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Stop black and white thinking: *Russula* subgenus *Compactae* (*Russulaceae*, *Russulales*) in Europe revised

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Abstract *Russula* subgenus *Compactae* is a group of ectomycorrhizal basidiomycetes, usually with large pileate fruitbodies. European members of the group are characterised by the absence of bright colours on the surfaces of their pilei, the context turning grey to black after cutting, the abundance of short lamellulae in the hymenophore, and spores with an inamyloid suprahilar spot and with low reticulate ornamentation. Our multi-locus phylogenetic study confirmed that this morphological delimitation corresponds to a well-supported clade. Within this clade, 16 species are recognised in Europe, of which five belong to the *R. albonigra* lineage and were described in a previous study, while eleven are fully described in this study. The application of the names *R. acrifolia*, *R. adusta*, *R. anthracina*, *R. atramentosa*, *R. densissima*, *R. nigricans* and *R. roseonigra* is based on the position of sequences retrieved from types or authentic material. Based on type sequences, *R. fuliginosa* is synonymised with *R. anthracina* and two varieties of *R. anthracina* are considered synonyms of *R. atramentosa*. The application of the name *R. densifolia* is based on a morphological match with the traditional species interpretation and the neotype specimen. Three species are described as new, *R. marxmuelleriana* sp. nov., *R. picrophylla* sp. nov. and *R. thuringiaca* sp. nov. This study recognises three major lineages and two species with isolated positions within the European *Compactae* and a morphological barcode was assigned to the species using an analysis of 23 selected characters. A search of publicly available sequences from the UNITE database revealed that the majority of species are host tree generalists and widely distributed in temperate and Mediterranean areas of Europe. *Russula adusta* is the only species so far proven to form ectomycorrhiza exclusively with conifers.

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INTRODUCTION

The genus *Russula* is a large genus of ectomycorrhizal fungi with a worldwide distribution (Buyck et al. 2018, Looney et al. 2018). Species within this genus are characterised by their white or pale stipe and lamellae, often contrasting with the brightly coloured pileus, their brittle flesh due to the context composed of sphaerocytes (i.e., globose cells), and their spores with amyloid ornamentation (Romagnesi 1967, Sarnari 1998, Buyck et al. 2008). *Russula* species make a significant contribution to the fungal biomass (Tedersoo et al. 2010) and are important components in many ecosystems as ectomycorrhizal symbionts (Singer 1986, Buyck et al. 1996, Twieg et al. 2007, Geml et al. 2009, Liao et al. 2014) and as dietary elements for small invertebrates and larger animals (Fogel & Trappe 1978, Keller & Snell 2002). Furthermore, many species are harvested for human consumption (Buyck 2008, Marley 2010, Dugan 2011, Perez-Moreno et al. 2021). The taxonomic history of the genus is rich, and includes several European monographs devoted to this genus (for a chronological overview see Romagnesi 1967 and Sarnari 1998).

The majority of *Russula* members with an absence of bright colours but dominance of black, brown, grey and white tinges; with frequent lamellulae in the hymenophore; and often large and compact basidiomata were traditionally grouped into *Russula* subg. *Compactae* (Romagnesi 1967, Sarnari 1998). Since the introduction of DNA sequencing, multiple phylogenetic studies showed that the traditional morphological concept of *R.* subg. *Compactae* refers to a polyphyletic group (Miller & Buyck 2002, Looney et al. 2016, Buyck et al. 2018). Part of the subgenus in its traditional circumscription, namely *R.* subsection *Ochricompactae*, is currently considered to belong to the genus *Multifurca*, which comprises both former *Lactarius* and *Russula* species (Buyck et al. 2008). The remaining species formerly included in the subgenus based on morphology are now classified into five subgenera: 1) *R.* subg. *Compactae*; 2) *R.* subg. *Malodorae*; 3) *R.* subg. *Brevipedum*; 4) *R.* subg. *Archaeae*; and 5) the recently described *R.* subg. *Glutinosae* (Buyck et al. 2018, 2020). Out of these five subgenera, *R.* subg. *Malodorae* and *R.* subg. *Glutinosae* are not reported from Europe (Buyck et al. 2018, 2020). The relation among these subgenera is not yet clear, as various recently published phylogenies of the genus *Russula* show different topologies (see

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Buyck et al. 2018 for an overview). However, several of these studies suggest *R*. subg. *Compactae* is sister to *R*. subg. *Archaeae*, and *R*. subg. *Glutinosae* is a sister to both of them and the most primitive group of the genus *Russula* (Looney et al. 2016, Buyck et al. 2018, 2020).

Species within *R*. subg. *Compactae* s.str. (Buyck et al. 2018) are macroscopically characterised by thick-fleshed basidiomata with dull-coloured (i.e., white, brown, grey to black) pilei, lamellulae arranged in a regular pattern and a context that is typically blackening, possibly with intermediate reddening, rarely browning or without colour change. Microscopically, they have spores with an inamyloid suprahilar spot. When present, hymenial cystidia are mostly minutely capitate with one central knob, while pileocystidia often have two eccentric terminal knobs (Buyck et al. 2018). The subgenus includes some well-known species already described in the classical European literature on mycology, such as *R. nigricans* and *R. adusta*. This rather dull-coloured group of species, however, did not attract the attention to the same extent as other 'colourful groups' (Buyck & Adamčík 2013) and only fourteen species (and some varieties and forms) have been described within this subgenus in Europe (Romagnesi 1967, 1985, Reumaux et al. 1996, Sarnari 1998, Pidlich-Aigner 2015, De Lange et al. 2021). All European representatives of the subgenus are classified within *R*. section *Nigricantinae* (Buyck et al. 2018). So far there is only a single phylogenetic study on the European species of the section, limited to the *R. albonigra* lineage (De Lange et al. 2021), which recognised four more new species in this species complex and suggests a higher diversity of the subgenus in Europe due to the possible presence of multiple species complexes. In the present study, we use sequence data of four DNA markers and detailed morphological observations to test the taxonomic status of the remaining European species within *R*. subg. *Compactae*.

MATERIAL AND METHODS

Sampling

This study includes the data from De Lange et al. (2021) and collections from Austria (1), Belgium (20), Czech Republic (1), France (15), Germany (21), Italy (10), Slovakia (8), Spain (3) and Sweden (24). The collections are deposited in the Herbarium Universitatis Gandavensis (GENT) or were requested from the University of Innsbruck (IB), the Muséum National d'Histoire Naturelle de Paris (PC), the Institute of Botany, Slovak Academy of Sciences (SAV), the University of Vienna (WU) and from the personal collections of Felix Hampe & Jochen Girwert (FH), Jesko Kleine (JK) (duplicates stored in GENT) and Helga Marxmüller (MxM) – the latter now deposited in the State Museum of Natural History Karlsruhe (KR). Some additional collections (GENT) from outside Europe were included due to the lack of relevant sequence data from other continents (Table 1).

