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Overview of the European species of the genus *Clitocella* (*Entolomataceae*, *Agaricales*) with notes on extralimital taxa

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Key words

Agaricomycetes
Basidiomycota
Rhodocybe
taxonomy
Tricholomatineae

Abstract A revision, based on morphological and multigene analysis, of the *Clitocella* species currently present in Europe is provided. Portions of nrITS rDNA, nr28S rDNA (LSU), RNA polymerase II second largest subunit (*RPB2*), translation elongation factor 1-alpha (*EF-1α*), and ATPase subunit 6 (*ATP6*), were used to sort out the relationships of the species within the genus. Three subgenera were recognized: *Clitocella* subg. *Clitocella* encompassing *C. popinalis*, *C. colorata*, *C. mundula*, *C. nigrescens*, *C. obscura* and the new species *C. solaris* from Switzerland; the new *Clitocella* subg. *Paraclitopilus* including *C. fallax* and *C. blancii*; and the new *Clitocella* subg. *Rhodopleurella* for accommodating *C. termitophila*, a peculiar entity characterized by a pleurotoid habit and growing on decaying, abandoned termite nests in the Dominican Republic. *Clitocella colorata* originally described from China is here reported and described for the first time in Europe (Italy and Estonia). *Rhodocybe cupressicola* and *Clitopilus ammophilus* are reduced to later synonyms of *Rhodopaxillus nigrescens*; similarly, *Clitopilus amarus* is treated as a later synonym of *Omphalia fallax* while *Rhodocybe amarella* and *R. ochraceopallida* of *Rhodopaxillus blancii*. Finally, Austrian and Swedish herbarium collections identified as *Rhodocybe*, a doubtful taxon considered by several modern authors occasionally as either a similar but distinct species from *R. popinalis* or as a dwarfish, puny and odourless form of *R. popinalis*, have been proved to be *R. tugrulii*, a species recently described from Turkey and Estonia, and also later reported from Italy and USA.

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INTRODUCTION

The pink-spored genus *Rhodocybe*, typified by *Agaricus caelatus*, is a genus morphologically circumscribed within the *Entolomataceae* by a very variable basidiome shape (clitocyboid, collybioid, mycenoid, omphalinoid, pleurotoid or tricholomatoid), and basidiospores which are angular-pustulate only in polar view, but almost smooth to nodulose, undulate or pustulate in side-view (Baroni 1981, Noordeloos 1983, 1988a, 2012a, Singer 1986, Contu 1999, 2002). The species are saprotrophic and widely distributed in temperate and tropical ecosystems in the northern and southern hemispheres (e.g., Maire 1926, Singer & Digilio 1952, Dennis 1953, 1961, Singer 1969, Pegler 1977, Horak 1978, 1979, Moser 1978, Baroni 1981, 1999, Ovrebo & Baroni 1988, Baroni & Halling 1992, Baroni & Horak 1994, Baroni & Watling 1999, Baroni & Gates 2006, Gröger 2006, Vila et al. 2007a, b, 2009, Henkel et al. 2010, Noordeloos & Gates 2012, Kluting et al. 2014, Vizzini et al. 2016, 2018). Traditionally, infrageneric classifications and species circumscriptions have placed heavy reliance on morphological characters. Identification is strongly dependent on observations of a rather limited set of characters, such as pileus colour, type of stipe attachment to pileus, presence/absence of hymenial pseudocystidia, presence/absence of clamp connections, basidiospore size and ornamentation, and pileipellis structure (Baroni 1981, Noordeloos 1983, 1988a, 2012a, Carassai et al. 2000, Contu 2002).

The first comprehensive molecular phylogenetic analysis of the *Entolomataceae* was conducted by Co-David et al. (2009) using a multigene approach which included the nuclear large subunit ribosomal DNA (nrLSU/28S), the nuclear RNA polymerase subunit II (*RPB2*) and the mitochondrial small subunit (mtSSU) gene regions. Even though that analysis was significantly affected by a limited taxon sampling, nevertheless it revealed that in the *Entolomataceae* it is possible to recognize two main monophyletic clades: one containing the agaricoid genus *Entoloma* s.lat. and the sequestrate genera *Richoniella* and *Rhodogaster* (named the Entoloma clade) and the other containing the genera *Clitopilus* and *Rhodocybe* (the Rhodocybe-Clitopilus clade). Consequently, Co-David et al. (2009) concluded that only two genera should be recognized within the *Entolomataceae*: *Entoloma* for all the species in the Entoloma clade and *Clitopilus* for all the species in the Rhodocybe-Clitopilus clade. Baroni & Matheny (2011), based on an analysis of a larger subset of species of the Rhodocybe-Clitopilus clade, obtained strong support for four major clades (Clitopilus-Rhodocybe p.p., Clitopilopsis, Rhodocybe s.str. and Rhodophana clades) worthy of being recognized as independent segregate genera. Finally, Kluting et al. (2014), redefined the classification of genera within the *Entolomataceae*. Focusing on the classification of genera within the Rhodocybe-Clitopilus clade sensu Co-David et al. (2009), they carried out an in-depth molecular phylogenetic analysis using a set of three independent protein-coding genes (*RPB2*, the

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mitochondrial ATP synthase subunit 6 (*ATP6*) and the nuclear translation elongation factor subunit 1-α (*EF-1α*)) coupled with a robust taxon sampling for this group, recognized five distinct lineages in the clade, corresponding to the genera *Clitopilus*, *Rhodocybe* s.str., *Clitocella*, *Clitopilopsis* and *Rhodophana*.

The aim of the present paper is to provide a detailed overview of the species of *Clitocella* present in Europe based on morphological and molecular phylogenetic multigene analyses (nrITS, nr28S, *RPB2*, *EF-1α* and *ATP6*) of collections from different areas, comparing them also with the *Clitocella* species recently described from Asia and Central and South America (Silva-Filho et al. 2018, Baroni et al. 2020, Jian et al. 2020, Mao et al. 2022). *Clitocella* was established to accommodate the rhodocyboid species with crowded, narrow, long-decurrent lamellae, absence of clamp connections, and thin-walled, obscurely pustulate binucleate basidiospores (Kühner & Lamoure 1971, Kluting et al. 2014).

MATERIAL & METHODS

Morphological studies

Macroscopic morphological features were studied in fresh specimens. The following abbreviations are employed: L = number of lamellae reaching the stipe; l = number of lamellulae between each pair of lamellae. Microscopic structures were examined in dried material using different mounting media: water, L4 (Clémençon 1972), Melzer's reagent, ammoniacal Congo red, phloxine, Cresyl blue and Cotton blue. Dried pieces of the samples were rehydrated in water and mounted in L4. All microscopic measurements were carried out with a Nikon Eclipse 80i microscope, using immersion oil at ×1000 magnification. Basidiospore measurements were made by capturing images of a single visual field with multiple spores (taken from lamellar squashes of exsiccated material of mature specimens) which were then measured using the DS-L1 Nikon camera control unit. Basidiospore dimensions excluded the hilar appendix and are given as (a)b–*c*–d(e), where (a) = minimum value, b = (average minus standard deviation), *c* = *average*, d = (average plus standard deviation) and (e) = maximum value; Q = (minimum−) average minus standard deviation –*average* –average plus standard deviation (−maximum) of ratio length/width; V = (minimum−) average minus standard deviation – *average* – average plus standard deviation (−maximum) of the volume. The approximate spore volume was calculated as that of an ellipsoid (Gross 1972, Meerts 1999). The notation [n/m/p] indicates that measurements were made on 'n' randomly selected spores from 'm' basidiomes of 'p' collections. A minimum of 30 spores were measured for each collection. Q indicates the quotient of length and width of the spores in side view. The width of the basidia was measured at the widest part, and the length was measured from the apex (sterigmata excluded) to the basal septum. Microscopy images were taken using a Nikon DS 5M digital connected to the microscope with both brightfield and interferential contrast optics. Macro- and microchemical testing of pigments were performed using basic solutions (5 % KOH and 10 % ammonia, separately). Chemical spot tests were performed on pileus surface, lamellae and stipe of fresh and/or dried basidiomes using 3 % and 10 % KOH, following Baroni (1978, 1981).

DNA extraction, amplification, and sequencing

DNA was extracted and amplified from dry specimens employing the methods reported in Alvarado et al. (2010, 2012). PCR amplification was performed with the primers ITSF1 and ITSF4 for the ITS region (Gardes & Bruns 1993, White et al. 1990); while LR0R and LR5 (Vilgalys & Hester 1990, Cubeta et al. 1991) were used to amplify the LSU/28S rDNA region; bRPB2-6F2 (reverse of bRPB2-6R2), bRPB2-7.1R2 and bRPB2-7R2 for the RNA polymerase II second largest subunit (*RPB2*) gene (Liu et al. 1999, Matheny et al. 2007), EF1-728F, EF1-983F and EF1-1567R (Carbone & Kohn 1999, Rehner & Buckley 2005) for the translation elongation factor 1-*α* (*EF-1α*) gene, and ATP6-3 (Kretzer & Bruns 1999) and ATP6-6r (Binder & Hibbett 2003) for the ATPase subunit 6 (*ATP6*).

PCR products were checked in 1 % agarose gels, and positive reactions were sequenced with PCR primers. Chromatograms were checked (using MEGA 6.0; Tamura et al. 2013) searching for putative reading errors, and these were corrected. The ITS, LSU, *RPB2*, *EF-1α* and *ATP6* alignments were carried out separately and checked on sight for possible errors in reading with MEGA 6.0 (Tamura et al. 2013), pre-aligned with its MUSCLE application and then manually corrected. In the ITS alignment the 18S region was trimmed. For ITS and LSU alignments gaps and variable regions were filtered using GBlocks version 0.91b software (Talavera & Castresana 2007) with less stringent selection allowing smaller final blocks and gap positions within the final blocks. After trimming both ends the gaps were treated as missing data (as question marks). Introns were delimited from the *EF-1α* sequences and excluded before analyses.

Phylogenetic analyses

BLAST (Altschul et al. 1990) was used to select the most closely related sequences from public databases (INSDC/GenBank https://www.ncbi.nlm.nih.gov/genbank/, UNITE https://unite.ut.ee/, BOLDSYSTEMS http://www.boldsystems.org/).

The data matrices of ITS, LSU, *RPB2*, *EF-1α* and *ATP6*, respectively, were assembled into a multilocus supermatrix. This matrix was analysed by using the Bayesian Inference (BI) and the Maximum Likelihood (ML) criteria through the MESQUITE (Maddison & Maddison 2017) software by which were obtained the .nex and .phy files.

The .nex file was loaded into MrBayes v. 3.2.7a (Ronquist & Huelsenbeck 2003) of the CIPRES Science Gateway v. 3.3 (Miller et al. 2010) and a Bayesian analysis was performed with the ITS–LSU–*RPB2*–*EF-1α*–*ATP6* partitioned (2 simultaneous runs, 6 chains, temperature set at 0.2, sampling every 1 000 generations) until reaching convergence parameters (standard deviation less than 0.01 and PSRF (Potential Scale Reduction Factor) (Gelman & Rubin 1992) equal to 1), after 2 690 000 generations. As required from the procedure, 25 % of the trees, those of the initial stretch and those of the final tail, were 'burned'.

The .phy file was loaded into the RAxML v. 8 program (Stamatakis 2014) using the standard search algorithm with 1 000 bootstrap cycles according to the GTR + GAMMA model. *Clitopilus prunulus* was used as outgroup following Baroni et al. (2020) and Mao et al. (2022). The trees in .tre format were read with the software SEAVIEW v. 4 (Gouy et al. 2010) and saved in a vector format for printing. Both BI and ML analyses produced the same topology. In Fig. 1 is shown the BI tree with the bootstrap values (MLB) combined with those of the posterior probabilities (BPP). Significance thresholds were indicated when higher than 0.95 for posterior probability (BPP) and 70 % for bootstrap (MLB). The lengths of the branches were estimated as average values on the sampled trees.

We estimated the best fit substitution model for each single alignment using the Bayesian information criterion (BIC) with jModelTest 2 (Darriba et al. 2012) and therefore selected the GTR+G+I model for all alignments. The accession numbers of the sequences used in the phylogenetic analysis are reported in Table 1.

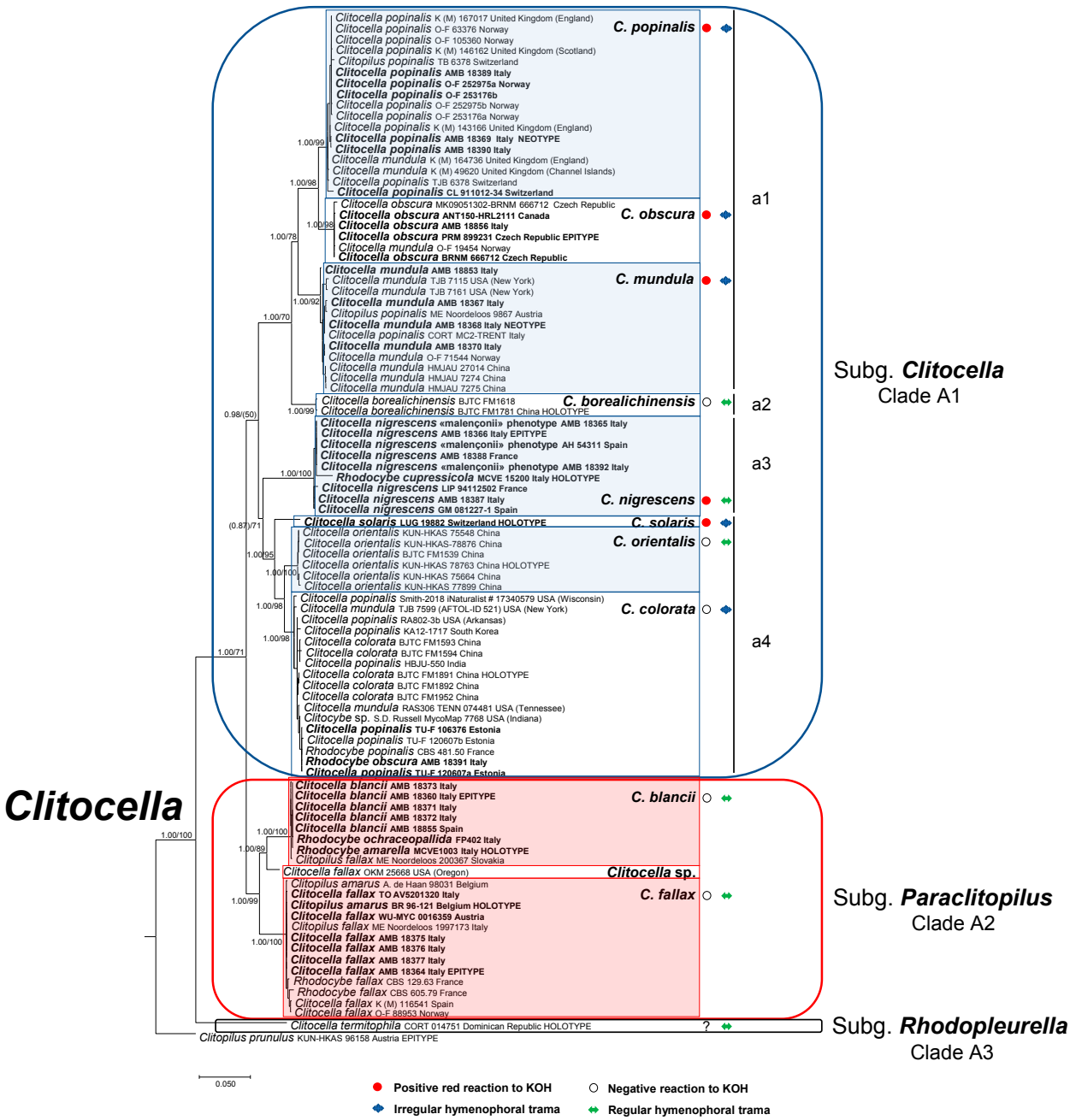

Fig. 1 Multilocus nrITS–nr28S(LSU)–*RPB2*–*EF-1α*–*ATP6* phylogram of the genus *Clitocella* (with *Clitopilus prunulus* as outgroup) obtained in MrBayes. Nodes were annotated if supported by ≥ 0.95 Bayesian PP (left) or ≥ 70 % ML BP (right). Non-significant support values are exceptionally represented inside parentheses.

RESULTS

Phylogenetic analyses

Both Bayesian and Maximum likelihood analyses produced the same topology; only the Bayesian tree with both BPP and MLB values is shown (Fig. 1). The multigene nrITS–nrLSU–*RPB2*–*EF-1α*–*ATP6* data matrix encompassed a total of 259 sequences (including 114 newly generated, 141 from INSDC/GenBank and 4 from UNITE) (62 ITS, 50 LSU, 71 *RPB2*, 42 *EF-1α*, 34 *ATP6*) from 94 samples of 12 taxa. The alignment is 3404 bp long (gaps included).

Except for *Clitocella termitophila*, the other species of *Clitocella* included in the present analysis clustered together forming a monophyletic lineage (BPP = 1.00, MLB = 71 %). *Clitocella termitophila* was sister to all the other species of *Clitocella* (BPP = 1.00, MLB = 100 %) (Fig. 1).

Three major clades (A1–A3) are recognized in *Clitocella* hereafter indicated as *Clitocella* subg. *Clitocella* (BPP = 0.98, MLB = 50 %), *Clitocella* subg. *Paraclitopilus* (BPP = 1.00, MLB = 99 %), and *Clitocella* subg. *Rhodopleurella*, respectively. Within the clade A1, four minor clades are present, a1 (BPP = 1.00, MLB = 78 %) (*C. popinalis*, *C. mundula*, *C. obscura*), a2 (BPP = 1.00, MLB = 99 %) (*C. borealichinensis*), a3 (BPP = 1.00, MLB = 100 %) (*C. nigrescens*), and a4 (BPP = 1.00, MLB = 95 %) (*C. solaris*, *C. orientalis*, *C. colorata*). The clade A2 consists of a clade (BPP = 1.00, MLB = 100 %) including all the sequences of *C. fallax* of the dataset (epitype included, except for *C. fallax* OKM 25668 USA which represents a different, undescribed new species), *Clitopilus amarus* A. d. Haan 98031 KC885963, and *Clitopilus amarus* holotype; and a clade (BPP = 1.00, MLB = 100 %) including the five *C. blancii* sequences (epitype included), the misidentified *Clitocella fallax* 200367 ME Noordeloos Slovakia, *Rhodocybe amarella* MCVE1003 holotype, and *Rhodocybe ochraceopallida* FP402. The clade A3 consists only of *C. termitophila*.

Based on these phylogenetic results, an updated taxonomic arrangement of *Clitocella* species is proposed.

Table 1 Taxa, vouchers, locations, and accession numbers of the DNA sequences used in the phylogenetic analyses. Sequences in **bold** were generated in this study.

Species (revised name)	Label	Voucher	State	GenBank Accession No.					Reference
				nrITS	**nrLSU**	*RPB2*	*EF-1α*	*ATP6*	
Clitocella blancii	*Clitocella blancii*	AMB 18360 Epitype	Italy	**ON502686**	**ON502626**	**ON524537**	**ON524566**	–	**This study**
	Clitocella blancii	AMB 18371	Italy	**ON502687**	**ON502627**	**ON524538**	**ON524567**	–	**This study**
	Clitocella blancii	AMB 18372	Italy	**ON502688**	**ON502628**	**ON524539**	**ON524568**	–	**This study**
	Clitocella blancii	AMB 18373	Italy	–	–	**ON524540**	**ON524569**	–	**This study**
	Clitocella blancii	AMB 18855	Spain	**ON502689**	**ON502629**	–	–	–	**This study**
	Clitopilus fallax	ME Noordeloos 200367	Slovakia	–	GQ289210	GQ289276	–	–	Co-David et al. 2009
	Rhodocybe amarella	MCVE 1003 holotype of *Rhodocybe amarella*	Italy	**ON502690**	–	–	–	–	**This study**
	Rhodocybe ochraceopallida	FP402	Italy	**ON502691**	–	–	–	–	**This study**
Clitocella borealichinensis	*Clitocella borealichinensis*	BJTC FM1618	China	OL966942	OL966946	OL989912	–	OL989922	Mao et al. 2022
	Clitocella borealichinensis	BJTC FM1781 Holotype	China	OL966943	OL966957	OL989913	OL989917	OL989923	Mao et al. 2022
Clitocella colorata	*Clitocella colorata*	BJTC FM1593	China	OL966940	–	–	–	–	Mao et al. 2022
	Clitocella colorata	BJTC FM1594	China	OL966941	–	–	–	–	Mao et al. 2022
	Clitocella colorata	BJTC FM1891 Holotype	China	OL966944	OL966955	OL989914	OL989918	OL989924	Mao et al. 2022
	Clitocella colorata	BJTC FM1892	China	OL966945	OL966956	OL989915	OL989919	OL989925	Mao et al. 2022
	Clitocella colorata	BJTC FM1952	China	–	OL966958	OL989916	OL989920	OL989926	Mao et al. 2022
	Rhodocybe obscura	AMB 18391	Italy	**ON502692**	**ON502630**	**ON524541**	–	–	**This study**
	Clitocella popinalis	TU-F 120607a	Estonia	**ON502693**	**ON502631**	**ON524542**	–	–	**This study**
	Rhodocybe popinalis	TU-F 120607b	Estonia	UDB031317	–	–	–	–	UNITE
	Clitocella popinalis	CBS 481.50	France	FJ770397	–	–	–	–	Hartley et al. 2009
	Rhodocybe popinalis	TU-F 106376	Estonia	UDB011645	–	–	–	–	UNITE
	Clitocella popinalis	KA12-1717	South Korea	KR673647	–	–	–	–	Kim et al. 2015
	Clitocella popinalis	HBJU-550	India	KU561066	–	–	–	–	Kour et al. 2016
	Clitocella popinalis	RA802-3b	USA: Arkansas	MK217434	–	–	–	–	Alanbagi et al. 2020, unpubl.
	Clitocella popinalis	Smith-2018 iNaturalist # 17340579	USA: Wisconsin	MK573922	–	–	–	–	Russell 2019, unpubl.
	Clitocella mundula	TJB 7599 (AFTOL-ID 521)	USA: New York	–	–	KC816953	KC816863	KC816783	Kluting et al. 2014
	Clitocella mundula	RAS306 TENN 074481	USA: Tennessee	MT237519	–	–	–	–	Matheny et al. 2020, unpubl.
	Clitocybe sp.	S.D. Russell MycoMap 7768	USA: Indiana	MK532767	–	–	–	–	Russell 2019, unpubl.
Clitocella fallax	*Clitocella fallax*	AMB 18364 Epitype	Italy	**ON502696**	**ON502634**	**ON524546**	**ON524573**	**ON934200**	**This study**
	Clitocella fallax	AMB 18375	Italy	**ON502694**	**ON502632**	**ON524543**	**ON524570**	–	**This study**
	Clitocella fallax	AMB 18376	Italy	**ON502695**	**ON502633**	**ON524544**	**ON524571**	**ON934199**	**This study**
	Clitocella fallax	TO AV5201320	Italy	**ON502697**	–	–	–	–	**This study**
	Clitocella fallax	AMB 18377	Italy	–	–	**ON524545**	**ON524572**	**ON934198**	**This study**
	Rhodocybe fallax	CBS 605.79	France	AF357018	–	–	–	–	Hofstetter et al. 2002
	Clitopilus amarus	A. d. Haan 98031	Belgium	KC885963	–	–	–	–	Morgado et al. 2016
	Clitopilus amarus	BR A. d. Haan 96-121 Holotype	Belgium	**OP002024**	**OP002025**	**OP021856**	–	–	**This study**
	Clitopilus fallax	ME Noordeloos 1997173	Italy	–	GQ289209	GQ289275	–	–	Co-David et al. 2009
	Clitopilus scyphoides	WU-MYC 0016359	Austria	**ON922913**	–	**ON934196**	–	–	**This study**
	Rhodocybe fallax	CBS 129.63	France	AF357017	AF223166	EF421018	–	–	Hofstetter et al. 2002
	Clitocella fallax	O-F 88953	Norway	–	–	KC816936	KC816845	KC816767	Kluting et al. 2014
	Clitocella fallax	K (M) 116541	Spain	–	–	KC816938	KC816847	KC816769	Kluting et al. 2014
Clitocella mundula	*Clitocella mundula*	HMJAU 27014	China	–	MN065722	MN148159	MN166270	MN133779	Jian et al. 2020
	Clitocella mundula	HMJAU 7275	China	–	MN065723	MN148160	MN166271	MN133780	Jian et al. 2020
	Clitocella mundula	HMJAU 7274	China	–	MN065724	MN148161	MN166272	MN133781	Jian et al. 2020
	Clitocella mundula	AMB 18367	Italy	**ON502698**	**ON502635**	**ON524547**	–	–	**This study**
	Clitopilus popinalis	ME Noordeloos 9867	Austria	–	GQ289213	GQ289280	–	–	Co-David et al. 2009
	Clitocella mundula	AMB 18370	Italy	**ON502700**	**ON502637**	**ON524549**	–	–	**This study**
	Clitocella mundula	AMB 18368 neotype	Italy	**ON502699**	**ON502636**	**ON524548**	–	–	**This study**
	Clitocella mundula	AMB 18853	Italy	**ON502701**	**ON502638**	**ON524550**	**ON524574**	–	**This study**

Table 1 (cont.)

