Hebeloma pamphiliense is a member of the Tubaria furfuracea clade (Agaricales, Tubariaceae)

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HEBELOMA PAMPHILIENSE IS A MEMBER OF THE *TUBARIA FURFURACEA* CLADE (*AGARICALES*, *TUBARIACEAE*)

Abstract
Based on molecular data Hebeloma pamphiliense *is showed to be an albinotic form of a species of the* Tubaria furfuracea *clade.*

Riassunto
Sulla base di dati molecolari viene dimostrato che Hebeloma pamphiliense *è una forma albina di una specie del complesso facente capo a* Tubaria furfuracea.

Key words: *Basidiomycota, Agaricomycetes*, albinotic taxa, ITS sequences, molecular phylogeny, taxonomy.

Introduction

The genus *Hebelomina*, typified by *H. domardiana* Maire, was established by Maire (1935) for pale-coloured *Hebeloma*-like fungi with whitish lamellae, white spore-print and smooth spores. So far, seven species have been described in this genus (Huijsman, 1946, 1978; Alessio & Nonis, 1977; Natarajan & Raman, 1980, 1983; Dessi & Contu, 1993; Gennari, 2002; Vesterholt, 2005; Fraiture & Hayova, 2006; Cittadini *et Al*., 2008). Most of them are extremely rare or even known only by the type specimens. Morphologically, the described species are heterogeneous, terricolous or lignicolous and the taxonomic position of the genus and its species was long debated (Huijsman, 1978; Neville & Roux 1997; Fraiture & Hayova, 2006) even though preliminary data indicated that *Hebelomina* is an artificial assemblage.

In particular, the phylogenetic analyses by Moncalvo *et Al*. (2002) have shown that the lignicolous *Hebelomina neerlandica* Huijsman is an albinotic *Gymnopilus* P. Karst., close to *G. penetrans* (Fr.) Murrill; Vesterholt (2005) considered the terricolous *H. domardiana* a white-spored *Hebeloma*. Consequently, the genus *Hebelomina* has been recently included in *Hebeloma* (Fr.) P. Kumm. (Vesterholt 2005) as subsection *Hebelomina* (Maire) Beker, U. Eberh. & Vesterh. of section *Denudata* and *H. domardiana* recombined in *Hebeloma*. Accordingly, Cittadini *et Al*. (2008) transferred on the basis of only morphological data *Hebelomina neerlandica* and *H. pallida* Dessi & Contu in *Gymnopilus*, *Hebelomina mediterranea* A. Gennari in *Hebeloma* and described a new species in the "*Hebelomina* complex" as *Hebeloma pamphiliense* Cittadini, Lezzi & Contu.

After collecting new specimens in the type area and re-evaluating the original material we have decided to infer the phylogenetic position of *Hebeloma pamphiliense* based on a ITS

sequence analysis. Specimens of *Tubaria furfuracea* (Fr.) Gillet found not so far from the type area, were also sequenced.

Materials and methods

DNA extraction, amplification and sequencing Genomic DNA was isolated from 10 mg of a dried herbarium specimen from three collections (see Tab. 1), by using the DNeasy Plant Mini Kit (Qiagen, Milan Italy) according to the 42 manufacturer's instructions. Universal primers ITS1F/ITS4 were used for the ITS region amplification (White *et Al*., 1990; Gardes & Bruns, 1993). Amplification reactions were performed in a PE9700 thermal cycler (Perkin-Elmer, Applied Biosystems) following Vizzini *et Al*. (2014). The PCR products were purified with the AMPure XP kit (Beckman) and sequenced by MACROGEN Inc. (Seoul, Republic of Korea). The sequences were submitted to GenBank (www.ncbi.nlm.nih.gov/genbank) and their accession numbers are reported in Fig. 1 and Tab. 1.