Morphological analysis

The macroscopic descriptions are based on observations from fresh material, with terminology following Vellinga (1988), colour codes referring to Kornerup & Wanscher (1978), guaiac reactions referring to Chalange (2014), and spore print colour codes referring to the scale of Romagnesi (1967). Lamellae density is noted as L+l, with L referring to lamellae and l referring to lamellulae. The microscopic description and terminology follow Adamčík et al. (2019). Microscopic characters were studied from dried material, spores were observed in Melzer's reagent, elements of the hymenium and pileipellis were observed in a 1 % solution of Congo red in modified L4 (Clémençon 1972) by replacing Invadin IFC with SDS (Sodium dodecyl sulfate) after c. 10 s pre-treatment in KOH 10 %. Basidiospores were observed at magnification of 1000× under a Nikon Eclipse Ni-U microscope with Nikon DsFi3 camera and measured using computer software (Nikon Nis Elements). Measurements of spore ornamentation, and line drawings of spores were made based on stacked photographs (Extended Depth of Field, Nikon Nis Elements module) at an original magnification of 5000×. Measurements of other elements were made using an eyepiece micrometer (at magnification of 1000×) and line drawings (at original magnifications of 1500×) were prepared with the aid of a camera lucida (Olympus U-DA) on an Olympus CX21 microscope. The microscopic descriptions are based on at least three collections where available. The total number of measurements is at least 40, except for less abundant elements (i.e., pileocystidia) where the total number of measurements is at least 20 (unless rare than the exact number is noted in the description). Tissues were mounted in Cresyl Blue (Buyck 1989) and sulfovanillin (Caboň et al. 2017) to observe colour changes of cystidium contents; mounted in carbolfuchsin (Romagnesi 1967) and further treated with HCl (10 %) to observe the presence of incrustations. All cited collections in the species descriptions have been sequenced, at least for the ITS nrDNA region.

Molecular analysis

DNA extraction and amplification was performed at the Centre for Molecular Phylogeny and Evolution (CeMoFE) of Ghent University or at the Slovak Academy of Sciences. DNA from fresh material was extracted using the CTAB extraction described in Nuytinck & Verbeken (2003). DNA from dried material was extracted using a modified CTAB protocol (Tel-zur et al. 1999; for modification see De Lange et al. 2021) or using the EZNA Fungal DNA Mini Kit (Omega Bio-Tek Inc., Norcross, GA, USA) following the manufacturer's instructions. Protocols for PCR amplification follow Le et al. (2007) or Caboň et al. (2017). Four nuclear markers were amplified: 1) the internal transcribed spacer region of ribosomal DNA (ITS), comprising the ITS1 and ITS2 spacer regions and the ribosomal gene 5.8S, using primers ITS1-F and ITS4 (White et al. 1990, Gardes & Bruns 1993); 2) a part of the ribosomal large subunit 28S region (LSU), using primers LR0R and LR5 (Moncalvo et al. 2000); 3) the region between the conserved domains 6 and 7 of the second largest subunit of the RNA polymerase II (*RPB2*), using primers bRPB2-6F and fRPB2-7cR or bRPB2-7.1R (Liu et al. 1999, Matheny 2005); and 4) the translation elongation factor 1-alpha (*EF-1α*), using primer pairs EF1-1018F and EF1-1620R or tef1F and tef1R (Morehouse et al. 2003, Stielow et al. 2015). PCR products were either directly sequenced at Macrogen Europe (Amsterdam, the Netherlands) or at the Seqme company (Dobříš, Czech Republic), or first purified using the Qiaquick PCR Purification Kit (Qiagen, Hilden, Germany). Forward and reverse sequences were assembled into contigs and edited where needed with BioloMICS (BioAware SA NV, Hannut, Belgium). All generated sequences were deposited in GenBank (www.ncbi.nlm.nih.gov) (Table 1).

Dataset construction

The dataset contains sequences either generated by the authors of this study or retrieved from public databases. To increase global taxon sampling, sequences found through name search and BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) were included. Only samples with at least one protein-coding gene sequence available (*RPB2* or *EF-1α*) were included in the multi-locus dataset. To estimate spatial distribution and host tree preference of the studied taxa, we analysed relevant metadata from publicly available barcode ITS sequences deposited in UNITE (https://unite.ut.ee/) (see summarised information on UNITE species hypotheses (SHs) in Fig. S1) as a separate

Table 1 Specimens and GenBank accession numbers of DNA sequences generated in this study or used in the multi-locus phylogenetic analysis.