Species (revised name)	Label	Voucher	State	GenBank Accession No.					Reference
				nrITS	**nrLSU**	*RPB2*	*EF-1α*	*ATP6*	
Clitocella mundula (cont.)	*Clitocella mundula*	O-F 71544	Norway	–	–	KC816950	KC816860	KC816780	Kluting et al. 2014
	Clitocella mundula	TJB 7115	USA: New York	–	–	KC816951	KC816861	KC816781	Kluting et al. 2014
	Clitocella mundula	TJB 7161	USA: New York	–	–	KC816952	KC816862	KC816782	Kluting et al. 2014
	Clitocella popinalis	CORT MC2-TRENT	Italy	–	–	KC816973	–	KC816798	Kluting et al. 2014
Clitocella nigrescens	*Clitocella nigrescens*	AMB 18366 Epitype	Italy	**ON502704**		**ON524553**	**ON524576**	–	**This study**
	Clitocella nigrescens	AMB 18387	Italy	**ON502705**	**ON502640**	**ON524554**	–	–	**This study**
	Clitocella nigrescens	AH 54311	Spain	**ON502703**	**ON502639**	**ON524551**	–	–	**This study**
	Clitocella nigrescens	GM 081227-1	Spain	**ON502706**	**ON502641**	**ON524555**	–	–	**This study**
	Clitocella nigrescens	AMB 18392	Italy	**ON502709**	**ON502643**	**ON524557**	–	–	**This study**
	Clitocella nigrescens	LIP 94112502	France	**ON502702**	–	–	–	–	**This study**
	Clitocella nigrescens	AMB 18365	Italy	–	–	**ON524552**	**ON524575**	–	**This study**
	Clitocella nigrescens	AMB 18388	France	**ON502707**	**ON502642**	**ON524556**	–	–	**This study**
	Rhodocybe cupressicola	MCVE 15200 holotype of *Rhodocybe cupressicola*	Italy	**ON502708**	–	–	–	–	**This study**
Clitocella obscura	*Clitocella obscura*	BRNM 666712	Czech Republic	**ON502710**	**ON502644**	**ON524558**	–	–	**This study**
	Clitocella obscura	MK09051302-BRNM 666712	Czech Republic	KX271753	–	–	–	–	Vizzini et al. 2016
	Clitocella obscura	PRM 899231	Czech Republic	**ON502711**	**ON502645**	**ON524559**	–	–	**This study**
	Clitocella obscura	AMB 18856	Italy	**ON502712**	**ON502646**	**ON524560**	**ON524577**	–	**This study**
	Clitocella mundula	O-F 19454	Norway	–	–	KC816954	KC816864	KC816784	Kluting et al. 2014
	Clitocella mundula	ANT150-HRL2111	Canada	**MN992316**	**ON923665**	**ON934195**	–	–	**This study**
Clitocella orientalis	*Clitocella orientalis*	KUN-HKAS 75548	China	MN061333	MN065727	MN148164	MN166275	MN133784	Jian et al. 2020
	Clitocella orientalis	KUN-HKAS 75664	China	MN061332	MN065726	MN148163	MN166274	MN133783	Jian et al. 2020
	Clitocella orientalis	KUN-HKAS 77899	China	–	MN065725	MN148162	MN166273	MN133782	Jian et al. 2020
	Clitocella orientalis	KUN-HKAS 78763 Holotype	China	–	MN065728	MN148165	MN166276	MN133785	Jian et al. 2020
	Clitocella orientalis	KUN-HKAS 78876	China	MN061334	MN065729	MN148166	MN166277	MN133786	Jian et al. 2020
	Clitocella orientalis	BJTC FM1539	China	–	OL966947	OL989911	OL989921	–	Mao et al. 2022
Clitocella popinalis	*Clitocella popinalis*	O-F 252975a	Norway	**ON502713**	**ON502647**	**ON524561**			**This study**
	Rhodocybe popinalis	O-F 253176a	Norway	UDB017726	–	–	–	–	UNITE
	Rhodocybe popinalis	O-F 252975b	Norway	UDB037336	–	–	–	–	UNITE
	Clitocella popinalis	AMB 18369 Neotype	Italy	**ON502715**	**ON502649**	**ON524563**	–	–	**This study**
	Clitocella popinalis	O-F 253176b	Norway	**ON502714**	**ON502648**	**ON524562**	–	–	**This study**
	Clitocella mundula	K (M) 49620	United Kingdom	–	–	KC816948	KC816858	KC816778	Kluting et al. 2014
	Clitocella popinalis	K (M) 143166	United Kingdom	–	–	KC816971	KC816878	KC816796	Kluting et al. 2014
	Clitocella popinalis	K (M) 146162	United Kingdom	–	–	KC816970	KC816877	KC816795	Kluting et al. 2014
	Clitocella mundula	K (M) 164736	United Kingdom	–	–	KC816949	KC816859	KC816779	Kluting et al. 2014
	Clitocella popinalis	K (M) 167017	United Kingdom	–	–	KC816972	KC816879	KC816797	Kluting et al. 2014
	Clitocella popinalis	O-F 63376	Norway	–	–	KC816974	KC816880	KC816799	Kluting et al. 2014
	Clitocella popinalis	O-F 105360	Norway	–	–	KC816975	KC816881	KC816800	Kluting et al. 2014
	Clitocella popinalis	TJB 6378	Switzerland	–	–	KC816976	KC816882	KC816801	Kluting et al. 2014
	Clitocella popinalis	TB 6378	Switzerland	–	AF261285	GU384654	–	–	Moncalvo et al. 2002, Baroni et al. 2011
	Clitocella popinalis	AMB 18389	Italy	**ON502716**	**ON502650**	**ON524564**	–	–	**This study**
	Clitocella popinalis	AMB 18390	Italy	**ON502717**	**ON502651**	–	–	–	**This study**
	Clitocella popinalis	CL 911012-34	Switzerland	**ON502718**	**ON502652**	**ON524565**	–	–	**This study**
Clitocella solaris	*Clitocella solaris*	LUG 19882 Holotype	Switzerland	**ON922914**	**ON923666**	**ON934197**	–	–	**This study**
Clitocella sp.	*Clitocella fallax*	OKM 25668	USA: Oregon	–	–	KC816937	KC816846	KC816768	Kluting et al. 2014
Clitopilus prunulus	*Clitopilus prunulus*	KUN-HKAS 96158 Epitype	Austria	NR_172770	MN065691	MN148129	MN166240	MN133745	Jian et al. 2020
Rhodopleurella termitophila	*Clitocella termitophila*	CORT 014751 Holotype	Dominican Republic	–	–	MN893319	–	–	Baroni et al. 2020

TAXONOMY

Clitocella Kluting, T.J. Baroni & Bergemann, Mycologia 106(6): 1135. 2014

Clitocella Kluting, T.J. Baroni & Bergemann, in Kluting, A Revised Generic Classification for the Rhodocybe-Clitopilus clade, Thesis, Middle Tennessee State University: 20. 2013, nom. inval., Art. 32.1 (a) (Shenzhen Code, Turland et al. 2018).

Synonym. *Rhodocybe* sect. *Decurrentes* (Konrad & Maubl.) Singer, Lilloa 22: 609. 1951, *partim*.
Type. Clitocella popinalis (Fr.) Kluting, T.J. Baroni & Bergemann.
Synonym. *Agaricus popinalis* Fr., Syst. Mycol. 1: 194. 1821, nom. sanct.

Basidiomes centrally stipitate to pleuropodal (*C. termitophila*), usually clitocyboid, white, greyish, grey-brown or purplish grey. *Pileus* small to medium-sized (5–120 mm), opaque, glabrous, smooth or matted tomentose or matted fibrillose, usually covered with a white bloom, fleshy. *Lamellae* subdecurrent to long-decurrent, narrow or very narrow (up to 4 mm), and close to crowded or very crowded with an even edge. *Stipe* equal and glabrous, pubescent, floccose or fibrillose, often with basal white rhizomorphs. *Context* usually with farinaceous to cucumber-like smell and taste bitter. *Spore-print* incarnate-pink. Surfaces of the dried basidiomes reddening or not in KOH. *Basidiospores* thin-walled (wall up to 0.2–0.4 µm thick), minutely and often obscurely angular in polar view with 7–12 facets and ornamented with obscure or sometimes distinct scattered undulating pustules or minute bumps visible in side and frontal views under light microscope, slightly cyanophilic and inamyloid, binucleate. *Hymenophoral trama* regular (consisting of parallel cylindrical hyphae) or irregular (composed by interwoven hyphae). *Hymenial cystidia* usually lacking, but if present then quite rare, arranged in small clusters as cheilocystidia. *Pseudocystidia* absent. *Clamp connections* absent.

Notes — It is a widespread saprotrophic genus known from Europe, Asia, North, South and Central America in forested or in grassy areas and also on dunes (Baroni 1981, Contu 2002, Noordeloos 1988a, 2012a, Moreau et al. 2008, Kluting et al. 2014, Kour et al. 2016, Silva-Filho et al. 2018, Baroni et al. 2020, Jian et al. 2020, Mao et al. 2022). *Clitocella* species are usually terrestrial but *C. termitophila* grows on arboreal nests of neotropical termites (Baroni et al. 2020). Thirteen are validly published species of *Clitocella* present in Index Fungorum (http://www.indexfungorum.org/names/Names.asp). Phylogenetically it is sister to the genus *Clitopilus*, typified with *Agaricus prunulus*. The highly supported clade *Clitocella* + *Clitopilus* is sister to *Clitopilopsis*, typified with *Agaricus hirneolus* (Co-David et al. 2009, Kluting et al. 2014, Morgado et al. 2016, Vizzini et al. 2016, Sánchez-García & Matheny 2017, Boccardo & Dovana 2019, Baroni et al. 2020, Sánchez-García et al. 2020, Mao et al. 2022). Most species of *Clitopilus* show the same clitocyboid habit as *Clitocella* but are distinguished by basidiospores which are ornamented with pustules arranged in longitudinal ridges (Noordeloos 1988b, 2012b). *Clitopilopsis* differs by subdistant lamellae, basidiospores with thickened walls 0.5–0.8(–0.9) µm, nearly smooth in all views, and round or obscurely angular in polar view, and multiseptated (1–4 septate) hymenial cystidia (Kluting et al. 2014, Jian et al. 2020). *Rhodocybe* s.str. has basidiospores ornamented with prominent, random isolated pustules in side and frontal views, distinctly angular in polar view, and hymenial cystidia, when present, can be pseudocystidia with brightly coloured contents (Kluting et al. 2014).

Part of the species currently recognized in *Clitocella* had previously been included in *Rhodocybe* sect. *Decurrentes* as morphologically delimited by Baroni (1981), Singer (1986), and Contu (2002). Baroni (1981) identified two characters, the reddening or not of the surfaces of the dry basidiome with KOH, and the type of hymenophoral texture (regular of parallel oriented hyphae, or irregular of confusedly interwoven hyphae), as important for distinguishing species.

Subgenus Clitocella

It is distinguished by a usually pale grey, grey, dark grey, violaceous black pileus, basidiome surfaces unchanging or turning grey or black when bruised or with age, usually with a positive, reddish, KOH reaction, a usually irregular hymenophoral trama (intertwined hyphae) and globose, subglobose, broadly ellipsoid to ellipsoid basidiospores, which are obscurely to clearly angular, and weakly to clearly pustulate.

Clitocella popinalis (Fr.) Kluting, T.J. Baroni & Bergemann, Mycologia 106(6): 1138. 2014 — Fig. 2, 3

Basionym. *Agaricus popinalis* Fr., Syst. Mycol. (Lundae) 1: 194. 1821, nom. sanct.
Synonyms. *Clitopilus popinalis* (Fr.) P. Kumm., Führer Pilzk.: 97. 1871.
Paxillus popinalis (Fr.) Ricken, Die Blätterpilze: 94. 1911. — *Clitocybe popinalis* (Fr.) Bres., Iconogr. Mycol. 4: 160. 1928.
Rhodopaxillus popinalis (Fr.) Konrad & Maubl., Révision des Hymenomycetes de France: 327. 1937.
Paxillopsis popinalis (Fr.) J.E. Lange, Fl. Agaric. Danic. 4: 49. 1939.
Clitopilopsis popinalis (Fr.) Kühner ex Konrad & Maubl., Encycl. Mycol. (Paris) 14: 379. 1949 '1948'.
Rhodocybe popinalis (Fr.) Singer, Lilloa 22: 609. 1951 '1949'.
Paxillopsis popinalis var. *pallida* J.E. Lange, Fl. Agaric. Danic. 5 (Taxon. Consp.): 104. 1940.
Rhodocybe popinalis f. *pallida* (J.E. Lange) Bohus, in Bohus, Locsmándi & Vasas, Beitr. Kenntn. Pilze Mitteleur. 9: 46. 1994.
Rhodocybe popinalis var. *pallida* (J.E. Lange) P.-A. Moreau, Doc. Mycol. 33 (132): 36. 2004.
Rhodocybe popinalis var. *insititia* Bon, Doc. Mycol. 11(41): 47. 1980.
Rhodocybe popinalis f. *insititia* (Bon) Courtec., Doc. Mycol. 18(72): 50. 1988.
Rhodocybe popinalis var. *hollosii* Babos (as '*hollosi*'), in Babos, Bohus, Locsmándi & Vasas, Beitr. Kenntn. Pilze Mitteleur. 9: 45. 1994.
Rhodocybe popinalis var. *sordidula* P.-A. Moreau, Bull. Trimestriel Soc. Mycol. France 113(4): 338. 1997.
??*Rhodocybe popinalis* var. *macrospora* A. Kaur, Atri & M. Kaur (as '*macrosporus*'), J. New Biol. Rep. 2(3): 261. 2013.
Clitopilus mundulus var. *nigrescens* Sacc., Syll. Fung. 5: 700. 1887.
Paxillus mundulus var. *arenosus* Hruby, Verh. Naturf. Vereins Brünn 67: 17. 1936.
Rhodocybe mundula f. *luteolamellata* Bohus (as '*luteomellata*'), in Babos, Bohus, Locsmándi & Vasas, Beitr. Kenntn. Pilze Mitteleur. 9: 47. 1994.
Rhodocybe mundula var. *rubescens* Locsmándi & Vasas, in Babos, Bohus, Locsmándi & Vasas, Beitr. Kenntn. Pilze Mitteleur. 9: 48. 1994.
Clitocella popinalis (Fr.) Kluting, T.J. Baroni & Bergemann, in Kluting, A Revised Generic Classification for the Rhodocybe-Clitopilus clade, Thesis, Middle Tennessee State University: 22. 2013, nom. inval., Art. 32.1 (a) (Shenzhen Code, Turland et al. 2018).
Neotype. AMB 18369 (designated by G. Consiglio, Index Fungorum 417: 1. 2019).

Selected iconography — Allard (1991: 32), Wilhelm (1992: 195), Courtecuisse & Duhem (1994: n° 974), Hausknecht & Zuccherelli (1998: 127), Lavorato & Contu (2001: 349, as *R. obscura*), Moreau (1997: Atlas, planche 336), Ludwig (2000: t. 167, 74.15.B, D, p. 169), Eyssartier & Roux (2011: 616), Overall (2011: f. 5, p. 29), Padovan et al. (2020: 252, below).

Selected descriptions — Kühner & Lamoure (1971: 18), Baroni (1981: 97), Allard (1991: 32), Moreau (1997: 337).

Pileus 20–60(–90) mm, fleshy, convex then applanate, depressed in old basidiomes, sometimes with a broad low obtuse umbo; margin at first involute, soon straight, not translucently striate, entire, sometimes undulate; surface dry, glabrous (smooth), not or only slightly hygrophanous, covered at first with a minute white soon disappearing pruina that persists on the margin, under the pruinose covering, grey, ash-grey, purplish grey, brownish grey, blackish grey (whitish in albinotic forms), often dark-spotted on the margin (as *Lepista panaeola*), with age usually fading to alutaceous beige starting from the centre, paler, whitish on the margin. *Lamellae* L = 50–70, l = 1–3(–4),

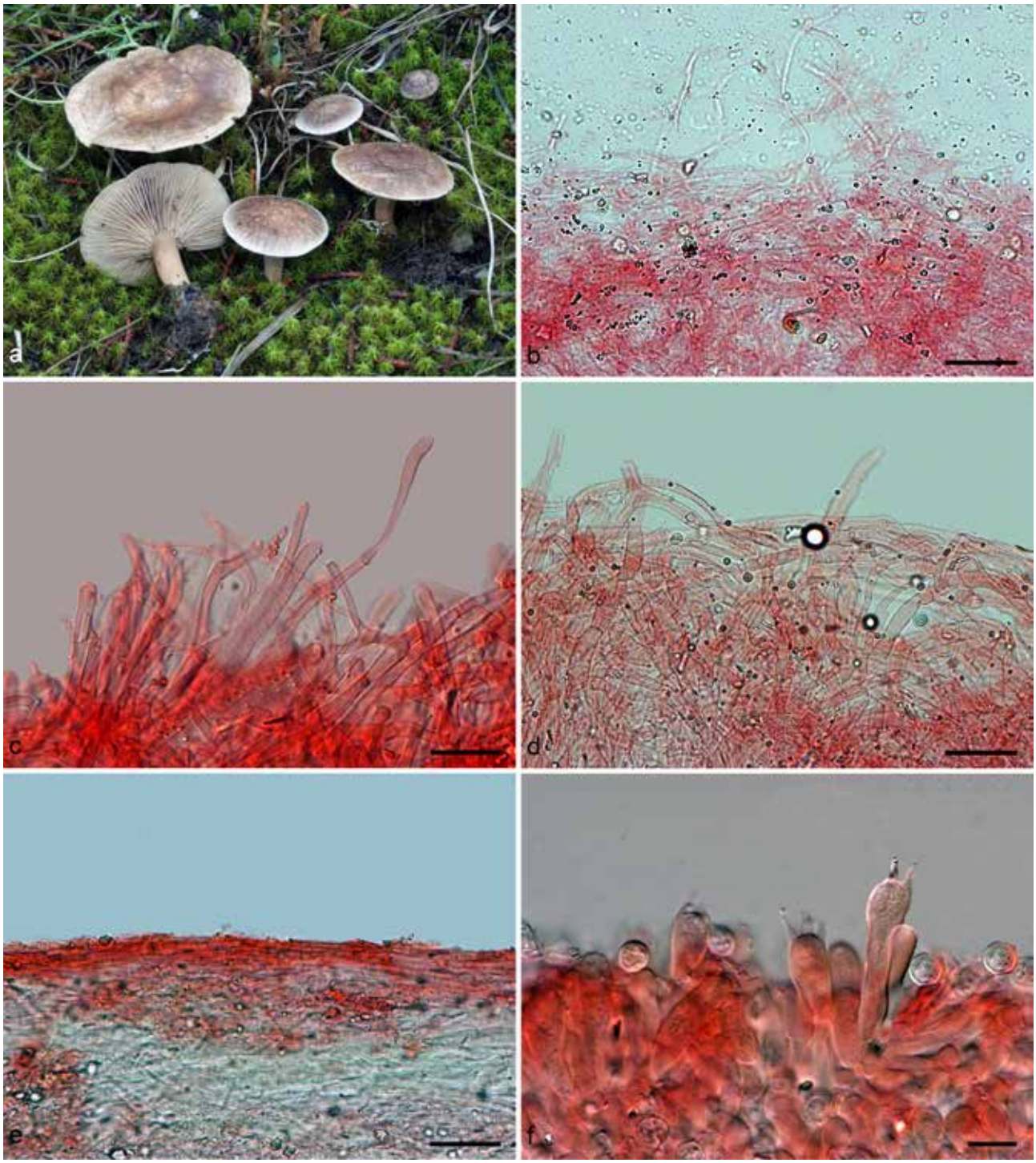

Fig. 2 *Clitocella popinalis*. a. Basidiomes (AMB 18369, neotype); b, c. pileipellis (AMB 18369, (neotype); d. pileipellis (AMB 18389); e. stipitipellis (AMB 18369, neotype); f. basidia and basidiospores (CL 91101234). b–f in ammoniacal Congo red. — Scale bars: b–e = 30 µm, f = 10 µm. — Photos: a by M. Maletti, b–f by M. Marchetti.

crowded, narrow, up to 4 mm broad, adnate-subdecurrent when young, then subdecurrent to strongly decurrent, cream grey, pale grey brown, then pinkish grey, usually unchanging on handling, rarely turning pale grey, with a concolorous, entire edge. *Stipe* 15–60(–80) × 4–18 mm, cylindrical or tapering downwards, rarely broadened at base, solid, stuffed with age, dry, smooth, fibrillose, pale grey to grey brownish, often with white rhizomorphs. *Context* rather crumbly, white to pale grey in the pileus, white to pale ochraceous in the stipe. *Smell* strongly farinaceous to rancid farinaceous (cucumber-like). *Taste* quite bitter, farinaceous, rubbery. *Spore-print* pinkish.

Basidiospores (4.9–)5.4–*5.8*–6.2(–6.9) × (4.1–)4.7–*5.1*–5.4(–6.0) µm [149/6/6], Q = (0.98–)1.06–*1.15*–1.24(–1.41), V = (45.5–)64.0–*78.8*–93.6(–122) µm^3, (rarely) globose, usually subglobose to broadly ellipsoid, angular and adaxially flattened in side view (with a clear suprahilar depression), subglobose to broadly ellipsoid and angular in frontal view (10–12 facets), clearly angular in polar view (7–10 facets), distinctly undulate-pustulate in all views in Cotton blue, hilar appendage up to 1 µm long, contents smooth, uni- to pluriguttulate, wall cyanophilic, slightly congophilic, pale yellow in water, yellow in Melzer's (inamyloid). *Basidia* 25–40 × 6–8 µm, clavate-4-spored, with many inner greenish guttulae. *Hymenophoral trama* irregular, consisting of cylindrical, 3–8 µm wide interwoven hyphae. *Hymenial cystidia* absent. *Subhymenium* 20–30 µm thick, *textura intricata* type, elements short and 2.5–4 µm wide. *Pileipellis* a cutis of parallel to interwoven cylindrical hyphae, the most superficial are often anticlinally oriented, thin (1–3 µm wide),

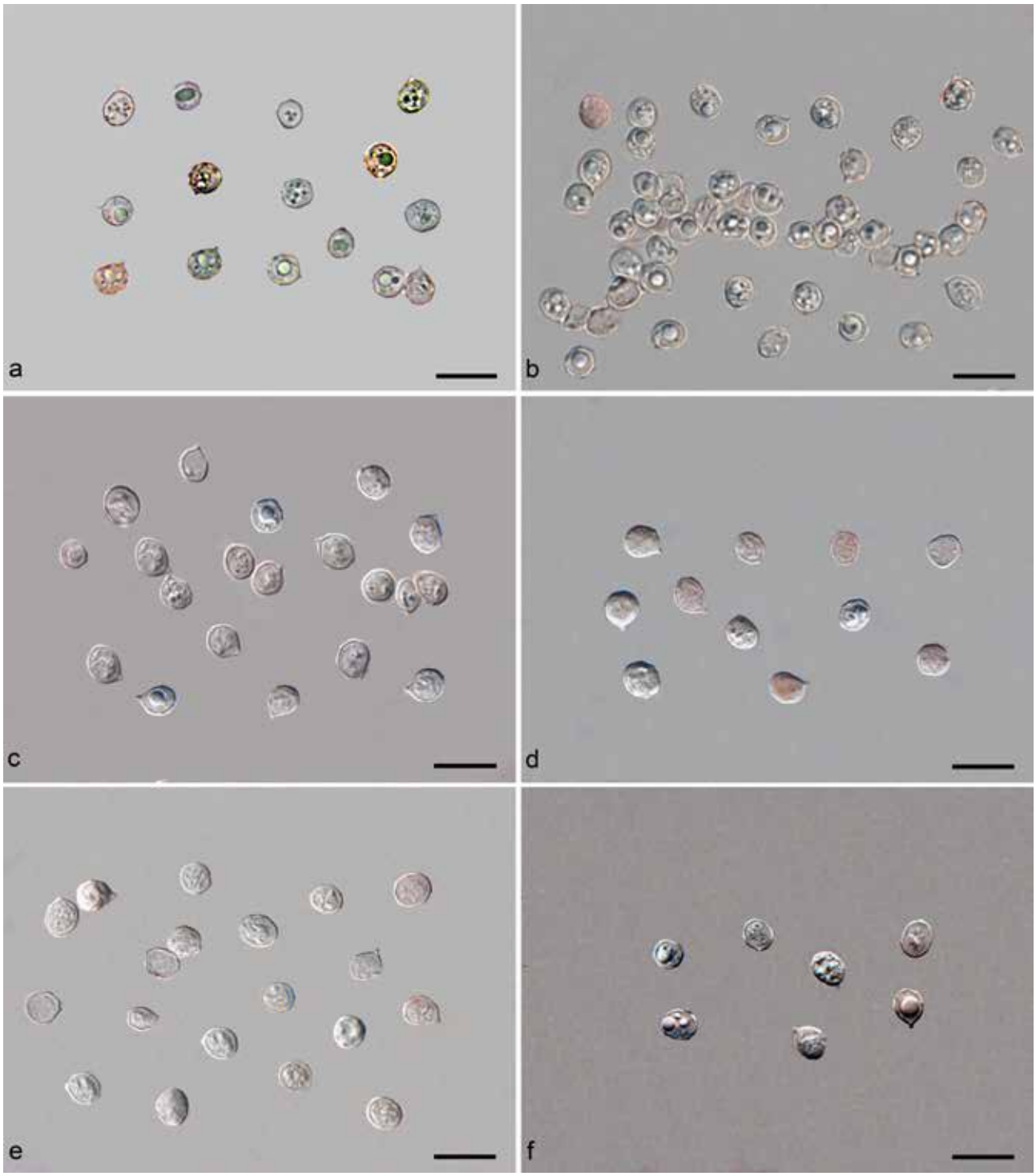

Fig. 3 *Clitocella popinalis*. Basidiospores. a. AMB 18369 (neotype); b, c. AMB 18389; d. CL 91101234; e. O-F 253176; f. O-F 252975. a–f in ammoniacal Congo red. — Scale bars = 10 µm. — Photos by M. Marchetti.

flexuous, with obtuse apex, and immersed in a gelatinous matrix, the innermost ones are 3–4 µm wide; pigment minutely incrusting, patchlike, some hyphae containing tiny yellowish lipid guttules; thromboplerous hyphae present; abundant crystalline deposits of acicular form. *Subpellis* of 4–6 µm wide parallel hyphae. *Stipitipellis* a cutis of parallel, 2–5 µm wide thin- to medium-walled hyphae (wall up to 0.4 µm thick), sometimes with some erect, caulocystidioid-like versiform elements. *Clamp connections* absent.

Chemical spot-test reactions — KOH on dried basidiomes surfaces (pileus, lamellae and stipe) produces a reddish colour.

Specimens examined. Italy, Vicenza, Breganze, Collina, in a meadow near *Picea sitchensis* and *Abies alba*, 8 May 2005, *G. Battaglia*, AMB *18390* (as *Rhodocybe obscura*); ibid., 4 Nov. 2009, *G. Battaglia*, AMB *18389* (as *Rhodocybe obscura*); Pesaro-Urbino, Piobbico, Monte Grino, among mosses under *Cedrus atlantica* and *Cupressus arizonica*, 26 Oct. 2009, *M. Maletti*, AMB *18369* (**neotype**). – Norway, Vest-Agder, Farsund, Jvijosanden, ved Kvijoodden, dune pasture, dense vegetation, 11 Oct. 2011, *K. Høiland*, O-F *253176*; Vest-Agder, Kristiansand, Hamresanden, Kristiansand, strandeng i kanten mot sand (beach meadow at the edge against sand), 19 Sept. 2015, *A. Huvestad*, *I.-L. Fonneland*, *U. Hammering*, O-F *252975*. – Switzerland, surroundings of Zurich, in a mixed forest with *Picea abies* and *Fagus sylvatica*, 12 Oct. 1991, *C. Lavorato*, C. Lavorato *91101234* (as *Rhodocybe obscura*).

Notes — *Clitocella popinalis* is a species so far reported for Europe where it is widespread (e.g., Kühner & Lamoure 1971, Baroni 1981, Allard 1991, Wilhelm 1992, Moreau 1997, Hausknecht & Zuccherelli 1998, Eyssartier & Roux 2011, Overall 2011, Noordeloos 2012a) and for Morocco (Malençon & Bertault 1975). It usually grows in open grasslands, meadows, gardens

or in grassy spots in forested areas, sometimes on maritime dunes (Guinberteau & Courtecuisse 1993, Noordeloos 1988a). *Rhodocybe popinalis* var. *macrospora* (Kaur et al. 2013) found on a mixed cattle and horse dung heap from Punjab, India, with smell and taste not distinctive, pileus 7–16 mm broad, deeply depressed at the centre; surface moist, white to pinkish white, rarely with greyish brown shades; pinkish to brownish orange lamellae, and very angular basidiospores 8.5–13.6 × 6–8.5 µm (Q = 1.52) surely does not represent *C. popinalis*. Given the very poor description of the basidiospores, it could represent an undescribed species of *Clitocella* subg. *Paraclitopilus* (see below) or even a species of *Entoloma*. Another collection from India named *C. popinalis* (Kour et al. 2016) is *C. colorata* (Fig. 1 and phylogenetic analysis in Mao et al. 2022). *Rhodocybe popinalis* var. *insititia* is characterized by a depressed pileus and a lateral stipe growing on *Ammophila arenaria* (Bon 1980).

