treat *Hebelomina* as a synonym of *Hebeloma*. Our studies on the genus *Hebeloma* allow us to assign some *Hebelomina* species and collections to species of *Hebeloma*. The remaining species of *Hebelomina* we were able to study appear to belong to *Tubaria*, *Gymnopilus* and another, as yet undetermined and unplaced genus, which is discussed in the context of *Hydropus* and *Mycopan*. Some of the transfers have already been made. As we are uncertain of the circumscription and species level taxonomy of these genera, we have refrained

from any further taxonomic transfers of species to other genera. We summarize our information and conclusions under Taxonomic Comments. Formal nomenclatural and taxonomic information are given in the Taxonomic Conspectus.

One of the challenges of writing this paper has been the selection of which taxon names to use to refer to certain species, taxonomic types or collections. Within this article, the latest transfer of a species to a genus is treated as the current name and this is the name we have used in the Taxonomic Conspectus. We have tried to follow this convention apart from in the species headings in the Taxonomic Comments part. There we use the genus name *Hebelomina* (if available) to indicate certain morphological traits. Where we refer to collections we have not seen ourselves, we adopt the taxon names used in the herbarium, in the sequence submission or applied in publications pertaining to the material.

### The *Hebelomina* syndrome

The dimensions, shape and colour of the basidiospores are important characters in the taxonomy of many genera of Agaricales, including *Hebeloma*. Within *Hebeloma* the spores are usually warty rough, and the ornamentation is developed within the epitunica (Cléménçon 1977) or what is equated to the perispore by Besson & Bruchet (1972). Unfortunately,



**Figure 2** – *Hebelomina*-like collections: A & B, *Hebeloma laetitia* HJB13642; C, *Hebeloma vaccinum* HJB11012; D, *Hebeloma sinapizans* GC00110402; E, *Gymnopilus* cf. *penetrans* HJB11491. Photos P. Cullington (A–B), H.J. Beker (C), G. Corriol (D) and A. de Haan (E); photos A–D reproduced from Beker et al. (2016).

the terminology of the spore layers by different authors is somewhat confused. A widely applied terminology was presented in the Dictionary of Fungi (Kirk et al 2008). They define the spore wall (eusporium) structure working outwards as follows:

- endosporium (endospore, corium), usually thin and the last to develop during sporogenesis;
- episporium, the thick fundamental layer which determines the shape of the spore;
- exosporium (exospore, epitunica, trachytectum, tunica), a layer derived from the episporium but chemically distinct and frequently responsible for the ornamentation and the outer spore layer if the following layers disappear;
- perisporium (mucostratum, myxosporium), a layer, frequently fugacious, enveloping the whole spore;
- ectosporium (sporothecium), hardly visible outer layer.

The first three layers are the spore wall proper. The perisporium and ectosporium are of extrasporal origin (Kirk et al. 2008) and, within *Hebeloma*, are often seen to loosen around the spore; we will here refer to them collectively as the perispore.

Within *Hebelomina* the intraspecific dimension and shape of the spores is relatively constant, however, the interspecific variation is quite large. This also appears to be true for the dextrinoidity of the spores, which can vary quite markedly from species to species but appears reasonably constant within a species. However, the colour of the spores and the ornamentation of the spores across all species appear rather constant. *Hebelomina* spores, under the microscope, appear colourless, i.e. hyaline. The spore deposit is whitish. We have only once seen a spore deposit from such a collection. Fraiture & Hayova (2006), Huijsman (1978), Volders (1997) and others commented that it appeared difficult to obtain a good spore print because the spores, although usually produced in large amount, remain on the gills and when it was possible to obtain a spore deposit from a *Hebelomina* collection they observed that it was not pure white but very pale brownish. With regard to the ornamentation there does not appear to be any. Fraiture & Hayova (2006) noted that *Hebelomina* often had basidiomes that were whitish or very pale, at least when young, and that the spores were very particular, being whitish and smooth under the light microscope. They conjectured that the presence of those special features in the different *Hebelomina* species could be explained by a mutation, inducing the loss of pigmentation of the carpophores and changing the brown and ornamented spores of *Hebeloma* and *Gymnopilus* into whitish and smooth “hebelominoid” spores.

Huijsman (1978) and Beker et al. (2016) suggested that the spore has formed but not the exospore and perispore. It appears that a deviation from the normal development causes the exospore (or at least that layer of the spore wall made up of pillars and spaces between them that account for the ornamentation) and the perispore not to develop or to develop only in a very rudimentary fashion. Certainly, for the *Hebelomina*-like collections we have studied, the spores have the normal length that would be expected for that species (or sometimes slightly shorter) and the dextrinoidity of the spores (that apparently arises within the episporium and not on the exospore and perispore) corresponds to the norm for the species. It appears that it is just the spore wall that has not properly formed

and hence the spores are smooth and hyaline with no obvious perispore and no ornamentation. The cheilocystidia and other basidiome structures are quite typical for the given species. However, this does not fully explain why *Hebelomina*-like collections have basidiomes whose pileus appears paler than is typical for that species (see fig. 2). It is interesting to note that we have two species for which *Hebelomina*-like basidiomes have been collected from more or less exactly the same spot but in different years.

## MATERIALS AND METHODS

Details, including authority names, of *Hebelomina* and *Hebelomina*-like collections discussed in this paper are given in the Taxonomy part of the paper. All other authority names of fungi can be found in MycoBank (Robert et al. 2013, www.mycobank.org) or Index Fungorum (Index Fungorum Partnership 2017, www.indexfungorum.org).

Methods for studying the morphology and for obtaining DNA sequence data from fungal specimens have been described before by Beker et al. (2016) and Eberhardt et al. (2016) and references therein. Sequences newly published in the context of this study have been submitted to GenBank (accession no. MF039233–MF039287). Herbarium, collection accession numbers, country, collector and collection date are given in the GenBank records. Other sequences were downloaded from GenBank and UNITE (<https://unite.ut.ee>, Kõljalg et al. 2005).

Five datasets were assembled. There are two datasets of subgroups of *Hebeloma*. The *Hebeloma* sect. *Denudata* dataset is based on a pruned six-loci-dataset (fewer collections per species considered, ITS, mitSSU V6 and V9 regions, *TEF1a*, *MCM7* and *RPB2*) of Eberhardt et al. (2016), enriched by sequences belonging to *Hebelomina*-like members of *Hebeloma* sect. *Denudata*. The other dataset represents *Hebeloma* sect. *Sinapizantia* and sect. *Velutipes* and is based on the pruned five-loci-dataset (ITS, mitSSU V6 and V9 regions, *TEF1a*, and *RPB2*) assembled by Grilli et al. (2016).