Table 1. Features of the sequenced collections

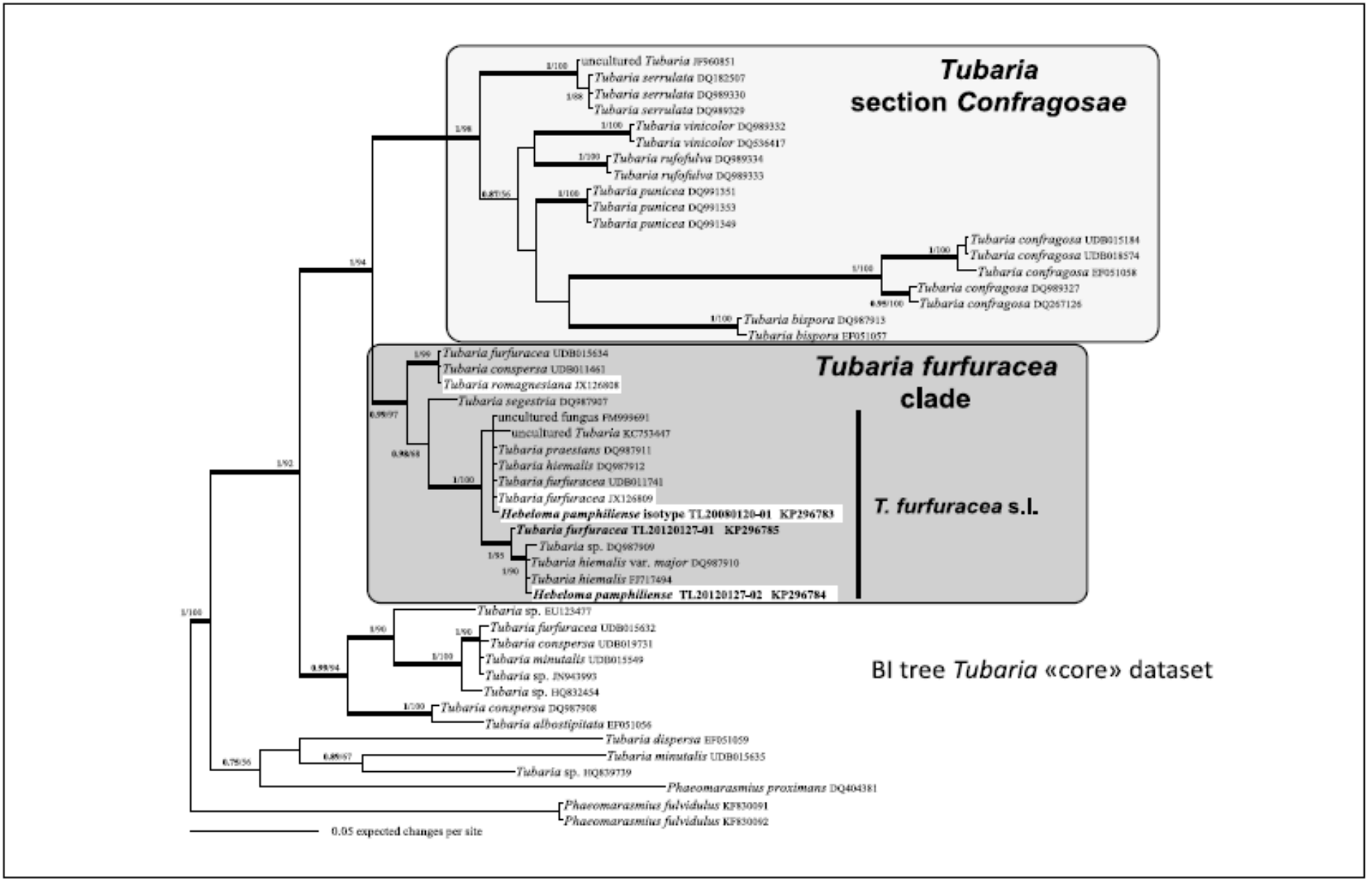
TAXON	COLLECTION DATA	ITS-GENBANK ACC. NUMBERS	SPORE DIMEN-SIONS (µm)	CHEILO-CYSTIDIA (FORM AND DIMENSION) (µm)	ELEMENTS OF THE HYMENO-PHORAL TRAMA (µm)
Hebeloma pamphiliense	Isotype, Italy, Rome, Villa Pamphili, on *Quercus ilex* debris, 20 Jan 2008, leg. T. Lezzi, TL20080120-01	KP296783	6.6-8.3 × 4.8-6.4	Mainly capitate, 25-32 × 4.5-6.5	× 4.0-9.1
Hebeloma pamphiliense	Italy, Rome, Villa Pamphili, on *Quercus ilex* debris, 27 Jan 2012, leg. T. Lezzi, TL20120127-02	KP296784			
Tubaria furfuracea	Italy, Rome, Villa Pamphili, on *Quercus ilex* debris, 27 Jan 2012, leg. T. Lezzi, TL20120127-01	KP296785	6.7-7.4 × 4.0-5.1	Mainly capitate, 37-49 × 6.7-9.5	× 4.1-8.5