Clitocella popinalis has often been confused with *C. mundula* and/or *C. obscura* (see below). These three species are phylogenetically closely related and form a strongly supported clade (Fig. 1; BPP = 1.00, MLB = 78 %). They share a pileus with pale to dark grey tinges, a reddish reaction to KOH of the basidiome surfaces, and an irregular hymenophoral trama. The basidiomes of *C. popinalis* are usually unchanging on bruising, but rare collections whose surfaces turned red and then eventually blackish grey were reported (Wilhelm 1992, Babos et al. 1994).

The albinotic forms of *C. popinalis* (Lange 1940, Babos et al. 1994, Moreau 1997, 2004) differ from *C. mundula* in the non-blackening surfaces, pileipellis elements with inner yellowish lipidic droplets, and larger basidiospores with evident pustules (Allard 1991, Moreau 1997). Additionally, *C. popinalis* is associated with grasses, whereas *C. mundula* is considered a woodland species.

Clitocella obscura differs from *C. popinalis* in dark grey to blackish pileus and lamellae, longer basidiospores reaching and sometimes exceeding 7 µm in length, well-developed filiform cheilocystidia, and growing in *Picea* litter in montane forests (see below).

Clitocella obscura (Pilát) Vizzini, Consiglio & M. Marchetti, *comb. nov.* — MycoBank MB 845483; Fig. 4–6

Basionym. *Rhodopaxillus obscurus* Pilát, Česká Mykol. 6(6–7): 97. 1952.

Based on *Rhodopaxillus obscurus* Pilát, Klíč k Určování Našich Hub Hřibovitých a Bedlovitých [Agaricales Agaricalium Europaeorum Clavis Dichotomica] (Praha: Brazda): 167 (1951), nom. inval., Art. 36.1. (Shenzhen Code, Turland et al. 2018).

See also *Rhodopaxillus obscurus* Pilát, Sborník Národního Musea v Praze (Acta Musei Nationalis Pragae) B 9 (2: Botanica 1): 67 (1953), a superfluous validation.

Synonyms. *Clitopilopsis obscura* (Pilát) M.M. Moser, in Gams, Kl. Krypt.-Fl., Edn. 2 2b: 109. 1955. *Rhodocybe obscura* (Pilát) M.M. Moser, in Gams, Kl. Krypt.-Fl., Edn 3 2b/2: 151. 1967.

Clitopilus obscurus (Pilát) Noordel. & Co-David, in Co-David, Langeveld & Noordeloos, Persoonia 23: 163. 2009.

Clitocella obscura (Pilát) Vizzini, Sesli, T.J. Baroni, Antonín & I. Saar, Phytotaxa 267(1): 13. 2016 nom. invalid., erroneous citation of the basionym, Art. 41.5 (Shenzhen Code, Turland et al. 2018).

Holotype. PRM 668718 (as *Rhodopaxillus obscurus*).

Epitype. PRM 899231 (designated here, MBT 10008921).

Selected iconography — Pilát (1952: 96), Moreau (1997: Atlas, planche 339), Ludwig (2000: t. 162, 74.1, p. 164).

Selected descriptions — Pilát (1953: 67), Baroni (1981: 95), Enderle (1980–1981: 32), Moreau (1997: 340).

Pileus 30–100 mm, convex then applanate, without umbo, depressed in old basidiomes, margin at first involute, then straight, not translucently striate, entire to undulate, lobate; surface dry, glabrous (smooth), not or only slightly hygrophanous, at first covered with a minute white soon disappearing pruina (which often fragments concentrically) that persists on the margin; under the pruinose covering dark grey, dark brownish grey, blackish. *Lamellae* medium crowded, L = 40–60, l = (1–)2–3(–4) subdecurrent to long decurrent, often furcate (bifid) at stipe apex and towards pileus margin, at first pale grey, then dark grey, brownish to slate, with pinkish tones, never turning grey black on handling or bruising, with an even, concolorous or paler edge. *Stipe* short, 20–40 × 8–20 mm, usually tapering downwards, white floccose-squamulose, with a white mycelioid tomentum aggregating the litter and white rhizomorphs; concolorous with the pileus or paler. *Context* solid, firm, whitish, never turning black when cut or when bruised. *Smell* farinaceous, cucumber-like. *Taste* farinaceous, bitter. *Spore-print* pinkish.

Basidiospores (4.0–)5.9–*6.4*–7.0(–8.0) × (3.6–)4.6–*4.9*–5.2(–6.2) µm [487/9/9], Q = (0.85–)1.21–*1.32*–1.42(–1.70), V = (31.4–)66.0–*81.7*–97.3(–151) µm^3, rarely subglobose, broadly ellipsoid to ellipsoid in side and frontal view, angular and adaxially flattened in side view, angular in polar view (7–10 facets), hilar appendage up to 1 µm long, contents smooth, uni- to pluriguttulate, wall cyanophilic, slightly congophilic, pale yellow in water, yellow in Melzer's (inamyloid). *Basidia* 25–40 × 6.5–9 µm, clavate, 4-spored, sterigmata up to 4–6 µm long, with homogeneous contents or guttulate with many inner greenish drops. *Hymenophoral trama* at first regular then irregular, consisting of cylindrical, 2–6 µm wide interwoven hyphae. *Subhymenium* 10–30(–40) µm thick, *textura intricata* type (pseudoparenchymatous), elements short and 2.5–5 µm wide (Fig. 5b–c). *Cheilocystidia* 15–80(–150) × (3–)3.5–6(–7) µm, narrow cylindrical to versiform, colourless, thin-walled, very rare to abundant, scattered or clustered, flexuous, sometimes forked or constricted at apex, with rounded apex (Fig. 6b–h). *Pileipellis* a cutis of parallel to interwoven cylindrical 3–6 µm wide hyphae, wall up to 0.3–0.5 µm thick, the most superficial are strictly repent to rarely erect, straight to flexuous, with obtuse apex, sometimes immersed in a thin gelatinous matrix, and with a brownish intracellular pigment and an epiparietal pigment in the form of small dark brown plaques; thromboplerous hyphae absent. *Subpellis* of 3–7 µm wide parallel hyphae. *Stipitipellis* a cutis of parallel, 2–6 µm wide hyphae, sometimes with some adscending, caulocystidioid-like versiform elements. *Clamp connections* absent.

Chemical spot-test reactions — KOH on dried basidiomes surfaces (pileus, lamellae and stipe) produces a reddish colour.

Specimens examined. Canada, Québec, Anticosti, *Picea laxa* glauca litter, 8 Sept. 2015, *R. Lebeuf*, ANT1*50*-HRL*2111* (as *Clitocella mundula*). – Czech Republic, Central Bohemia, near the village of Roblín, Český kras region, karstic area with the background of limestone, in silvis, 11 June 1944, *A. Pilát*, PRM *668718* (**holotype**, as *Rhodopaxillus obscurus*); Central Bohemia, near the village and castle of Karlštejn, Český kras region, karstic area with the background of limestone, in picetis, 4 Aug. 1944 and 2 July 1951, *A. Pilát*, PRM *668719* and PRM *668722* (as *Rhodopaxillus obscurus*); Central Bohemia, near the village Srbsko, Český kras region, karstic area with the background of limestone, in picetis, 27 July 1944, *A. Pilát*, PRM *668725* (as *Rhodopaxillus obscurus*); Černá v Pošumaví (Šumava Protected Landscape Area), Český Krumlov District, South Bohemian Region, Vápenný vrch hill, in a forest of *Picea abies*, 17 Aug. 2008, *M. Kříž* & *Z. Egertová*, D *2237-38*; Bílichov, Džbán Nature Park, Samotínský potok valley, in a forest of *Picea abies*, 9 Oct. 2010, *M. Kříž* & *D. Marounek*, PRM *899231* (**epitype**, as *Rhodocybe obscura*); Brno District, Mokrá, Mokersky les forest, under *Picea abies*, 12 Sept. 2001, *A. Vágner*, MK *09051302*-BRNM *666712*. – Italy, Bolzano, Passo Montecroce, in a forest of *Picea abies*, 28 Aug. 2020, *M. Maletti*, AMB *18856*.

Notes — The species was described as *Rhodopaxillus obscurus* by Pilát (1952) from *Picea* woods in calcareous soil, Czechoslovakia, in areas (Central Bohemia) which are now part of the Czech Republic. The protologue described the species as characterized by robust basidiomes (pileus 40–100 mm diam), dark grey, brownish grey, fuscous grey tinges all over the basidiome (pileus, lamellae and stipe), absence of hymenial cystidia, and basidiospores minutely verrucose, 7–8 × 5.5–6 µm. Baroni (1981) first found in the holotype collection (PRM 668718) and other original material the presence (not reported by Pilát 1951,

Fig. 4 *Clitocella obscura*. Basidiomes. a. PRM 899231 (epitype); b. AMB 18856; c, d. ANT150-HRL2111; e. D2237-38; f. PRM 668718 (holotype). — Photos: a by M. Kříž, b by M. Maletti, c, d by R. Lebeuf, e by M. Kříž, f by M. Marchetti.

1952, 1953) of scattered to clustered filamentous cheilocystidia along all the lamellar edge. Our reanalysis of the holotype, and the study of other ancient and recent collections from the Czech Republic, Italy, and Canada (Québec) (see above) has confirmed the presence of filamentous cystidia except for MK09051302-BRNM 666712. Its geographical distribution is limited to Europe and North America so far, and includes the Czech Republic (Pilát 1952), Slovakia (Fábry 1977), Germany (Enderle 1980–1981, Ludwig 2001), Sweden (Baroni 1981, Noordeloos 2012a), Norway (O-F 19454, Fig. 1), Italy (AMB 18856, Fig. 1) and Canada (ANT150-HRL2111, Fig. 1), mainly associated with *Picea* species (*Picea abies* in Europe, *Picea laxa* (= *P. glauca*) in Canada).

As all attempts (also including Illumina MiSeq technology) to obtain molecular data from the *Rhodopaxillus obscurus* holotype failed, a collection from the Czech Republic (PRM 899231), the morphological characteristics of which fit well the protologue, the morphological data of the holotype and the descriptions of most of the authors, was selected as epitype.

The unique combination of features such as dark blackish grey colours all over the basidiome, unchanging context, the presence of filamentous cheilocystidia, and its typically growing under *Picea*, is diagnostic, and distinguishes *C. obscura* from the morphologically similar *C. popinalis*, *C. mundula*, and *C. nigrescens*.

Clitocella colorata may have very rare cheilocystidia in some collections but usually shows a very pale-coloured depressed pileus, blackening basidiome surfaces, negative reaction with KOH, smaller basidiospores, and it is not strictly associated with *Picea* (but coniferous wood, mainly *Pinus* or mixed coniferous and broad-leaved woods) (see below).

Some collections previously reported as *C. obscura* from Italy (AMB 18391, Battaglia 2006; C. Lavorato 91101234, Lavorato & Contu 2001) based on our molecular phylogenetic analyses (Fig. 1), turned out to be *C. colorata* and *C. popinalis*, respectively. The French collections named as *Rhodocybe obscura* by Riousset & Bon (1994), Guinberteau et al. (1998), Bobinet & Dupuy (2000) and Berger et al. (2008), due to their growth

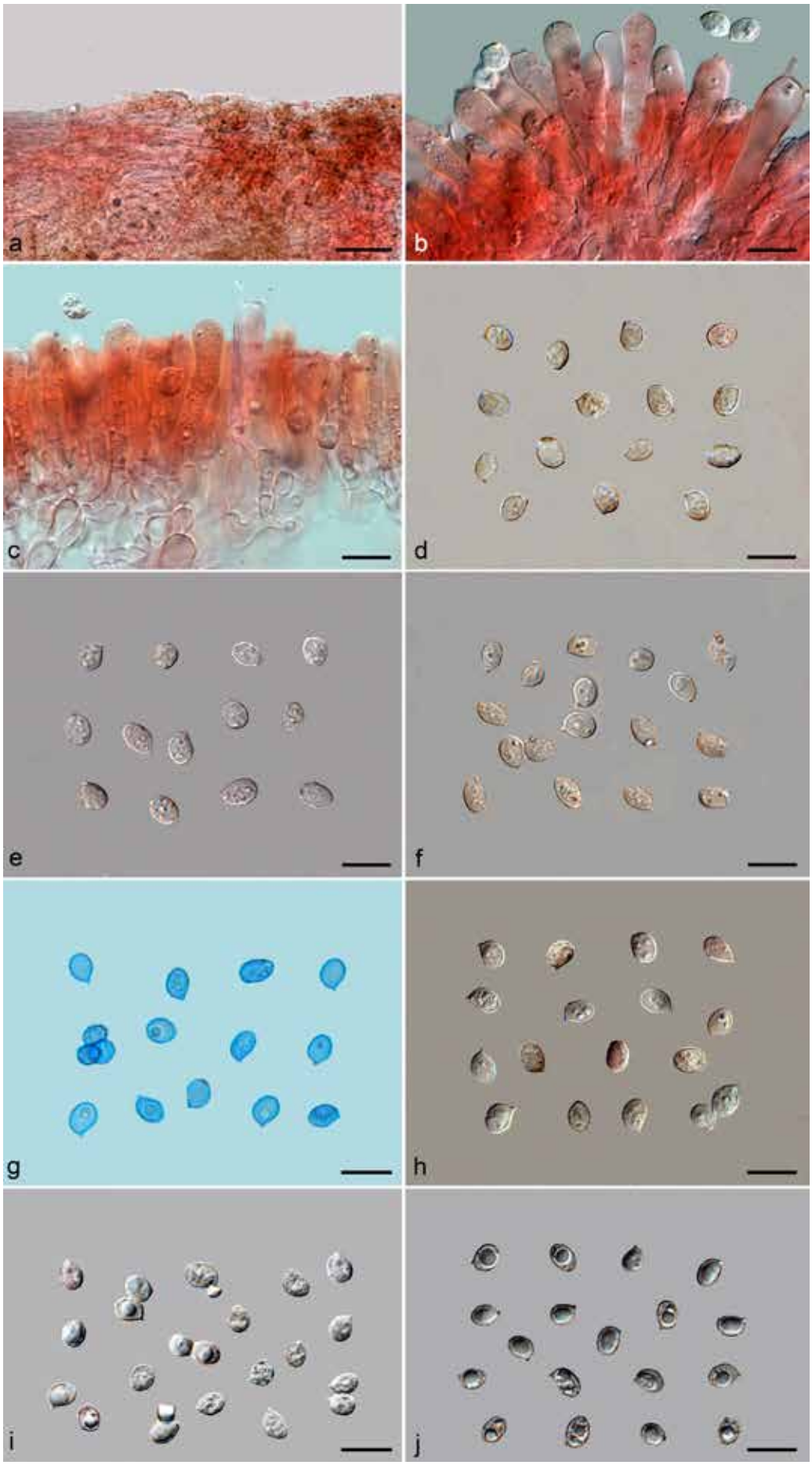

Fig. 5 *Clitocella obscura*. Microscopic features. a. Pileipellis (BRNM 666712); b. hymenium and basidiospores (BRNM 666712); c. hymenium and subhymenium (ANT150-HRL2111); d. basidiospores (PRM 668718, holotype); e. basidiospores (PRM 668722); f. basidiospores (PRM 668725); g. basidiospores (BRNM 666712); h. basidiospores (PRM 899231, epitype); i. basidiospores (ANT150-HRL2111); j basidiospores (AMB 18856). a–f, h–j in ammoniacal Congo red, g in Cotton blue. — Scale bars: a = 30 µm, b–j = 10 µm. — Photos by M. Marchetti.

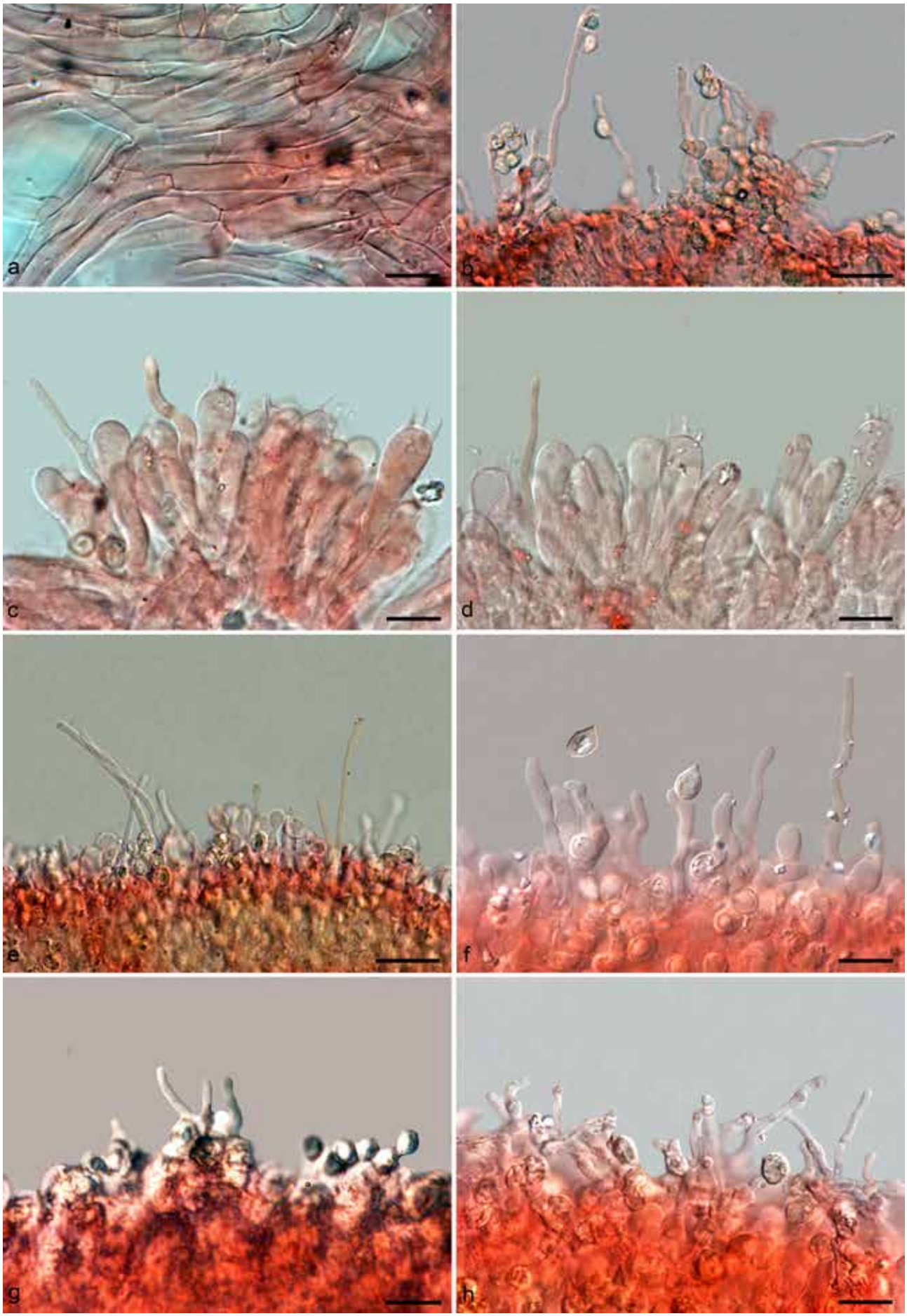

Fig. 6 *Clitocella obscura*. Microscopic features. a. Elements of the hymenophoral trama (ANT150-HRL2111); b. cheilocystidia (PRM 668718, holotype); c. cheilocystidia (PRM 668719); d. cheilocystidia (PRM 668722); e. cheilocystidia (D2237-38); f. cheilocystidia (PRM 899231, epitype); g. cheilocystidia (AMB 18856); h. cheilocystidia (ANT150-HRL2111). a–h in ammoniacal Congo red. — Scale bars: a, c–d, f–h = 10 µm, b, e = 20 µm. — Photos by M. Marchetti.

under *Cupressus* and absence of cheilocystidia, are referable to *C. nigrescens*, as previously also highlighted by Moreau et al. (2008).

Clitocella mundula (Lasch) Kluting, T.J. Baroni & Bergemann, Mycologia 106(6): 1138. 2014 — Fig. 7, 8

Basionym. *Agaricus mundulus* Lasch, Linnaea 4: 526. 1829, nom. sanct.
Synonyms. *Paxillus mundulus* (Lasch) Fr., Öfvers. Kongl. Vetensk.-Akad. förhandl, 18(1): 27. 1861.
Clitopilus mundulus (Lasch) P. Kumm., Führer Pilzk.: 9. 1871.
Paxillus amarellus var. *mundulus* (Lasch) Quél., Enchir. Fung.: 92. 1886.
Rhodopaxillus mundulus (Lasch) Konrad & Maubl., Icon. Select. Fung. 4: pl. 278. 1934.
Paxillopsis mundula (Lasch) J.E. Lange, Fl. Agaric. Danic. 4: 48. 1939.
Clitopilopsis mundula (Lasch) Kühner ex Konrad & Maubl. (as '*mundulus*'), Encycl. Mycol. 14: 379. 1949 '1948'.
Rhodocybe mundula (Lasch) Singer, Lilloa 22: 609. 1951 '1949'.
Clitocella mundula (Lasch) Kluting, T.J. Baroni & Bergemann, in Kluting, A Revised Generic Classification for the Rhodocybe-Clitopilus clade, Thesis, Middle Tennessee State University: 22. 2013, nom. inval., Art. 32.1 (a) (Shenzhen Code, Turland et al. 2018).
Neotype. AMB 18368 (designated by G. Consiglio, Index Fungorum 417: 1. 2019).

Selected iconography — Neukom (1994: 115), Breitenbach & Kränzlin (1995: 116, pl. 100), Moreau (1997: Atlas, planche 338), Ludwig (2000: 169, t. 167, 74.15.E), Eyssartier & Roux (2011: 616), Padovan et al. (2020: 252, above).

Selected descriptions — Baroni (1981: 98), Neukom (1994: 113), Moreau (1997: 339).

Pileus 20–80 mm, at first convex-applanate but soon depressed, rarely with an obtuse umbo, margin involute for a long time then straight, not translucently striate, entire, sometimes undulate to lobate; surface dry, glabrous (smooth), not hygrophanous, minutely hoary to pruinose-pubescent, usually cracking starting from the margin, and forming several concentric zones, white, pale cream, beige-ochraceous, rarely with grey hues, usually darker in the centre, sometimes with ochraceous spots towards the margin, often staining blackish grey on handling or contact with plant debris. *Lamellae* L = 40–70, l = 1–4(–6), crowded, narrow, up to 3 mm broad, decurrent to long decurrent, rarely intervenose, pale cream, pale buff, with pinkish hues at maturity, commonly blackening on handling in fresh basidiomes, with a concolorous or paler, entire edge. *Stipe* 10–50 × 5–14 mm, cylindrical or tapering downwards, sometimes broadened at apex, central to somewhat eccentric, solid, stuffed with age, dry, smooth to fibrillose-tomentose, concolorous with the pileus, whitish to pale beige-ochraceous, with abundant basal mycelium which aggregates the litter and giving rise to whitish rhizomorphs. *Context* rather crumbly, white to pale ochraceous, usually unchanging, rarely slightly greying when cut. *Smell* usually strongly farinaceous to rancid farinaceous, sometimes farinaceous only after handling. *Taste* quite bitter, farinaceous. *Spore-print* pinkish, dirty brownish pink.
Basidiospores (4.0–)4.9–*5.4*–5.8(–6.8) × (3.4–)4.0–*4.3*–4.6(–5.3) µm [186/4/4], Q = (1.01–)1.15–*1.24*–1.33(–1.56), V = (26.2–)42.40–*53.3*–64.2(–87.8) µm^3, rarely globose, subglobose to broadly ellipsoid in side and frontal view, clearly angular when young but obscurely angular when mature in frontal and polar view, with obscure, indistinct minute pustules or bumps in all views, hilar appendage up to 1 µm long, contents smooth, uni- to pluriguttulate, wall cyanophilic, slightly congophilic, pale yellow in water, yellow in Melzer's (inamyloid). *Basidia* 17–35 × 6.5–8 µm, cylindro-clavate, 4-spored, rarely 2-spored, sterigmata up to 6 µm long, with homogeneous contents or guttulate with many inner greenish drops. *Hymenophoral trama* irregular, consisting of cylindrical, 2–8 µm wide interwoven hyphae. *Hymenial cystidia* absent. *Subhymenium* 20–40 µm thick, *textura intricata* type, elements short and 2–3 µm wide. *Pileipellis* a cutis of parallel to interwoven cylindrical 2–5 µm wide hyphae, wall up to 0.3–0.5 µm thick, the most superficial are strictly repent to erect, hyaline and smooth or, in the dark-

Fig. 7 *Clitocella mundula*. Basidiomes. a. AMB 18370; b. AMB 18368 (neotype); c. AMB 18367; d. AMB 18853. — Photos: a–c by M. Maletti, d by G. Consiglio.

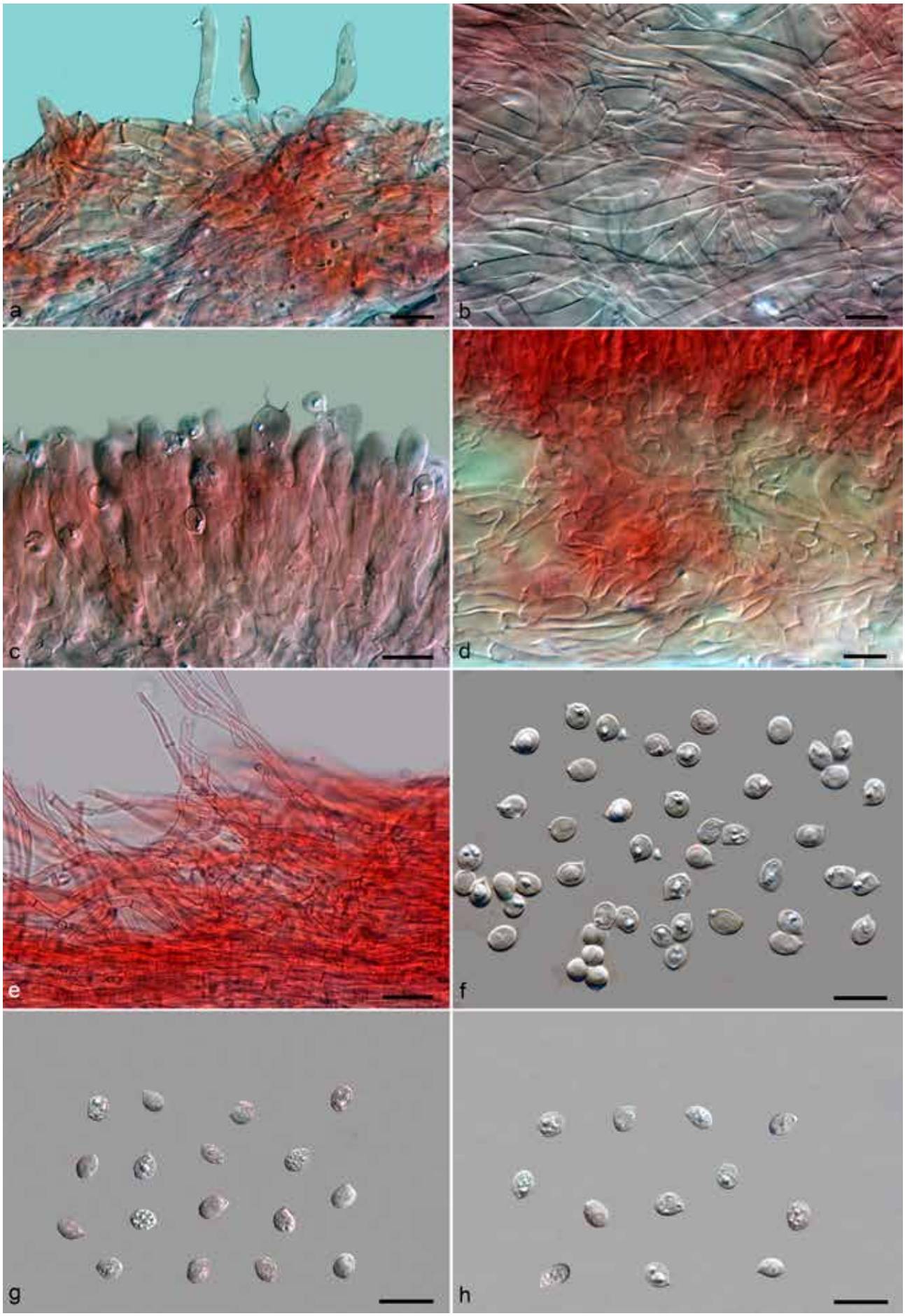

Fig. 8 *Clitocella mundula*. Microscopic features. a. Pileipellis (AMB 18368, neotype); b. elements of the hymenophoral trama (AMB 18368, neotype); c. hymenium and subhymenium (AMB 18368, neotype); d. subhymenium and hymenophoral trama (AMB 18368, neotype); e. stipitipellis (AMB 18368, neotype); f. basidiospores (AMB 18368, neotype); g. basidiospores (AMB 18367); h. basidiospores (AMB 18370). a–h in ammoniacal Congo red. — Scale bars = 10 µm. — Photos by M. Marchetti.

coloured forms, brownish due to epiparietal encrusting (small plaques) and/or intracellular pigment; terminal elements pileocystidioid, sometimes clustered, thin-walled, straight to flexuous, subcylindrical to fusiform, 8–25 × 3–5 µm, with obtuse to acute apex; thromboplerous hyphae absent. *Subpellis* of 3–8 µm wide parallel hyphae. *Stipitipellis* a cutis of parallel, 2–4(–5) µm wide hyphae, with some adscending, caulocystidioid-like straight to flexuous versiform elements, scattered or clustered, often multiseptated, with obtuse to acute apex. *Clamp connections* absent.