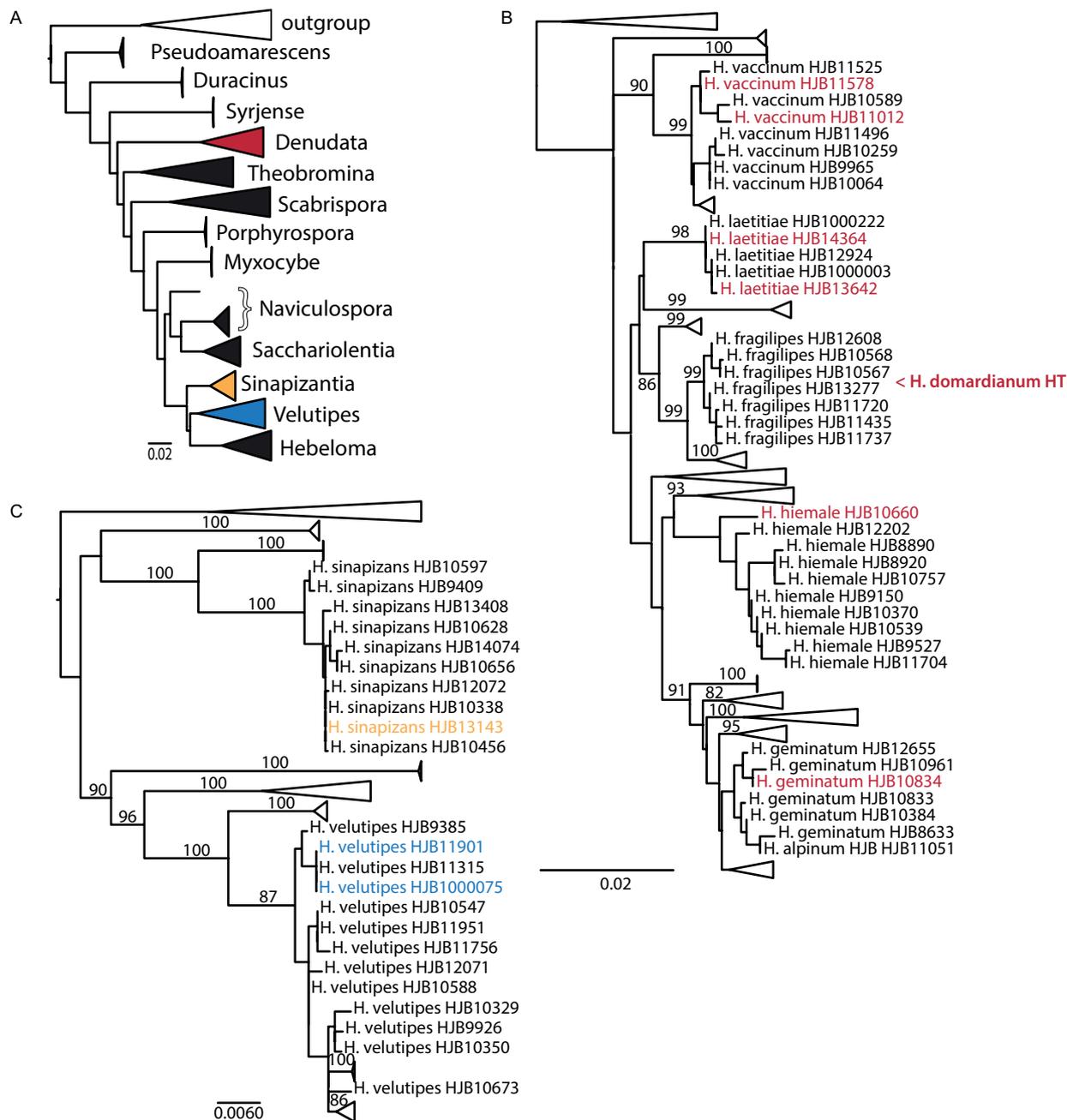
One dataset each was assembled from ITS sequences for the genera *Gymnopilus* and *Tubaria*. The *Gymnopilus* dataset was assembled using data from diverse authors and studies (i.e. Moser et al. 2001, Rees et al. 2002, 2004, Guzmán-Dávalos et al. 2003, 2008, 2009, Holec 2005, Boyle et al. 2006, Arhipova et al. 2012, Osmundson et al. 2013, Holec et al. 2016). After preliminary tests, sequences were omitted from the analysis that did not further illuminate the putative taxonomic placement of *Hebelomina*-like *Gymnopilus* collections. These included sequences that were not identified to species, some non-European taxa, the majority of sequences from material of non-European origin as well as a number of sequences from European material. The *Tubaria* dataset includes ITS data from diverse authors (i.e. Matheny et al. 2007, Antonín et al. 2012, Vizzini et al. 2014, Deepna Latha et al. 2016) and newly generated sequences.

The last dataset was assembled to illuminate the placement of the type sequence of the *Hebelomina*-like *Hebeloma microsporium*. BLAST searches against GenBank and UNITE of ITS and LSU data suggested that, at the time (Feb. 2017), there were no ITS data of closely related species pub-

lished, either named or unnamed. The best named matches were with a New Zealand sample of *Pleurella ardesiaca* (JQ694106) and less than 90% similarity (618 bp), followed by *Baeospora myosura* with at most 83% similarity (636 bp). The dataset (concatenated data of ITS, LSU and SSU; not all loci for all collections sequenced) was selected after preliminary tests with datasets published by Moncalvo et al. (2002), Bodensteiner et al. (2004) and Matheny et al. (2006, 2015), emended by selected data from other works (Wilson

& Desjardin 2005, Padamsee et al. 2008, Sánchez-García et al. 2014), and newly generated data of *Hydropus* collections.

