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Musumecia gen. nov. in the Tricholomatoid clade (Basidiomycota, Agaricales) related to Pseudoclitocybe

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Abstract

Musumecia, a new genus of Agaricales, is described to accommodate the new species *Musumecia bettlachensis*. Based on a combined ITS– and LSU–rDNA Bayesian, Maximum Likelihood and Maximum Parsimony analysis, *Musumecia* clearly clusters within the Tricholomatoid clade, where it is sister to *Pseudoclitocybe*. *Musumecia* is distinguished from allied genera by a unique combination of macro- and micromorphological characters, including basidiomes with a clitocyboid/hygrophoroid habit, emerging from a fleshy pseudosclerotial mass (pseudosclerotium), decurrent and thick lamellae, a brown darkening of both lamellae and stipe, whitish-cream spore print, elongated non-siderophilous basidia, smooth, acyanophilous and inamyloid basidiospores, and the absence of both cystidia and clamp-connections.

Recent multigene phylogenetic analyses focused on Agaricales (Matheny et al. 2006) have led to the recognition of several monophyletic clades. Among these, the well supported Tricholomatoid clade encompasses four families, the Tricholomataceae R. Heim ex Pouzar s.s, the Lyophyllaceae Jülich, the Entolomataceae Kotl. & Pouzar, the Mycenaceae Overeem, and the *Catathelasma* clade (Matheny et al. 2006, Ammirati et al. 2007). Recent work by Binder et al. (2010) and Vizzini et al. (2010a) indicate that *Infundibulicybe* Harmaja, *Pseudoclitocybe* (Singer) Singer, *Trichocybe* Vizzini, and *Singerocybe* Harmaja can be included in the Tricholomatoid clade as well.

The aim of this study is to describe a new genus, *Musumecia*, to accommodate *Musumecia bettlachensis* sp. nov., a fungus collected from France. According to molecular and morphological features it belongs to the Tricholomatoid clade and is inassimilable to any of the extant genera.

Material and methods

Morphology

The micromorphological descriptions are based upon study of herbarium material. The observations of microscopic characters were made on dried material rehydrated in 3% KOH and stained in Congo red, Cresyl Blue, Cotton Blue and Melzer's reagent. Cotton Blue was also used to check the siderophilous granulation in the basidia (Baroni 1981). Spore measurements are based on means of 90 spores from three collections, stained in Melzer's reagent. The width of basidia was measured at the widest part, and the length was measured from the apex (sterigmata excluded) to the basal septum. In the macro- and micromorphological descriptions the following abbreviations are used: Q=the quotient of length and width of the spores in side view; Qm=average quotient; L=no. of entire lamellae; l=no. of lamellulae between each pair of entire lamellae. Colour designations in the format

"(4A1)" refer to plate, column, and row of Kornerup and Wanscher (1978). Herbarium abbreviations are according to Thiers (2011). Author citations follow the 'Index fungorum – authors of fungal names' (<www.indexfungorum.org/authorsoffungalnames.htm>). The type material is housed at TO. The Latin description of the new taxon is deposited in MycoBank (<www.mycobank.org/DefaultPage.aspx>).

DNA extraction, PCR amplification, and DNA sequencing

Genomic DNA was isolated from 1 mg of herbarium specimens (Table 1), by using the DNeasy Plant Mini Kit according to the manufacturer's instructions. Universal primers ITS1F/ITS4 were used for the ITS region amplification (White et al. 1990, Gardes and Bruns 1993) and primers LR0R/LR7 (Vilgalys and Hester 1990, Vilgalys lab, unpubl., <www.botany.duke.edu/fungi/mycolab>) for the LSU rDNA amplification. Amplification reactions were performed in a PE9700 thermal cycler following Vizzini et al. (2010b). The PCR products were purified with the AMPure XP kit and sequenced by DiNAMYCODE srl and MACROGEN Inc. The sequences were assembled and edited with the phred/phrap/consed software suite. The sequences were submitted to GenBank (accession no. in Table 1, Fig. 4), and the alignments and phylogenetic tree are available at TreeBASE (<www.treebase.org>) under accession no. 11507.

Table 1. Collections newly sequenced in this study.