Chemical spot-test reactions — KOH on dried basidiomes surfaces (pileus, lamellae and stipe) produces a reddish colour.

Specimens examined. Italy, Pesaro-Urbino, Parchiule, in a mixed forest of broad-leaved trees (*Quercus pubescens*, *Q. cerris* and *Carpinus betulus*), 17 Aug. 1989, M. Maletti, AMB *18367*; Bardineto (SV), in a mixed forest of broad-leaved trees, 10 Oct. 1998, G. Consiglio, M. Chiari & C. Papetti, AMB *18853*; Pesaro-Urbino, Parco Mirafiori, in a mixed forest of broad-leaved trees and conifers, Oct. 2003, M. Maletti, AMB *18370*; Siena, Monte Amiata, under *Populus* sp., 10 Oct. 2008, M. Maletti, AMB *18368* (**neotype**).

Notes — *Clitocella mundula* is characterized by medium-sized to large clitocyboid basidiomes with a pale-coloured pileus (whitish, yellowish grey, pale cream to dark smoke-grey) usually with several concentric zones, a positive reddish KOH reaction, the absence of hymenial cystidia, subglobose to sometimes broadly ellipsoid obscurely angular basidiospores with obscure minute pustules or bumps and is usually found in forested habitats (Baroni 1981, Moreau 1997, Kluting et al. 2014, Jian et al. 2020).

It grows scattered or in groups on soil in coniferous or mixed coniferous broad-leaved woods. It is widely distributed in Eurasia, North and South America (Baroni 1981, Neukom 1994, Moreau 1997, Eyssartier & Roux 2011, Noordeloos 2012a, Kluting et al. 2014, Jian et al. 2020) and Malençon & Bertault (1975) also reported a single collection from North Africa (Morocco, under *Quercus ilex*). *Clitocella mundula* and *C. popinalis* are easily misidentified and confused (see Fig. 1 where the collections are reported with the original determinations). *Agaricus mundulus* Lasch (1829) has always been considered closely related to *A. popinalis* Fr. (1821) from the beginning. Fries (1838, 1857, 1874) distinguished *A. mundulus* from his *A. popinalis* by the thin-fleshed, pale, minutely villose, blackening pileus. The fundamental works of Baroni (1981) and Moreau (1997) made it possible to identify further distinctive characters between the two entities, namely the growth in forested areas, the slightly smaller and obscurely pustulate basidiospores, and the absence of lipidic guttulae inside the pileipellis elements as diagnostic of *C. mundula* vs *C. popinalis*.

On the contrary, some authors who have not considered these distinctions clearcut, reduced *Agaricus mundulus* to a later synonym of *Agaricus popinalis* (e.g., Noordeloos 1983, 1988a, Wilhelm 1992, Babos et al. 1994, Contu 1999, 2000, 2002, Carassai et al. 2000, Ludwig 2001). The distinguishing morphological characters highlighted by Baroni (1981) and Moreau (1997) between the two taxa are instead confirmed by our observations on further collections. The phylogenetic analysis clearly indicates *C. mundula* as being molecularly distinct from *C. popinalis* (Fig. 1). According to the literature and our observations, pileus colour is quite variable in *C. mundula* and its dark-coloured variants could be confused with *C. popinalis* if not checked microscopically.

Clitocybe himantiigena from Paraguay (Spegazzini 1918) was considered a later synonym of *Rhodocybe mundula* (isabelline colour, absence of hymenial cystidia, subglobose basidiospores 5–6 µm) by Baroni (1981) who examined the type collection. Singer (1951 ‘1949) transferred it to *Rhodocybe* and then provided a more detailed description, including microscopic features based on Argentine collections (Singer 1950, 1969). As Singer’s concept of *R. himantiigena* (dark grey pileus, basidiospores 4.3–8 × 3.7–5 µm, presence of filiform, cylindro-clavate, rarely branched cheilocystidia) is very different from the original one, Baroni (1981), who studied the holotype, established the new species *R. semiarboricola* for *R. himantiigena* sensu Singer, adding the data that it is a species without positive (red) reaction in KOH. Probably unaware of Baroni’s considerations, Silva-Filho et al. (2018), based on a Brazilian collection that shared the same morphological characteristics as the Argentine ones described by Singer, combined *R. himantiigena* instead of *R. semiarboricola* in *Clitocella*.

Clitocella colorata L. Fan & N. Mao, in Mao, Lv, Xu, Zhao & Fan, MycoKeys 88: 161. 2022 — Fig. 9, 10

Holotype. China. Shanxi Province, Qinshui County, Lishan Mountain, N35°36.49' E112°11.7', alt. 1150 m, 26 July 2021, on the ground in broad-leaved forest dominated by *Quercus* sp., *N. Mao* MNM340 (BJTC FM1781).

Selected iconography — Mao et al. (2022: f. 3b–d).

Selected description — Mao et al. (2022: 161).

Pileus 20–80 mm wide, convex to plano-convex, usually with a shallow to profound depression at the centre; margin not translucently striate, enrolled then straight, sometimes slightly uplifted, largely lobated, undulating; surface dry, minutely hoary to pruinose-pubescent, usually cracking starting from the margin, and forming several concentric zones, under the hoary overlay white to yellowish white, greyish white to greyish brown, pinkish white; context white to greyish white, 1.0–1.5 mm thick. *Lamellae* L = 40–60, l = (1–)2–4, crowded, narrow, up to 3 mm broad, thin and fragile, decurrent, at first white to yellowish white, becoming yellowish brown on drying, with an entire and concolorous edge. *Stipe* 20–45 × 4–15(–18) mm, central to slightly eccentric, cylindrical, equal, pale white to yellowish brown, smooth, usually with long white rhizomorphs. *Smell* farinaceous-rancid (rancid flour-like). *Taste* farinaceous, bitter. *Spore-print* pink. Pileus, lamellae and stipe turning black when bruised or in old basidiomes.

Basidiospores (4.7–)5.1–*5.5*–5.9(–6.8) × (3.7–)4.1–*4.3*–4.6 (–5.0) µm [137/3/3], Q = (1.07–)1.18–*1.28*–1.38(–1.58), V = (38.6–)46.3–*54.9*–63.5(–78.8) µm^3, (rarely) globose, usually subglobose to broadly ellipsoid, angular in side view (without a clear suprahilar depression), subglobose to broadly ellipsoid and slightly angular in frontal view (10–12 facets), slightly angular in polar view (8–10 facets), obscurely undulate-pustulate in all views in Cotton blue, hilar appendage up to 1 µm long, contents smooth, uni- to pluriguttulate, wall cyanophilic, slightly congophilic, pale yellow in water, yellow in Melzer’s (inamyloid). *Basidia* 18–35 × 4–8 µm, clavate, 4-spored, rarely 2-spored, sterigmata up to 4 µm long, with homogeneous contents or guttulate with many inner greenish drops. *Hymenophoral trama* subregular to irregular, composed of subparallel to interwoven, hyaline, thin-walled, cylindrical to inflated hyphae, 3–6 µm wide. *Hymenial cystidia* usually absent; in AMB 18391 scattered colourless, thin-walled, narrow cylindrical, 20–55 × 3–6 µm cheilocystidia, sometimes with clavate to subcapitate apex, were observed. *Subhymenium* 20–30 µm thick, *textura intricata* type, elements short and 2–4 µm wide. *Pileipellis* a cutis of parallel to interwoven, 2–4 µm wide cylindrical hyphae, the most superficial are immersed in a thin gelatinous matrix; terminal elements rarely erect, subcylindrical or with an inflated apex, sometimes with a pale yellow to yellowish brown epiparietal (as small plaques) pigment. *Subpellis* made up of parallel to interwoven, slightly loosely arranged, hyaline, cylindrical, 3–7 µm wide hyphae. *Stipitipellis* a cutis composed of parallel, compactly arranged, thin-walled (wall up to 0.4 µm thick), 2–5 µm wide cylindrical hyphae, usually encrusted with yellowish brown pigment; caulocystidioid elements very rare to absent. *Clamp connections* absent.

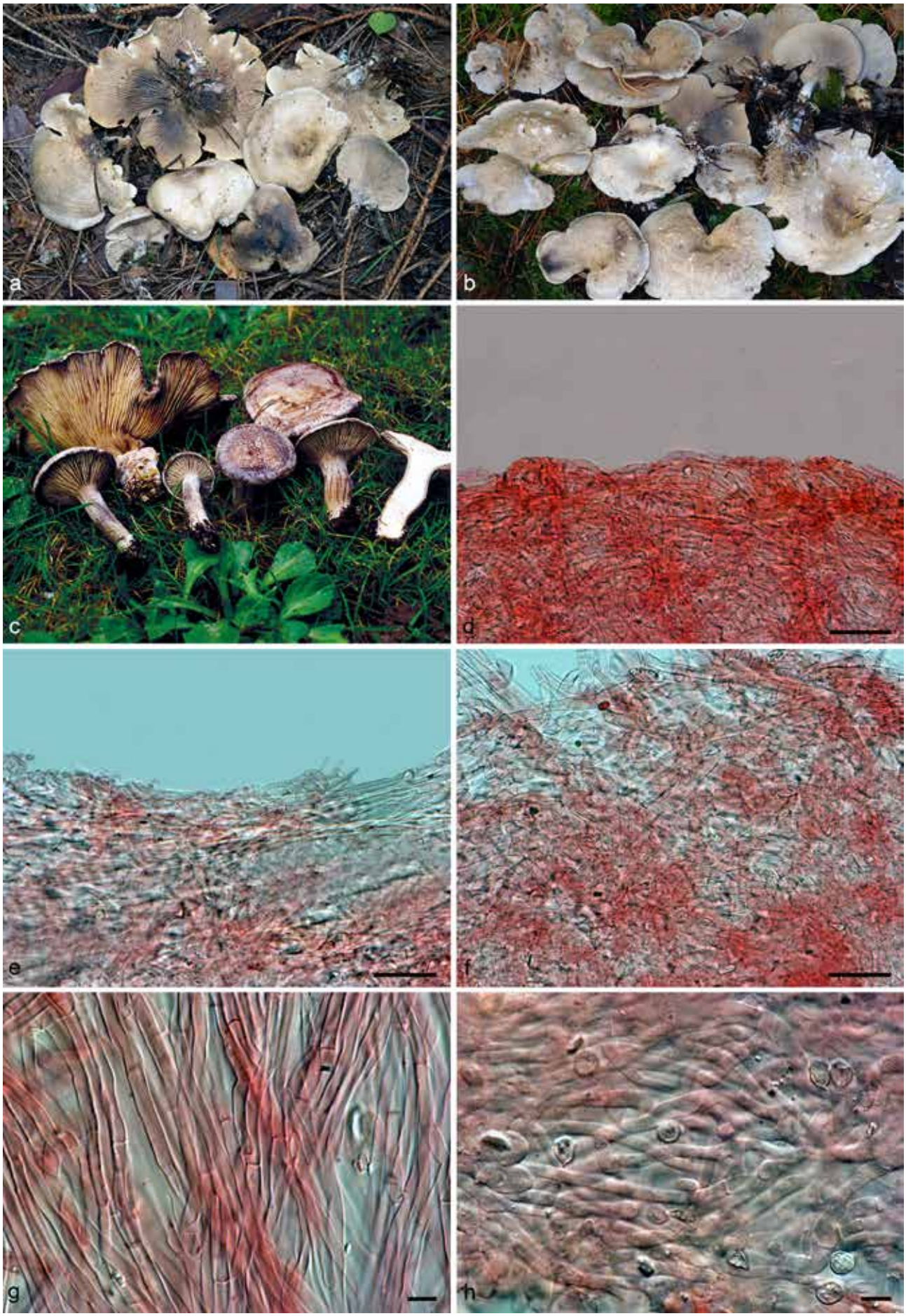

Fig. 9 *Clitocella colorata*. Basidiomes. a. TU 120607; b. TU 106376; c. AMB 18391. Microscopic features. d. pileipellis (TU 106376); e. pileipellis (AMB 18391); f. pileipellis (TU 120607); g, h. elements of the hymenophoral trama (AMB 18391). d–h in ammoniacal Congo red. — Scale bars: d–f = 30 µm, g–h = 10 µm. — Photos: a, b by L. Vello, c by G. Battaglia, d–h by M. Marchetti.

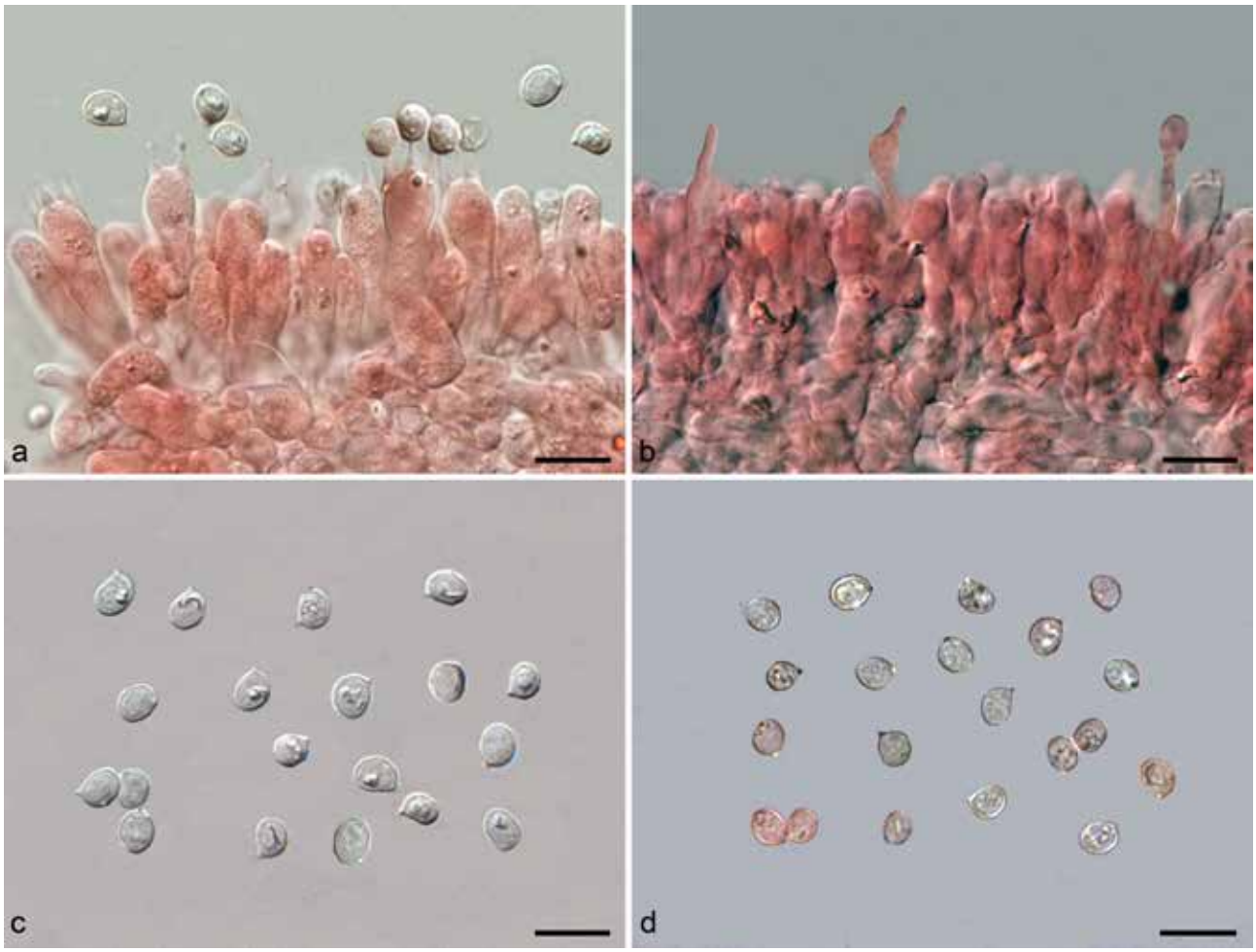

Fig. 10 *Clitocella colorata*. Microscopic features. a. Hymenium and basidiospores (TU 120607); b. hymenium (with cheilocystidia) and subhymenium (AMB 18391); c. basidiospores (TU 120607); d. basidiospores (AMB 18391). a–b, d in ammoniacal Congo red, c in water. — Scale bars: a–d = 10 µm. — Photos by M. Marchetti.

Chemical spot-test reactions — KOH on dried basidiomes surfaces (pileus, lamellae and stipe) produces no reaction (negative).

Specimens examined. Estonia, Võru county, Antsla municipality, Karula parish, Karula rahvuspark, Ähijärve, in a mixed forest, 1 Sept. 2016, *V. Liiv*, TU *120607* (as *Rhodocybe popinalis*); Saare county, Kärla commune, Kärla parish, Joempa, in a pine forest (*Pinus sylvestris*), 14 Oct. 2008, *V. Liiv*, TU *106376* (as *Rhodocybe popinalis*). – Italy, Vicenza, Barbarano Vicentino, in a mixed forest of broad-leaved trees and conifers (*Picea sitchensis* and *Abies alba*), 8 July 1998, *G. Battaglia*, AMB *18391* (as *Rhodocybe obscura*).

Notes — *Clitocella colorata* has recently been described from Shanxi province (North China or Huabei) China on soil or rotten wood in coniferous (*Pinus*) or broad-leaved (*Quercus*) forest (Mao et al. 2022). Our analysis highlighted that the new species has a wider geographical distribution, and it is also present in India, South Korea, USA (Arkansas, Indiana, New York, Tennessee, Wisconsin) and in Europe (France, Italy, and Estonia) (Fig. 1; Mao et al. 2022). *Clitocella colorata* is characterized by its clitocyboid basidiomes, a usually pale-coloured pileus surface (white to yellowish white, greyish white to greyish brown, pink-white), (globose) subglobose to broadly ellipsoid basidiospores slightly angular and with minute pustules or bumps, hyphae of pileipellis with pale yellow to yellowish brown intracellular or parietal pigment, and the surfaces of dried basidiomes show no reddish reaction in KOH. In the original description, no reference is made to a possible colour change of the basidiome surfaces, its smell and taste are not reported, the hymenial cystidia are indicated as absent, and the hymenophoral trama as regular (Mao et al. 2022). Our observations based on collections from Italy and Estonia (AMB 18391, TU 106376, TU 120607) highlighted that pileus, lamellae, and stipe surface stain strongly black when bruised or in age (Fig. 9a–c), smell is farinaceous, taste is bitter, the light-yellow pigment in the pileipellis is also present as epiparietal minutely encrusting material, and the hymenophoral trama is subregular at first but then irregular and composed of interwoven hyphae. In addition, rare and scattered cheilocystidia, 20–55 × 3–6 µm, thin-walled, gracile, flexuous, cylindrical or with a clavate to subcapitate apex are present in the collection from Italy (AMB 18391). The Italian and Estonian collections are from mixed coniferous forests. The blackening of the surfaces is also noticeable in f. 3b, c within the article by Mao et al. (2022) and in the photo of dehydrated basidiomes provided by Kour et al. (2016) for an Indian collection (HBJU-550/HK550 CUH AM033) from a coniferous forest (dominated by *Cedrus deodara*) wrongly identified as *C. popinalis* (Fig. 1). This blackening is not reported in the morphological description by the Indian authors who described smell and taste as strongly farinaceous and bitter, respectively.

Morphologically, *C. colorata* can be easily confused with *C. mundula* and *C. popinalis* which, however, have dried basidiome surfaces producing a reddish reaction in KOH (Baroni 1981, Moreau 1997, Kluting et al. 2014; our observations).

Clitocella mundula shares with *C. colorata* the clitocyboid habit (strongly depressed pileus), the pale-coloured pileus surface and blackening of the basidiomes surfaces, the growth in woods, but differs mainly in the obscurely angular basidiospores with indistinct pustules or bumps (Baroni 1981, Neukom 1994, Moreau 1997). *Clitocella popinalis* shows basidiome surfaces usually unchanging on handling, a dark-coloured pileus slightly depressed only in senescing basidiomes, is usually associated

with grasses, and has slightly broader and longer basidiospores than those of *C. colorata* (Baroni 1981, Moreau 1997, Overall 2011, Kluting et al. 2014, Jian et al. 2020).

Based on molecular data (Fig. 1; Mao et al. 2022), *C. orientalis* is sister to *C. colorata* with strong statistical support (BPP = 1.00; MLB = 98 %). *Clitocella orientalis*, so far known only from China, shares with *C. colorata* the same negative reaction when KOH is applied on the dried basidiome surfaces and the growth in woods, but it is distinguished by a paler whitish pileus, non-blackening surfaces and the viscid pileus and stipe (clearly gelatinized pileipellis and stipitipellis) (Jian et al. 2020). Among the other pale-coloured *Clitocella* species, *C. pallescens*, established without molecular data based on a single collection from Paraná (Brazil), differs from *C. colorata* in a smaller (13–30 mm wide) white to pastel grey pileus, infundibuliform when young, smaller basidiospores (4–5 × 3–4.3 µm) hardly reaching 5 µm in length, almost smooth or with very minute and obscure angles in polar view, and growing on rotten wood (Silva-Filho et al. 2018). *Clitocella borealichinensis*, described from the same province where *C. colorata* was originally found (Shanxi province, North China) is extremely difficult to differentiate with respect to the latter, and it is mainly distinguished by more delicate and minuter basidiome (pileus 13–50 mm wide, stipe 20–32 × 2–8 mm) with a pileus surface devoid of pink tone, non-blackening basidiome surfaces, smaller basidiospores, (3.8–)4–5(–5.5) × 3.8–4.5 µm, on average 4.61 (± 0.42) × 4.06 (± 0.18), and peculiar nrLSU–*RPB2*–*EF-1α*–*ATP6* sequences (Mao et al. 2022).

Clitocella nigrescens (Maire) Consiglio, Index Fungorum 430: 1. 2020 — Fig. 11–13

Basionym. *Rhodopaxillus nigrescens* Maire, Bull. Soc. Hist. Nat. Afr. N. 36(3): 31. 1945.

Synonyms. *Clitopilopsis nigrescens* (Maire) Konrad & Maubl., Encycl. Mycol. 14: 380. 1949 ‘1948’.

Rhodocybe nigrescens (Maire) P.-A. Moreau, Contu & Guinb., Micol. Veg. Medit. 23(1): 38. 2008.

Clitopilus ammophilus Malençon, Trav. Inst. Sci. Chérifien, Sér. Bot. Biol. Vég. 33: 19. 1975.

Rhodocybe ammophila (Malençon) Pacioni & Lalli 1984, Micol. Ital. 13(1): 78, nom. illegit., Art. 53.1 (Shenzhen Code, Turland et al. 2018) (non *Rhodocybe ammophila* E. Horak 1978).

Clitocella ammophila (Malençon) Consiglio, Index Fungorum 430: 1. 2020.

Rhodocybe malençonii Pacioni & Lalli, Doc. Mycol. 14(56): 56. 1985 ‘1984’.

Rhodocybe malençonii f. *alba* Contu (as ‘*malençoni*’), Rev. Catal. Micol. 22: 13. 1999.

Rhodocybe cupressicola Carassai, Papa & Contu, Micol. Veget. Medit. 15(1): 65. 2000.

Rhodocybe horakii Pacioni & Lalli, Micol. Ital. 13(1): 78. 1984, nom. illegit., Art. 52.1 (Shenzhen Code, Turland et al. 2018). The circumscription includes the type of a name (*Rhodocybe ammophila* E. Horak) which ought to have been adopted.

Rhodocybe obscura (Pilát) Singer s. Riousset & Bon, Doc. Mycol. 23(92): 49. 1994; s. Guinberteau et al. (1998), Bull. Soc. Mycol France 114(2): 37; s. Bobinet & Dupuy, Bull. Soc. Bot. Centre-Ouest 31: 585. 2000, s. Berger et al., Cah. mycol. nant. 20: 43. 2008 (non s. Pilát).

Holotype. MPU 8603 (as *Rhodopaxillus nigrescens*).
Epitype. AMB 18366 (designated here, MBT 10008920).

Selected iconography — Malençon (in Malençon & Bertault 1975: 18, pl. 1, as *Clitopilus ammophilus*), Tabarés (1988: lam. 343, as *Rhodocybe malençonii*), Contu & Farci (1997: Fungi Mediterranei Rariores 25, as *Rhodocybe malençonii*), Carassai et al. (2000: 67, as *Rhodocybe cupressicola*), Ludwig (2000: 165, t. 163, pl. 74.2, 74.2.A, 74.2.B), Contu (2002: 111, f. 10, as *Rhodocybe malençonii*; f. 11 as *R. cupressicola*), Mua & Melis (2002: 19, as *Rhodocybe malençonii*), Moreau et al. (2008: 35, Photo 1–2, as *Rhodocybe malençonii*; 39, photo 3–4, as *Rhodocybe nigrescens*), Guinberteau (2011: 89, as *Rhodocybe malençonii*), Merino Alcántara (2018: http://www.micobotanicajaen.com/Revista/Articulos/DMerinoA/SetasDunas005/Rhodocybe%20malen%C3%A7onii.pdf as *Rhodocybe malençonii*).