Taxon	Voucher collection (herbarium)	Country	ITS	LSU	*RPB2*	*EF-1α*
Russula acrifolia	2018 ST01 (GENT)	Sweden	OM833115	OM860227	ON148365	ON015985
	FH 2014 ST03 (GENT, FH*)	Germany	OM833110	OM860222	ON148360	ON015980
	LD 16-022 (GENT)	Sweden	MW172319°	MW182479°	MW306683°	MW273325°
	MxM R-010115 (KR)	France	OM833108	–	–	–
	PC0728045 (PC)	France	OM833109	–	–	–
	RDL 18-012 (GENT)	Sweden	MW172320°	MW182480°	MW306684°	MW273326°
	RDL 18-013 (GENT)	Sweden	OM833111	OM860223	ON148361	ON015981
	RDL 18-017 (GENT)	Sweden	OM833112	OM860224	ON148362	ON015982
	RDL 18-021 (GENT)	Sweden	MW172321°	MW182481°	ON148359	MW273327°
	RDL 18-037 (GENT)	Sweden	OM833113	OM860225	ON148363	ON015983
	RDL 18-040 (GENT)	Sweden	OM833116	OM860228	ON148366	ON015986
	RDL 18-045 (GENT)	Sweden	OM833114	OM860226	ON148364	ON015984
Russula aff. *acrifolia*	r-05065	United States	JF834363°	JF834510°	JF834460°	–
	r-07018	United States	JF834370°	JF834515°	JF834465°	–
Russula adusta	LD 16-025 (GENT)	Sweden	MW172316°	–	MW306682°	MW273322°
	LD 16-029 (GENT)	Sweden	OM833064	–	–	–
	PC0728042 (PC)	France	OM833065	–	–	–
	RDL 18-014 (GENT)	Sweden	OM833066	–	–	–
	RDL 18-015 (GENT)	Sweden	OM833067	–	–	–
	RDL 18-016 (GENT)	Sweden	OM833068	–	–	–
	RDL 18-020 (GENT)	Sweden	MW172317°	MW182477°	–	MW273323°
	RDL 18-024 (GENT)	Sweden	OM833069	–	–	ON015963
	RDL 18-025 (GENT)	Sweden	OM833077	–	–	–
	RDL 18-028 (GENT)	Sweden	MW172318°	MW182478°	–	MW273324°
	RDL 18-030 (GENT)	Sweden	OM833078	OM860204	–	ON015964
	RDL 18-031 (GENT)	Sweden	OM833071	–	–	–
	RDL 18-033 (GENT)	Sweden	OM833072	–	–	–
	RDL 18-034 (GENT)	Sweden	OM833073	–	–	–
	RDL 18-035 (GENT)	Sweden	OM833074	–	–	–
	RDL 18-039 (GENT)	Sweden	OM833079	–	–	ON015965
	RDL 18-048 (GENT)	Sweden	OM833075	–	–	–
	Rom. 58-431 (PC)	France	OM833076	–	–	–
Russula albonigra	JK RUS 13090603 (JK*)	Germany	MW172296°	MW182461°	MW306670°	–
	SAV-F 20177 (SAV)	Slovakia	MW172298°	MW182463°	MW306672°	MW273311°
	SAV-F 20197 (SAV)	Slovakia	MW172299°	MW182464°	MW306673°	MW273312°
	SAV F-3220 (SAV)	Belgium	OM833121	–	–	–
	SAV-F 3465 (SAV)	Slovakia	MW172293°	MW182460°	MW306669°	MW273309°
	SAV-F 4776 (SAV)	Slovakia	MW172297°	MW182462°	MW306671°	MW273310°
Russula aff. *albonigra*	r-04105	United States	JF834355°	JF834503°	JF834452°	–
	r-05068	United States	JF834364°	JF834521°	JF834461°	–
Russula ambusta	FH 2008 ST01 (GENT, FH*)	Germany	MW172300°	MW182465°	–	–
	SAV-F 3358 (SAV)	Slovakia	MW172301°	MW182466°	–	–
Russula anthracina (type of *R. fuliginosa*)	**IB92/454 (IB)**	Italy	HG798529°	–	–	–
Russula anthracina	FH RUS 14091001 (GENT)	Slovakia	MW172330°	MW182487°	MW306693°	MW273333°
	FH RUS 14091201 (GENT, JK*)	Slovakia	MW172331°	MW182488°	MW306694°	MW273334°
	Rom. 56-62 (PC)	France	OM833169	–	–	–
Russula archaeosuberis	BB 12.085 (PC)	Italy	KY800355°	KU237593°	KU237878°	KU238019°
	RDL 16-055 (GENT)	Italy	OM833177	OM860252	ON148391	ON016012
Russula ashihoi	KD 18-002 (CAL)	India	MT893201°	–	–	–
	KD 18-023 (CAL)	India	MT893202°	–	–	–
Russula atramentosa	FH0170824-02 (GENT, FH*)	Germany	MW172324°	MW182483°	MW306687°	MW273329°
	FH 2010 ST03 (GENT, FH*)	Germany	OM833140	–	–	–
	FH 2011-002R (GENT, FH*)	Belgium	MW172322°	MW182482°	MW306685°	MW273328°
	FH 21-004 (FH*)	Germany	OM833149	–	–	–
	IB91/58 (IB)	Italy	OM833146	–	–	–
	JK RUS 14091101 (JK*)	Slovakia	OM833139	–	–	–
	PC0735191 (PC)	France	OM833142	–	–	–
	RDL 16-050 (GENT)	Italy	MW172323°	–	MW306686°	–
	RDL 16-065 (GENT)	Italy	OM833141	–	–	ON016000
Russula atramentosa (invalid type of *R. anthracina* var. *carneifolia*)	Rom. 53-86 (PC)	France	OM833144	–	–	–
Russula atramentosa	Rom. 57-102 (PC)	France	OM833143	–	–	–
Russula atramentosa (invalid type of *R. anthracina* var. *insipida*)	Rom. 57-64 (PC)	France	OM833145	–	–	–
Russula atramentosa	JK RUS 16111003 (GENT, JK*)	Italy	OM833138	–	–	–
	SAV F-1810 (SAV)	Slovakia	OM833148	–	–	–
	SAV F-4236 (SAV)	Slovakia	OM833147	–	–	–
Russula camarophylla	MPG11-7-09 (PC)	Spain	KY800353°	KU237579°	KU237865°	KU238006°
Russula cantharellicola	**UC1999420**	United States	KF306036°	–	–	–
Russula cortinarioides	BB 07.103 (PC)	United States	KP033480°	KP033491°	KP033502°	KU237985°
	BB 07.104 (PC)	United States	KP033482°	KP033493°	KP033504°	–
	BB 07.111 (PC)	United States	KP033483°	KP033494°	KP033505°	–
	BB 07.131 (PC)	United States	KP033484°	KP033495°	KP033506°	–
	BB 07.133 (PC)	United States	KP033485°	–	KP033507°	–
Russula densifolia	FH 2006 ST02 (GENT, FH*)	Germany	OM833156	–	–	–
	FH 2006 ST03 (GENT, FH*)	Germany	OM833155	–	–	–

Table 1 (cont.)