Sequence alignment and phylogenetic analysis

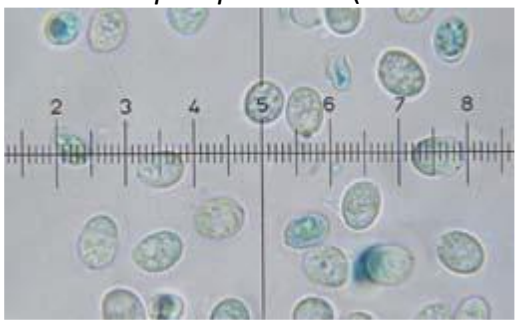
The sequences obtained in this study were checked and assembled using Geneious v.5.3 (Drummond *et Al*., 2010). A preliminary BLAST search showed *Hebeloma pamphiliense* is a member of the genus *Tubaria* (W.G. Sm.) Gillet. Consequently, sequences were combined with published *Tubaria* ITS rDNA sequences selected from GenBank and UNITE (http://unite.ut.ee) databases on the basis of the greatest similarity based on BLASTsearch, outcomes of a recent phylogenetic study focused on *Tubaria* (Matheny *et Al*., 2007), and subsequent phylogenetic analysis (preliminary trees not shown).

The alignment was generated using MAFFT (Katoh *et Al*., 2002) with default conditions for gap openings and gap extension penalties. The alignment was then imported into MEGA v.5.0 (Tamura *et Al*., 2011) for manual adjustment. Best-fit models were estimated by both the Akaike information criterion (AIC) and the Bayesian information criterion (BIC) with jModelTest 0.1.1 (Posada, 2008) to provide a substitution model for the alignment. Phylogenetic analyses were performed using the Bayesian Inference (BI) and Maximum Likelihood (ML) approaches. Following Matheny *et Al*., (2007), *Phaeomarasmius fulvidulus* Singer and *P. proximans* (A.H. Sm. & Hesler) Singer were chosen as outgroup species. The BI was performed with MrBayes 3.1.2

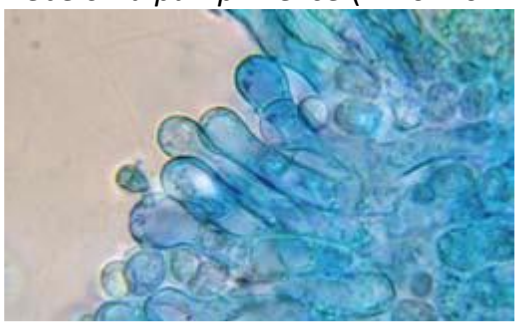
Fig. 1. Bayesian phylogenetic tree from the ITS (ITS1-5.8S-ITS2) sequence alignment of *Tubaria* species, with *Phaeomarasmius fulvidulus* and *P. proximans* as outgroup taxa. BPP values (in bold) ≥ 0.75 and MLB values ≥ 50% are shown on the branches. Thickened branches indicate Bayesian posterior probability >0.95 and ML bootstrap support >90%. For each sequence taxon name and Genbank/UNITE number are given. Newly sequenced collections are in bold. Albinotic collections are highlighted in white and marked by an asterisk.