Selected descriptions — Maire (1945: 31, as *Rhodopaxillus nigrescens*), Malençon (in Malençon & Bertault 1975: 17, 19 as *Clitopilus ammophilus*), Pacioni & Lalli (1984a: 78, as *Rhodocybe ammophila*), Contu (1989: 24, as *Rhodocybe malençonii*), Moreno et al. (1994: 251, as *Rhodocybe malençonii*, including also photos of basidiospores observed under SEM, Scanning Electron Microscopy), Hausknecht & Zuccherelli (1996: 60), Carassai et al. (2000: 65, as *Rhodocybe cupressicola*), Lunghini & Perrone (2000: 31), Contu (2002: 109, as *Rhodocybe malençonii*; 112 as *R. cupressicola*), Mua & Melis (2002: 18, as *Rhodocybe malençonii*), Moreau et al. (2008: 34, 36, as *Rhodocybe malençonii*; 38, 40, as *Rhodocybe nigrescens*), Merino Alcántara (2018: http://www.micobotanicajaen.com/Revista/Articulos/DMerinoA/SetasDunas005/Rhodocybe%20malen%C3%A7onii.pdf, as *Rhodocybe malençonii*).

Pileus 25–130(–150) mm, fleshy, convex then applanate, depressed in the centre in old basidiomes (usually *Pleurotus*-like), margin involute for a long time, not striate, undulate; surface dry to slightly gelified in the centre, smooth, not hygrophanous, ochraceous beige, alutaceous, ochraceous grey, ash-grey, sometimes entirely white, paler at margin, often black-spotted. *Lamellae* L = 45–60, l = 1–2(–3), crowded, long adnate, subdecurrent to long decurrent, 4–8 mm broad, detachable from the context, pale grey, cream, yellowish, then pinkish, with a concolorous undulate edge. *Stipe* (10–)20–70(–90) × 10–30 mm, solid, central to eccentric, terete, clavate, sometimes enlarged at apex (when lamellae are long decurrent), long tapering to slightly rooting in basidiomes growing deep in the sand and then also coalescent, white mycelium at base that aggregates the growth substrate and grains of sand, smooth to fibrillose-costolate at the insertion point of the lamellae, whitish to pale ochraceous-grey. *Context* up to 20 mm thick in the pileus, white, sometimes with green-blue hues at stipe apex, usually unchanging when cut (a faint greyish colour-change in a young basidiome is mentioned by Maire 1945). *Smell* faintly farinaceous, but described differently by the various authors, not peculiar (Pacioni & Lalli 1984a as *R. ammophila*, Mua & Melis 2002 as *R. malençonii*), farinaceous to raphanoid (Aparici & Mahiques 1996 as *R. malençonii*), virose-nauseating (Malençon in Malençon & Bertault 1975 as *C. ammophilus*, Contu 1989, 2002 as *R. malençonii*), virose, non-farinaceous (Lejay 2004 as *R. malençonii*), pleasant of freshly opened oyster (Guinberteau 2010, 2011 as *R. malençonii*), faint and complex, spermatic, subfarinaceous (Carassai et al. 2000, Contu 2002 as *R. cupressicola*), farinaceous to spermatic, of oyster, watermelon (Moreau et al. 2008 and Mir et al. 2017 as *R. nigrescens*). *Taste* bitter. *Spore-print* pink. No part of the basidiome turns noticeably black or grey, even after handling.

Basidiospores (6.0–)7.0–*7.7*–8.3(–9.9) × (4.5–)5.5–*5.9*–6.4(–8.3) µm [597/11/10], Q = (1.03–)1.19–*1.30*–1.40(–1.63), V = (73.9–)113–*143*–174(–315) µm^3, ovoid to largely ellipsoid, ellipsoid in side view and frontal view, minutely angular in polar view (8–10 facets), almost smooth to weakly nodulose-pustulate to verrucose in all views, rounded to slightly attenuated apically, with clear suprahilar depression, hilar appendage up to 1 µm long, contents smooth, uni- to pluriguttulate, wall cyanophilic, slightly congophilic, pale yellow in water, yellow in Melzer’s (inamyloid). *Basidia* 25–45(–50) × 7–10(–10.5) µm, cylindrical-clavate, frequently long-pedicellate, mostly 4-sporic, rarely 2-sporic, sterigmata up to 6 µm long, with many inner guttulae; intermixed with basidioles and sometimes with sterile versiform elements not exceeding the level of the basidia. *Subhymenium* as *textura intricata* type consisting of short and intertwined, 2–4 µm wide elements. *Hymenophoral trama* regular of parallel, hyaline to pale yellow-brown cylindrical 2.5–5(–7) µm wide hyphae, in the centre (*mediostratum*), slightly divergent towards the subhymenium, walls up to 0.5(–0.8) µm thick. *Pileipellis* a cutis of subparallel to intertwined, 2–5(–6) µm wide, sometimes slightly gelified hyphae, pigment yellow-brown, intracellular, or minutely encrusting, with rare to common clusters of erect pileocystidioid hyphae (Fig. 12a–c), terminal elements subcylindrical to long lageniform, sinuous, sometimes bifid,

Fig. 11 *Clitocella nigrescens*. Basidiomes. a. AMB 18392; b. AH 54311; c. AMB 18387; d. AMB 18366 (epitype); e. AMB 18365; f. GM 081227-1; g. MCVE 15200 (holotype of *Rhodocybe cupressicola*); h. AMB 18388. — Photos: a by E. Brugaletta, b by L. Sánchez, c, d by G. Consiglio, e by L. Perrone, f by G. Mir, g by E. Carassai, h by P. Boisselet.

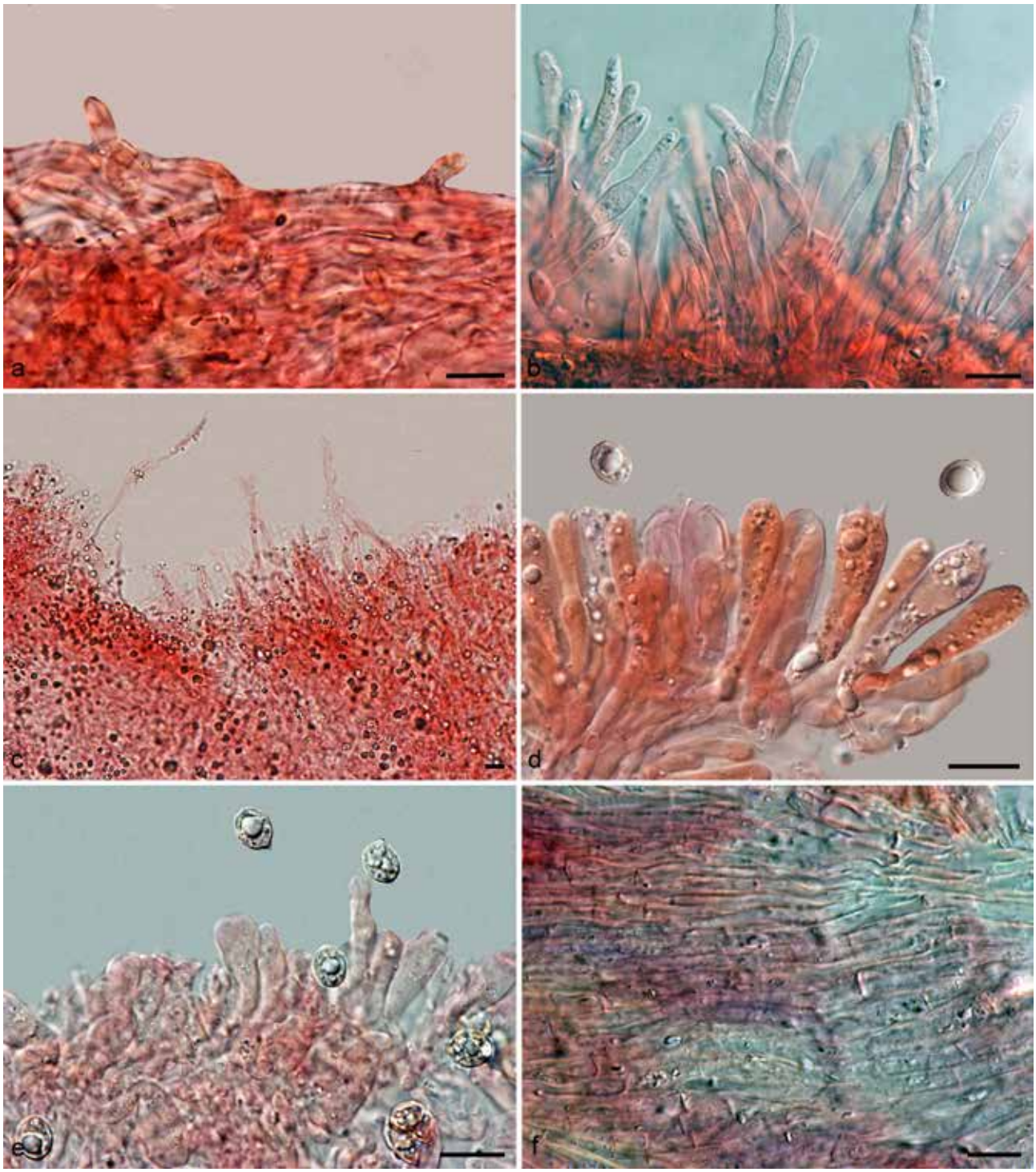

Fig. 12 *Clitocella nigrescens*. Microscopic features. Pileipellis. a. MCVE 15200 (holotype of *Rhodocybe cupressicola*); b. AMB 18365; c. LIP 9211066. Hymenium and basidiospores. d. AMB 18366 (epitype); e. LIP 9211066. Hymenophoral trama. f. MCVE 15200 (holotype of *Rhodocybe cupressicola*). a–f, d in ammoniacal Congo red. — Scale bars = 10 µm. — Photos by M. Marchetti.

apex rounded to acute, 10–60(–120) × 1.5–4(–5) µm; thromboplerous hyphae and polymorphic, yellow-brown refractive crystalline deposits frequent. *Subpellis* of 3–6 µm wide hyphae. *Stipitipellis* a cutis of yellowish parallel cylindrical 2–6 µm wide hyphae, pigment parietal or minutely encrusting, polymorphic, refractive crystalline deposits abundant, with emergent, single or in clusters, caulocystidioid hyphae (hyphoid hairs), clavate to subcylindrical, 1–2.5 µm wide. *Clamp connections* absent.

Chemical spot-test reactions — KOH on dried basidiomes surfaces (pileus, lamellae and stipe) produces an orange to light reddish colour.

Specimens examined. France, Charente-Maritime, Île d'Oléron, under *Cupressus macrocarpa* on dunes, 5 Nov. 1992, *J. Guinberteau*, LIP 9211066 and 21 Nov 1994, *J. Guinberteau*, LIP 94112502; Kerbihan, Saint-Pierre-Quiberon, Morbihan, under *Cupressus* spp., 16 Feb. 2020, *P. Boisselet*, AMB 18388. – Italy, Sassari, Alghero, on a sandy dune with *Juniperus oxycedrus*, 5 Nov. 2008, *G. Consiglio*, *L. Perrone* & *L. Setti*, AMB *18365*; Ragusa, Randello, on sand, under *Pinus halepensis* and *Cupressus sempervirens*, 16 Jan. 2014, *E. Brugaletta*, AMB *18392*; ibid., 23 Dec. 2018, *G. Consiglio*, *E. Brugaletta*, *C. Signorino* & *L. La Spina*, AMB *18366* (**epitype**); ibid., 29 Nov. 2019, *G. Consiglio*, *E. Brugaletta*, *A. Gennari*, *A. Mannina*, *M. Pulvirenti*, *C. Signorino*, *L. La Spina* & *G. Visentin*, AMB 18387; Macerata, Corridonia, S. Claudio, under *Cupressus sempervirens*, 1 Dec. 1999, *E. Carassai* & *M. Papa*, MCVE 15200 (holotype of *Rhodocybe cupressicola*). – Spain, Mallorca, Ala Mesquida, Capdepera, on a fixed dune with *Juniperus phoenicea* subsp. *turbinata* and *Pinus halepensis*, 27 Dec. 2008, *F. Lillo*, *G. Mir* & *J. Planas*, GM 081227-1; Menorca, Sa Torreta, Maó, on fixed dune with *Pinus halepensis* and *Juniperus* spp., 7 Dec. 2012, *J. Cuesta, C. Mascaró* & *J.F. Mateo*; Viladecans, Pineda del Remolar, on a dune under *Pinus pinea*, 10 Nov. 2015, *L. Sánchez*, AH 54311.

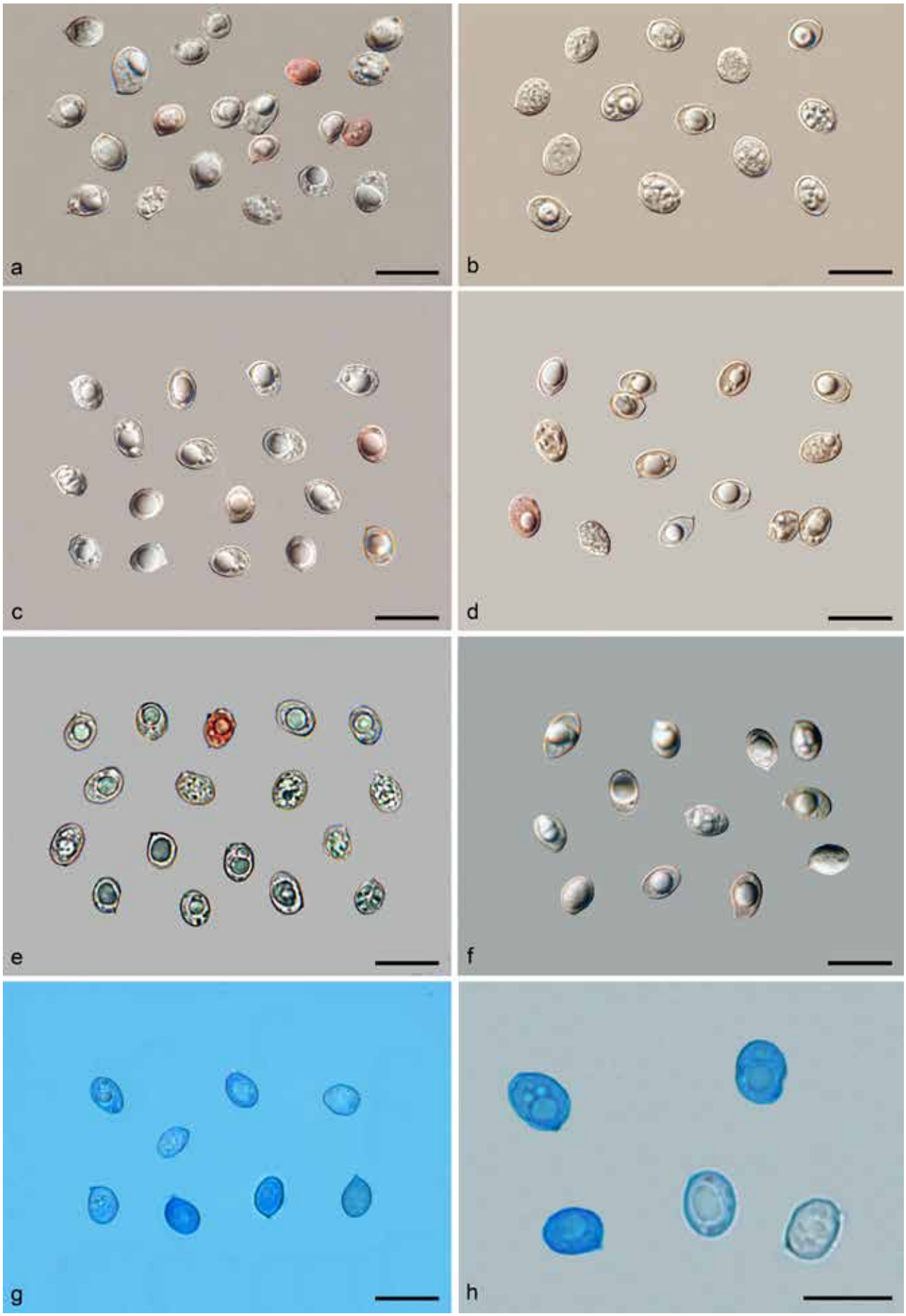

Fig. 13 *Clitocella nigrescens*. Microscopic features. Basidiospores. a. MCVE 15200 (holotype of *Rhodocybe cupressicola*); b. GM081227-1; c. AMB 18366 (epitype); d. AH 54311; e AMB 18365; f. AMB 18388; g. MCVE 15200; h. AMB 18365. a–f, in ammoniacal Congo red, g–h in Cotton blue. — Scale bars = 10 µm. — Photos by M. Marchetti.

Notes — *Clitocella nigrescens* grows gregarious or in small tufts, on white dunes (*Euphorbio-Ammophiletum arenariae*) and grey dunes (*Festuco-Galietum arenarii*, *Artemisio-Ephedretum distachyae*) (Guinberteau 2010) or in retrodunal areas (in litter of *Cupressus*, *Juniperus*, *Pinus*, *Eucalyptus*), both in Mediterranean and Atlantic coasts (Algeria, Morocco, Tunisia, France, Italy, Spain) from late autumn to winter. White capped forms are known from Morocco, France, and Italy (Malençon & Bertault 1975, Contu 1999, Moreau et al. 2008).

The *Rhodocybe* species typically growing on dunes and in sandy areas has long been referred to as *R. malençonii*. It was first described as *Clitopilus ammophilus* by Malençon (in Malençon & Bertault 1975) based on two collections from the Atlantic coast of Morocco growing on pure sand under *Acacia cyanophylla* (current name *Acacia saligna*, *Fabaceae*) and *Tetraclinis articulata* (*Cupressaceae*). Given its alutaceous ochre pileus colours, Malençon considered the species to be morphologically related to *Clitopilus truncatus* (now *Rhodocybe gemina*) but differing in its arenicolous habitat, paler pileus surface, a cyathiform pileus in old basidiomes (*Clitocybe*- to *Panus* like habit), bitter taste and larger basidiospores. Pacioni & Lalli (1984a) reported the species from coastal dunes (*Ammophiletum*) in central Italy and coastal dunes (*Agropyretum*) and retrodunal pine forest in Tunisia and combined it in *Rhodocybe*. Later, Pacioni & Lalli (1984b) introduced the new name *Rhodocybe malençonii* for *R. ammophila* sensu Pacioni & Lalli (1984a) preoccupied by *R. ammophila* E. Horak (1978). Finally, Consiglio (2020) combined it in *Clitocella*. Subsequent findings confirmed its presence in North Africa (Tunisia and Morocco), France, Italy and Spain, mainly on shifting coastal dunes (also called white dunes) of both Mediterranean and Atlantic coasts (Contu 1989, 1998, 1999, 2002, Ortega et al. 1991, Pérez-De-Gregorio & Vidal 1994, Moreno et al. 1994, Aparici & Mahiques 1996, Hausknecht & Zuccherelli 1996, Contu & Farci 1997, Guinberteau 1997, 1999, 2011, Contu & Signorello 1999, Lunghini & Perrone 2000, Monti et al. 2001, Mua & Melis 2002, Moreau et al. 2008, Merino Alcántara 2018). Carassai et al. (2000) have recently described the new species *R. cupressicola* from Italy and France as differing from *R. malençonii* mainly in having a pileus with ash-grey tinges at first, then grey to ochraceous, often black-spotted starting from the margin (as *Lepista panaeola*), only a faintly bitterish taste, absence of gelified matrix in the pileipellis and growth not strictly confined to dunes, but in coastal ruderal areas in the litter of *Cupressus sempervirens* (Carassai et al. 2000, Contu 2002). Moreau et al. (2008) after revising the holotype of *Rhodopaxillus nigrescens* (MPU 8603) from Algeria (under *Eucalyptus*, Maire 1945), proposed it as a priority synonym of *R. cupressicola* on a morphological basis. The species had hitherto been neglected by most mycologists except for Konrad & Maublanc (1948) who had recombined it into *Clitopilopsis* and Pilát (1952) who compared it to his new species *Rhodopaxillus obscurus*. Based on the study of several collections attributable to *R. nigrescens* from France, Spain and Italy, Moreau et al. (2008) tentatively essayed to keep *R. malençonii* separate from *R. nigrescens* proposing a spate of minor distinguishing characters such as i) *R. malençonii*: pileus soon depressed, white to ochraceous-beige to grey-brown, often dark speckled; lamellae long decurrent, yellowish cream then pinkish; stipe white, often attenuate-rooting at base, deep-seated in the sand; context white sometimes with grey-blue hues; smell strong, of oyster or strongly farinaceous on cutting; taste bitter; spores with an evident supraapicular depression; basidia attenuated at base; hymenophoral trama with distinct mediostratum, 50–70 µm thick, hymenopodium divergent, 30–40 µm thick; pileipellis as a xerotrichoderm, subpellis and hypoderma not differentiated; habitat on white dunes (*Euphorbio-Ammophiletum*, *Ephedretum*; ii) *R. nigrescens*: pileus convex then applanate, depressed only lately, grey to ochraceous grey; lamellae adnate to subdecurrent, pale grey, pale yellow to cream, then pinkish; stipe white, whitish to ochraceous-grey, terete to subrooting; context whitish; smell faint, farinaceous to spermatic; taste only slightly bitterish; spores without an evident supraapicular depression; basidia only slightly attenuated at base; hymenophoral trama with a hardly distinct, 20–30 µm thick mediostratum, hymenopodium divergent, 20–25 µm thick; pileipellis an ixotrichoderm with repent elements, subpellis with yellow encrusting pigment, hypoderma thick, consisting of thin hyphae; *habitat* in the litter of *Cupressus macrocarpa* (Atlantic areas), or of *C. sempervirens* (Mediterranean areas), on limestone sand. Our observations on 10 collections from France, Italy, and Spain have shown that the alleged distinctive features listed above have been over-emphasized by Moreau et al. (2008) and that these fade between one collection and another. Therefore, the two entities are here considered as expressions (phenotypes) of a single species, which for reasons of priority must be named *C. nigrescens*. Molecular analyses supported this statement (Fig. 1). The holotypes of *Clitopilus ammophilus* (MPU 3564) and *Rhodopaxillus nigrescens* (MPU 8603) are in poor conservation conditions and therefore not sequenceable, but the sequences obtained from the holotype of *Rhodocybe cupressicola* (MCVE 15200) and from collections identified as *R. malençonii* and *R. nigrescens* by French, Italian and Spanish mycologists are clearly conspecific (Fig. 1).

Clitocella obscura differs in growing on *Picea* litter, presence of filiform cheilocystidia, and smaller basidiospores (see above and Baroni 1981, Moreau 1997).

The collections from France identified as *Rhodocybe obscura* by Riousset & Bon (1994), Guinberteau et al. (1998), Bobinet & Dupuy (2000) and Berger et al. (2008), due to their growth in thermophilic areas, absence of cheilocystidia, and very large basidiospores, are referable to *C. nigrescens* (see above).

Clitocella solaris Musumeci, Consiglio & Vizzini, *sp. nov*. — MycoBank MB 845489; Fig. 14

Etymology. solaris, because of its constant exposition to sunshine, in an open, sunny area.

Holotype. LUG 19882.

Pileus very small, 5–10 mm, at first subglobose, then irregularly convex, soon plano-convex to applanate (flattened), without umbo, usually depressed in the centre; margin incurved then straight, not translucently striate, shortly crenate, undulate; surface not hygrophanous, dry, minutely felted, pubescent-sericeous, sub-velvety, sometimes concentrically cracked, whitish cream, incarnate-cream with micaceous sheen. *Lamellae* L = 25–40, l = 1–2(–3), not crowded, decurrent to long decurrent, sometimes forked at stipe apex, thick, up to 2 mm broad, whitish, whitish cream with incarnate tinges, with a concolorous to paler, smooth edge. *Stipe* 5–17 × 1.5–2.5 mm, tenacious, squat, subcylindrical with an attenuated or enlarged to clavate base, sometimes with white rhizomorphs, surface light brown to incarnate, covered with a soon-vanishing, fine, whitish bloom. *Context* very thin, inconspicuous, whitish cream, no part of the basidiome staining black or grey, even after handling. *Smell* subfarinaceous to cucumber-like. *Taste* subfarinaceous. *Sporeprint* not obtained.

Basidiospores (5.0–)5.5–*5.9*–6.3(–6.5) × (4.0–)4.2–*4.6*–5.0(–5.2) µm [40/2/1], Q = (1.00–)1.16–*1.29*–1.42(–1.55), V = (44.4–)54.3–*66.5*–78.6(–87.8) µm^3, ellipsoid to broadly ellipsoid or even subglobose in side and frontal view, hilar appendage obvious, usually with clear suprahilar depression, minutely angular in polar view, asperulate, weakly nodulose in all views, contents smooth, uni- to pluriguttulate, wall inamyloid, non-dextrinoid. *Basidia* 23–40(–47) × 7–9 µm, clavate, mostly 4-sporic, rarely 2-sporic, sterigmata up to 4 µm long. *Hyme-*

Fig. 14 *Clitocella solaris*. a. Habitat. Basidiomes. b, c. (LUG 19882, holotype). Microscopic features. d. elements of the pileipellis (LUG 19882, holotype); e. basidiospores (LUG 19882, holotype); f. elements of the hymenophoral trama (LUG 19882, holotype). d–e in water, f in ammoniacal Congo red. — Scale bars = 10 µm. — Photos by E. Musumeci.

nophoral trama at first subregular then irregular, *textura intricata* like, consisting of cylindrical, 2–7 µm wide, colourless, thin-walled hyphae, walls rarely faintly coloured or with encrusting pigment. *Hymenial cystidia* not observed. *Pileipellis* a cutis of subparallel to intertwined, 2–7 µm wide, sometimes slightly gelified hyphae, pigment yellow-brown, parietal or rarely encrusting. *Subpellis* hardly differentiated, hyphae (3–10 µm wide) scarcely pigmented and very rarely encrusted. *Stipitipellis* lacking caulocystidia, superficial hyphae (2–5 µm wide) scarcely pigmented, in places finely encrusted, central hyphae of trama gelatinized, often sinuous-diverticulate, 2–8 µm wide. *Clamp connections* absent.

Chemical spot-test reactions — KOH on fresh and dried basidiomes surfaces (pileus, lamellae and stipe) produces a reddish colour.

Habitat & Distribution — Gregarious, on moss pads in open and sunny areas. So far known only from the *locus typicus*.

Specimens examined. France, Departement Haut-Rhin, Alsace, Schlierbach, hilly, open area, sunny all day long, 243 m a.s.l., with seedlings of *Betula pubescens* and at some distance (at least 30 m) two *Pinus sylvestris* trees, on sandy-pebbly, alluvial soil, silty substrate rich in woody debris and carbonate, surface partly colonized by mosses, small shrubs, and lichens, five basidiomes found on moss pads of *Rhacomitrium canescens* s.lat. in the vicinity of young plants of *B. pubescens*, 7 Oct. 2021, *E. Musumeci*, LUG 19882 (**holotype**); ibid., 12 Oct. 2021, *E. Musumeci*, 1232-21. Other fungal species found nearby: *Bonomyces arnoldii*, *Gymnopus impudicus*, *Hygrocybe conica*, *Hygrocybe acutoconica*, *Omphalina pyxidata* and *Tephroderma fuscopallens*.