Taxon	Voucher collection (herbarium)	Country	ITS	LSU	*RPB2*	*EF-1α*
Russula densifolia (cont.)	FH 2014 ST05 (GENT, FH*)	Germany	OM833162	–	–	–
	FH 2014 ST06 (GENT, FH*)	Germany	OM833154	–	–	–
	FH RUS 14091103 (GENT, FH*)	Slovakia	OM833153	–	–	–
	FH RUS 15101001 (GENT, FH*)	Germany	OM833163	–	–	–
	FH RUS 15101002 (GENT, FH*)	Germany	OM833157	–	–	–
	MxM R-9407/KR-M-0070924 (KR)	France	OM833151	–	–	–
	RDL-15-23-08-2014 (GENT)	Belgium	OM833152	OM860231	ON148380	ON016001
	RDL 16-001/2 (GENT)	Belgium	MW172325°	MW182484°	MW306688°	MW273330°
	RDL 17-014 (GENT)	Belgium	OM833164	–	–	–
	RDL 17-020 (GENT)	Belgium	OM833159	OM860233	ON148382	ON016003
	RDL 17-023 (GENT)	Belgium	OM833158	OM860232	ON148381	ON016002
	RDL 17-024 (GENT)	Belgium	MW172327°	MW182486°	MW306690°	MW273332°
	RDL 18-052 (GENT)	Belgium	MW172326°	MW182485°	MW306689°	MW273331°
	Rom. 63-131 (PC)	France	OM833160	–	–	–
	Rom. 71-150 (PC)	France	OM833161	–	–	–
	SAV F-3162 (SAV)	Slovakia	OM833165	–	–	–
	SAV F-3372 (SAV)	Slovakia	OM833166	–	–	–
	SAV F-3386 (SAV)	Slovakia	OM833167	–	–	–
Russula densissima	FH 2014 ST04 (GENT, FH*)	Germany	MW172328°	–	MW306691°	–
	FH 2010 ST02 (GENT, FH*)	Germany	MW172329°	–	MW306692°	–
	Rom. 73-131 (PC)	France	OM833150	–	–	–
Russula cf. *dissimulans*	TENN:070021 (TENN)	United States	KT933979°	KT933840°	KT933911°	–
Russula cf. *eccentrica*	BB 07.044 (PC)	United States	KP033479°	KP033490°	KP033501°	KU237937°
	BB 07.132 (PC)	United States	KP033478°	KP033489°	KP033500°	KU237926°
Russula cf. *fistulosa*	EDC 14-073 (GENT)	Zambia	OM833171	OM860237	ON148385	ON016006
Russula cf. *fistulosa* var. *grata*	BB 06.089 (PC)	Madagascar	KP033477°	KP033488°	KP033499°	–
Russula aff. *fistulosa*	AV 18-052 (GENT)	Guinea	OM833173	OM860250	ON148387	ON016008
Russula fortunae	**Corrales180 (TUC)**	Panama	KM594806°	–	–	–
	Ovrebo5504 (TUC)	Panama	MN130087°	–	–	–
Russula gossypina	BB 06.002 (PC)	Madagascar	KY800350°	KU237450°	KU237736°	KU237886°
Russula indonigra	**AG 15-873 (CAL)**	India	MT889672°	–	–	–
	AG 16-1335 (CAL)	India	MT889670°	–	–	–
Russula khanchanjungae	**AV KD KVP 09-106 (GENT)**	India	KR364129°	JN389004°	JN375607°	–
Russula lateriticola	BB 06.031 (PC)	Madagascar	KP033476°	KP033487°	KP033498°	KU237888°
Russula latolamellata	**GDGM 79561 (GDGM)**	China	MN275543°	–	MK880660°	MT085574°
	GDGM 79562 (GDGM)	China	MN275544°	–	–	–
	GDGM 79563 (GDGM)	China	MN275545°	MN839557°	MT085632°	MT085604°
Russula marxmuelleriana	FH 2009 ST02 (GENT, FH*)	Germany	OM833119	OM860229	–	–
	RDL 17-009 (GENT)	Belgium	OM833120	OM860230	ON148369	ON015988
Russula nigricans	FH 20-066 (GENT, FH*)	Germany	OM833136	–	–	–
	RDL 16-002 (GENT)	Belgium	OM833122	OM860240	ON148370	ON015989
	RDL 16-004/1 (GENT)	Belgium	OM833123	–	ON148371	ON015990
	RDL 16-005 (GENT)	Belgium	OM833124	OM860241	ON148372	ON015991
	RDL 16-007 (GENT)	Belgium	OM833129	–	–	–
	RDL 16-009 (GENT)	Belgium	OM833130	–	–	–
	RDL 16-011 (GENT)	Belgium	OM833128	–	–	–
	RDL 16-069 (GENT)	Italy	OM833125	–	–	–
	RDL 17-001 (GENT)	Belgium	OM833127	OM860243	ON148374	ON015993
	RDL 17-002 (GENT)	Belgium	OM833131	OM860244	ON148375	ON015994
	RDL 17-003 (GENT)	Belgium	OM833132	OM860245	ON148376	ON015995
	RDL 17-004 (GENT)	Belgium	MW172332°	MW182489°	MW306695°	MW273335°
	RDL 17-005 (GENT)	Belgium	MW172333°	MW182490°	MW306696°	MW273336°
	RDL 17-007 (GENT)	Belgium	MW172334°	MW182491°	MW306697°	MW273337°
	RDL 17-008 (GENT)	Belgium	OM833133	OM860246	ON148377	ON015996
	RDL 18-050 (GENT)	Belgium	OM833134	–	–	ON015997
	RDL 18-051 (GENT)	Belgium	OM833135	OM860247	ON148378	ON015998
	RDL 18-061 (GENT)	Belgium	OM833126	OM860242	ON148373	ON015992
Russula aff. *nigricans*	r-01003	United States	JF834331°	JF834479°	JF834428°	–
	UBC:F30152 (UBC)	Canada	KX812835°	KX812859°	KX813643°	–
Russula nigrifacta	RDL 16-028 (GENT)	Italy	MW172307°	–	MW306676°	MW273316°
	RDL 16-044 (GENT)	Italy	MW172308°	MW182470°	MW306677°	MW273317°
	RDL 16-063 (GENT)	Italy	MW172306°	–	–	MW273315°
	SAV-F 1501 (SAV)	Slovakia	MW172302°	MW182467°	MW306674°	MW273314°
	SAV-F 3006 (SAV)	Slovakia	MW172305°	MW182469°	MW306675°	–
Russula nigrocarpa	**GDGM 79720 (GDGM)**	China	MN688794°	MN839585°	MT085662°	MT085630°
	GDGM 79721 (GDGM)	China	MN688795°	–	–	–
Russula ochrobrunnea	**GDGM 79718 (GDGM)**	China	MN688792°	MN839584°	MT085661°	MT085629°
	GDGM 79719 (GDGM)	China	MN688793°	–	–	–
Russula picrophylla	2018 ST02 (GENT)	Sweden	OM833101	OM860217	ON148356	ON015978
	FH 2005 ST02 (GENT, FH*)	Germany	OM833103	–	–	–
	FH 2008 ST03 (GENT, FH*)	Germany	OM833092	OM860219	–	–
	FH RUS 14081335 (GENT, FH*)	Germany	OM833091	–	–	–
	JK RUS 13090806 (JK*)	Germany	OM833089	OM860208	ON148347	ON015969
	LD 16-026 (GENT)	Sweden	OM833087	–	–	–
	LD 16-027 (GENT)	Sweden	OM833088	–	ON148346	ON015968
	MxM R-01091994/KR-M-0071291 (KR)	France	OM833090	–	–	–
	MxM R-9154/KR-M-0071292 (KR)	France	OM833105	–	–	–

Table 1 (cont.)