Species	**GenBank acc. no.**		**Source, locality and substrate**
	ITS	**LSU**	
Musumecia bettlachensis	JF926520	JF926521	TO HG2284 (type collection), France, Alsace, Dept. Haut Rhin, Bettlach, 2 Oct 2010, on *Abies alba* litter
Pseudoclitocybe cyathiformis	JF926522	JF926523	TO HG2285, Italy, Tuscany, Grosseto, Rocchette di Fazio, 22 Dec 2008, on *Quercus cerris* litter
Pseudoclitocybe expallens	JF926524	JF926525	TO HG2286, Italy, Tuscany, Grosseto, Scanzano, 28 Dec 2009, on grassy soil

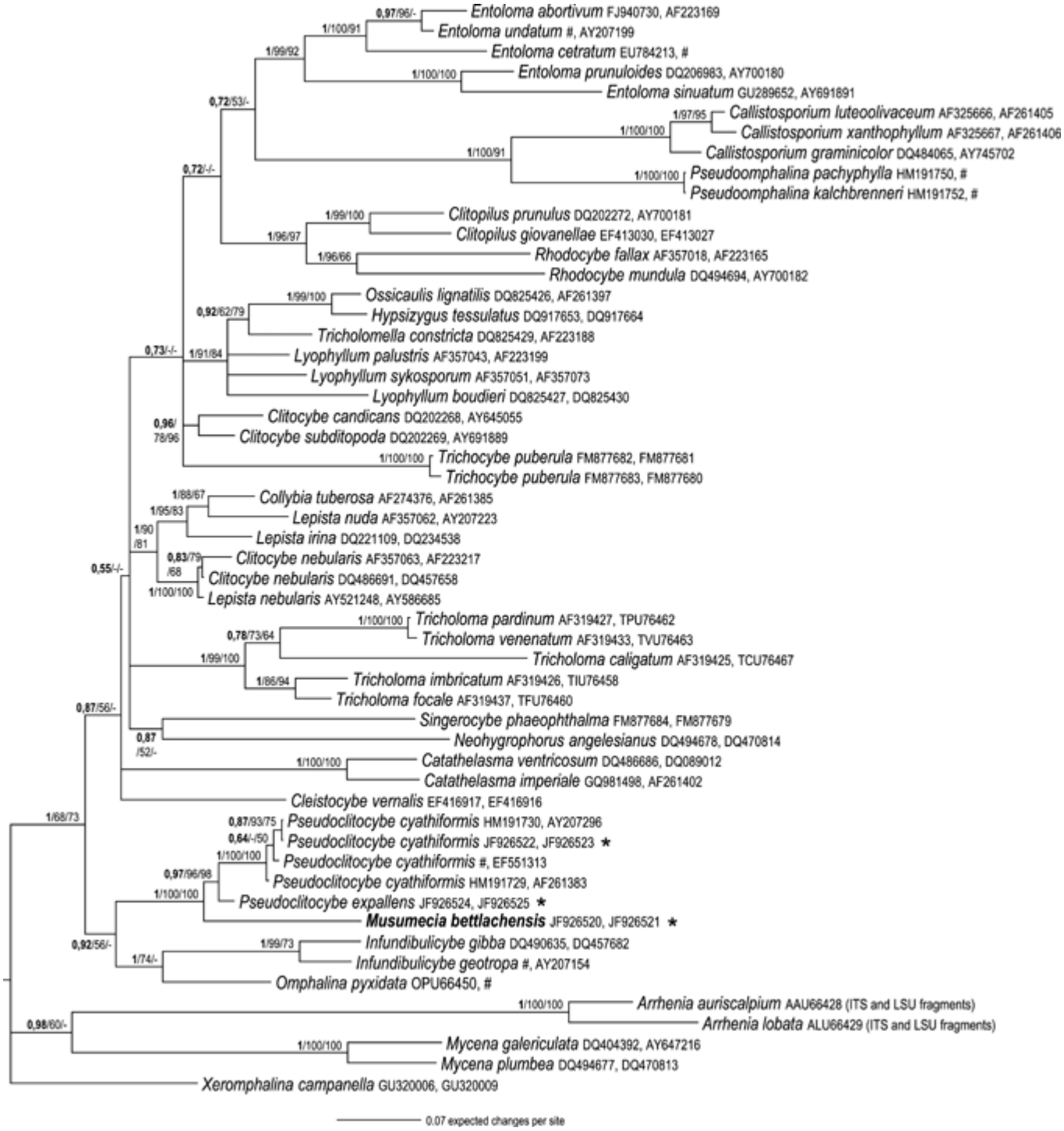

Figure 4. Bayesian phylogram obtained from the combined ITS and LSU rDNA sequences of the Tricholomatoid clade. *Xeromphalina campanella* (Hygrophoroid clade) was used as outgroup. Support values (BPP, in bold, MLB and MPB) above 50% are given above branches. The # symbol indicates the missing of ITS or LSU sequence, respectively. * refers to samples sequenced in this work and reported in Table 1.