Notes — *Clitocella solaris* has to be placed within *Clitocella* subg. *Clitocella* (Fig. 1) where it is circumscribed by a unique combination of characters such as the small-sized basidiomes (pileus not exceeding 10 mm diam), a whitish cream pileus surface, distant (spaced) lamellae, a positive KOH reaction, an unchanging, not staining black context, subfarinaceous smell and taste, absence of hymenial cystidia and clearly angular, subglobose, broadly ellipsoid to ellipsoid basidiospores with evident bumps in Cotton blue. Molecularly, it is sister (BPP = 1.00, MLB = 95 %) to a clade formed by *C. colorata* and *C. orientalis* (Fig. 1), species which exhibit larger basidiomes, a negative

KOH reaction, crowded lamellae, and differently shaped basidiospores (Jian et al. 2020, Mao et al. 2022). *Clitocella popinalis* has a larger pileus and stipe, a usually dark-coloured pileus surface (purplish grey, brownish grey, blackish grey) crowded lamellae, and subglobose to broadly ellipsoid wider basidiospores (5.1 µm on average) (see above).

Clitocella* subg. *Paraclitopilus Vizzini & Consiglio, *subg. nov.* — MycoBank MB 845479

Etymology. The species of this subgenus have a habit similar to that of *Clitopilus* species with central stipe and white to pale-coloured pileus.

Habit like that of the centrally-stipitate *Clitopilus* species, pileus white to cream coloured under the white pruinose covering, surfaces of both fresh and dried basidiomes not staining grey or black when bruised or in age and with a negative KOH reaction, hymenophoral trama regular, basidiospores ellipsoid to oblong, amygdaliform, sporal Q on average exceeding 1.30, obscurely angular, often adhering in tetrads.

Type. *Omphalia fallax* Quél.

Clitocella fallax (Quél.) Kluting, T.J. Baroni & Bergemann, Mycologia 106(6): 1138. 2014 — Fig. 15, 16

Basionym. *Omphalia fallax* Quél., C. r. Assoc. Franç. Avancem. Sci. 24(2): 617. 1896 ‘1895’.

Synonyms. *Clitocybe fallax* (Quél.) Sacc. & Trotter, Syll. Fung. 21: 42. 1912.

Rhodopaxillus fallax (Quél.) Maire, Bull. Soc. Linn. Lyon 6(3): 19. 1927.

Paxillopsis fallax (Quél.) J.E. Lange, Fl. Agaric. Danic. 4: 49 1939.

Rhodocybe fallax (Quél.) Singer, Farlowia 2: 549. 1946.

Clitopilopsis fallax (Quél.) Kühner ex Konrad & Maubl., Les Agaricales. Encycl. Mycol. 14: 380. 1949 ‘1948’.

Clitopilus fallax (Quél.) Vila & Contu, Boll. Assoc. Micol. Ecol. Romana 25(77–78): 12. 2009.

Clitopilus amarus A. de Haan, Sterbeeckia 18: 32. 1998.

Clitopilus fallax (Quél.) Kühner & Romagn., Fl. Analyt. Champ. Supér. (Paris): 173. 1953, nom. inval. (basionym not mentioned).

Rhodocybe fallax s. Cetto, I Funghi dal vero 6, pl. 2316. 1989 (= *Clitocybe martiorum* J. Favre ?).

Lectotype. *Omphalia fallax* Quél., C. r. Assoc. Franç. Avancem. Sci. 24 (2): 617. 1896 ‘1895’, pl. 6, f. 5. (selected by G. Consiglio, Index Fungorum 415: 1. 2019).

Epitype. AMB 18364 (designated by G. Consiglio, Index Fungorum 415: 1. 2019).

Selected iconography — Lonati (1988: 11 as *R. fallax*), Pluvinage (1993: 8 as *R. fallax*), Hausknecht & Zuccherelli (1996: 59 as *R. fallax*), Vila (2000: pl. 944), Ludwig (2000: 168, t. 166, pl. 74.11, 74.11.A, 74.11.B, as *R. fallax*), Contu (2002: f. 3, p. 102, as *R. fallax*, same photo by A. Zuccherelli as in Hausknecht & Zuccherelli 1996: 59), Contu (2009: 20, as *Clitopilus fallax*), Eyssartier & Roux (2011: 616 as *R. fallax*).

Selected descriptions — Baroni (1981: 102 as *R. fallax*), Noordeloos (1983: 41; 1988a: 80 as *R. fallax*), Lonati (1988: 10 as *R. fallax*), Contu (2002: 99 as *R. fallax*).

Pileus 10–50 mm, convex, then applanate, usually depressed in the centre, with or without a weak rounded umbo; margin involute when young, then straight or reflexed, strongly wavy-undulating when old, sometimes slightly ribbed as in *Tricholoma stiparophyllum* or *Hygrophorocybe nivea*; surface dry, smooth, minutely tomentose, pruinose, then subglabrous, sometimes cracking with age, not hygrophanous, not translucently striate, white, sometimes with slight cream or ochre tinges in the centre when old. *Lamellae* L = 50–70, l = 1–2(–3), crowded, arcuate-decurrent, 3–5 mm broad, pale, then yellowish, finally tinged with pink, with smooth, entire, concolorous edge. *Stipe* 10–50 × 2–7(–10) mm, cylindrical, often tapering and recurved towards the base, solid, white, subtomentose or pruinose to flocculose at apex and fibrillose below, usually with white rhizomorphs at the base. *Context* solid, white. *Smell* not distinctive to fragrant, aromatic, resembling that of *Clitocybe inornata* (now *Atractosporocybe inornata*) according to Maire (1927). *Taste* usually very bitter, rarely almost mild. No part of the basidiome staining

Fig. 15 *Clitocella fallax*. Basidiomes. a. AMB 18364 (epitype); b. AMB 18376; c. AMB 18375; d. TO AV5201320. — Photos: a by M. Maletti; b–c, by G. Consiglio; d by O. Chiarello.

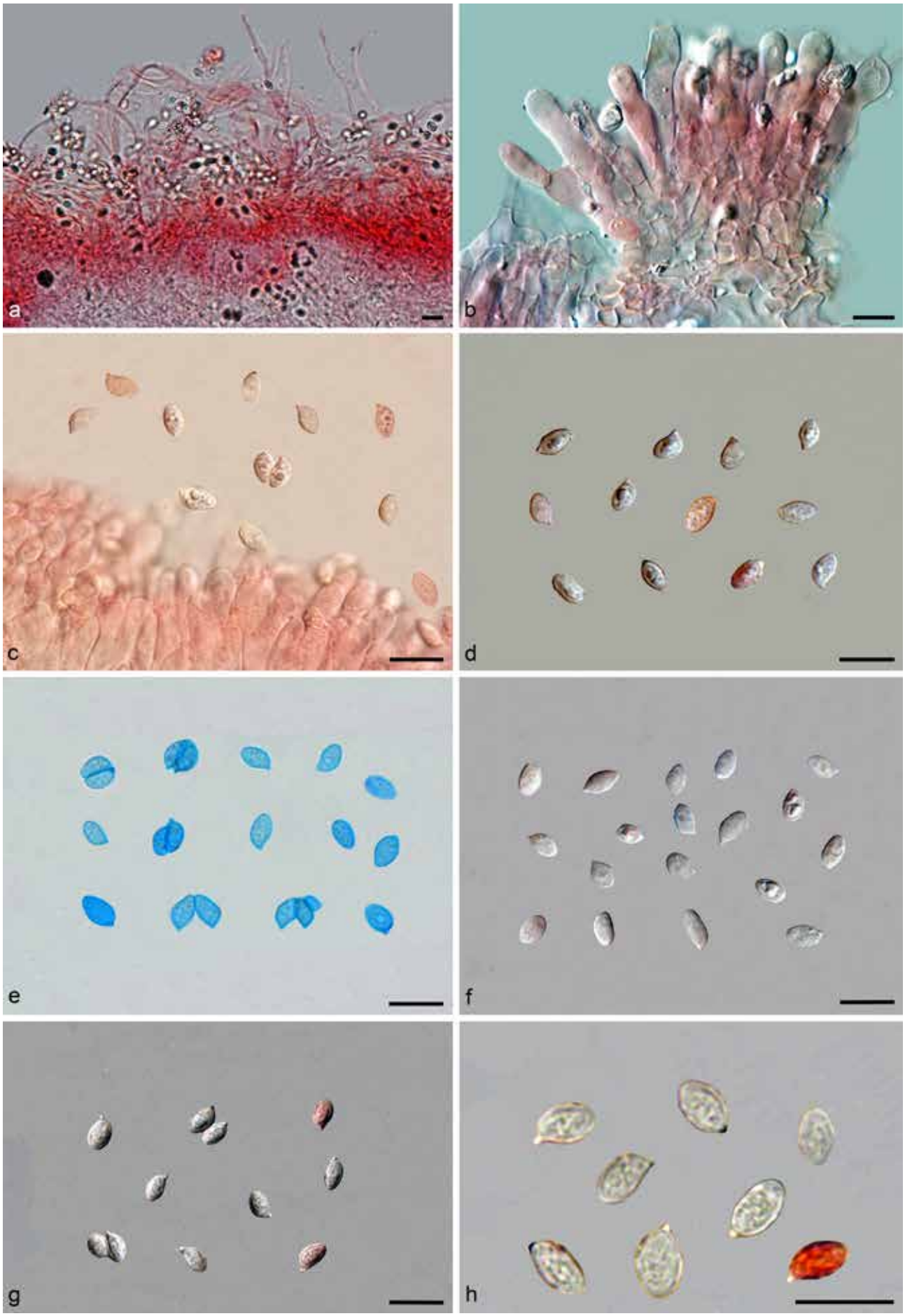

Fig. 16 *Clitocella fallax*. Microscopic features. a. Pileipellis (AMB 18364, epitype); b. hymenium and subhymenium (AMB 18364, epitype); c. hymenium and basidiospores (AMB 18377); d–h. basidiospores (d AMB 18364, epitype; e AMB 18377; f WU-MYC 0016359; g–h BR 96-121, holotype of *Clitopilus amarus*). a–d, f–h in ammoniacal Congo red, e in Cotton blue. — Scale bars = 10 µm. — Photos by M. Marchetti.

black or grey, even after handling. *Spore-print* pale cream pink. *Basidiospores* (4.9–)5.8–*6.6*–7.3(–8.9) × (3.1–)3.7–*4.1*–4.6(–7.1) µm [283/7/7], Q = (0.99–)1.44–*1.60*–1.75(–2.29), V = (27.3–)42.1–*59.8*–77.4(187) µm³, oblong to amygdaliform in side view, oblong, ovoid-ellipsoid in frontal view, minutely angular in polar view (8–9 facets), weakly nodulose-pustulate to verrucose in all views, rounded to slightly attenuated apically, often adhering in tetrads, very thin-walled, rare sclerospores with up to 1 µm thick wall, hilar appendage up to 1 µm long, contents smooth, uni- to pluriguttulate, wall cyanophilic, pale yellow in water, yellow in Melzer's. Rare spores show some weak longitudinal ribs (as in *Clitopilus*). *Basidia* 18–30 × (5–)6–11 µm, cylindrical to clavate-cylindrical, 4-spored, rarely 2-spored, sterigmata up to 4 µm long, with rare cyanophilic contents (bodies). *Subhymenium* (10–)20–30 µm thick, consisting of *textura intricata* short elements, 2.5–5 µm wide. *Hymenial cystidia* absent. *Hymenophoral trama* regular to subregular of parallel to slightly intervowen cylindrical, thin-walled hyphae, 3–10(–15) µm wide, sometimes inflated at septa. *Pileipellis* a cutis of narrow, 2.5–6.0(–9) µm wide, subparallel to loosely intertwined cylindrical hyphae, thin-walled (wall up to 0.4 µm thick), sometimes inflated at septa, white to pale yellowish; terminal ascending (erect) elements rare to frequent, slightly gelified, single or in clusters, sinuous, subcylindrical with rounded to capitulate apex, 1.5–4 µm wide; thromboplerous hyphae with yellowish grey contents present; pigment absent to pale yellow, parietal or rarely minutely incrusting some hyphae of the pileipellis, polymorphic, refractive crystalline deposits frequent. *Subpellis* of subparallel 5–7 µm wide hyphae, with pale yellow parietal pigment. *Stipitipellis* consisting of parallel, 2–6 µm wide cylindrical repent hyphae, producing clusters of erect, clavate to cylindrical caulocystidioid hyphae (elements), with frequent refractive crystalline deposits. *Clamp connections* absent.

Chemical spot-test reactions — KOH on dried basidiomes surfaces (pileus, lamellae and stipe) produces no reaction (negative).

Specimens examined. Austria, Toter Mann, Untertansleiten, 16 Aug. 1996, *A. Hausknecht* & *G. Kovacs*, WU-MYC *0016359* (as *Clitopilus scyphoides*). – Belgium, Schilde, Schildehof, with *Urtica* and *Rubus* under *Quercus* and *Populus*, 24 Aug. 1996, *A. de Haan*, BR *96-121* (holotype of *Clitopilus amarus*). – Italy, Bologna, Parco Cavaioni, in a mixed forest of broad-leaved trees with *Quercus pubescens* and *Q. cerris*, 10 Sept. 2002, *G. Consiglio*, *G. Perdisa* & *E. Franceschini*, AMB *18375*; Sassari, Luras, Carana, in a mixed forest of broad-leaved trees, 1 Nov. 2008, *G. Consiglio*, *M. Contu*, *L. Perrone* & *L. Setti*, AMB *18376*; Pesaro-Urbino, Piobbico, Monte Grino, under *Cedrus atlantica* and *Cupressus arizonica*, 26 Oct. 2009, *M. Maletti*, AMB *18364* (**epitype**); ibid., 17 Nov. 2010, *G. Consiglio*, *M. Maletti* & *G. Perdisa*, AMB *18377*; Vicenza, Brogliano, in a mixed coniferous plantation on *Abies alba* litter, 20 May 2013, *O. Chiarello*, TO *AV5201320*.

Notes — The species grows gregarious, in autumn, in the litter of deciduous (*Alnus*, *Eucalyptus*, *Robinia*, *Castanea*, *Populus*, *Quercus*), coniferous (*Abies*, *Cedrus*, *Cupressus*, *Pinus*) and mixed forest, rarely on bare soil, also in grasslands (*Corynephoretum*) on fairly dry, sandy soil. It is widespread in Europe but everywhere quite rare and prefers nitrophilous, man-disturbed (anthropogenic) areas (Maire 1927, Babos 1973, Baroni 1981, Noordeloos 1983, 1988a, 2012a, Lonati 1988, Pluvinage 1993, Hausknecht & Zuccherelli 1996, Ludwig 2001, Contu 2002, 2009, Gröger 2006).

Clitocella fallax can be confused morphologically with some centrally-stipitate *Clitopilus* species, *Hygrophorocybe nivea*, some species of *Clitocybe* sect. *Candicantes*, or *Ripartites tricholoma*, but its usually very bitter context and basidiospore structure are diagnostic. An Italian molecularly checked collection (TO AV5201320; Fig. 1), strangely exhibited a non-bitter, mild taste. The basidiospores of *C. fallax* are very thin-walled and only slightly pustulate. Therefore, it is very important to stain them very well, e.g., in Cotton blue, to recognize their angular pustulate nature. *Clitopilus amarus* is conspecific and later synonym of *C. fallax* (Fig. 1) based on the collection A. d. Haan 98031 and the holotype (BR A. d. Haan 96-121). This molecular relationship between *Clitopilus amarus* and *C. fallax* was already present in the phylogenetic trees elaborated by Morgado et al. (2016), Jatuwong et al. (2017) and Baroni et al. (2020), using only the nrITS sequence of the non-type collection *Clitopilus amarus* A. d. Haan 98031. *Clitopilus amarus* was described from Belgium as resembling *Clitocybe phyllophila*, but with crowded, arcuate, deeply decurrent lamellae, pale pink-brown spores, with 6 longitudinal, weakly pronounced ridges, 5.5–6.5 × 4–4.5 µm, amygdalifom to rhombiform, and growing in mixed broad-leaved forest with *Quercus*, *Populus*, *Urtica* and *Rubus* (De Haan 1998). Our re-examination of the holotype has revealed that most of its spores are typical of *Clitocella*, but that some are endowed with weak longitudinal ribs resulting from the fusion of several pustules (Fig. 16g–h). These rare ribs had misled De Haan, making him describe the alleged new taxon as a *Clitopilus*.

A similar case of mixed sporal ornamentation had been recognized in a true *Clitopilus* when Morgado et al. (2016) described *Clitopilus reticulosporus*, a new species from Austria and Hungary growing on rotting wood, whose basidiospores, observed under scanning electron microscopy, exhibit a very peculiar reticulate ornamentation resembling an intermediate form between the clitopiloid type with longitudinal ribs, and the rhodocyboid type with irregular bumps. A reticulate ornamentation was also recently detected in *Clitopilus subscyphoides* by Jian et al. (2023).

Clitocella fallax is easily differentiated from all other *Clitocella* species by a unique combination of pruinose white basidiomes, non-blackening surfaces which are unchanging with KOH, regular hymenophoral trama, and oblong to amygdaliform basidiospores. In particular, *C. fallax* differs from the phylogenetically related *C. blancii* (Fig. 1) mainly in the white pileus, the larger basidiospores with a different Q and with more evident nodulose-pustulate ornamentations in all views and growth usually in nitrophilous, man-disturbed not strictly thermophilous areas (see below and Baroni 1981, Noordeloos 1983, 1988a, 2012a, Lonati 1988, Hausknecht & Zuccherelli 1996, Ludwig 2001, Contu 2002, 2009, Gröger 2006).

Within *Clitocella* subg. *Clitocella*, small specimens of *C. mundula* and the white forms of *C. popinalis* (*R. popinalis* var. *hollosiae* and *R. popinalis* var. *pallida*; Allard 1991, Babos et al. 1994, Moreau 1997, 2004) can be confused with *C. fallax* but they differ in the lamellae turning black on handling or greying with age, a brown-red to orange KOH reaction on basidiome surfaces (above all on dried specimens), a hymenophoral trama of interwoven hyphae and subglobose to largely ellipsoid up to 6(–6.5) µm long spores (Baroni 1981, Babos et al. 1994, Moreau 1997; our observations). *Clitocella pallescens* from Paraná (Brazil) has a smaller, 13–30 mm wide pileus, infundibuliform when young, smaller basidiospores hardly reaching 5 µm in length, an irregular hymenophoral trama, and grows on rotten wood (Silva-Filho et al. 2018).

Gracile forms of *C. fallax* (pileus 10–20 mm wide, infundibuliform, stipe 10–30 × 1.5–3 mm) from Switzerland growing on bare soil (Breitenbach & Kränzlin 1995) are similar to those described by Baroni (1981) for North America, non-checked molecularly. The presence of *C. fallax* in North America is still questionable. The only sequence from an American collection named *C. fallax* present in public databases, OKM 25668 (CORT:25668 OKM) USA (Oregon), represents a distinct undescribed species, sister to *C. blancii* (Fig. 1).

Clitocella blancii (Maire) Consiglio, Index Fungorum 415: 1. 2019 — Fig. 17–19

Basionym. *Rhodopaxillus blancii* Maire, Bull. Soc. Hist. Nat. Afr. N. 36: 30. 1945.

Synonyms. *Clitopilopsis blancii* (Maire) Konrad & Maubl., Encycl. Mycol. 14: 380. 1949 '1948'.

Clitopilus blancii (Maire) Contu, Boll. Assoc. Micol. Ecol. Romana 25(77–78): 17. 2009.

Rhodocybe ochraceopallida Ballero & Contu, Mycotaxon 48: 1. 1993.

Clitopilus ochraceopallidus (Ballero & Contu) Noordel. & Co-David, in Co-David, Langeveld & Noordeloos, Persoonia 23: 163. 2009.

Rhodocybe amarella Consiglio, D. Antonini, M. Antonini & Contu, in Consiglio, Antonini, Antonini & Contu, Riv. Micol. 47(4): 319. 2004.

Clitopilus amarellus (Consiglio, D. Antonini, M. Antonini & Contu) Noordel. & Co-David, in Co-David, Langeveld & Noordeloos, Persoonia 23: 160. 2009.

Lectotype. MPU 312238 (selected by G. Consiglio, Index Fungorum 415: 1. 2019).

Epitype. AMB 18360 (designated by G. Consiglio, Index Fungorum 415: 1. 2019).

Selected iconography — Maire (1945: f. 3, p. 30, as *Rhodopaxillus blancii*), Consiglio et al. (2004: 320, as *Rhodocybe amarella*), La Rocca (2005: 15, as *Rhodocybe ochraceopallida*), Contu (2009: 16, 18–19, as *Clitopilus blancii*), Eyssartier & Roux (2011: 604, as *Clitopilus blancii*), Deneyer (see Appendix, as *Clitocella blancii*) as *Rhodocybe ochraceopallida*, Corriol & Hannoire (2012: 42, as *Rhodocybe blancii*).

Selected descriptions — Maire (1945: 30, as *Rhodopaxillus blancii*), Ballero & Contu (1993: 1, as *Rhodocybe ochraceopallida*), Consiglio et al. (2004: 319, as *Rhodocybe amarella*), La Rocca (2005: 13, as *Rhodocybe ochraceopallida*), Contu (2009: 17, as *Clitopilus blancii*).

Pileus 20–70(–100) mm, at first convex, then applanate and finally depressed in the centre, frequently with an umbo, which is small narrow and acute in young basidiomes, low and obtuse in older ones; margin involute for a long time, sometimes perpendicular to the pileus surface, undulate, wavy and usually at first slightly costolate-sulcate (ribbed) as in *Tricholoma stiparophyllum* and *Hygrophorocybe nivea*, not translucently striate; surface dry, non-hygrophanous, slightly tomentose, velvety, initially covered with a white hoary-pruinose aeriferous coating (as in *Clitocybe* sect. *Candicantes*) which is often soon more or less concentrically cracked; under the hoary coating, alutaceous ochre, chamois, grey-brown, then uniformly fading

Fig. 17 *Clitocella blancii*. Basidiomes. a. AMB 18360 (epitype); b. FP402; c. AMB 18371; d. AMB 18372; e. AMB 18373; f. AMB 18855. — Photos: a, e by M. Maletti, b by F. Padovan, c–d by G. Consiglio, f by E. Suárez.

to pale yellow, grey-brown, pale pinkish ochre when drying. *Lamellae* L = 40–60, l = (1–)2–4(–5), crowded, arcuate-decurrent, 3–4 mm broad, pale, yellowish cream, very late with pink tinges, with a smooth, concolorous edge. *Stipe* 20–50 × 2–8 mm, cylindrical to subclavate towards the base, rarely curved, sometimes flared at apex, solid, smooth to slightly pruinose at apex, concolorous with the pileus surface but paler, whitish to pale yellowish, solid, with a basal white cottony mycelial tomentum often subtended by white rhizomorphs. *Context* white, unchanging. *Smell* indistinct to faintly fruity, mealy when cut. *Taste* mealy and very bitter, but mild is some collections. No part of the basidiome staining black or grey, even after handling. *Spore-print* pale pink.

Basidiospores (4.0–)5.0–*5.5*–6.1(–7.3) × (3.0–)3.6–*4.0*–4.4(–5.7) µm [567/10/9], Q = (0.95–)1.24–*1.38*–1.51(–1.84), V = (19.2–)35.7–*47.4*–59.1(–94.3) µm^3, quite variable in shape, subglobose to largely ellipsoid, ellipsoid, amygdalo-ellipsoid in side view, apex rounded to ogival, attenuated-pointed, ovoid in frontal view, almost smooth to weakly undulate-verrucose in side view, with minute warts, pustules barely noticeable in Cotton blue, minutely angular (4–7 facets) in polar view, with clear suprahilar depression, often occurring in tetrads, hilar appendage up to 1.5 µm long, contents smooth, uni- to pluriguttulate, wall slightly cyanophilic, pale yellow in water, yellow in Melzer's (inamyloid). *Basidia* 18–30(–40) × 5.5–7(–7.5) µm, cylindrical, cylindrico-clavate, 4-spored, sterigmata up to 4 µm long, with

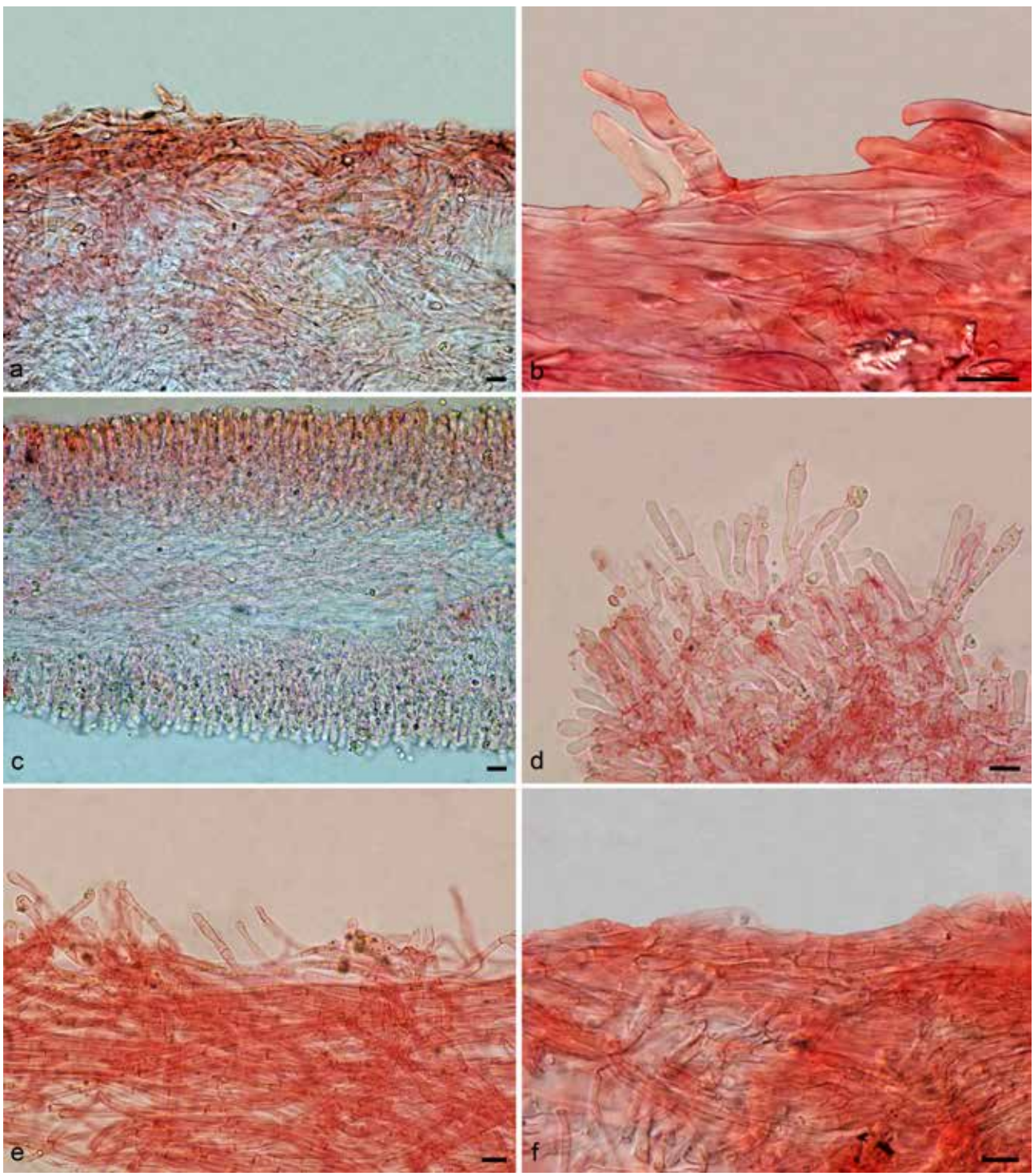

Fig. 18 *Clitocella blancii*. Microscopic features. a. Pileipellis (AMB 18855); b. pileipellis (AMB 18360, epitype); c. hymenophoral trama (AMB 18855); d. hymenium (lamellar edge) (AMB 18855); e. stipitipellis (AMB 18855); f. stipitipellis (AMB 18360, epitype). a–f in ammoniacal Congo red. — Scale bars: a–f = 10 µm. — Photos: a, c–d, e by E. Suárez, b, f by M. Marchetti.