Alignments of DNA sequences were done in MAFFT version 7 (online, <http://mafft.cbrc.jp/alignment/server/>) using the E-INS-i option (Katoh & Standley 2013) with slight adjustments by eye. Maximum Likelihood analyses in RAxML versions 7 or 8 (Stamatakis 2014) were run locally or through the Cipres Portal (Miller et al. 2010), in 10 or 100 replicates, selecting the tree with the maximum likelihood, and



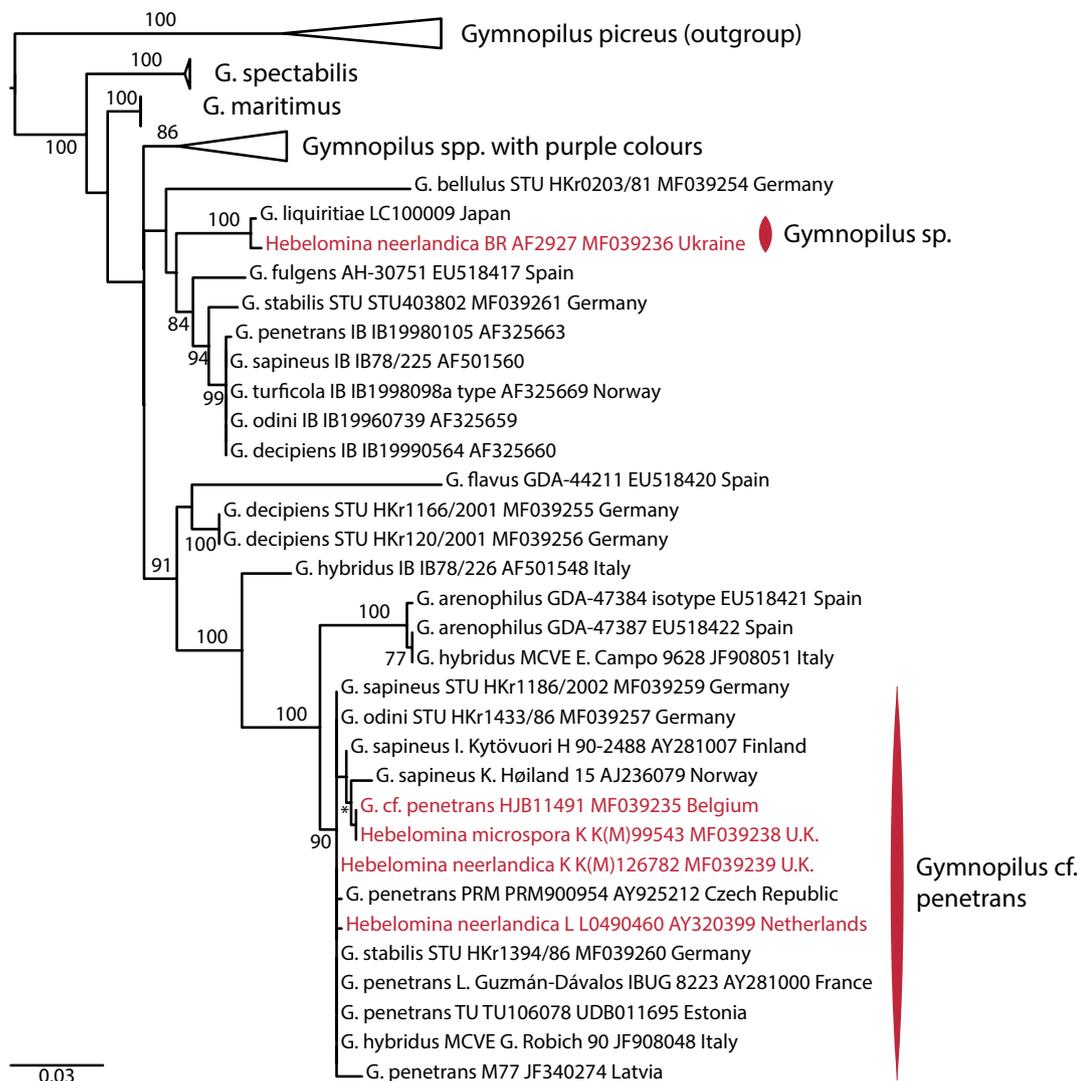
**Figure 3** – Placement of *Hebelomina*-like collections in *Hebeloma* in ML results of five or six-loci-datasets and 1000 replicates of bootstrap. A, overview of the genus *Hebeloma*, following the tree in figure 12F of Beker et al. (2016); B, *Hebeloma* sect. *Denudata*. The type of *Hebelomina*, *H. domardianum*, could not be sequenced, but has been morphologically assigned to *Hebeloma fragilipes* (see arrowhead); C, *Hebeloma* sect. *Sinapizantia* and *Velutipes*. *Hebelomina*-like collections are indicated in the colour corresponding to their respective *Hebeloma* sections.

500–1000 replicates of Fast Bootstrap. Trees were depicted using FigTree version 1.4.2 (Rambaut 2014). Alignments and trees were submitted to TreeBASE (study accession number TB2:S20948) where all GenBank accession numbers are listed, including those which were omitted from the figures. Sequence similarity values were calculated in PAUP\* (Swofford 2000) using the default settings for DNA data and pairwise alignments if only two sequences were compared, or (in the context of *Baeospora myosura*), a multiple alignment spanning the ITS1-5.8S-ITS2 between the CATT and the TTGAC motif.

## RESULTS

Maximum Likelihood analyses were done primarily to illustrate the taxonomic placement of *Hebelomina* and *Hebelomina*-like collections. The results of the phylogenetic analyses are shown in figs 3–6. Clades without immediate interest for

this study have been collapsed. Fully resolved trees can be viewed and downloaded from TreeBASE. Taxonomic clade annotations in fig. 3 follow our own studies (Beker et al. 2016). HJB-numbers (Beker et al. 2016) refer to collections held in the private collection of H.J. Beker, or to database records of our project database (Beker et al. 2016). Identifications in fig. 4 are a consensus between submitter information and the taxonomic opinion indicated by Species Fungorum (Kirk 2018). Matheny et al. (2007) and Vizzini et al. (2014) are followed in fig. 5. Sequences are identified by their GenBank or UNITE accession numbers and, where available, by collection numbers and country of origin. In fig. 6, sequences are identified by collection or AFTOL numbers referred to in GenBank accessions. Genbank accession numbers are added for collections with only a single GenBank accession available. Clade annotation in fig. 6 follows Matheny et al. (2006) and submitter information. In fig. 6, dashed lines are used for the backbone of the tree to indicate that the phylogenetic



**Figure 4** – Placement of *Hebelomina*-like collections in *Gymnopilus* according to ITS ML results with 1000 bootstrap replicates. \* – 98. Clade names are tentative. Species names of sequences follow submission or original publications. Species names are followed by (if available) herbarium abbreviation, collection or collectors number, sequence accession number and country of origin. *Hebelomina*-like collections and clades including *Hebelomina*-like collections are indicated in red.

reconstruction is necessarily unreliable considering the phylogenetic diversity within the dataset and the small number of loci.