Sequence alignment and phylogenetic analysis

The sequences obtained in this study were checked and assembled using Geneious (Drummond et al. 2011), and compared to those available in the GenBank database (<www.ncbi.nlm.nih.gov/Genbank/>) using the blastn algorithm. Based on the blastn results,

sequences were selected according to the outcomes of recent phylogenetic studies on Agaricales (Matheny et al. 2006, Binder et al. 2010). A combined analysis of ITS and LSU sequences was carried out using sequences from the same strain or specimen. *Xeromphalina campanella* (GU320006, GU320009) was used as outgroup. Single alignment for each dataset was generated using MAFFT (Katoh et al. 2002) with default conditions for gap openings and gap extension penalties. The sequence alignment, its manual adjustment, and the best-fit models estimation follow Vizzini et al. (2010b). The GTR+G and GTR+I+G substitution models were used in the ITS and LSU analysis, respectively. A partitioned matrix was used in all the analyses. Molecular–phylogenetic analyses were performed using the Bayesian Inference (BI), Maximum Likelihood (ML) and Maximum Parsimony (MP) approaches. BI of phylogeny using Monte Carlo Markov Chains (MCMC) was carried out with MrBayes (Huelsenbeck and Ronquist 2001). Four incrementally heated simultaneous MCMC were run over 10 000 000 generations, under model assumption. Trees were sampled every 1000 generations resulting in an overall sampling of 10 001 trees. The "burn-in" value was evaluated using Tracer (Rambaut and Drummond 2007). The first 20% of trees was discarded as "burn-in". For the remaining trees, a majority rule consensus tree showing all compatible partitions was computed to obtain estimates for Bayesian Posterior Probabilities (BPP). Branch lengths were estimated as mean values over the sampled trees. Only BPP values over 50% are reported in the resulting trees. This Bayesian analysis was repeated three times, always using random starting trees and random starting values for model parameters to test the independence of the results from the revisiting of the prior topologies during chain growth (Huelsenbeck et al. 2002). ML estimation was performed through RAxML (Stamatakis 2006) with 1000 bootstrap replicates (Felsenstein 1985) using the GTRGAMMA and GTRGAMMAI (for ITS and LSU, respectively) 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 –x 12345 as a random seed to invoke the novel rapid bootstrapping algorithm. MP analysis was performed using PAUP* (Swofford 2002) using the heuristic search mode with 100 random addition sequence replicates and tree bisection–reconnection (TBR) branch swapping, but keeping only 10 trees per replicate in order to discover possible islands of maximum parsimony. All character states were treated as unordered and equally weighted. Gaps were treated as missing data. Branch robustness was estimated by nonparametric bootstrapping (Felsenstein 1985) with 500 replicates with 10 random addition replicates per bootstrap. Only bootstrap values over 50% are visualized in the resulting tree (MPB). Support values for major clades that are supported in BI, ML and MP are visualized in the resulting tree. pairwise% identity values for the *Musumecia bettlachensis* and closely related sequences were calculated using MEGA (Tamura et al. 2007).

Musumecia Vizzini & Contu gen. nov.

Mycobank no. MB 561609

Habitus hygrophoroideus vel clitocyboideus. A genero Pseudoclitocybe, cui proximus est, differt lamellis distantibus spissisque, sporis haud amyloideis atque in structura molecularis DNAe (spatiis internis transcriptis ITS et LSU).

Type: *Musumecia bettlachensis* sp. nov.

Etymology

Named after the Swiss mycologist Enzo Musumeci, the collector of the species.

Musumecia bettlachensis Vizzini & Contu sp. nov. (Fig. 1–3)

Figure 1.

Musumecia bettlachensis. Basidiomes (from the holotype). (a) young clustered basidiomes with pink lamellae and evident pseudosclerotial basal mass, (b) basidiomes with pink–yellow lamellae. Scale bars=2 cm.