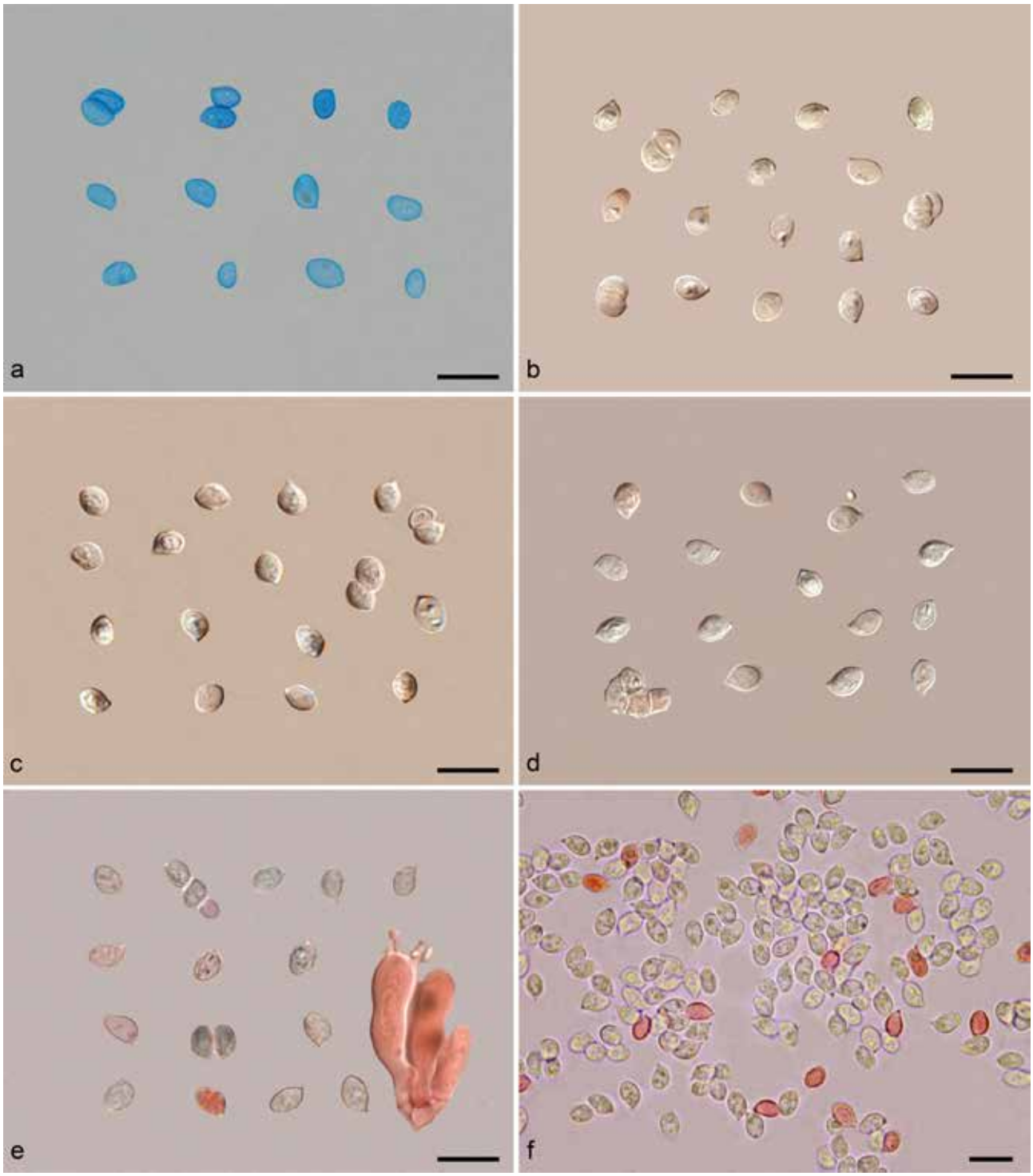

Fig. 19 *Clitocella blancii*. Microscopic features. Basidiospores. a. AMB 18360 (epitype); b. CAG 91/304 (holotype of *Rhodocybe ochraceopallida*); c. AMB 18371; d. MCVE 1003 (holotype of *Rhodocybe amarella*); e. basidiospores, basidia and subhymenium (AMB 18360, epitype); f. AMB 18855. a in Cotton blue, b–f in ammoniacal Congo red. — Scale bars = 10 µm. — Photos: a–e M. Marchetti, f by E. Suárez.

cyanophilic contents (guttulae, bodies). *Subhymenium* poorly differentiated, 10–20 µm thick, *textura intricata* type, with short elements, 2.5–5 µm wide. *Hymenial cystidia* absent. *Hymenophoral trama* regular to subregular of parallel subcylindrical, 3–8 µm wide hyphae, sometimes swollen, inflated at septa. *Pileipellis* as a xerocutis of subparallel to intertwined cylindrical hyphae, 2–6 µm wide, wall up to 0.4 µm thick, with terminal elements commonly erect (subtrichoderm structure), cylindrical to subfusiform, sometimes inflated towards the base; pigment pale brownish yellow parietal, minutely encrusting and also intercellular, with frequent refractive polymorphic to rosette like crystalline deposits. *Subpellis* of subparallel 4–7 µm wide hyphae. *Stipitipellis* consisting of parallel, 2–5(–6) µm wide cylindrical repent hyphae, producing clusters of erect, clavate to cylindrical caulocystidioid, 4–7 µm wide hyphae (elements), rarely with acute apex, sometimes uniseptate, with frequent refractive crystalline deposits.

Chemical spot-test reactions — KOH on dried basidiomes surfaces (pileus, lamellae and stipe) produces no reaction (negative).

Specimens examined. Italy, Pesaro-Urbino, Piobbico, Monte Grino, under *Cedrus atlantica* and *Cupressus arizonica*, 28 Oct. 2007, *M. Maletti*, AMB *18373*; ibid., 3 Nov. 2009, *G. Consiglio*, *M. Maletti* & *L. Setti*, AMB *18372*; ibid., 26 Oct. 2009, *M. Maletti*, AMB *18360* (**epitype**); Sassari, Luras, in a mixed forest of broad-leaved trees, 1 Nov. 2008, *G. Consiglio*, *M. Contu*, *L. Perrone* & *L. Setti*, AMB *18371*; Gorizia, Redipuglia, Sacrario di Redipug-

lia, on litter under *Cupressus sempervirens*, 14 Jan. 2016, *M.C. Magnozzi*, AMB *19302*; Medio Campidano, Marina di Arbus, Piscinas, under *Juniperus phoenicea*, 1 Dec. 1991, *M.* Contu, CAG *91/304* (holotype of *Rhodocybe ochraceopallida*); Grosseto, Capalbio, Riserva WWF di Burano, sandy dunes with *Juniperus phoenicea*, 29 Nov. 1989, *F. Padovan*, FP*402* (as *Rhodocybe ochraceopallida*); Sassari, Aglientu, Rena Majore, under *Pistacia lentiscus* in a forest of *Pinus pinea*, 3 Nov. 2003, *G. Consiglio*, *D. Antonini*, *M. Antonini* & *L. Perrone*, MCVE *1003* (holotype of *Rhodocybe amarella*). – Spain, Teruel, Albarracín, Dehesa El Canalón, under *Juniperus thurifera*, 20 Nov. 2019, *E. Suárez*, AMB *18855*.

Notes — *Clitocella blancii* is a gregarious xerophilic (thermophilic) species growing in the litter of autochthonous and allochthonous trees present in the Mediterranean basin, such as *Pinus halepensis*, *P. pinaster*, *P. pinea*, *Cedrus atlantica*, *Cupressus* spp., *Eucalyptus* spp., *Juniperus* spp., and *Pistacia lentiscus*. It is quite rare and fruits in autumn-winter. So far surely known from Algeria, France, Italy, and Spain.

Originally described as *Rhodopaxillus blancii* from Algeria (loc. Mostaganem), under *Pinus halepensis* (Maire 1945), as similar to *Clitocybe infundibuliformis* (now *Infundibulicybe gibba*), the species was later combined in *Clitopilopsis* by Konrad & Maublanc (1949). Since then, the species had been neglected and passed into oblivion until Contu (2009) who, after having reported it from Sardinia and Tuscany in the litter of *Cupressus* and *Eucalyptus*, combined it into *Clitopilus*, following the doctrine of Co-David et al. (2009). Finally, the species has recently been combined in *Clitocella* by Consiglio (2019). The lectotype of *Rhodopaxillus blancii* (MPU 312238) is in poor conservation conditions and poisoned with mercuric chloride and arsenic trioxide (Caroline Loup, pers. comm.), and is therefore not usable for both sequencing and microscopical analysis. Consequently, an Italian collection (AMB 18360) whose morphological features fit well those of the original description (Maire 1945), the collections recently described by authoritative authors (e.g., Contu 2009, Eyssartier & Roux 2011), as well as of six collections from Italy and Spain (see below), was designated by Consiglio (2019) as epitype to preserve current usage of the name and to serve as a reference specimen.

The molecular analysis in the present work provided conclusive evidence that *Rhodocybe ochraceopallida* and *R. amarella*, both described from Sardinia (Ballero & Contu 1993 and Consiglio et al. 2004, respectively), the first under *Juniperus phoenicea* and the second under *Pistacia lentiscus*, are conspecific with *C. blancii* (Fig. 1). Both species were established as the authors were unaware of Maire's publication. The re-examination by us of the holotype collections (MCVE 1003 and CAG 91/304) revealed microscopic features that fit perfectly into the variability of *C. blancii*. Macromorphologically, *R. ochraceopallida* is deviant only for the mild, non-bitter taste (Ballero & Contu 1993, Contu 1998, 1999, 2002, 2009, La Rocca 2005), but as pointed out above, there are also collections of *C. fallax* without a bitter taste. While the holotype of *R. amarella* was successfully sequenced, that of *R. ochraceopallida* failed, but an ITS sequence was obtained from the FP 402 Padovan's collection (Tuscany, *Juniperus phoenicea*) recognized by Contu (2002) as representative of *R. ochraceopallida*. The presence of *C. blancii* in France is well-documented (Eyssartier & Roux 2011, Corriol & Hannoire 2012, Moreau & Poumarat, pers. comm.) as well as in Spain (Aparici & Mahiques 1996 as *R. fallax*; AMB 18855, Fig. 1, 17f).

Clitocella blancii is distinguished from *C. fallax* mainly in a pileus with pale leathery-brown, ochre or pinkish tinges, smaller basidiospores almost smooth in side view and with a different Q, and growing in thermophilous areas (see above and Ballero & Contu 1993, Consiglio et al. 2004, Contu 2009).

Clitocella* subg. *Rhodopleurella Vizzini & Consiglio, *subg. nov*. — MycoBank MB 845481

Etymology. The name of the epithet is derived from the Greek words ῥόδον (rose-coloured) and πλευρά (lateral) and refers to the eccentric stipe of members of the genus.

The subgenus is distinguished from *Clitocella* by its pleurotoid habit (eccentric stipe), growth on decaying, abandoned termite nests in tropical rain forest, and a different *RPB2* sequence. To date, the new subgenus has only been reported from the Dominican Republic.

Type. *Clitocella termitophila* T.J. Baroni & Angelini, in Baroni, Angelini, Bergemann, Lodge, Lacey, Curtis & Cantrell, Mycol. Progr. 19(10): 1087. 2020.

Notes — *Clitocella termitophila* is sister to the clade consisting of *Clitocella* subg. *Clitocella* and subg. *Paraclitopilus* (Fig. 1) and represents an independent evolutive line. This species occupied a position outside the core of the *Clitocella* species already in the phylogenetic analyses by Baroni et al. (2020) and Mao et al. (2022). Its thin-walled basidiospores with obscure, rounded angularity in polar view and an obscurely pustulate-bumpy surface are typical features also of the other species of *Clitocella* (Kluting et al. 2014, Baroni et al. 2020). However, the ellipsoid basidiospores, the eccentric stipe, and the habit of growing on decaying woody materials of an arboreal termite nest (Baroni et al. 2020) are diagnostic features for this subgenus. The other species of *Clitocella* typically produce subglobose to broadly ellipsoid or amygdaliform basidiospores, all have a central stipe, and none is lignicolous as they are found growing on decaying leaves, humus, or soil in various temperate habitats (Kluting et al. 2014).

The status of Agaricus parilis Fr., Observ. Mycol. 2: 214. 1818 — Fig. 20

Agaricus parilis was described by Fries (1818, 1821) as an agaric with depressed ash grey pileus, greyish lamellae, blackish grey stipe and without distinctive smell and taste. It was considered by Gillet (1874) and Quélet (1886) as a *Clitocybe* and an *Omphalia*, respectively. Kühner & Romagnesi (1954) provided the first detailed description of it as *Clitopilus parilis*, indicating that it has a *Rhodophyllus undatus* (now *Entoloma undatum*)/*Clitocybe senilis* like habit, and is close to *R. popinalis* but without a farinaceous smell and taste. Singer (1962) then combined it in *Rhodocybe*. Baroni (1981) included *Agaricus parilis* in the paragraph "excluded, doubtful, and insufficiently known species" of his world monographic work on *Rhodocybe*, since there is no type collection. Arnolds (1982) described from the Netherlands *R. parilis* collections very similar to the French ones of Kühner & Romagnesi (1954). Noordeloos (1983, 1988a, 2012a), while recognizing that *R. parilis* is a species very close to *R. popinalis* and of which it could perhaps only be a dwarf form, doubtfully maintains it as a distinct species based on smaller basidiomes (pileus 12–25 mm, stipe × 2–4 mm), slightly narrower basidiospores (3.5–4.5 µm wide), smell none, and taste mild.

Rhodocybe parilis sensu Kühner & Romagnesi (1954), Arnolds (1982) and Noordeloos (1983, 1988a, 2012a) was followed, among others, by Moser & Jülich (1985–1996), Bresinsky & Einhellinger (1987), Bon (1989), Cetto (1989), De Vries & Arnolds (1994), Hausknecht & Noordeloos (1998), Contu (2000), Ludwig (2001), and Gröger (2006).

The nrITS, nr28S, *RPB2* and *EF-1α* sequences have newly obtained from seven collections named *R. parilis* (six from Austria, cited in Hausknecht & Noordeloos 1998 and one from Sweden) (Table 2). All these collections have turned out to be

Fig. 20 *Rhodocybe parilis* (collections from Austria). Basidiomes. a. WU-MYC 0004222; b. WU-MYC 0006178; c. WU-MYC 0006320; d. WU-MYC 0010084. — Photos by A. Hausknecht.

Table 2 Revised names, vouchers, locations, and accession numbers of the DNA sequences of the examined *Rhodocybe parilis* collections.

Species (revised name)	Label	Voucher and State	GenBank Accession No.			
			nrITS	nrLSU	*RPB2*	*EF-1α*
Rhodocybe tugrulii	*Rhodocybe parilis*	WU-MYC 0003753, Austria	OP363993	OP363998	OP381081	–
Rhodocybe tugrulii	*Rhodocybe parilis*	WU-MYC 0004222, Austria	OP363991	–	–	–
Rhodocybe tugrulii	*Rhodocybe parilis*	WU-MYC 0006178, Austria	–	OP364000	–	–
Rhodocybe tugrulii	*Rhodocybe parilis*	WU-MYC 0006320, Austria	OP363992	OP363997	OP381080	OP381083
Rhodocybe tugrulii	*Rhodocybe parilis*	WU-MYC 0010084, Austria	OP363995	–	–	–
Rhodocybe tugrulii	*Rhodocybe parilis*	WU-MYC 0022202, Austria	OP363994	OP363999	OP381082	OP381084
Rhodocybe tugrulii	*Rhodocybe parilis*	GB-013 1395, Sweden	OP363996	OP364001	–	–

Rhodocybe tugrulii (data not shown), a species so far known from Turkey and Estonia (Vizzini et al. 2016), Italy (Boccardo & Dovana 2019) and USA (Horman 2018) as growing in the litter of coniferous trees. The morphological characters of *R. tugrulii* fit quite well those of *R. parilis* sensu Noordeloos (1983, 1988a, 2012a), except for the mealy to subspermatic smell and the wider basidiospores × (4.0–)4.3–5.5(–5.9) µm of the former (Vizzini et al. 2016, Horman 2018, Boccardo & Dovana 2019). Further studies will be needed to clarify the relationships between these two taxa.

These data once again underline, as previously stated by Kluting et al. (2014) and Vizzini et al. (2016), that *Rhodocybe* sect. *Decurrentes* as morphologically circumscribed by Baroni (1981), Singer (1986) and Contu (2002) (typified with *A. mundulus*, species with a *Clitopilus*-like habit, greyish or greyish brown, centrally stipitate basidiomes, decurrent to subdecurrent lamellae, and absence of both coloured pseudocystidia and clamp connections) is not a monophyletic assemblage and entities with a *C. mundula*/*C. popinalis* habit has arisen at least twice in the rhodocyboid fungi (in *Clitocella* and *Rhodocybe* s.str.).

Specimens examined (*Rhodocybe parilis*). Austria, Ziersdorf, Kiblitz, auf Weg im Mischwald, 17 Sept. 1984, *A. Hausknecht* & *R. Schütz*, WU-MYC *0003753*; Niederösterreich, Gmünd, Sandgrube Breitensee, auf Sandboden bei Fichte (*Picea*), 22 Sept. 1984, *L. Sandmann* & *A. Hausknecht*, WU-MYC *0004222*; Niederösterreich, Maissau, Sondorferstrasse, 16 Oct. 1991, *A. Hausknecht*, WU-MYC *0006178*; Niederösterreich, Gmünd, Sandgrube Breitensee, Waldrand bei *Pinus*, 6 Aug. 1987, *L. Sandmann* & *A. Hausknecht*, WU-MYC *0006320*; Burgenland, Oberwart, Eisenberg-Badersdorf, 21 June 1987, *A. Hausknecht* & *W. Klofac*, WU-MYC *0010084*; Niederösterreich, Grossreipersdorf, Feldberg, *Pinus*, 17 Aug. 2002, *A. Hausknecht*, WU-MYC *0022202*. – Sweden, Skane, Maglehem, Ravlunda skjutfalt, amongst mosses on sandy soil, 23 Oct. 1983, *L. Örstadius*, GB-*013 1395*.

DISCUSSION

Eight species of *Clitocella* are recognized for the European territory in the present paper. Based on molecular data, *Clitocella blancii*, *C. fallax*, *C. nigrescens*, *C. popinalis* and *C. solaris*, would appear to be present only in Europe so far (Fig. 1). *Clitocella obscura* is present in Europe and North America (Canada). *Clitocella mundula* and *C. colorata* are present in Europe, Asia, and North America (USA).

Clitocella blancii and *C. nigrescens* are thermophilic species; *C. popinalis* and *C. solaris* usually grow in grasslands, fields, mossy areas, while *C. colorata*, *C. fallax*, *C. mundula* and *C. obscura* in forested areas.

Clitocella blancii and *C. fallax* form an evolutionary lineage separate from the rest of the *Clitocella* species (*Clitocella* subg. *Clitocella*) and constitutes *Clitocella* subg. *Paraclitopilus*. The latter is morphologically well circumscribed by a *Clitopilus*- to *Clitocybe*-like habit, a pale-coloured white to light alutaceous ochre pileus usually without grey tinges, basidiome surfaces unchanging, not staining grey or black when bruised or in age, and with a negative reaction to KOH, regular hymenophoral trama, and ellipsoid to oblong, amygdaliform, obscurely to minutely angular, obscurely pustulate basidiospores, sometimes with an almost smooth outline. The similarity of *C. fallax* to species of *Clitopilus* is so striking that anomalous collections of the former, due to the presence of rare spores with pustules arranged in weak longitudinal ribs, were described as *Clitopilus amarus* by De Haan (1998).

Clitocella subg. *Clitocella* is distinguished by a usually pale grey, grey, dark grey, blackish violaceous pileus, basidiome surfaces unchanging or staining grey or black when bruised or with senescence, usually with a positive, reddish reaction to KOH, a usually irregular hymenophoral trama (intertwined hyphae) and globose, subglobose, broadly ellipsoid to ellipsoid basidiospores, which are minutely to clearly angular and weakly to clearly pustulate. Within this subgenus, clade a1 (BPP = 1.0, MLB = 78 %) encompasses a peculiar trio, *C. popinalis*, *C. mundula* and *C. obscura*. Morphologically also closely related (grey pileus and lamellae, reddish reaction of the basidiome surfaces to KOH and irregular hymenophoral trama are the shared features), they form a natural group of species that are often misidentified and easily confused with each other. The lack of monophyly for collections of *C. mundula*, *C. obscura* and *C. popinalis* borrowed from herbaria in Europe (as *R. mundula*, *R. obscura* and *R. popinalis* in Fig. 1 and Table 1) is likely due to misidentifications. *Clitocella nigrescens* shows broad phenotypic plasticity but its large basidiospores and association with dunes or retrodunal trees are diagnostic. *Clitocella solaris* and *C. colorata* have pale-coloured pilei.

Clitocella subg. *Rhodopleurella* represents an independent evolutive unit from tropical rain forest. It consists so far only of *C. termitophila*, a species distinguished by pleuropodal basidiomes, ellipsoid basidiospores, and growing on decaying, abandoned arboreal termite nests.

KEY TO THE EUROPEAN SPECIES OF CLITOCELLA

1. Pileus grey, dark grey, yellowish brown 2
1. Pileus almost white to pastel grey, light ochraceous-pink 6
2. Pileus surface of dried basidiomes with a positive reddish KOH reaction 3
2. Pileus surface of dried basidiomes with a negative KOH reaction . . . . . *C. colorata*
3. Cheilocystidia present, lamellae when mature dark grey, black, growth under *Picea* . . . . . *C. obscura*
3. Cheilocystidia absent, lamellae when mature not dark grey, black, not associated with *Picea* 4
4. Growing on dunes or in association with hind dune trees, basidiospores broadly ellipsoid to ellipsoid, exceeding on average 7 µm in length ((6.0–)7.0–7.7–8.3(–9.9) µm) . . . . . *C. nigrescens*
4. Usually not growing on dunes or in hind dune thickets, basidiospores subglobose to broadly ellipsoid not exceeding on average 7 µm in length 5
5. Usually occurring in forested systems, basidiome surfaces turning black when old and/or on bruising, basidiospores not exceeding on average 5 µm in width and obscurely pustulate . . . . . *C. mundula*
5. Usually occurring in grassland systems, basidiome surfaces not turning black when old and/or on bruising, basidiospores exceeding on average 5 µm in width and clearly pustulate . . . . . *C. popinalis*
6. Pileus surface of dried basidiomes with a positive reddish KOH reaction, basidiospores subglobose to ellipsoid, angular, sporal Q not exceeding 1.30 on average 7
6. Pileus surface of dried basidiomes with a negative KOH reaction, basidiospores ellipsoid to oblong, amygdaliform, obscurely angular, sporal Q exceeding 1.30 on average. 8
7. Pileus small, up to 10 mm diam, lamellae spaced . . . . . *C. solaris*
7. Pileus larger, lamellae crowded . . . . . go back to couplet 4 . . . . . (albinotic forms of *C. nigrescens*, ... *C. popinalis* and *C. mundula*; see Allard 1991, ... Babos et al. 1994, Contu 1999, Moreau 2004, ... Moreau et al. 2008)
8. Pileus white under the white pruinose coating, sometimes with faint pale cream or pale ochre tinges only when old, basidiospores longer than 6 µm on average, nitrophilic species . . . . . *C. fallax*
8. Pileus pale leathery-brown, ochre, pale pinkish ochre under the white pruinose coating, basidiospores shorter than 6 µm on average, thermophilic species . . . . . *C. blancii*

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REFERENCES

Allard C. 1991. Note concernant Rhodocybe popinalis. Bulletin Trimestriel de la Fédération Mycologique Dauphiné-Savoie 121: 32–34, photo 3.

Altschul SF, Gish W, Miller W, et al. 1990. Basic local alignment search tool. Journal of Molecular Biology 215: 403–410.

Alvarado P, Manjón JL, Matheny PB, et al. 2010. Tubariomyces, a new genus of Inocybaceae from the Mediterranean region. Mycologia 102(6): 1389–1397.

Alvarado P, Moreno G, Manjón JL. 2012. Comparison between Tuber gennadii and T. oligospermum lineages reveals the existence of the new species T. cistophilum (Tuberaceae, Pezizales). Mycologia 104(4): 894–910.