Taxon	Voucher collection (herbarium)	Country	ITS	LSU	*RPB2*	*EF-1α*
Russula picrophylla (cont.)	RDL 16-027 (GENT)	Italy	OM833093	OM860209	ON148348	ON015970
	RDL 16-031 (GENT)	Italy	MW172313°	MW182474°	MW306679°	MW273319°
	RDL 16-034 (GENT)	Italy	OM833094	OM860210	ON148349	ON015971
	RDL 16-049 (GENT)	Italy	OM833095	OM860211	ON148350	ON015972
	RDL 16-056 (GENT)	Italy	OM833096	OM860212	ON148351	ON015973
	RDL 16-057 (GENT)	Italy	OM833097	OM860213	ON148352	ON015974
	RDL 16-058 (GENT)	Italy	MW172314°	MW182475°	MW306680°	MW273320°
	RDL 18-026 (GENT)	Sweden	MW172315°	MW182476°	MW306681°	MW273321°
	RDL 18-029 (GENT)	Sweden	OM833102	OM860218	ON148357	ON015979
	RDL 18-049 (GENT)	Sweden	OM833098	OM860214	ON148353	ON015975
	RUS 18111501 (JK*)	Spain	OM833099	OM860215	ON148354	ON015976
	RUS 18111502 (JK*)	Spain	OM833100	OM860216	ON148355	ON015977
	SAV F-3234 (SAV)	Spain	OM833104	–	–	–
Russula cf. *polyphylla*	BB 07.134 (PC)	United States	KP033486°	KP033497°	KP033508°	KU238023°
	BB 07.023 (PC)	United States	KP03348°	KP033492°	KP033503°	KU237986°
Russula roseonigra	FH 2014 ST01 (GENT, FH*)	Germany	MW172336°	–	MW306698°	MW273338°
	FH RUS 14091311 (GENT, FH*)	Czech Republic	OM833106	–	–	–
	RDL 16-024 (GENT)	Italy	MW172337°	MW182492°	MW306699°	MW273339°
	WU36644 (WU)	Austria	OM833107	OM860220	ON148358	–
Russula sp.	AV 17-013 (GENT)	Mexico	OM833176	OM860238	ON148390	ON016011
	EDC 14-280 (GENT)	Cameroon	OM833175	OM860239	ON148389	ON016010
	EDC 14-390 (GENT)	Cameroon	OM833172	OM860249	ON148386	ON016007
	EDC 14-424 (GENT)	Togo	OM833174	OM860251	ON148388	ON016009
	FH 12-064 (GENT, FH*)	Thailand	MN130076°	–	MN380517°	–
	FH 18-057 (GENT, FH*)	Panama	OM833117	OM860221	ON148367	ON015987
	FH 18-090 (GENT, FH*)	Panama	OM833168	OM860234	ON148383	ON016004
	FH 18-092 (GENT, FH*)	Panama	OM833170	OM860235	ON148384	ON016005
	FH 18-119 (GENT, FH*)	Panama	OM833137	OM860248	ON148379	ON015999
	HMAS:267774 (HMAS)	China	KX441104 °	KX441351°	KX442092°	–
	HMAS:269796 (HMAS)	China	KX441169°	KX441416°	KX442157°	–
Russula sp. (as *R. albonigra*)	MCVE15300	Italy	JF908707°	–	–	–
Russula sp.	RITF3122	China	MH911600°	MH911611°	MH911626°	–
	RW 1625 (GENT)	Belgium	OM833118	OM860236	ON148368	–
Russula sp. 1	RW 1975 (GENT)	Italy	MW172309°	MW182471°	–	–
Russula thuringiaca	FH 19-032 (GENT, FH*)	Germany	OM833084	–	–	–
	FH 20-056 (GENT, FH*)	Germany	OM833085	–	–	–
	FH 2008 ST02 (GENT, FH*)	Germany	OM833083	–	–	–
	FH 2010 ST06 (GENT, FH*)	Germany	OM833082	OM860207	–	–
	FH 2011 ST01 (GENT, FH*)	Germany	OM833080	OM860205	–	ON015966
	FH 2014 ST02 (GENT)	Germany	OM833081	OM860206	ON148345	ON015967
	SAV F-3359 (SAV)	Slovakia	OM833086	–	–	–
Russula ustulata	**AV 16-019 (GENT)**	Norway	MW172312°	MW182473°	MW306678°	MW273318°
	SAV 2610 (SAV)	Italy	MW172310°	MW182472°	–	–
	PRM 924452 (PRM)	Czech Republic	MW172311°	–	–	–

In **bold**: types; * personal herbarium; ° sequences not generated in this study

dataset. After an initial analysis of all found sequences, those of compromised quality were omitted from the dataset and the maximum number of sequences representing the same molecular operational taxonomic unit (MOTU) was reduced to six. We used the following strategy to add UNITE sequences to the dataset. Name searches were performed on each distance threshold to find corresponding SHs, and for each of these SHs at a < 3 % threshold the 3 % SH it is included in was determined. Each different 3 % SH was then tracked for all included SHs at lower levels until < 0.5 %. The representative sequences of all these < 0.5 % SHs were included in the dataset. A similar approach was performed based on the best blastn (https://unite.ut.ee/analysis.php) hits of selected representative haplotypes of each species recognised in our multi-locus analysis to ensure that corresponding SHs without an attached name were included. Among the SHs matching our species concepts, we selected sequences provided by metadata on hosts (from ectomycorrhizal root tips) and distribution.

Phylogenetic analysis

Four samples of species in *R.* subg. *Archaeae* were used as an outgroup, because the recent phylogenies of the genus place this subgenus as sister to *R.* subg. *Compactae* (Buyck et al. 2020).

Sequences were aligned using the online version of the multiple sequence alignment program MAFFT v. 7 (Katoh & Toh 2008), using the E-INS-i strategy. Trailing ends of the alignments were trimmed and the alignments were, when necessary, manually edited in MEGA7 (Kumar et al. 2016). The alignments can be obtained from the Open Science Framework (https://doi.org/10.17605/OSF.IO/8UD3F). The alignments were partitioned into following partitions: ITS (-LSU)-alignment: ITS1, 5.8S, ITS2, (LSU); *RPB2*-alignment: the *RPB2* intron and the first, second and third codon positions of the exon; *EF-1α*-alignment: the first and second intron and the first, second and third codon positions. PartitionFinder2 was used to find the appropriate partitioning scheme and substitution models using the Akaike information criterion (AICc) with a greedy search over all models (Guindon et al. 2010, Lanfear et al. 2012, 2017). Maximum likelihood (ML) analyses were conducted with IQ-Tree v. 1.6.12 (Nguyen et al. 2015, Chernomor et al. 2016) using standard bootstrapping analysis (1 000 replicates). Bayesian inference (BI) was executed with MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). Two independent parallel runs of one cold and three heated chains were run for ten million (single-locus datasets) or twenty million generations (multi-locus dataset) with a sample frequency of 100. Potential Scale Reduction Factor (PSRF) values approached 1.0. Convergence and Effective Sample Size (ESS) statistics of the runs