TAXONOMIC COMMENTS

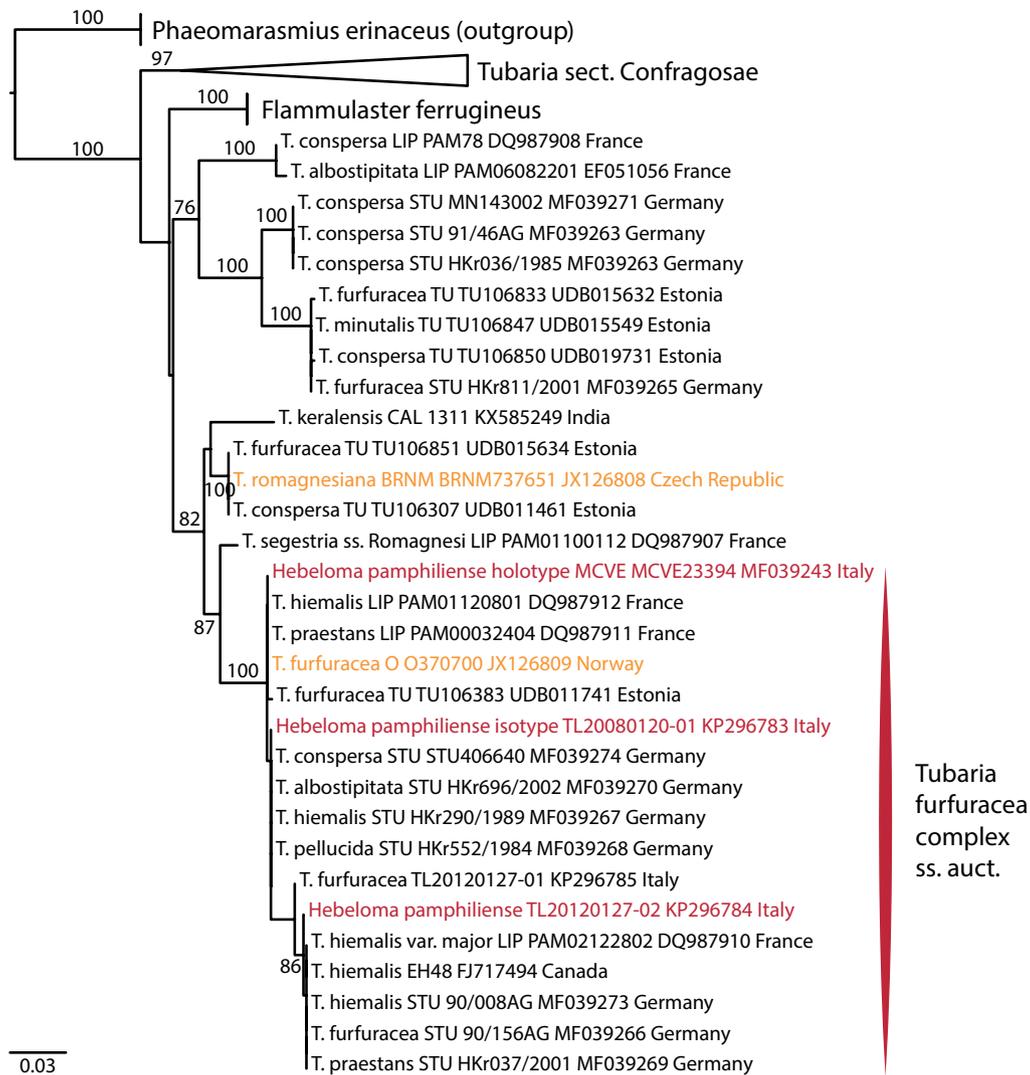
***Hebeloma* [sect. *Denudata*] subsect. *Hebelomina*** (Maire) Beker, U.Eberh. & Vesterh.

In Eberhardt et al. (2016) *Hebeloma* [sect. *Denudata*] subsect. *Clepsydroidea*, with type *Hebeloma cavipes* Huijsman was erected for members of *Hebeloma* sect. *Denudata* characterized by the shape of the cheilocystidia, which are usually on average more than 40 µm long, significantly swollen at the apex and constricted below the apex (as for all taxa within *Hebeloma* sect. *Denudata*) but then also significantly swollen in the lower half, giving the cheilocystidia an hour-

glass appearance. Often, the cheilocystidia also have thickened walls in the narrow median part of the cheilocystidium. Included in this section is *Hebeloma fragilipes*, which is conspecific with *Hebeloma domardianum* (Eberhardt et al. 2016; see also under *Hebeloma domardianum*). As described in detail below collections referred to *Hebelomina* belong to several sections of *Hebeloma* as well as to other genera. As a result, we no longer accept *Hebeloma* subsect. *Hebelomina* as a section of *Hebeloma*.

***Hebelomina domardiana*** Maire

Original material as well as Maire’s notes and watercolour drawings (fig. 1) have been recovered. While we have been unable to amplify DNA from the type, we have studied the material morphologically and are confident that this collection is conspecific with *Hebeloma fragilipes* (Beker et al.



**Figure 5** – Placement of *Hebelomina*-like collections in *Tubaria* according to ITS ML results with 1000 bootstrap replicates. Species names of sequences follow original submission or publications. Species names are followed by (if available) herbarium abbreviation, collection or collectors number, sequence accession number and country of origin. *Hebelomina*-like collections and clades including *Hebelomina*-like collections are indicated in red. Albinotic collections (*vide* Antonín et al. 2012) are indicated in orange. The indication of the *T. furfuracea* complex follows Matheny et al. (2007) and Vizzini et al. (2014).

2016). Although the spores are typical ‘*Hebelomina*’ spores, i.e. smooth and of inflated appearance, they have the correct length for *Hebeloma fragilipes*, and the cheilocystidia exhibit the typical median thickening of this species. The name *Hebelomina domardiana* was published earlier than the name *Hebeloma fragilipes*, but having hyaline spores it is hardly typical. As a result, we have made a proposal (Beker et al. 2015) to conserve the name *Hebeloma fragilipes* against the name *Hebeloma domardianum*. *Hebeloma fragilipes* has recently been recommended for conservation by the Nomenclatural Committee (May 2017). Beker et al. (2016), anticipating this decision, list *Hebeloma domardianum* as a synonym of *Hebeloma fragilipes*. This is followed in the conspectus below.