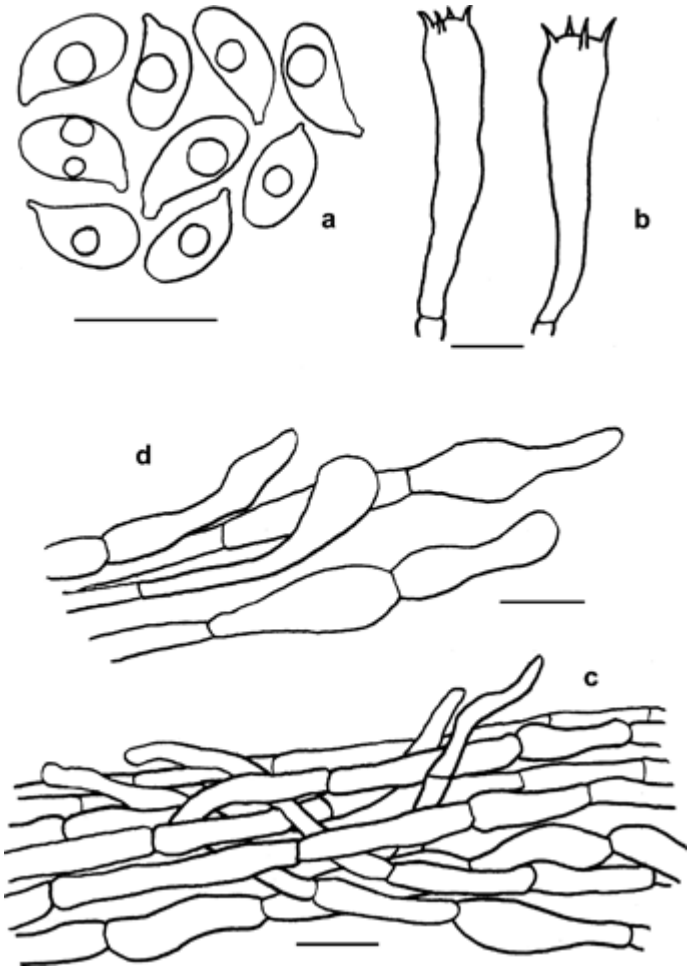

Figure 3. *Musumecia bettlachensis*. Microscopic features (from the holotype). (a) spores, (b) basidia, (c) pileipellis elements, (d) caulocystidioid elements of the stipitipellis. Scale bars=10 μm.

Mycobank no. MB 561610

Ex massa basali alba erumpens sicut Lyophyllum conglobatum. Pileus 2–8 cm, carnosus, convexo-semiglobosus dein explanatus et in senectute revolutus, umbonatus, haud hygrophanus, siccus, albus vel cremeo-albidus. Lamellae haud confertae, adnato-subdecurrentes, latiusculae, sat spissae, in juventute roseo-salmoneae deinde salmoneae vel ex albidae cremeo-isabellinae postremo brunneae. Stipes 2–8×0.5–1.0 cm, centralis, haud elongatus, cylindraceus vel superne incrassatus, pileo concolor, deinde brunneus, pruinosus vel leviter flocculosus, plenus deinde fistulosus. Caro compacta, in stipite fibrosa, cremeo-albida vel pallide cremeo-ochracea. Odor debilis, haud gratis, sapor mitis. Sporarum pulvis in pileo solum visa, cremeo-albida.Sporae 5.5–8.5×3.5–5.0 μm, hyalinae, haud amyloideae, haud dextrinoideae, haud cyanophilae, laeves, ellipsoideo-subamygdaliformes vel subpyriformes-lacrimoideae, raro subcylindraceae, crassotunicatae, apiculus parce manifestus Basidia: 32–45×5–8 μm, elongata, clavata, granulatione siderophila destitutis, haud fibulata. Trama lamellaris regularis vel subregularis, ex hyphis elongatis, plerumque cylindraceis, 8–30 μm latis, efformata. Cystidia nulla. Pilei cutis: suprapellis in ixocute efformata, hyphae 4–17 μm latae, plerumque elongatae; subcutis ex hyphis largioribus, 6–32 μm latis efformata. Stipiti cutis leviter gelata, ex hyphis elongatis, interdum apicibus inflatis vel furcatis, caulocystidiformibus, 4–18 μm latis efformata. Fibulae nullae. Habitat: caespitosa in nemore cum Abies alba et Fraxinus excelsior, sub Abiete alba inventa. Hiemalis. Ex Gallia solum cognita species.