Tubaria
section Confragosae
uncultured Tubaria JF960851
Tubaria serrulata DQ182507
Tubaria serrulata DQ989330
Tubaria serrulata DQ989329
Tubaria vinicolor DQ989332
Tubaria vinicolor DQ536417
Tubaria rufofulva DQ989334
Tubaria rufofulva DQ989333
Tubaria punicea DQ991351
Tubaria punicea DQ991353
Tubaria punicea DQ991349
Tubaria confragosa UDB015184
Tubaria confragosa UDB018574
Tubaria confragosa EF051058
Tubaria confragosa DQ989327
Tubaria confragosa DQ267126
Tubaria bispora DQ987913
Tubaria bispora EF051057
Tubaria furfuracea
clade
Tubaria furfuracea UDB015634
Tubaria conspersa UDB011461
Tubaria romagnesiana JX126808
Tubaria segestria DQ987907
uncultured fungus FM999691
uncultured Tubaria KC753447
Tubaria praestans DQ987911
Tubaria hiemalis DQ987912
Tubaria furfuracea UDB011741
Tubaria furfuracea JX126809
Hebeloma pamphiliense isotype TL20080120-01 KP296783
Tubaria furfuracea TL20120127-01 KP296785
Tubaria sp. DQ987909
Tubaria hiemalis var. major DQ987910
Tubaria hiemalis EF717494
Hebeloma pamphiliense TL20120127-02 KP296784
T. furfuracea s.l.
Tubaria sp. EU123477
Tubaria furfuracea UDB015632
Tubaria conspersa UDB019731
Tubaria minutalis UDB015549
Tubaria sp. JN943993
Tubaria sp. HQ832454
Tubaria conspersa DQ987908
Tubaria albostipitata EF051056
Tubaria dispersa EF051059
Tubaria minutalis UDB015635
Tubaria sp. HQ839739
Phaeomarasmius proximans DQ404381
Phaeomarasmius fulvidulus KF830091
Phaeomarasmius fulvidulus KF830092
0.05 expected changes per site
BI tree Tubaria «core» dataset

Hebeloma pamphiliense (TL20120127-02). Photo by Tomaso Lezzi

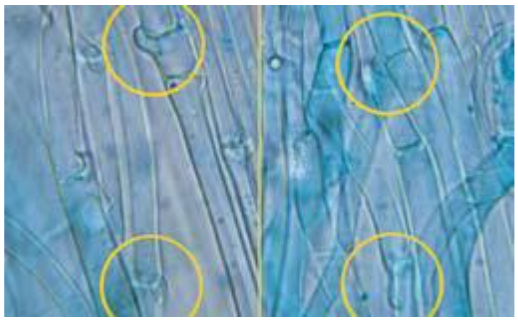


Hebeloma pamphiliense (TL20120127-02). Spores. Photo by Tomaso Lezzi



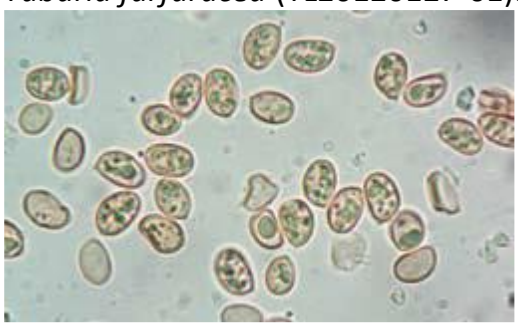
Hebeloma pamphiliense (TL20120127-02). Cheilocystidia. Photo by Tomaso Lezzi