#### *Hebelomina maderaspatana* Natarajan & Raman

After much effort to loan the type from the University of Madras we received the following communication from Professor N. Raaman: “I am sorry to inform you that the holotype of *Hebeloma maderaspatana* has been lost and as Prof. K. Natarajan was expired, I could not confirm the availability of the holotype of *Hebeloma maderaspatana*.” From the original description, where the species is described as having no cystidia and with an epicutis with no mention of an ixocutis, we doubt this is a *Hebeloma* but cannot suggest to which genus this might belong.

#### *Hebelomina mediterranea* A.Gennari

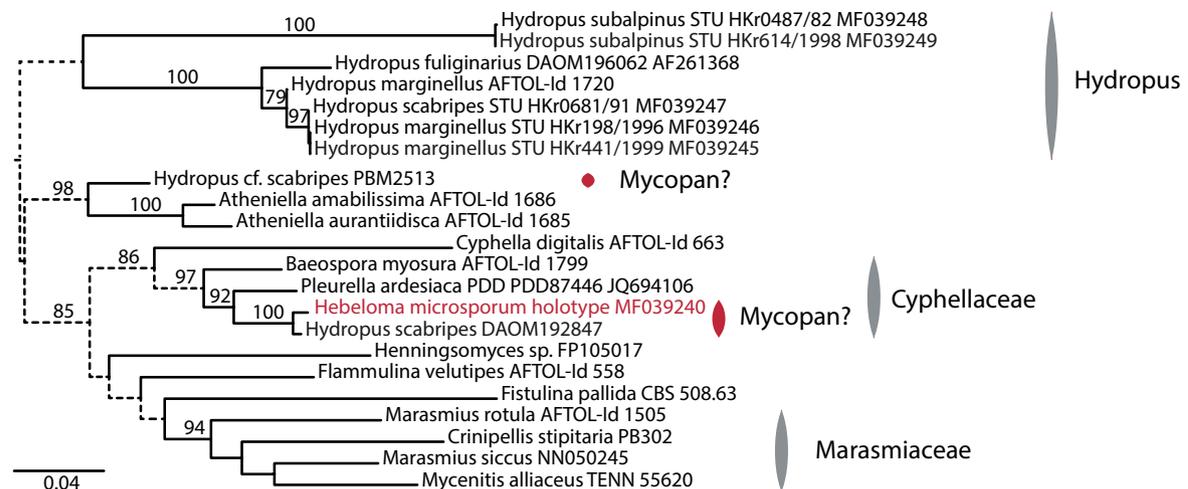
This species was originally described in *Hebelomina* and has spores typical of such collections, where the exospore and perispore have not formed, leaving smooth spores. Otherwise, including the spore length, morphologically and molecularly this is *Hebeloma velutipes* Bruchet. In Grilli et al. (2016) this was synonymised with *Hebeloma velutipes*. This is followed in the conspectus below.

#### *Hebelomina microspora* Alessio & Nonis

Alessio & Nonis (1977) originally erected this species to replace *Hebelomina microspora* Huijsman (Huijsman 1946: 31), invalidly published without a Latin diagnosis (Art. 39.1; McNeill et al. 2012). Contu (in Cittadini et al. 2008) transferred the species of Alessio & Nonis to *Hebeloma*, without true conviction (“almeno temporaneamente”) and without having seen the type. However, some information given in the original description and the protologue, in particular the amyloidity of the spores, argues strongly against the assignment to *Hebeloma*. The habitat, growing on wood, though not unseen in ectomycorrhizal formers, is not in favour of an assignment to any genus of ectomycorrhizal fungi.

We have examined the holotype of this taxon, which is not in good condition. We have not been able to find any spores. However, the cheilocystidia and pleurocystidia, the latter being numerous, do not correspond to any *Hebeloma* we have ever seen and are more like those found in taxa like *Baeospora*. While we are uncertain of the genus it is certainly not a *Hebeloma*. Molecular data from the type suggests it may be distantly related (although by no means clearly) to *Baeospora* and the Australian genus *Pleurella* that have been tentatively placed in the Cyphellaceae (Sánchez-García et al. 2014, supplement). There is no close sequence match for the ITS of this collection, but a reasonably good LSU match (99%, 601 bp) to the sequence of a collection originally identified as *Hydropus scabripes* (AF042635; Bodensteiner et al. 2004). In the molecular analysis published in this work and in fig. 6, it is in a rather isolated position in relation to other members of the genus *Hydropus*. Possibly prompted by the result of Bodensteiner et al. (2004), Redhead (2013) erected the monospecific genus *Mycopan* for *Hydropus scabripes*. If the type of *Mycopan* is indeed the same species as collection DAOM192847, then it would appear likely that *Hebeloma microsporum* is a member of *Mycopan*.

The basionym of *M. scabripes* is *Prunulus scabripes* Murrill (Murrill 1916). It was recombined by Singer (1961



**Figure 6** – Tentative placement of the holotype of the *Hebelomina*-like *Hebeloma microsporum* in the Agaricales according to ITS + partial LSU results with 1000 replicates of bootstrap. Dotted lines indicate those relationships that are the most likely to be misrepresented as the result of the taxon selection (see text).

[1962]) into *Hydropus*. The type of *M. scabripes* has been described by Murrill (1916) and Maas Geesteranus & Hausknecht (1993) cite some results of type studies of *C. Bas*. A few additional details are given in Bas (1999). Alessio & Nonis (1977) described the type they assigned to *Hebeloma microsporium*. Based on these descriptions and our own observations, it is not possible to conclude whether *M. scabripes* and *Hebeloma microsporium* may be congeners or even conspecifics. The latter does not appear likely. With regard to some important characters, even though the spore size roughly corresponds between the descriptions of Murrill (1916) and Alessio & Nonis (1977), the spore size cited in Maas Geesteranus & Hausknecht (1993) is larger. (This could be due to two-spored basidia in part of the material: Bas (1999) described the basidia as two-spored in the material he saw; neither Murrill (1916) nor Alessio & Nonis (1977) described the basidia; we saw four-spored basidia in the type material of *Hebeloma microsporium*.) The description of the spore shape differs between Murrill (1916) and Alessio & Nonis (1977), as does the description of the stipe surface at the apex (minutely and densely scabrous versus pruinose). Also important is the difference in habitat, “in grass at roadside in thin woods” (Murrill 1916) vs. growing on wood (Alessio & Nonis 1977).