Type: France, Alsace, Dept Haut Rhin, Bettlach, 460 m a.s.l., 2 Oct 2010, leg. E. Musumeci (holotype: TO HG2284, duplicate in herb. pers. Musumeci 6423-10).

Pileus 2–8 cm broad, subglobose-hemispheric at first, with the disc slightly umbonate, then expanding to plane, finally shallowly depressed; margin broadly decurved and inrolled at first, then horizontal, finally broadly undulate, not pellucid-striate, sometimes minutely ribbed. Surface dry, not hygrophanous, at first sericeous, finely tomentose-fibrillose streaked with fine fibrils, then glabrous and smooth in age; colour pure white (4A1), ivory-white (4 B2 C2) or cream-white (5A3), with darker sordid cream-brown (5C3) spots when moist or in age. Lamellae [L=(20) 25–32; l=1–2(3)] interspersed with lamellulae, broadly adnate at first, becoming decurrent to long decurrent, distant, thick, 2–6 mm broad, rarely anastomosed, at times intervenose or forked towards the stipe; at first pale salmon-pink (8A2), then becoming ochre-yellow (3A3-4) and finally greyish-brown (4D4), with an even concolorous edge. Stipe 2–8×0.5–1.0 cm, cylindrical or somewhat broadened towards the apex, slightly bulbous at the base, usually flexuous, subcartilagineous to fleshy, solid then fistulose, caespitose, arising from a white pseudosclerotioid flattened mass incorporating plant debris and particles of soil (Fig. 1a); surface finely pruinose-floccose, at first concolorous with the pileus, then brownish (4D4, 4E5). Rhizomorphs present, conspicuous, white (Fig. 2a). Context quite firm, fibrous in the stipe, whitish cream with alutaceous hues (3A3-4), 4-7(10) mm thick at pileus disc. Smell faint but unpleasant, taste mild. Spore-print (on pileus): whitish-cream (4A3).

Figure 2. *Musumecia bettlachensis*. Basidiomes. (a) mature basidiomes with white rhizomorphs, (b) mature basidiomes with cream–brown spotted pileus and grey-brownish lamellae. Scale bars=2 cm.

Spores: (5) 5.5–8.5×3.5–5.0 µm, on average 7.0×4.2 µm, Q=1.4–1.8, Qm=1.65, hyaline, smooth, wall thin or somewhat thickened, mono-biguttulate, inamyloid, non-dextrinoid, acyanophilous, ellipsoid to subamygdaliform, rarely cylindrical in face view, pyriform to lacrymoid in profile, not in tetrads (Fig. 3a). Basidia 32–45×5–8 µm, clavate to narrowly clavate, not siderophilous, usually 4-spored, rarely 2-spored (Fig. 3b). Subhymenium filamentous. Hymenophoral trama regular to subregular, hymenopodial layer consists of 3–12 µm wide hyphae, central trama made up of 8–30 µm wide hyphae, slightly thick-walled, long cylindrical to subphysaloid, rarely allantoid, hyaline, not encrusted. Cheilocystidia and pleurocystidia absent. Pileipellis a slightly gelified cutis; hyphae 4–17 µm wide, cylindrical or sinuate, smooth, hyaline or pale yellow in KOH, with scattered erect and repent terminal elements, cylindrical to fusiform-lageniform, 30–60×3.5–8.0 µm; pigment parietal when present, faintly yellow in KOH (Fig. 3c). Pileitrama hyphae 6–32 µm in diameter, cylindrical, broadly cylindrical, subphysaloid or inflated, smooth, walls usually slightly thickened, refractive, hyaline to faintly yellow in KOH, with rare pseudoclamps. Stipitipellis slightly gelified, hyphae 4–18 µm wide, slightly pigmented, not encrusted, thick-walled (wall up to 0.8 µm thick), with scattered, caulocystidia-like, clavate to pyriform or forked at apex, erect and repent terminal cells (Fig. 3d). Stipititrama hyphae 5–30 µm wide, cylindrical-subphysaloid, swollen at times, rarely suballantoid and thick-walled (wall up to 0.8 µm thick). Thromboplerous hyphae (= oleiferous hyphae sensu Clémençon 2004) rare. Clamp connections absent in whole basidiome. Pseudosclerotial mass of hyaline, thin-walled and clampless, 3–12 µm wide hyphae intermixed with rare thromboplerous hyphae.