Hebeloma pamphiliense (TL20120127-02). Cheilocystidia. Photo by Tomaso Lezzi

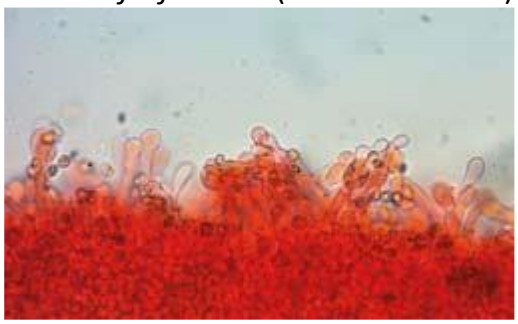


Hebeloma pamphiliense (TL20120127-02). Clamp connections. Photo by Tomaso Lezzi

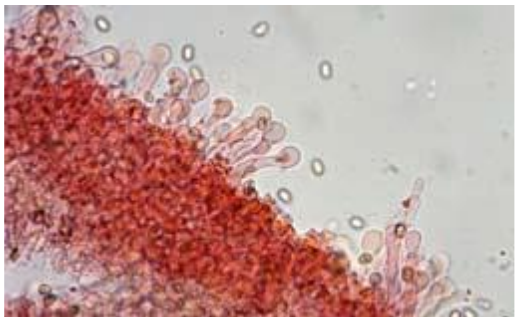
Tubaria furfuracea (TL20120127-01). Spores (1000×). Photo by Tomaso Lezzi



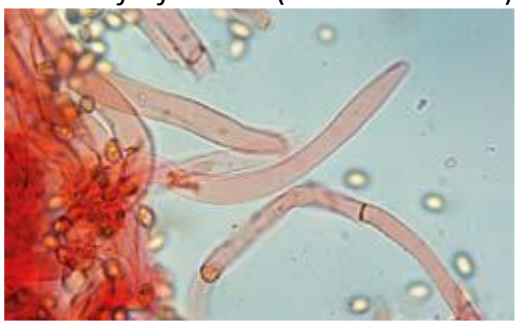
Tubaria furfuracea (TL20120127-01). Cheilocystidia (400×). Photo by Tomaso Lezzi



Tubaria furfuracea (TL20120127-01). Cheilocystidia (400×). Photo by Tomaso Lezzi



Tubaria furfuracea (TL20120127-01). Lamellar hyphae (400×). Photo by Tomaso Lezzi



Tubaria furfuracea (TL20120127-01). Photo by Tomaso Lezzi

(Huelsenbeck & Ronquist, 2001) with four incrementally heated simultaneous Monte Carlo Markov Chains (MCMC) run over 10 million generations, under GTR+Γ evolutionary model. Trees were sampled every 1 000 generations resulting in an overall sampling of 10 001 trees; the first 2 500 trees were discarded as "burn-in" (25%). For the remaining trees, a majority rule consensus tree showing all compatible partitions was computed to obtain estimates for Bayesian Posterior Probabilities (BPP). ML estimation was performed through RAxML v.7.0.4 (Stamatakis, 2006) with 1 000 bootstrap replicates (Felsenstein, 1985) using the GTRGAMMA algorithm to perform a tree inference and search for a good topology. Support values from bootstrapping runs (MLB) were mapped on the globally best tree using the "-f a" option of RAxML and "-x12345" as a random seed to invoke the novel rapid bootstrapping algorithm. Only BPP values over 0.75 and MLB over 50% are reported in the resulting tree (Fig. 1). Pairwise % identity values of ITS sequences were calculated using MEGA 5.10 (Tamura *et Al*., 2011).

Results

Both Bayesian and Maximum likelihood analyses produced the same topology; therefore, only the Bayesian tree with both BPP and MLB values is shown (Fig. 1). The ITS data matrix comprises a total of 48 sequences (including 36 from GenBank and 9 from UNITE). In the obtained Bayesian phylogenetic tree (Fig. 1), our three collections (TL20080120-01, TL20120127-01 and TL20120127-02) fall in a well-supported clade (hereafter designed as *T. furfuracea* s.l.; BPP = 1; MLB = 100) in the *Tubaria furfuracea* clade (BPP = 0,99; MLB = 97). The sequences of the *T. furfuracea* s.l. clade share a pairwise % identity value of 98.7. The clade is sister (BPP = 0,98, MLB = 68) to a *T. segestria* sequence (DQ987907).