We are aware of several sequenced collections identified as *Hydropus scabripes* or similar species (i.e. *Hydropus trichoderma* or *Hydropus paradoxus*), of which some – represented by PBM2513 in fig. 6 – are molecularly closely related to each other. Based on the available data and in the absence of molecular data from the type of *M. scabripes*, we suspect the majority opinion is that, if the type of *M. scabripes* was sequenced, it would fall into this group. However, we have come across a number of presumably misidentified collections of *Hydropus scabripes* (data not published) of widely differing taxonomic associations. A single probably misidentified collection (STU HKr0681/91), originally identified as *Hydropus scabripes*, is even closely related to DAOM196062, allegedly representing the type species of *Hydropus*, *Hydropus fuliginarius*. None of the other sequences identified as *Hydropus scabripes* (*Hydropus paradoxus*, *Hydropus trichoderma*) is closely related to *Hebeloma microsporium* or *Hydropus scabripes* DAOM192847 (fig 6). Thus, not knowing the rationale behind Redhead’s (2013) erection of *Mycopan*, it is not clear to what genus *Hebeloma microsporium* should be assigned, but it is clearly not a member of *Hebeloma*. Following the recommendations of Vellinga et al. (2015), it would be premature to make any taxonomic changes or erect a new genus at this time. For want of a better name we follow Contu (in Cittadini et al. 2008) and list the species in the *Conspetus* as *Hebeloma microsporium*.

### *Hebelomina neerlandica* Huijsman

We have studied the holotype and, while we have not been able to generate an ITS sequence, we have no doubt that this is a species of *Gymnopilus* P.Karst. The original description (Huijsman 1978) described the habitat as fallen branchlets of *Pinus sylvestris*. This would be typical for lignicolous saprotrophes. The yellow trama, the small ellipsoid spores, the epicutis without ixocutis and the shape of the cheilocystidia

all indicate *Gymnopilus*. The formal transfer to this genus was done by Contu in Cittadini et al. (2008).

### *Hebelomina pallida* Dessi & Contu

This species is described as growing on the wood of *Eucalyptus*. It is not a *Hebeloma* according to the protologue. Contu (in Cittadini et al. 2008) transferred the species to *Gymnopilus*, based on its similarity to *Gymnopilus neerlandicus* (*Hebelomina neerlandica*) and its association in the field with numerous basidiomes of *G. cf. penetrans* on wood, a *Eucalyptus camaldulensis* stump. Unfortunately, and despite many requests, we have been unable to loan the type and hence cannot comment further on this taxon.

### *Hebeloma pamphiliense* Cittadini, Lezzi & Contu

This light-spored taxon was described in *Hebeloma*. We have studied the holotype both morphologically and molecularly. It appears to be a species of *Tubaria* (W.G.Sm.) Gillet, possibly *Tubaria furfuracea* (Pers.) Gillet, results which have been illustrated in a recent paper (Vizzini et al. 2014). The partial ITS sequence from the holotype of *Hebeloma pamphiliense* confirms the placement of the isotype by Vizzini et al. (2014). However, it should be noted that the molecular identification of *T. furfuracea* and allies is by no means clear. What is called by common consent the “*T. furfuracea* complex” or “*Tubaria furfuracea* s. lat.” (Matheny et al. 2007, Vizzini et al. 2014; fig. 5), contains in Europe one or two ITS species, but it is not clear how these ITS species relate to described species. Furthermore, this clade is not the only one competing for the name of *T. furfuracea* or species from its context. There are at least three distinct clades (see also Vizzini et al. 2014) including ITS sequences named by acclaimed mycologists, suggesting that type studies of European *Tubaria* species may not necessarily support the synonymy of *Hebeloma pamphiliense* with *T. furfuracea* or any of the members of the described species of the *T. furfuracea* complex once the taxonomy and nomenclature of these taxa have been cleared up. Antonín et al. (2012 and literature cited therein) report on additional albinotic collections of *Tubaria* (see fig. 5). One of these (BRNM737651 JX126808) clusters with another group of *T. furfuracea* collections that, judging from ITS data, belong to a species that is not included in the same *T. furfuracea* complex as *Hebeloma pamphiliense*.

*Tubaria furfuracea* is the type species of *Tubaria* and one could argue that all of the instances of *T. furfuracea* as well as the type of *Hebeloma pamphiliense* will probably remain in *Tubaria*, irrespective of the clade in which the type of *T. furfuracea* will nest. However, the generic limits of *Tubaria* are phylogenetically not clear-cut in relation to *Flammulaster* and *Phaeomarasmium* (see also Matheny et al. 2007, Vizzini et al. 2014). Although it is likely that the type of *H. pamphiliense* is part of the group of taxa that will remain in *Tubaria*, at least as long as the identities of *Flammulaster carpophilus* and *Phaeomarasmium excentricus* (according to Kirk 2018 considered synonymous with *P. rimulincola*) are not clear, it does appear premature to transfer *Hebeloma pamphiliense* to *Tubaria*.

### Other *Hebelomina*-like *Hebeloma* collections examined from *Hebeloma* section *Denudata*, fig. 3B

**Estonia:** Surju (approx. N58.23; E24.70; alt. approx. 220 m a.s.l.) in mixed woodland, 28 Aug. 1989, *J. Vesterholt* 89-497 (HJB10660).

**Commentary** – This collection was identified as *Hebeloma hiemale* Bres. in Beker et al. (2016). It has been analysed both morphologically and molecularly. In all respects other than the spore ornamentation and colour it is identical with *Hebeloma hiemale*. This is also the collection from Estonia that was studied by Vesterholt and is described fully in Vesterholt (2005) in the context of the erection of *Hebeloma* subsect. *Hebelomina*.

**Denmark:** Sydjylland, Tisvilde Hegn, eastern end (approx. N56.02; E12.03; alt. approx. 10 m a.s.l.) under *Betula* sp., *Picea* sp., 24 Sep. 2003, *T. Læssøe* 11137 (HJB10834).

**Commentary** – This collection was identified as *Hebeloma geminatum* Beker, Vesterh. & U.Eberh. (Eberhardt et al. 2015, Beker et al. 2016). The collection has been studied both morphologically and molecularly. In all respects other than the spore ornamentation and colour, it is identical with *Hebeloma geminatum*. We have just this one *Hebelomina*-like collection of *Hebeloma geminatum* at our disposal.

**England:** Buckinghamshire, Stoke Common (approx. N51.5566930; W0.5771430; alt. approx. 75 m a.s.l.) on acid, sandy, wet soil in mixed woodland under *Quercus* sp., *Salix* sp., 7 Sep. 2010, *P. Cullington* s.n. (HJB13642); Buckinghamshire, Stoke Common (approx. N51.5566930; W0.5771430; alt. approx. 75 m a.s.l.) on acid, sandy, wet soil in mixed woodland under *Quercus* sp., *Salix* sp., 13 Sep. 2014, *P. Cullington* s.n. (HJB14364); fig. 2A–B.