Habitat and distribution

Densely gregarious and caespitose, emerging from a conglobate fleshy pseudosclerotial mass in a mixed wood with *Abies alba* and *Fraxinus excelsior*, on argillose to stony-sandy soil, collected under *Abies alba* together with *Lyophyllum boudieri*, *Mycena rosea*, *Pterula subulata*, *Macrocystidia cucumis*, *Stropharia cyanea*, *Galerina stylifera* and *Lactarius salmonicolor*. Autumn. The new species is so far known only from the type locality.

Etymology

The specific epithet refers to Bettlach, the French locality where the type collection was made.

Additional specimens examined (paratypes)

France: Alsace, Dept. Haut Rhin, Bettlach, 460 m a.s.l., 2 Oct 2010 (over 100 basidiomata), leg. E. Musumeci (type: TO HG2284, duplicate in herb. pers. Musumeci 6423-10); 9 Oct 2010 leg. E. Musumeci (25 basidiomata, herb. pers. Musumeci 6500-10); 15 Oct 2010 (4 basidiomata), leg. E. Musumeci (herb. pers. Musumeci 7020-10).

Molecular analyses

The amplification of the ITS and LSU regions was successful for the *Musumecia bettlachensis*, *Pseudoclitocybe cyathiformis* (Bull.) Singer, and *P. expallens* (Pers.) M. M. Moser specimens, yielding a PCR product ranging from 650–699 bp (ITS) and from 1097–1423 bp (LSU). Comparing these sequences with those from GenBank revealed that *Musumecia bettlachensis* belongs to the Tricholomatoid clade as defined by Matheny et al. (2006) and Binder et al. (2010). The ITS data matrix comprises a total of 51 sequences (including 48 from GenBank). This dataset is 813 base pairs long, and contains 524 (64.5%) variable sites. Of these, 402 (49.4%) are parsimony-informative. The LSU data matrix comprises a total of 50 sequences (including 47 from GenBank). This dataset is 1122 base pairs long, and contains 330 (29.4%) variable sites. Of these, 206 (18.4%) are parsimony-

informative. The combined dataset comprises a total of 54 taxa (including 48 from GenBank) and is 1935 base pairs long. The topologies of the combined ITS and LSU Bayesian, Maximum Likelihood and Maximum Parsimony trees are congruent, and all the analyses have reported high support values for most branches (Fig. 4). *Musumecia bettlachensis* clusters sister to *Pseudoclitocybe* sequences, forming a strongly supported clade with 100% branch support in all the performed analyses. Within this clade, the five *Pseudoclitocybe* sequences (four of *P. cyathiformis* and one of *P. expallens*) display a pairwise% identity of 96.2% and 99.5% for the ITS and the LSU regions, respectively. The *Musumecia bettlachensis* sequences compared with the five *Pseudoclitocybe* show a pairwise% identity of 92.9% (ITS) and 97.6% (LSU). The resulting *Musumecia* and *Pseudoclitocybe* clade is in turn sister to a clade formed by *Omphalina pyxidata* (Bull.) Quél. and *Infundibulicybe*.

Discussion

Based on our phylogenetic analysis of the Tricholomatoid clade (Fig. 4), *Musumecia bettlachensis* is sister to *Pseudoclitocybe*, with high BPP, MLB and MP bootstrap values. However, its macro- and micromorphological features and its ITS and LSU pairwise% identity values are sufficiently different from those of *Pseudoclitocybe cyathiformis* and *P. expallens* to warrant the erection of a new genus: *Musumecia*. The clade consisting of *Musumecia* and *Pseudoclitocybe* is sister to a clade formed by *Omphalina* and *Infundibulicybe*: this result is consistent with the analysis by Binder et al. (2010), where *Infundibulicybe* and *Pseudoclitocybe* are shown to be sister taxa, and *Omphalina* sequences are not considered.