Discussion

Hebeloma pamphiliense is a *Tubaria*

Hebeloma pamphiliense was established on morphological basis on the ground of collections from the Villa Pamphili Park (Rome); it is apparently terricolous but growing on *Quercus ilex* debris and cupules (Cittadini *et Al*., 2008). The phylogenetic analysis (Fig. 1) highlighted that *H. pamphiliense* is a *Tubaria*. The genus *Tubaria* (*Tubariaceae* Vizzini) is polyphyletic and heterogeneous. The number and the identity of the species belonging to this very difficult complex is still debated and the taxonomic problems have still to be solved (Matheny *et Al*., 2007). In their phylogenetic analysis, Matheny *et Al*. (2007) recovered two major groups in the *Tubaria* core, viz. *Tubaria* section *Confragosae* (Singer) Matheny and the *Tubaria furfuracea* complex.

The first group, recognized as a strongly monophyletic clade, encompasses *T. bispora* Matheny, P.-A. Moreau, M.A. Neves & Vellinga, *T. confragosa* (Fr.) Harmaja, *T. punicea* (A.H. Sm. & Hesler) Ammirati, Matheny & P.-A. Moreau, *T. rufofulva* (Cleland) D.A. Reid & E. Horak, *T. serrulata* (Cleland) Bougher & Matheny and *T. vinicolor* (Peck) Ammirati, Matheny & Vellinga; the group is distinguished morphologically from the other species of *Tubaria* by darker yellowish brown spore prints and resistance of spore walls to collapse in microscopic mounts Matheny *et Al*. (2007). The development of the partial veil is variable and ranging from an evanescent cortina to a membranous annulus. The second group, the *Tubaria furfuracea* complex, forming an unresolved polytomy in the Bayesian analysis by Matheny *et Al*. (2007), is distinguished mainly by the lighter spore prints (ochraceous) and spore walls that fail to revive (appearing collapsed) for some spores in microscopic mounts. Species in this group usually do not produce an annulus and include collections named *T. conspersa* (Pers.) Fayod, *T. furfuracea*, *T. hiemalis* Romagn. ex Bon, *T. hiemalis* var. *major* Bon & Trimbach, *T. pallidospora* J.E. Lange, *T. praestans* Romagn. ex E. Horak & P.-A. Moreau, *T. segestria* (Fr.) Boud. sensu Romagnesi, *Tubaria* sp., and "*Phaeomarasmius*" sp. Gates 0006.

The ITS sequences of the two *Hebeloma pamphiliense* collections (isotype included) and of the normally brown-pigmented *Tubaria* collection found about 200 m far from the type area (Tab. 1) matched well those of the *Tubaria furfuracea* s.l.: *T. furfuracea*, *T. hiemalis*, *T. hiemalis* var. *major* and *T. praestans* (Fig. 1).

The taxonomy of *Tubaria furfuracea* s.l. is very puzzling because of the lack of detailed molecular studies; almost all recent studies are based on morphological characters (Arnolds, 1982; Bon, 1992; Volders, 2002). Arnolds (1982) recognized three species: *Tubaria furfuracea* s.s. with evident velar remnants present at the pileus margin, spores (6.0)6.5–9.0(11) × (4.0)4.5– 5.5(6.5) µm, ellipsoid to ellipsoid-oblong, sometimes slightly constricted apically, cheilocystidia (30)34.5–53 × 4.5–7.5(9.5) µm, subcylindrical to slightly ventricose, at apex not to rather swollen, and (6.0)8.5–20(26) µm wide hymenophoral trama hyphae; *T. hiemalis* with scarce velar remnant, slightly larger spores (6.7)7.0–9.5(10.5) × 4.5–5.5(6.0) µm, usually distinctly apically swollen (capitate) cheilocystidia, (5)8.0–18(20) µm wide hymenophoral trama hyphae, and winter fructification; and *T. romagnesiana* Arnolds with distinct velar remnants at pileus margin, shorter spores [(5.8)6.0–8.2(8.5) × 4.0–5.2(5.5) µm], cylindrical or slightly ventricose cheilocystidia without a swollen to subcapitate apex, and only ± 4.0–10(14.5) µm wide hymenophoral trama hyphae. The same species concept was followed by Bon (1992) and Horak (2005). Volders (2002) after thorough morphological studies, considered all three species conspecific.