**Commentary** – These collections were determined morphologically and molecularly as *Hebeloma laetitiae* Quadr. in Beker et al. (2016). We only have these two *Hebelomina*-like collections of this taxon at our disposal, both from almost exactly the same location, but they were collected some four years apart. These are the only records of this taxon from a location other than the type location in Italy. They have been analysed both morphologically and molecularly. The pileus colour, although paler than the collections from the type location, still has some pink in it which appears to be an important character of this taxon.

**Belgium:** West Flanders, Westhoek (N51.0875333; E2.5753167; alt. approx. 0 m a.s.l.) on sandy soil in dune under *Salix repens*, 7 Sep. 2005, *H. Beker* HJB11012; West Flanders, Westhoek (N51.0874167; E2.5754000; alt. approx. 0 m a.s.l.) on sandy soil in dune under *Salix repens*, 5 Jun. 2006, *H. Beker* HJB11578; fig. 2C.

**Commentary** – These collections have been identified morphologically and molecularly as *Hebeloma vaccinum* Romagn. in Beker et al. (2016). They are both from almost exactly the same location in the Belgian sand dunes with dwarf *Salix*. The first collection was made in early September 2005; the second collection in early June 2006.

### Other *Hebelomina*-like *Hebeloma* collections examined from *Hebeloma* sections *Sinapizantia* and *Velutipes*, fig. 3C

**France:** Cher, Forêt Sectionale de l'Echalusse, D99 vers Lunery (approx. N46.9237140; E2.2394080; alt. approx. 125 m a.s.l.) on calcareous, clayey soil under *Carpinus* sp., *Quercus* sp., 4 Nov. 2000, *G. Corriol* 110402 (HJB13143), fig. 2D.

**Commentary** – This collection has been studied morphologically and molecularly and identified as *Hebeloma sinapizans* (Paulet) Gillet (Beker et al. 2016, Grilli et al. 2016). Aside from the spore ornamentation and colour the characters fit exactly with *Hebeloma sinapizans*.

**Italy:** Toscana, Prov. Arezzo, Tuscany (approx. N43.47; E11.86; alt. approx. 250 m a.s.l., 16 Oct. 2002, *A. Gennari* s.n. (K; database record HJB11901).

**Commentary** – This collection, originally labelled as *Hebelomina mediterranea*, appears to have been collected in the same location as the type but on the following day. As with the holotype, morphologically and molecularly, apart from the spores, this collection corresponds to *Hebeloma velutipes* (Beker et al. 2016, Grilli et al. 2016).

### Other *Hebelomina*-like *Gymnopilus* collections examined, fig. 4

**Belgium:** Antwerp, Gooreind (approx. N51.20; E4.96; alt. approx. 10 m a.s.l.) on litter in woodland under *Pinus nigra*, 15 Oct. 1998, *A. de Haan* s.n. (HJB11491), fig. 2E. **England:** Surrey, Oxshott Heath, Esher, north of sandy lane (approx. N51.33; W0.33; alt. approx. 75 m a.s.l.) on clayey, wet soil under *Betula* sp., *Quercus* sp., 14 Oct. 1984, *L. Spooner* s.n. (K(M)99543, HJB11609); Surrey, Esher common, north side of sandy lane (approx. N51.33; W0.33; alt. approx. 75 m a.s.l.) on rotten litter in mixed woodland under *Betula* sp., *Pinus* sp., *Quercus* sp., 7 Nov. 2004, *B.M. Spooner* s.n. (K(M)126782, HJB11608).

**Commentary** – We have examined only a small selection of the collections for *Hebelomina neerlandica* listed by Fraiture & Hayova (2006). Morphological and molecular data (fig. 4) support the inclusion of the analysed *Hebelomina*-like collections in the genus *Gymnopilus*. Although we are not able to resolve the taxonomy of the genus based on the available data, a placement near or in *G. penetrans* (Fr.) Murrill appears likely.

**Ukraine:** Novobilychi (approx. N50.45; E30.50; alt. approx. 180 m a.s.l.) on a dead trunk in mixed woodland under *Pinus sylvestris*, 14 Sep. 2004, *A. Fraiture* 2927 (BR, KW 29993; database record HJB11512).

**Commentary** – This collection has been described by Fraiture & Hayova (2006) and is listed by the authors under *Hebelomina neerlandica*. It clearly belongs to the genus *Gymnopilus* as currently interpreted, but it is not a member of the same species as the collections above. According to published sequence data (i.e. LC100009) it very likely represents a species other than *G. penetrans* or one of the other members of its group (*G. hybridus*, *G. sapineus*). The closest match is a sequence from Japan, identified as *G. liquiritiae*. This species is discussed by Holec (2005) and considered dubious. There are six ITS sequences published in GenBank

under the name *G. liquiritiae*, which are likely to belong to six different species.

## TAXONOMIC CONSPECTUS

*Hebeloma fragilipes* Romagn. (Romagnesi 1965: 341) – Type: France, Pinede du Mont-Po near Chantilly (Oise) (approx. N49.190; E2.170;1; alt. approx. 100 m a.s.l.) on grassy, mossy ground under *Betula* sp., 7 Sep. 1963, *H. Romagnesi* R63-179 (holo-: PC, barcode PC0090764; database record HJB1000031).

*Hebeloma domardianum* (Maire) Beker, U.Eberh. & Vesterh. (Vesterholt 2005: 102). – *Hebelomina domardiana* Maire (Maire 1935: 13) – Type: Algeria, Boudouaou, originally as [“Mauritania”], Forêt de L’Alma, under *Quercus*, 15 Dec. 1933, *R. Maire* 11028 (holo-: MPU; database record HJB1000106).

*Gymnopilus neerlandicus* (Huijsman) Contu (Cittadini et al. 2008: 16) – *Hebelomina neerlandica* Huijsman (Huijsman 1978: 490); replacement name for homotypic synonym – *Hebelomina microspora* Huijsman (Huijsman 1946: 31); **nom. inval.** (Art. 39.1; McNeill et al. 2012). – *Hebelomina microspora* Huijsman ex Huijsman (Huijsman 1978: 485); **nom. illegit.** (Art. 53.1; McNeill et al. 2012), non *Hebelomina microspora* Alessio & Nonis (Alessio & Nonis 1977: 19). – *Hebelomina huijsmaniana* Singer (Singer 1986: 612); as “nom. nov.”; **nom. illegit.** (Art. 52.1; McNeill et al. 2012) for *Hebelomina microspora* Huijsman. – Type: The Netherlands, Overijssel near Rijssen, on pine needles and branchlets of *Pinus sylvestris*, 24 Oct. 1943, *W.J. Reuvecamp* & *W.F. Smits* det. H. Huijsman (holo-: L, barcode L0053521; database record HJB1000038).