Pseudoclitocybe, typified by *Pseudoclitocybe cyathiformis*, is characterized on the basis of a clitocyboid habit (depressed pileus and decurrent lamellae), grey–brown–black pigmentation, a cutis-like pileipellis, a regular hymenophoral trama, smooth acyanophilous and amyloid spores, elongated non-siderophilous basidia, clampless hyphae (but clamp-connections are present at the base of the stipe and in the mycelium, Kuyper 1995), and absence of cystidia (Singer 1956, 1986, Harmaja 1974, Bigelow 1985, Ballero and Contu 1993, Kuyper 1995, Bon 1997, Watling and Turnbull 1998, Knudsen 2008).

Musumecia shares with *Pseudoclitocybe* the cutis-like pileipellis, the regular hymenophoral trama, the elongated basidia, the smooth acyanophilous spores, the absence of cystidia and of clamp connections in the basidiome, but it sharply differs by: 1) a *Hygrophorus*-like habit (non-depressed convex pileus and distant and thick bright coloured lamellae; 2) a brown darkening of both lamellae and stipe (a remarkable feature hardly seen in other clitocyboid taxa); 3) a caespitose growth, with stipes arising from a pseudosclerotial mass of mycelium; 4) non-amyloid spores; 5) lacking clamp-connections also in the mycelium.

With regard to the peculiar myceliar mass of *Musumecia*, according to our microscopic observations and molecular ITS analysis (data not shown), it is a true pseudosclerotium and not a mycocecidium derived from a modified host as in the mycoparasitic *Clitocybe sclerotioidea* (Bigelow 1965, Gregory 2007) and *Squamanita* spp. (Redhead et al. 1994, Vizzini and Girlanda 1997, Mondiet et al. 2007, Matheny and Griffith 2010).

From a morphological point of view, *Musumecia* could resemble, in the Tricholomatoid clade, *Clitocybe* (Fr.) Staude (typified by *C. nebularis* (Batsch) P. Kumm.), a genus differing by having more crowded and thin lamellae, clamped hyphae, basidia usually not so elongated, and a different way of growth since basidiomes do not originate by a fleshy basal myceliar mass (Singer 1986, Bon 1997, Raithelhuber 2004). The well-known and edible *Lyophyllum conglobatum* (Vittad.) M. M. Moser (probably only a growth form of *L. fumosum* (Pers.) P. D. Orton), with grey to greyish–brown

basidiomes arising from a pseudosclerotial mass, is distinguished by globose spores, clamped hyphae and basidia with siderophilous granulations (Consiglio and Contu 2002).

Within the *Hygrophoroid* clade (Matheny et al. 2006, Binder et al. 2010), *Hygrophorus* Fr. has not coalescent stipes, clamp connections, longer basidia and a bilateral hymenophoral trama (Singer 1986, Arnolds 1990).

References

- *Ammirati, J. F. et al. 2007. Cleistocybe, a new genus of Agaricales. Mycoscience 48: 282–289.*
- *Arnolds, E. 1990. Tribus Hygrophoreae. – In: Bas, C. et al (eds), Flora Agaricina Neerlandica 2. A. A. Balkema, pp. 115–133.*
- *Ballero, M. and Contu, M. 1993. Ecologia e tassonomia dei generi Pseudoclitocybe Sing. e Pseudoomphalina Sing. in Sardegna. Candollea 48: 601–606.*
- *Baroni, T. J. 1981. The genus Rhodocybe Maire (Agaricales). Beih. Nova Hedw 67: 1–194.*
- *Bigelow, H. E. 1965. The genus Clitocybe in North America: section Clitocybe. Lloydia 28: 139–180.*
- *Bigelow, H. E. 1985. North American species of Clitocybe, part. II. Cramer.*
- *Binder, M. et al. 2010. Amylocorticiales ord. nov. and Jaapiales ord. nov.: early diverging clades of Agaricomycetidae were dominated by corticioid forms. Mycologia 102: 865–880.*
- *Bon, M. 1997. Flore Mycologique d'Europe. 4. Les Clitocybes, Omphales et ressemblants. Doc Mycol. Mém. Hors-Sér. no.4. Amiens.*
- *Clémençon, H. 2004. Cytology and plectology of the Hymenomycetes. Bibl. Mycol 199: 1–488.*
- *Consiglio, G. and Contu, M. 2002. Il Genere Lyophyllum P. Karst. emend. Kühner, in Italia. Rivista di Micologia 45: 99–181.*
- *Drummond, A. J. et al. 2011. Geneious ver. 5.4<http://www.geneious.com/>.*
- *Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791.*
- *Gardes, M. and Bruns, T. D. 1993. ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. Mol. Ecol 2: 113–118.*
- *Gregory, D. C. 2007. The genus Clitocybe of California. MSc thesis, San Francisco State Univ.*
- *Harmaja, H. 1974. Pseudoclitocybe atra (Vel.) n. comb. Karstenia 14: 126–128.*
- *Huelsenbeck, J. P. and Ronquist, F. 2001. MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755.*
- *Huelsenbeck, J. P. et al. 2002. Potential applications and pitfalls of Bayesian inference of phylogeny. Syst. Biol 51: 673–688.*
- *Katoh, K. et al. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucl. Acids Res 30: 3059–3066.*
- *Knudsen, H. 2008. Pseudoclitocybe Singer. – In: Knudsen, H. and Vesterholt, J. (eds), Funga Nordica – agaricoid, boletoid and cyphelloid genera. Nordsvamp, p. 238.*
- *Kornerup, A. and Wanscher, J. H. 1978. Methuen handbook of colour, 3rd ed. Eyre Methuen & Co., Ltd.*
- *Kuyper, T. W. 1995. Pseudoclitocybe. – In: Bas, C. et al (eds), Flora Agaricina Neerlandica. Vol. 3. A. A. Balkema, pp. 92–93.*
- *Matheny, P. B. and Griffith, G. W. 2010. Mycoparasitism between Squamanita paradoxa and Cystoderma amianthinum (Cystodermateae, Agaricales). Mycoscience 51: 456–461.*
- *Matheny, P. B. et al. 2006. Major clades of Agaricales: a multi-locus phylogenetic overview. Mycologia 98: 982–995.*