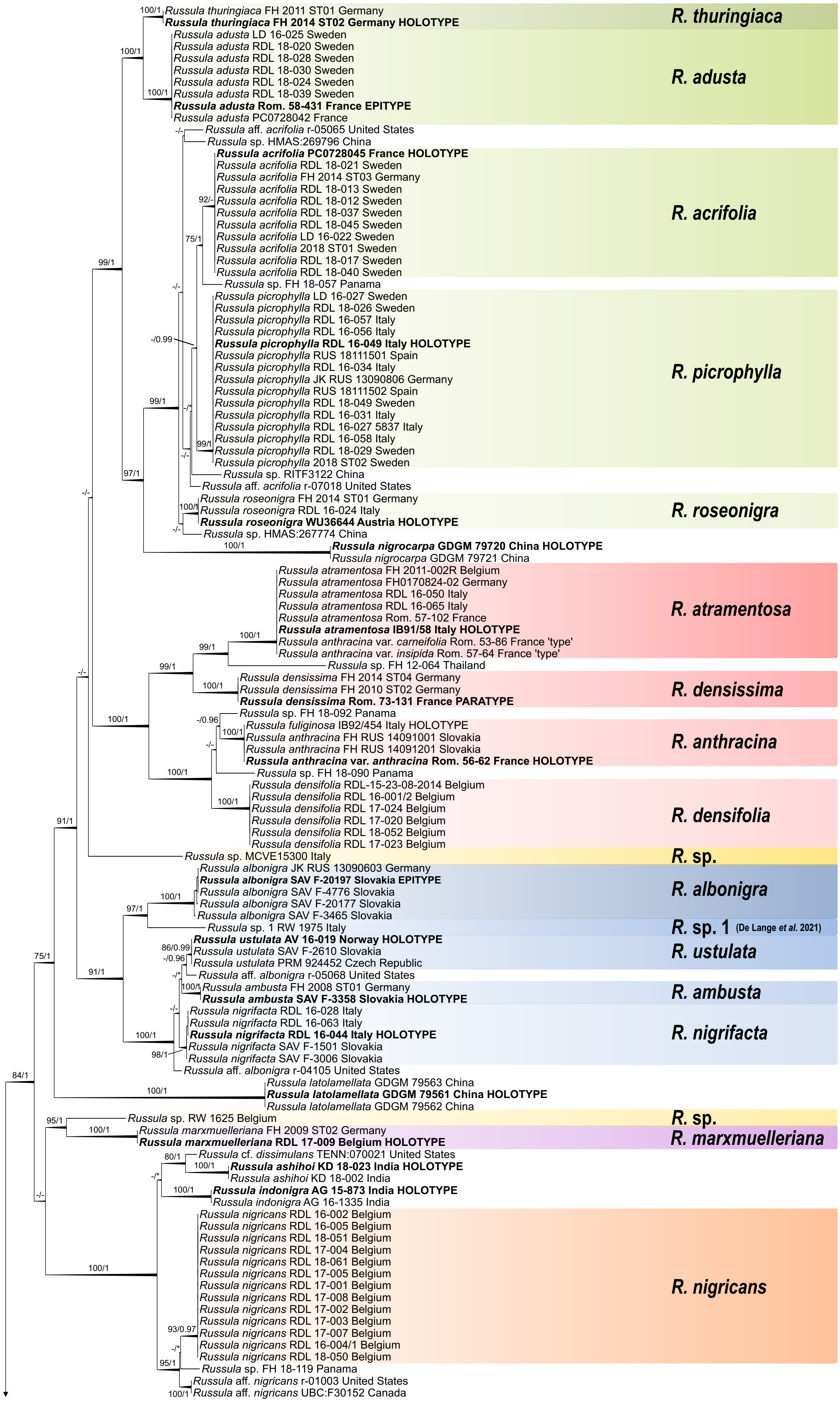

Fig. 1 Maximum Likelihood (ML) tree of *Russula* subg. *Compactae*, based on concatenated ITS, LSU, *RPB2* and *EF-1α* sequence data. ML bootstrap values ≥ 75 and BI posterior probabilities ≥ 0.95 are shown; * missing branch.

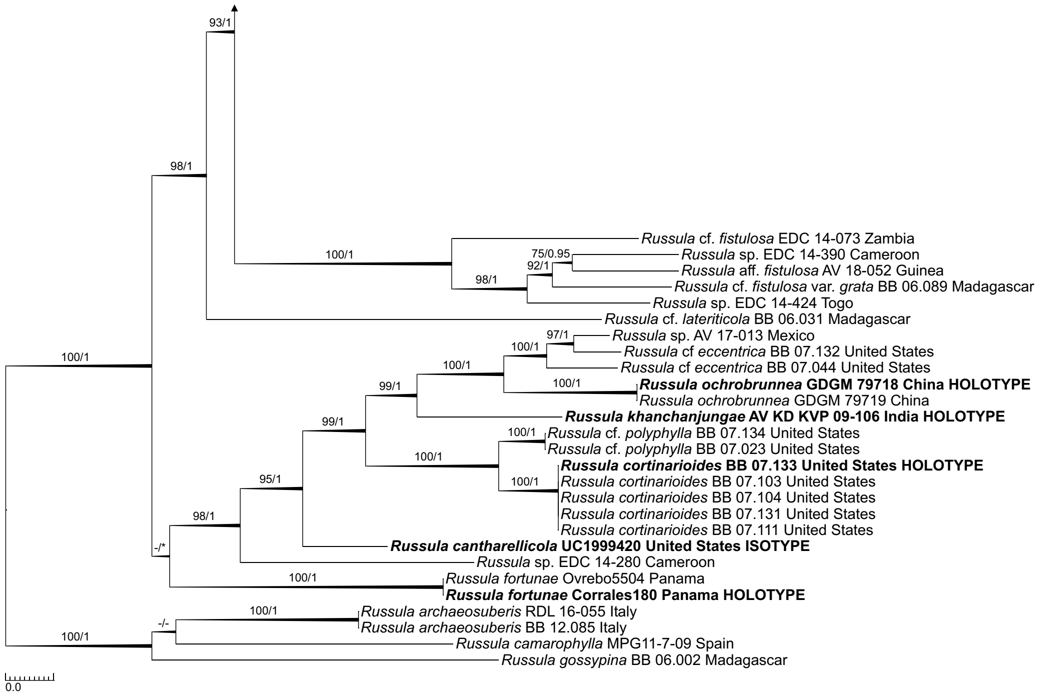

Fig. 1 (cont.)

were also examined with Tracer v. 1.7.1 (Rambaut et al. 2018). A burn-in sample of 20 % was excluded before constructing the majority rule consensus tree. Prior to the multi-locus analysis, analyses were performed on each alignment separately and visually checked for incongruence. Significant incongruence was assumed if two different relationships (one monophyletic and the other non-monophyletic) for any set of taxa were supported with bootstrap values (BS) ≥ 70 or posterior probabilities (PP) ≥ 90. The resulting gene trees did not show any supported conflicts, therefore all alignments could be concatenated for the multi-locus phylogenetic analyses.