*Gymnopilus pallidus* (Dessi & Contu) Contu (Cittadini et al. 2008: 17). – *Hebelomina pallida* Dessi & Contu (Contu & Dessi 1993: 104). – Type: Sardinia, prov. Cagliari, Serramanna, on dead wood of *Eucalyptus*, 5 Jul. 1992, *P. Dessi* & *M. Contu* 92/269 (holo-: CAG, n.v.).

*Hebeloma velutipes* Bruchet (Bruchet 1970: 127). – Type: France, Les Echets (Ain) (approx. N45.86; E4.90; alt. approx. 280 m a.s.l.) on clayey soil in deciduous woodland under *Corylus avellana*, 24 Sep. 1963, *G. Bruchet* BR63-20 (holo-: LY; database record HJB1000045).

*Hebeloma mediterraneum* (A.Gennari) Contu (Cittadini et al. 2008: 16). – *Hebelomina mediterranea* A.Gennari (Gennari 2002 [2003]: 312). – Type: Italy, Toscana, Arezzo, Val di Chiana, Civitella, under *Arbutus unedo*, *Cistus monspeliensis*, *Cistus salvifolius*, *Quercus ilex* and *Quercus pubescens*, 15 Oct. 2002, *S. Urci* 669 (holo-: MCVE; database record HJB1000075).

### Uncertain taxon

*Hebelomina maderaspatana* Natarajan & Raman (Natarajan & Raman 1980 [1981]: 72). Type: India, Tamil Nadu on litter

in groups, Indian Institute of Technology campus, Guindy, Madras, 3 Nov. 1978, *N. Raman* 2420 (holo-: Madras Univ. Bot. Lab. no. 2420, n.v.).

### Uncertain taxa excluded from *Hebeloma*

*Hebeloma microsporum* (Alessio & Nonis) Contu (Cittadini et al. 2008: 16). – *Hebelomina microspora* Alessio & Nonis (Alessio & Nonis 1977: 19). – Type: Italy, Parco della Rimembranza Augustae Taurinorum, on wood and roots in conifer forest, 5 May 1976, *B. Nonis* s.n. (holo-: herb. E. Rebaudengo, Ceva; database record HJB1000256).

*Hebeloma pamphiliense* Cittadini, Lezzi & Contu (Cittadini et al. 2008: 6). – Type: Italy, Roma, Lazio, Parco di Villa Pamphili, under *Quercus ilex*, 20 Jan. 2008, *M. Cittadini* & *T. Lezzi* 23394 (holo-: MCVE, database record HJB1000152; iso-: T. Lezzi private collection TL20080120-01, n.v.).

### Taxon not accepted

*Hebeloma* subject. *Hebelomina* (Maire) Beker, U.Eberh. & Vesterh. (Vesterholt 2005: 24). – *Hebelomina* Maire (Maire 1935: 13). – Type species: *Hebeloma domardianum* (Maire) Beker, U.Eberh. & Vesterh.

## DISCUSSION

In this work, we assemble and emend previous results concerning species and collections of *Hebelomina* and show that they belong to at least four different genera and eleven different species.

For the sake of completeness, in the context of the *Hebelomina* syndrome, the genus *Rapacea* with a single species *R. mariae* (Horak 1999) is worth mentioning. The species was recently recombined into the genus *Cortinarius* (Peintner et al. 2002a, 2002b, Fraiture & Hayova 2006, Soop 2010). At some point it had been suggested that *C. mariae* might be a member of *Hebelomina* (Soop 2010). Soop described this taxon as being white all over and with spores that appear totally smooth, dextrinoid, yellow-brown, not pale, producing an olivaceous-yellow spore print. According to Horak (1999) its spores were pale olivaceous-argillaceous, i.e. much paler than the normal colour of the spores in the genus *Cortinarius* and were inamyloid, but became brown in Melzer’s reagent (dextrinoid), and appeared smooth under the light microscope but minutely asperulate or with low net-like ridges under SEM. *Cortinarius mariae* appears to be closely related to other New Zealand *Cortinarius* species (Peintner et al. 2002b).

The difficulty in assigning *Hebelomina* ssp. and collections outside *Hebeloma* to species, and in the case of *Hebeloma microsporum*, even to genus or family, emphasises the need of detailed studies, including type studies, for these taxa. Deviating names within clades may be due to misidentifications, but most of all they reflect unclear species limits and shifts in time and differences between identifiers of how certain species have been perceived.

Although fig. 6 supports earlier results of Matheny et al. (2006) and Sánchez-García et al. (2014) that *Baeospora*

*myosura*, and, as we found out, the related *Hebeloma microsporium*, may be a member of the Cyphellaceae, we prefer to treat this result with caution, as the available data are sparse. Clades and clade support may be artefactual rather than a reflexion of a shared phylogenetic history of the clade members. However, we are sure that *Hebeloma microsporium* is not a member of *Hebeloma* and reasonably sure it is not a member of the groups studied in some detail by Matheny and co-workers (Bodensteiner et al. 2004, Padamsee et al. 2008, Sánchez-García et al. 2014, Matheny et al. 2015). It does appear likely that *Hebeloma microsporium* belongs to a group of light spored species. Whether or not *Hebeloma microsporium* is a candidate member of the genus *Mycopan* is again a question that can only be answered by a study of the type of the genus. Unfortunately, Redhead (2013) did not indicate whether the type has been re-studied or what the results were.

It is clear from the results above that the other taxa that have been taxonomically placed within *Hebelomina* appear to be aligned with brown spored species. While we are not able to determine the exact species for the non-*Hebeloma*-like *Hebelomina*, they all appear to be conspecific with members of their respective genera, mainly differentiated by the smooth spores (almost hyaline under the microscope). It is likely that this is a mutation which appears to occur occasionally within some of the brown-spored genera like *Gymnopilus*, *Hebeloma* and *Tubaria*, whereby the outer parts of the spore wall that contain pigmentation and ornamentation (exospore and perispore) appear not to have developed normally.

We conclude that *Hebelomina* is neither a genus nor a section of a genus and should be abandoned as a supraspecific taxon.

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