- *Mondiet, N. et al. 2007. The enigmatic Squamanita odorata (Agaricales, Basidiomycota) is parasitic on Hebeloma mesophaeum. Mycol. Res 111: 599–602.*
- *Raithelhuber, J. H. 2004. Mitteleuropäische Trichterlinge. Gattungen Clitocybe, Pseudolyophyllum und Paralepista. J. H. Raithelhuber.*
- *Rambaut, A. and Drummond, A. J. 2007. Tracer ver. 1.4<http://beast.bio.ed.ac.uk/Tracer>.*
- *Redhead, S. A. et al. 1994. Squamanita contortipes, the Rosetta Stone of a mycoparasitic agaric genus. Can. J. Bot 72: 1812–1824.*
- *Singer, R. 1956. New genera of fungi. Mycologia 48: 719–727.*
- *Singer, R. 1986. The Agaricales in modern taxonomy, 4rd ed. Koeltz Scientific Books.*
- *Stamatakis, A. 2006. RAxML-VI-HPC: Maximum Likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690.*
- *Swofford, D. L. 2002. PAUP*: phylogenetic analyses using parsimony (*and other methods), ver. 4.0b10. Sinauer.*
- *Tamura, K. et al. 2007. MEGA4: Molecular evolutionary genetics analysis (MEGA) software ver. 4.0. Mol. Biol. Evol 24: 1596–1599.*
- *Thiers, B. 2011. (continuously updated). Index herbariorum: a global directory of public herbaria and associated staff. New York Bot. Gard. Virtual Herb <http://sweetgum.nybg.org/ih/>.*
- *Vilgalys, R. and Hester, M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. J. Bacteriol 172: 4238–4246.*
- *Vizzini, A. and Girlanda, M. 1997. Squamanita umbonata (Sumst.) Bas, a mycoparasite of Inocybe oblectabilis (Britz.) Sacc. – preliminary note. Allionia 35: 171–175.*
- *Vizzini, A. et al. 2010a. Trichocybe, a new genus for Clitocybe puberula (Agaricomycetes, Agaricales). Fung. Div 42: 97–105.*
- *Vizzini, A. et al. 2010b. A new taxon in the Infundibulicybe gibba complex (Basidiomycota, Agaricales, Tricholomataceae) from Sardinia (Italy). Mycologia 103: 203–208.*
- *Watling, R. and Turnbull, E. 1998. British fungus flora. Agarics and Boleti. 8. Cantharellaceae, Gomphaceae and amyloid spored and xeruloid members of Tricholomataceae (excl. Mycena). R. Bot. Gard. Edinb.*
- *White, T. J. et al. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. – In: Innis, M. A. et al (eds), PCR protocols. Academic Press, pp. 315–322.*