Coalescent species delimitation approaches

For species delimitation under the multispecies coalescent model, a part of the multi-locus dataset, comprising only the European members of *R.* subg. *Compactae*, was used. A total of 18 potential species units (as proposed by the ML and BI trees) were evaluated as the full model. Two coalescent species delimitation methods were performed to test these species hypotheses. The specific parameter settings for both analyses follow De Lange et al. (2021). The first method was implemented in Bayesian Phylogenetics and Phylogeography, BP&P v. 4.3.8 (Yang 2015). We performed analysis A11 (Yang & Rannala 2014) for unguided species delimitation using rjMCMC algorithm 0 (Yang & Rannala 2010). As a second species delimitation method we used the STACEY v. 1.2.5 (Jones 2017) package implemented in BEAST2 (Bouckaert et al. 2019). The xml-file for the BEAST2 runs were prepared in BEAUTi v. 2.6.3 (Drummond et al. 2012). We used following partitions: for the nrDNA 1) 5.8S; 2) ITS1 + ITS2; and 3) LSU; for the protein coding loci the introns and the first, second and third codon positions of the exons. PartitionFinder2 was used to find the appropriate substitution models. Convergence and Effective Sample Size (ESS) statistics were examined with Tracer v. 1.7.1. LogCombiner v. 2.6.3 (Drummond & Rambaut 2007) was used to combine posterior samples. SpeciesDelimitationAnalyzer (Jones et al. 2014) was used to calculate the most likely number of clusters (i.e., putative species).

Nomenclature

The nomenclatural status of names is supported by a reference to relevant articles (ICNafp Art.) of the actual Code (Turland et al. 2018).

RESULTS

Multi-locus phylogenetic analyses

The final alignment contains 144 samples represented by 144 ITS, 104 LSU, 100 *RPB2* and 88 *EF-1α* sequences, of which 62 ITS, 49 LSU, 47 *RPB2* and 50 *EF-1α* sequences are newly published in this study (Table 1). We were able to gain ITS sequences of 75 % (80 % when the suggested types of the invalid names are included) of all studied types. A total of 11 type specimens of European *Compactae* are included in the analysis. Both ML and BI topologies were congruent and show similar supports. The supports are relatively high at almost all tree parts and node ranks, including supports at species level. All European *Compactae* samples are placed in the crown clade with the high support of BS = 84 and PP = 1.00 (Fig. 1). The European samples are clustered in 15 species clades and three singletons with a well delimited position. All members of the *R. albonigra* lineage are grouped in a well-supported clade confirming the phylogenetic delimitation of all species defined by the previous study of De Lange et al. (2021): *R. albonigra*, *R. ambusta*, *R. nigrifacta*, *R. ustulata* and an unnamed species (*Russula* sp. 1) represented by a single sequence. Based on the position of type sequences names were assigned to the species clades corresponding to *R. acrifolia*, *R. adusta*, *R. anthracina*, *R. atramentosa*, *R. densissima* and *R. roseonigra*. *Russula nigricans* was recognised by the position of the epitype-sequence in a preliminary analysis of the separate available markers used in this study (LSU, *RPB2* and *EF-1α*). It was not further included in the final multi-locus analysis due to the lack of an ITS-sequence. *Russula densifolia* was recognised by micromorphological comparison of the samples within the clade and the neotype (the DNA extraction failed). Three well-supported species clades contain no types and, to our knowledge, represent so far unrecognised taxa here