However, he distinguished two infraspecific taxa without distinctly capitate cheilocystidia, viz. *T. furfuracea* var. *furfuracea* with (8)10–20(30) µm wide trama hyphae and 6.5–9(11) ×

4.5–5.5(6.5) µm large spores and var. *furfuracea* f. *romagnesiana* (Arnolds) Volders with 4–10(15) µm wide trama hyphae and rather thick-walled, 6–8 × 4–5 µm large spores, and var. *hiemalis* (Romagn. ex Bon) Volders with 10–20(30) µm wide trama hyphae, 7–10(11) × 4.5–5 µm large spores and distinctly capitate cheilocystidia. Vesterholt (2012) considered all three species as phenotypic expressions of *T. furfuracea* s.l. without recognizing infraspecific taxa. In the analysis of the nrLSU sequences by Aime *et Al*. (2009), *T. furfuracea* and *T. hiemalis* are conspecific. According to our analysis (Fig. 1) *T. furfuracea*, *T. hiemalis*, *T. hiemalis* var. *major* and *T. praestans* seem to be conspecific (they share a pairwise % identity value of 98.7) whereas *T. romagnesiana* and *T. segestria* sensu Romagnesi occupy an independent position. Morphologically, our three collections share with *T. furfuracea* var. *hiemalis* the capitate cheilocystidia and with var. *furfuracea* the spore size, see Cittadini *et Al*. (2008) and Tab. 1. The albinotic *Tubaria* Albinotic entities belonging to the genus *Tubaria* (sometimes labeled as "*Leucotubaria*", see Bendiksen, 1980) are only rarely described in the literature (Bendiksen, 1980; Antonín *et Al*., 2012). *Tubaria hololeuca* Kühner ex E. Horak & P.-A. Moreau is the only white coloured *Tubaria* species formally described from Europe (Bon, 1992; Volders, 2002; Horak & Moreau, 2004).

It is characterized by very pale and small largely ellipsoid spores, 5.5-6.5 × 4.5-5 µm (tetrasporic basidia) up to 7(7,8) × 5.5 (bisporic basidia) and cylindrical to lageniform cheilocystidia. Bendiksen (1980) described an albinotic form of *T. furfuracea* from Norway which shows morphological features exactly superimposable to those present in our collections (capitate cheilocystidia *T. hiemalis*-like and 6.5-8.5 × 4.5-5.5 µm spores *T. furfuracea*-like). Antonín *et Al*. (2012), based on morphological and molecular data attributed a first albinotic collection from Norway (O 370700N-Bendiksen 191/79, Oslo, Grorud, Groruddammen, on soil, 18 Aug. 1979, leg. E. Bendiksen, cited in Bendiksen, 1980) to *T. furfuracea* (see sequence JX126809, Fig. 1) and a second one from the Czech Republic to *T. romagnesiana* (see sequence JX126808, Fig. 1).

The Norwegian collection is contaxic with the isotype collection of *Hebeloma pamphiliense*. According to our analysis, albinotic forms seem to be restricted to the *T. furfuracea* clade so far, and are apparently not described for the section *Confragosae*.

Conclusions

The *Hebelomina* genus (habit) is highly polyphyletic. Molecular analysis by Moncalvo *et Al*. (2002) has shown that *Hebelomina neerlandica* is a *Gymnopilus*. Those authors extend however prematurely their conclusions to the whole genus *Hebelomina*. Vesterholt (2005) considered the type species, *Hebelomina domardiana,* a *Hebeloma*. Finally, our analysis highlighted that *Hebeloma pamphiliense*, formally ascribed to *Hebeloma* sect. *Denudata* subsect. *Hebelomina*, is an albinotic form of a taxon in *Tubaria furfuracea* s.l.

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