Aparici R, Mahiques R. 1996. Rhodocybes de la zona litoral de «El Saler». Butlletí Societat Micològica Valenciana 2: 89–96.
Arnolds EJM. 1982. Ecology and coenology of macrofungi in grasslands and moist heathlands in Drenthe, the Netherlands. Part 2 Autecology. Part 3 Taxonomy (Bibliotheca Mycologica 90). Cramer, Vaduz.
Babos M. 1973. A magyarországi homokterületek ritka és érdekes gombafajai. I. Studia Botanica Hungarica 8: 3–24.
Babos M, Bohus G, Locsmandi C, et al. 1994. Über den Formenkreis von Rhodocybe popinalis (Fr.) Sing, und Rh. mundula (Lasch) Sing. Beiträge zur Kenntnis der Pilze Mitteleuropas 9: 45–50.
Ballero M, Contu M. 1993. New-sand-inhabiting Rhodocybe (Basidiomycetes, Agaricales). Mycotaxon 48: 1–4.
Baroni TJ. 1978. Chemical spot-test reactions – boletes. Mycologia 70: 1064–1076.
Baroni TJ. 1981. A revision of the genus Rhodocybe Maire (Agaricales). Nova Hedwigia, Beihefte 67: 1–194.
Baroni TJ. 1999. Rhodocybe pegleri sp. nov. with notes on Rhodocybe pseudonitellina from East Africa. Kew Bulletin 54: 777–782.
Baroni TJ, Angelini C, Bergemann SE, et al. 2020. Rhodocybe-Clitopilus clade (Entolomataceae, Basidiomycota) in the Dominican Republic: new taxa and first reports of Clitocella, Clitopilus, and Rhodocybe for Hispaniola. Mycological Progress 19: 1083–1099.
Baroni TJ, Gates GM. 2006. New species and records of Rhodocybe (Entolomataceae, Agaricales) from Tasmania. Australian Systematic Botany 19: 343–358.
Baroni TJ, Halling RE. 1992. New species of Rhodocybe from South America with a key to species. Mycologia 84(3): 411–321.
Baroni TJ, Hofstetter V, Largent DL, et al. 2011. Entocybe is proposed as a new genus in the Entolomataceae (Agaricomycetes, Basidiomycota) based on morphological and molecular evidence. North American Fungi 6(12): 1–19.
Baroni TJ, Horak E. 1994. Entolomataceae in North America III: New taxa, new combinations, and notes on species of Rhodocybe. Mycologia 86: 138–145.
Baroni TJ, Matheny PB. 2011. A re-evaluation of gasteroid and cyphelloid species of Entolomataceae from Eastern North America. Harvard Papers in Botany 16: 293–310.
Baroni TJ, Watling R. 1999. Taxonomic and mycogeographic notes on some Malaysian fungi IV. Notes on Clitopilus and Rhodocybe. Mycotaxon 72: 57–72.
Battaglia G. 2006. Rhodocybe obscura (Pilát) M.M. Moser. Rivista di Micologia 49(2): 137–142.
Berger C, Moliere A, Ouvrard G, et al. 2008. Récoltes intéressantes en 2007. Cahiers mycologiques nantais 20: 40–50 and photo 25.5.
Binder M, Hibbett DS. 2003. Oligonucleotides. http://www.clarku.edu/faculty/dhibbett/Protocols_Folder/Primers/Primers.htm [accessed 23 June 2022].
Bobinet P, Dupuy G. 2000. L'année 1999 en Oléron: récoltes intéressantes. Contribution n 42 au Programme d'inventaire et de cartographie des Mycota français. Bulletin de la Société Botanique du Centre-Ouest 31: 577–590.
Boccardo F, Dovana F. 2019. Prima segnalazione di Rhodocybe tugrulii in Italia. Annales Confederationis Europaeae Mycologiae Mediterraneensis 2016 (2019): 86–93.
Bon M. 1980. Quelques Agaricales "greffées" sur Ammophila arenaria (L.) Link. Documents Mycologiques 11(41): 47–54.
Bon M. 1989. Agaricomycètes de la région Languedoc-Cévennes (4ème partie). Documents Mycologiques 19(75): 25–46.
Breitenbach J, Kränzlin F. 1995. Champignons de Suisse, Tome 4: Champignons à lames. 2ème partie. Entolomataceae, Pluteaceae, Amanitaceae, Agaricaceae, Coprinaceae, Bolbitiaceae, Strophariaceae. Edition Mykologia, Lucerne, Switzerland.
Bresinsky A, Einhellinger A. 1987. Pilze, Flechten und andere Pflanzen aus Flugsandgebieten Südbayerns. Hoppea, Denkschriften der Regensburgischen Botanischen Gesellschaft 45: 413–460.
Carassai E, Papa M, Contu M. 2000. Rhodocybe cupressicola (Agaricales) spec. nov. dalle Marche, con chiave per il genere in Italia. Micologia e Vegetazione Mediterranea 15: 64–70.
Carbone I, Kohn LM. 1999. A method for designing primer sets for speciation studies in filamentous ascomycetes. Mycologia 91(3): 553–556.
Cetto B. 1989. I Funghi dal vero, volume 6. Ed. Saturnia, Trento.
Clémençon H. 1972. Zwei verbesserte Präparierlösungen für die microskopische Untersuchung von Pilze. Zeitschrift für Pilzkunde 38: 49–53.
Co-David D, Langeveld D, Noordeloos ME. 2009. Molecular phylogeny, and spore evolution of Entolomataceae. Persoonia 23: 147–176.
Consiglio G. 2019. Nomenclatural novelties. Index Fungorum 415: 1.
Consiglio G. 2020. Nomenclatural novelties. Index Fungorum 430: 1.
Consiglio G, Antonini D, Antonini M, et al. 2004. Rhodocybe amarella spec. nov. Una nuova specie della Sezione Decurrentes rinvenuta in Sardegna. Rivista di Micologia 47(4): 319–324.
Contu M. 1989. Agaricales des dunes sableuses de Sardaigne. Observations complémentaires sur Rhodocybe malenconii Pacioni et Lalli 1984. Bulletin de la Fédération Mycologique Dauphiné-Savoie 112: 24–26.
Contu M. 1998. Chiavi per la determinazione delle Agaricales della Sardegna. I. Clitopilus Kumm. e Rhodocybe R. Maire. Pagine di Micologia 9: 74–76.
Contu M. 1999. Ecologia e tassonomia del genere Rhodocybe R. Maire (Basidiomycetes, Entolomataceae) in Sardegna. Revista Catalana de Micologia 22: 5–14.
Contu M. 2000. L'Agaricus parilis ed il genere Rhodocybe R. Maire. Bollettino dell'Associazione Micologica ed Ecologica Romana 49–50: 3–8.
Contu M. 2002. Il genere Rhodocybe (Basidiomycetes, Entolomataceae) in Italia. I. Sezione Decurrentes. Micologia e Vegetazione Mediterranea 17(2): 95–114.
Contu M. 2009. Studi sul genere Clitopilus (incl. Rhodocybe) – I. Prima segnalazione in Italia di Clitopilus blancii comb. nov., nuove raccolte di Clitopilus giovanellae, iconografia di Clitopilus carneolus comb. nov. e ulteriori nuove combinazioni. Bollettino dell'Associazione Micologica ed Ecologica Romana 77–78: 15–31.
Contu M, Farci D. 1997. Fungi Mediterranei Rariores 25. Micologia e Vegetazione Mediterranea 12(1).
Contu M, Signorello P. 1999. Contributo alla conoscenza della flora micologica (Macromiceti) delle dune della Sicilia. Bollettino dell'Accademia Gioenia di Scienze Naturali 32(356): 31–45.
Corriol G, Hannoire C. 2012. Inventaires de Macromycètes dans les réserves naturelles de Prats-de-Mollo, La Forêt de la Massane, le Mas Larrieu, et Mantet (Pyrénées Orientales, France). Rapport final. Conservatoire botanique national des Pyrénées et de Midi-Pyrénées (CBN-PMP).
Courtecuisse R, Duhem B. 1994. Champignons de France et d'Europe. Delachaux et Niestlé, Lausanne.
Cubeta MA, Echandi E, Abernethy T, et al. 1991. Characterization of anastomosis groups of binucleate Rhizoctonia species using restriction analysis of an amplified ribosomal RNA gene. Phytopathology 81: 1395–1400.
Darriba D, Taboada GL, Doallo R, et al. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772.
De Haan A. 1998. Clitopilus amarus nov. spec. een bittere Molenaar. Steerbeckia 18: 32–35.
De Vries B, Arnolds E. 1994. Veranderingen in de mycoflora van drie jeneverbesstruwelen. Coolia 37: 51–71.
Dennis RWG. 1953. Les Agaricales de l'Ile de la Trinité: Rhodosporae-Ochrosporae. Bulletin de la Société Mycologique de France 69: 145–198.
Dennis RWG. 1961. Fungi Venezuelani. Kew Bulletin 15: 67–156.
Enderle M. 1980–1981. Seltene oder interessante Pilze aus dem Ulmer Raum. Mitteilungen des Vereins für Naturwissenschaft und Mathematik in Ulm e.V. 31: 24–36.
Eyssartier G, Roux P. 2011. Le Guide des champignons France et Europe. Belin, Paris, France.
Fábry I. 1977. NiekoFko zriedkavých druhov zo skupiny Agaricales na Slovensku (Einige seltene Arten aus der Gruppe der Agaricales in der Slowakei). Česká Mykologie 31(1): 31–37.
Fries EM. 1818. Observationes mycologicae praecipue ad illustrandam floram suecicam. Vol. 2. Sumptibus G. Bonnieri, Havniae.
Fries EM. 1821–[1832]. Systema mycologicum: sistens fungorum ordines, genera et species, huc usque cognitas, quas ad normam methodi naturalis determinavit. Vol. 1. Ex Officina Berlingiana, Lundae, Sweden.
Fries EM. 1838. Epicrisis Systematis Mycologici. Upsaliae.
Fries EM. 1857. Monographia Hymenomycetum Sueciae. Upsaliae.
Fries EM. 1874. Hymenomycetes europaei. Upsaliae.
Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for Basidiomycetes – application to the identification of mycorrhizae and rusts. Molecular Ecology 2: 113–118.
Gelman A, Rubin DB. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7: 457–511.
Gillet CC. 1874. Les Hyménomycètes ou Description de tous les Champignons qui Croissent en France. Ch. Thomas, Alençon.
Gouy M, Guindon S, Gascuel O. 2010. SeaView version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Molecular Biology and Evolution 27(2): 221–224.
Gröger F. 2006. Bestimmungsschlüssel für Blätterpilze und Röhrlinge in Europa. Teil I. Regensburger Mykologische Schriften 13: 1–638.
Gross G. 1972. Kernzahl und sporenvolumen bei einigen Hymenogasterarten. Zeitschrift für Pilzkunde 38: 109–158.
Guinberteau J. 1997. La mycoflore des écosystèmes dunaires du Bas-Médoc (Gironde, France) – Approche écodynamique des mycocoenoses dunaires atlantiques. In: Favennec J, Barrère P (eds), Biodiversité et protection dunaire. Bordeaux, France, 17–19 April 1996: 242–261 + 4 planches couleur, 12 photos couleur. Lavoisier Tec & Doc, Paris.
Guinberteau J. 1999. Les champignons ont rendez-vous avec la dune. Spécial Champignons Magazine 16: 12–17.

Guinberteau J. 2010. Les champignons des dunes non boisées du littoral aquitain: un univers méconnu! Bulletin de la Société Linnéenne de Bordeaux 145 n.s., 38(3): 247–277.
Guinberteau J. 2011. Le petit livre des champignons des dunes. Éditions Confluences, Bordeaux.
Guinberteau J, Callac P, Boisselet P. 1998. Inventaires des communautés fongiques liées au Cupressus macrocarpa en zone littorale atlantique et données récentes sur les populations sauvages d'Agaricus bisporus. Bulletin de la Société mycologique de France 114(2): 19–38.
Guinberteau J, Courtecuisse R. 1993. Contribution à l'étude des macromycètes psammophiles de la Cote d'Argent (Littoral Aquitain). II – Sur quelques taxons rares ou critiques. Bulletin de la Société Mycologique de France 109(3): 123–147.
Hartley AJ, De Mattos-Shipley K, Collins CM, et al. 2009. Investigating pleuromutilin-producing Clitopilus species and related basidiomycetes. FEMS Microbiology Letters 297(1): 24–30.
Hausknecht A, Noordeloos ME. 1998. Neue oder seltene arten der Entolomataceae (Agaricales) aus Mittel- und Südeuropa. Österreichische Zeitschrift für Pilzkunde 8: 199–221.
Hausknecht A, Zuccherelli A. 1996. Ritrovamenti interessanti dal Ravennate. Agaricales con polvere sporale rosa. 4ª parte. Bollettino del Gruppo Micologico "G. Bresadola", n.s, 39(1): 19–70.
Hausknecht A, Zuccherelli A. 1998. Ritrovamenti interessanti dal Ravennate. 5ª parte: diverse Agaricales, nuovi reperti e aggiunte a gruppi già trattati e altri. Bollettino del Gruppo Micologico "G. Bresadola", n.s, 41(2): 91–134.
Henkel TW, Aime MC, Largent DL, et al. 2010. The Entolomataceae of the Pakaraima Mountains of Guyana III: new species of Rhodocybe. Mycoscience 51: 23–27.
Hofstetter V, Clémençon H, Vilgalys R, et al. 2002. Phylogenetic analyses of the Lyophylleae (Agaricales, Basidiomycetes) based on nuclear and mitochondrial rDNA sequences. Mycological Research 106(9): 1043–1059.
Horak E. 1978. Notes on Rhodocybe Maire. Sydowia 31: 58–80.
Horak E. 1979. Fungi Agaricini Novazelandiae. VII. Rhodocybe Maire. New Zealand Journal of Botany 17: 275–281.
Horman J. 2018. Rhodocybe tugrulii: First North American record. Long Island Sporeprint 26(1): 1, 4, 7.
Jatuwong K, Hyde KD, Karunarathna SC, et al. 2017. Two species of Clitopilus (Entolomataceae, Agaricales) from Northern Thailand. Chiang Mai Journal of Science 44(1): 115–124.
Jian SP, Bau T, Zhu XT, et al. 2020. Clitopilus, Clitocella, and Clitopilopsis in China. Mycologia 112(2): 371–399.
Jian SP, Wang XH, Deng WQ, et al. 2023. Clitopilus in southern China: two new species and comments on C. subscyphoides. Mycological Progress 22: 35.
Kaur A, Atri NS, Kaur M. 2013. A new variety of Rhodocybe popinalis (Entolomataceae, Agaricales) from coprophilous habitats of India. Journal on New Biological Reports 2(3): 260–263.
Kim CS, Jo JW, Kwag YN, et al. 2015. Mushroom Flora of Ulleung-gun and a newly recorded Bovista species in the Republic of Korea. Mycobiology 43(3): 239–257.
Kluting KL, Baroni TJ, Bergemann SE. 2014. Toward a stable classification of genera within the Entolomataceae: a phylogenetic re-evaluation of the Rhodocybe-Clitopilus clade. Mycologia 106(6): 1127–1142.
Konrad P, Maublanc A. 1949 '1948'. Les Agaricales. Encyclopédie Mycologique 14: 1–464.
Kour H, Kumar S, Sharma YP, et al. 2016. Clitocella (Entolomataceae) – a new genus record for India. Studies in Fungi 1(3): 130–134.
Kretzer AM, Bruns TD. 1999. Use of atp6 in fungal phylogenetics: an example from the Boletales. Molecular Phylogenetics and Evolution 13(3): 483–492.
Kühner R, Lamoure D. 1971. Agaricales de la zone alpine. Genre Rhodocybe R. Maire. Bulletin de la Société Mycologique de France 87(1): 15–23.
Kühner R, Romagnesi H. 1954. Compléments a la Flore Analytique: III. Especes nouvelles, critiques ou rares de Pleurotacées, Marasmiacées et Tricholomacées. Bulletin de la Société des Naturalistes d'Oyonnax 8: 73–131.
La Rocca S. 2005. Due rari basidiomiceti della Sicilia: Rhodocybe ochraceopallida e Agaricus freirei. Micologia e Vegetazione Mediterranea 20(1): 13–16.
Lange JE. 1940. Flora Agaricina Danica. Vol. 5. Recato A/S, Copenhagen, Denmark.
Lasch WG. 1829. Enumeratio Hymenomycetum pileatorum Marchiae Brandenburgicae, nondum in floris nostratibus nominatorum, cum observationibus in cognitos et novorum descriptionibus. Linnaea 4: 518–553.
Lavorato C, Contu M. 2001. Due interessanti Agaricales raccolte in Svizzera. Rivista di Micologia 44(4): 347–351.
Lejay P. 2004. Quelques trouvailles intéressantes faites aux sables d'or (22). Cahiers Mycologiques Nantais 16: 37–39.
Liu YJ, Whelen S, Hall BD. 1999. Phylogenetic relationships among Ascomycetes: evidence from an RNA Polymerase II subunit. Molecular Biology and Evolution 16(12): 1799–1808.
Lonati G. 1988. Funghi rari o poco conosciuti: Rhodocybe fallax (Quélet) Singer. Bollettino dell'Associazione Micologica ed Ecologica Romana 5(14): 10–12.
Ludwig E. 2000. Pilzkompendium. Band 1. Abbildungen. IHW-Verlag. Eching, Germany.
Ludwig E. 2001. Pilzkompendium. Band 1. Beschreibungen. IHW-Verlag. Eching, Germany.
Lunghini D, Perrone L. 2000. Una raccolta invernale a Torre Astura. Bollettino del'Associazione Micologica ed Ecologica Romana 49–50: 27–35.
Maddison WP, Maddison DR. 2017. Mesquite: a modular system for evolutionary analysis. Available at http://mesquiteproject.org.
Maire R. 1926. Études mycologiques (fascicule 2). Bulletin de la Société Mycologique de France 40(3): 293–317.
Maire R. 1927. Une Agaricacée peu connue. Bulletin bi-mensuel de la Société Linnéenne de Lyon 6(1): 19–21.
Maire R. 1945. Études mycologiques. Fascicule 5. Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 36: 24–42.
Malençon G, Bertault R. 1975. Flore des Champignons Supérieurs du Maroc. II. Travaux de l'Institut scientifique chérifien et de la Faculté des Sciences de Rabat, Série botanique et biologie végétale 33: 1–541.
Mao N, Lv J-C, Xu Y-Y, et al. 2022. Two new Clitocella species from North China revealed by phylogenetic analyses and morphological characters. MycoKeys 88: 151–170.
Matheny PB, Wang Z, Binder M, et al. 2007. Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). Molecular Phylogenetics and Evolution 43(2): 430–451.
Meerts P. 1999. The evolution of spores in agarics: do big mushrooms have big spores? Journal of Evolutionary Biology 12: 161–165.
Merino Alcántara D. 2018. Setas de Dunas 5. Micobotánica-Jaén año XIII nº 2. http://www.micobotanicajaen.com/Revista/Articulos/DMerinoA/SetasDunas005/SetasDunas005.pdf.
Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments workshop (GCE), 14 November 2010: 1–8. New Orleans, LA, USA.
Mir G, Melis JLL, Prats MC. 2017. Aportación al catálogo micológico de las Illes Balears. Menorca, III. Micobotánica-Jaén 12(2): 1–23.
Moncalvo JM, Vilgalys R, Redhead SA, et al. 2002. One hundred and seventeen clades of euagarics. Molecular Phylogenetics and Evolution 23(3): 357–400.
Monti G, Gorreri L, Marchetti M, et al. 2001. Funghi di ambienti dunali. Università degli studi di Pisa, Pisa.
Moreau P-A. 1997. Le genre Rhodocybe Maire: quelques observations sur le groupe R. mundula-R. popinalis. Bulletin de la Société Mycologique de France 113(4): 343–354 + atlas pl. 336–339.
Moreau P-A. 2004. Le genre Rhodocybe Maire: addenda. Documents Mycologiques 33(132): 36.
Moreau P-A, Contu M, Guinberteau J. 2008. Rhodocybe nigrescens comb. nov., un nom prioritaire pour R. cupressicola. Variabilité de l'espèce et comparaison avec Rhodocybe malenconii. Micologia e Vegetazione Mediterranea 23(1): 31–50.
Moreno G, Arenal F, González V. 1994. Algunos Agaricales de las playas de España peninsular. Cryptogamie Mycologie 15(4): 239–254.
Morgado LN, Noordeloos ME, Hausknecht A. 2016. Clitopilus reticulosporus, a new species with unique spore ornamentation, its phylogenetic affinities and implications on the spore evolution theory. Mycological Progress 15: 26.
Moser M. 1978. Keys to Agarics and Boleti (Polyporales, Boletales, Agaricales, Russulales). Fischer Verlag, Stuttgart, Germany.
Moser M, Jülich W. 1985–1996. Farbatlas der Basidiomyceten. Fischer Verlag, Stuttgart, New York.
Mua A, Melis M. 2002. Contributo allo studio ed alla divulgazione della micoflora ammofila (funghi delle dune). Parte seconda. Bollettino dell' Associazione Micologica ed Ecologica Romana 52–53: 9–21.
Neukom H-P. 1994. Pilz des Monats. Rhodocybe mundula (Lasch: Fr.) Sing. im Vergleich mit Rhodocybe popinalis (Fr.) Sing. Ein Beitrag zur Klärung zweier kritischer Arten. Schweizerische für Pilzkunde 5–6: 113–122.
Noordeloos ME. 1983. Notulae ad Floram Agaricinam Neerlandicam. I-III. Marasmiellus, Macrocystidia and Rhodocybe. Persoonia 12: 31–43.
Noordeloos ME. 1988a. Rhodocybe Maire. In: Bas C, Kuyper TW, Noordeloos ME, et al. (eds), Flora Agaricina Neerlandica. I: 77–82. Balkema, Rotterdam, The Netherlands.
Noordeloos ME. 1988b. Clitopilus Kumm. In: Bas C, Kuyper TW, Noordeloos ME, et al. (eds), Flora Agaricina Neerlandica. I: 82–85. Balkema, Rotterdam, The Netherlands.

Noordeloos ME. 2012a. Rhodocybe Maire. In: Knudsen H, Vesterholt J (eds), Funga Nordica, 2nd edition. Vol. 2. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera: 576–579. Nordsvamp, Copenhagen, Denmark.
Noordeloos ME. 2012b. Clitopilus (Fr.: Fr.) P. Kumm. In: Knudsen H, Vesterholt J (eds), Funga Nordica, 2nd edition. Vol. 2. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera: 515–517. Nordsvamp, Copenhagen, Denmark.
Noordeloos ME, Gates GM. 2012. The Entolomataceae of Tasmania. Fungal Diversity Research Series 22: 1–400.
Ortega A, Vizoso MT, Contu M. 1991. Notes sobre la micoflora xero-termofila y sabulicola de Andalucia (primera parte). Documents Mycologiques 21(82): 19–42.
Overall A. 2011. Fungi royale. Some interesting larger fungi of the Royal Parks – Part 2 saprobes. Field Mycology 12(1): 26–30.
Ovrebo CL, Baroni TJ. 1988. Three new species of Rhodocybe from Costa Rica. Mycologia 80(4): 508–514.
Pacioni G, Lalli G. 1984a. Entità micologiche del Parco Nazionale del Circeo. Micologia Italiana 13(1): 77–81.
Pacioni G, Lalli G. 1984b. Novitates. Documents Mycologiques 14(56): 56.
Padovan F, Lorenzon L, Campo E, et al. 2020. 1260 funghi della Provincia di Belluno-Atlante fotografico. Associazione micologica "Bresadola", Gruppo di Belluno-APS. Rasai di Seren del Grappa, Belluno, Italy.
Pegler DN. 1977. A preliminary agaric flora of east Africa. Kew Bulletin Additional Series 6: 1–615.
Pérez-De-Gregorio MÀ, Vidal JM. 1994. Aportació al coneixement dels macromicets de l'illa de Mallorca 1. Butlletí de la Societat Catalana de Micologia 16–17: 145–164.
Pilát A. 1951. Klíč k Určování Našich Hub Hřibovitých a Bedlovitých [Agaricales Agaricalium Europaeorum Clavis Dichotomica], Brázda, Praha (Prague).
Pilát A. 1952. Rudocechratka tmavá – Rhodopaxillus obscurus Pilát 1951 je snad totožná s africkou rudocechratkou cernající – Rhodopaxillus nigrescens Maire 1945. Česká Mykologie 6(6–7): 94–97.
Pilát A. 1953. Hymenomycetes novi vel minus cogniti Cechoslovakiae. II. Acta Musei Nationalis Pragae (Sborník Národního Musea v Praze) 9B(2): 1–109.
Pluvinage D. 1993. Récoltes Fédérales. Espèces intéressantes signalées dans notre region. Bulletin Trimestriel de la Fédération Mycologique Dauphiné-Savoie 128: 8, 13–19.
Quélet L. 1886. Enchiridion Fungorum in Europa media et praesertim in Gallia Vigentium. O. Doin, Lutetiae.
Rehner SA, Buckley E. 2005. A Beauveria phylogeny inferred from nuclear ITS and EF1-a sequences: evidence for cryptic diversification and links to Cordyceps teleomorphs. Mycologia 97(1): 84–98.
Riousset G, Bon M. 1994. Découverte en France de Rhodocybe obscura (Pilát) Mos. Documents Mycologiques 23(92): 49–50.
Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19(12): 1572–1574.
Sánchez-García M, Matheny PB. 2017. Is the switch to an ectomycorrhizal state an evolutionary key innovation in mushroom-forming fungi? A case study in the Tricholomatineae (Agaricales). Evolution 71(1): 51–65.
Sánchez-García M, Ryberg M, Khan FK, et al. 2020. Fruiting body form, not nutritional mode, is the major driver of diversification in mushroom-forming fungi. Proceedings of the National Academy of Sciences (PNAS) USA 117(51): 32528–32534.
Silva-Filho AGS, Teixeira-Silva MA, Cortez VG. 2018. New species, new combination, and notes on Clitocella and Rhodocybe (Entolomataceae) from Paraná state, Brazil. Darwiniana, nueva serie 6(1): 58–67.
Singer R. 1950. Type studies on Basidiomycetes IV. Lilloa 23: 147–246.
Singer R. 1951 '1949'. The Agaricales in modern taxonomy. Lilloa 22: 1–832.
Singer R. 1962. The Agaricales in modern taxonomy, 2nd ed. Cramer, Weinheim.
Singer R. 1969. Mycoflora australis. Nova Hedwigia, Beihefte 29: 1–405.
Singer R. 1986. The Agaricales in modern taxonomy. 4th ed. Koeltz Scientific Books, Koenigstein, Germany.
Singer R, Digilio APL. 1952. Prodromo de la flora agaricina Argentina. Lilloa 25: 1–462.
Spegazzini C. 1918. Reliquiae mycologicae tropicae. Boletín de la Academia Nacional de Ciencias en Córdoba 23(3–4): 365–541.
Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313.
Tabarés M. 1988. Rhodocybe ammophila (Malençon) Pacioni et Lalli, Làmina 343. Bolets de Catalunya vol. 7. Édit. Societat Catalana de Micologia, Barcelona, Spain.
Talavera G, Castresana J. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Systematic Biology 56(4): 564–577.
Tamura K, Stecher G, Peterson D, et al. 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. Molecular Biology and Evolution 30: 2725–2729.
Turland NJ, Wiersema JH, Barrie FR, et al. (eds). 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten, Germany.
Vila J. 2000. Rhodocybe fallax (Quélet) Singer, Làmina 944. Bolets de Catalunya vol. 19. Édit. Societat Catalana de Micologia, Barcelona.
Vila J, Contu M, Caballero F, et al. 2007a. Sinopsis del gènero Rhodocybe (Secc. Rhodocybe) en Europa y descripcion de R. formosa sp. nov. Boletín de la Sociedad Micológica de Madrid 31: 77–84.
Vila J, Contu M, Caballero F, et al. 2009. Nuevos datos sobre el género Clitopilus (incl. Rhodocybe) en la península Ibérica e Islas Canarias. Bollettino dell'Associazione Micologica ed Ecologica Romana 25(77–78): 3–14.
Vila J, Contu M, Ortega A, et al. 2007b. Appunti sul Genere Rhodocybe in Catalogna (Penisola Iberica) – (2° contributo). Rivista di Micologia 50(4): 291–311.
Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of Bacteriology 172: 4238–4246.
Vizzini A, Baroni TJ, Sesli E, et al. 2016. Rhodocybe tugrulii (Agaricales, Entolomataceae), a new species from Turkey and Estonia based on morphological and molecular data, and a new combination in Clitocella (Entolomataceae). Phytotaxa 267(1): 1–15.
Vizzini A, Ferrari RJ, Ercole E, et al. 2018. A new species of Rhodocybe sect. Rufobrunnea (Entolomataceae, Agaricales) from Italy. MycoKeys 10(36): 21–33.
White TJ, Bruns TD, Lee S, et al. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand D, Sninsky J, et al. (eds), PCR Protocols: a guide to methods and applications: 315–322. Academic Press, San Diego, USA.
Wilhelm M. 1992. Rhodocybe popinalis (Fr.) Sing. (= Rhodocybe mundula (Lasch: Fr.) Sing.?). Schweizerische Zeitschrift für Pilzkunde 1992(9–10): 193–198.

Appendix Basidiomes of *Clitocella blancii*. France, Piriac-sur-Mer, among litter of *Thuja*, 11 Nov. 2013, Y. Deneyer. — Photo by Y. Deneyer.