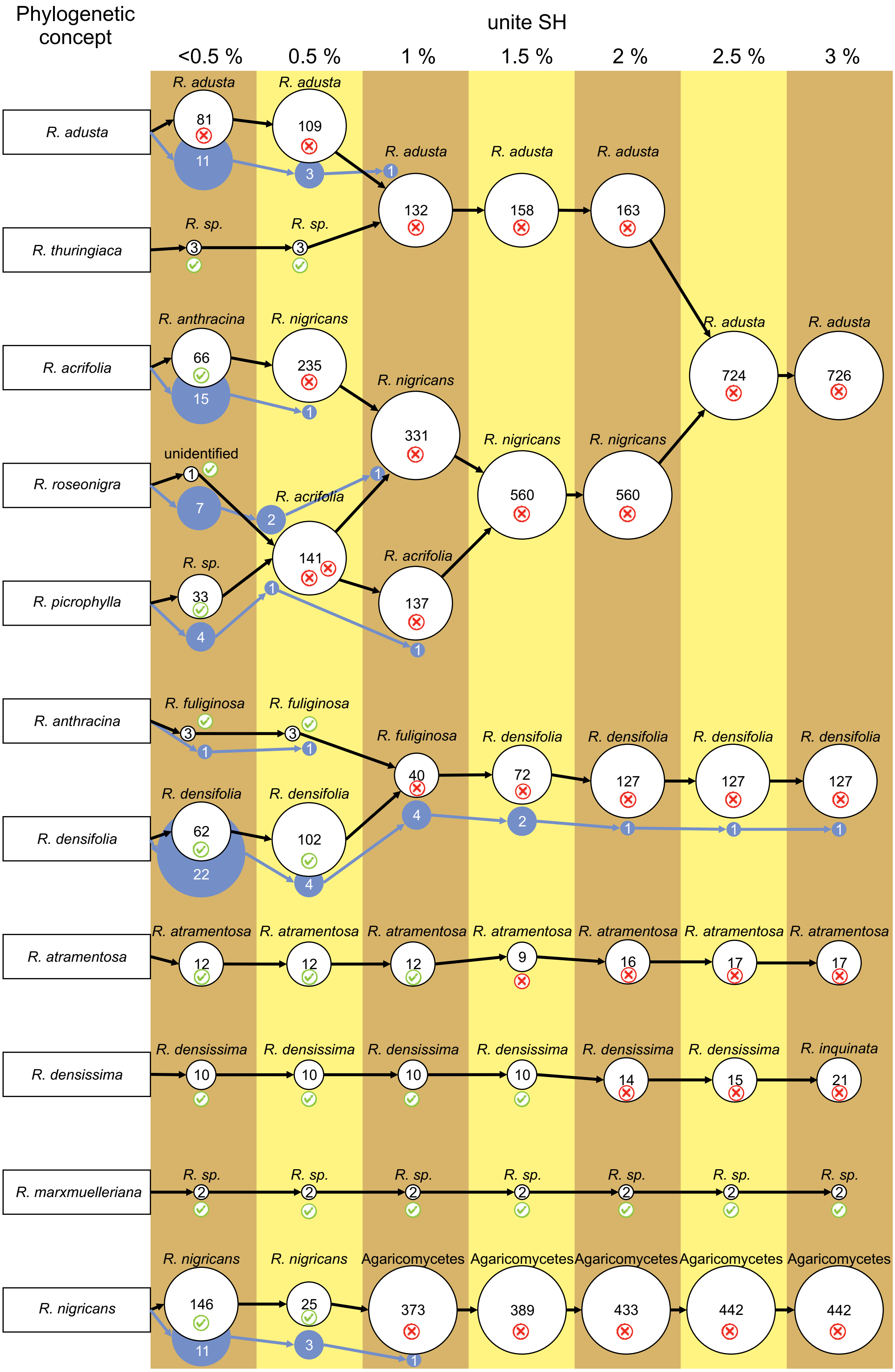

Fig. 2 Representation of the eleven studied *Compactae* species in the UNITE database at different distance thresholds. White circles give information about sequence numbers of the species hypothesis (SH) with the best match, the names above them are adopted from UNITE. Blue circles give information on numbers of SHs with at least one sequence corresponding to the phylogenetic concept of the species. Matches and mismatches of SHs to our phylogenetic concepts are labelled with green yes and red no marks respectively.

described as new species: *R. marxmuelleriana*, *R. picrophylla* and *R. thuringiaca*. Two European samples (RW 1625 and MCVE15300) are represented by a singleton sequence only and we did not include them in the morphological analyses, but they may represent separate species. Based on the position of type sequences and sequences of authentic material, *R. anthracina* var. *carneifolia* nom. inval. and *R. anthracina* var. *insipida* nom. inval. are synonyms of *R. atramentosa* and *R. fuliginosa* is synonym of *R. anthracina* var. *anthracina*.

Assignment of host trees and ecology based on analysis of publicly available ITS sequences

Our GenBank and UNITE search resulted in building an alignment of 673 ITS sequences in total, with 51 additional ITS sequences produced in this study compared to the multi-locus analysis and 478 additional sequences retrieved from public databases. The UNITE search did not gain any significant new information about the *R. albonigra* lineage compared to the previous study of De Lange et al. (2021). All but one species described in this study are covered at least by a single SH matching our phylogenetic species concept. SH2310086.08FU of *R. adusta* at the lowest clustering threshold of < 0.5 % probably contains sequences from different continents (North America and South-eastern China) that in our ITS tree (Fig. S2) form separate clusters and may correspond to different taxa. At the clustering threshold of 0.5 %, seven of the best matching SHs of eleven species make a good match, there is a good match for only three species at the 1 % threshold, for only two at 1.5 %, and at 2 % and higher only *R. marxmuelleriana* is supported (Fig. 2). Some phylogenetic species are covered by more than one species hypothesis, especially *R. densifolia* with sequences distributed among 23 SHs at the clustering threshold of < 0.5 %, and there are even representative sequences of multiple SHs across all clustering thresholds, ending with two SHs at 3 % that contain sequences of this phylogenetic species. A high number of SHs with a reference sequence corresponding to a single phylogenetic species at the clustering threshold of < 0.5 % is also retrieved in *R. acrifolia*, *R. adusta*, *R. nigricans* and *R. roseonigra*. The phylogenetic concept of *R. roseonigra* and *R. picrophylla* at the 0.5 % threshold corresponds to a single SH1961391.08FU labelled as *R. acrifolia*. The UNITE clustering and merging of SHs at higher ranks corresponds to the phylogenetic relationships (Fig. 2). The names assigned in UNITE to the best matching SHs at the clustering thresholds of < 0.5 % and 0.5 % correspond to the names in our phylogenetic study for *R. adusta*, *R. atramentosa*, *R. densifolia*, *R. densissima* and *R. nigricans.* A UNITE-search for *R. acrifolia* will lead, with high probability, to an incorrect identification. The best matching SHs for *R. thuringiaca* and *R. marxmuelleriana* at these thresholds are labelled *Russula* sp., which correspond to the status of the taxa described here as new species. *Russula picrophylla* is also a new species but the best matching SH is labelled *Russula* sp. only at the threshold of < 0.5 %. The best match search for *R. anthracina* gives *R. fuliginosa* at < 0.5 % and 0.5 %, which is correct because the UNITE name assignment is the synonym. UNITE also allows nomenclature search at all thresholds but < 0.5 %. Among the species that can be identified correctly based on sequence search at < 0.5 % and 0.5 % threshold, *R. adusta* has eight SHs with this name, *R. acrifolia* six, *R. anthracina* two, *R. densifolia* 22, *R. densissima* two and *R. nigricans* 27. Many of the SHs with the same name correspond to closely related taxa diversified by geographical distance, as apparent from our phylogenetic analyses (Fig. S1). Some homonymous SHs are even not related, for example *R. nigricans* SH1961379.08FU groups sequences of the *R. acrifolia* lineage. Our data does not show clear evidence for the occurrence of European species on continents outside of Europe, despite there is some unsupported grouping of non-European samples within European species clades (e.g., *R. acrifolia*, *R. adusta*, *R. atramentosa*, *R. densifolia and R. nigricans*) (Fig. S2). We hypothesize that this clustering is rather a result of a higher number of short (only ITS1 or ITS2) and low quality sequences in the analysis. A similar analysis without the additional European samples from public databases shows a clearer grouping and separation of European and non-European samples (data not shown). A similar conclusion about the distribution of species to be limited to continents or certain areas is also true for the species from other continents. The ITS-dataset shows a global species diversity of at least 194 species within *R.* subg. *Compactae.*

For nine of eleven *Compactae* species we retrieved information about at least one host species (usually from ectomycorrhizal root tips) (Table 2). Most of these species were sampled from root tips of both conifers and deciduous trees: *R. acrifolia*, *R. densifolia*, *R. nigricans*, *R. picrophylla*, *R. roseonigra* and *R. thuringiaca*. *Russula densissima* and *R. marxmuelleriana*,

Table 2 Countries of occurrence and host plants verified by root tips sequence data.

Species	Countries	Host plants
R. acrifolia	Estonia, France, Germany, Italy, Latvia, Russian Federation, Slovenia, Spain, Sweden, Switzerland	*Fagus sylvatica*, *Picea abies*, *Pinus sylvestris*, *Quercus*
R. adusta	Austria, Estonia, Finland, France, Italy, Netherlands, Poland, Russian Federation, Sweden, United Kingdom	*Larix decidua*, *Picea abies*, *Pinus cembra*, *Pinus koraiensis*, *Pinus sylvestris*
R. anthracina	Estonia, France, Italy, Slovakia	–
R. atramentosa	Austria, Belgium, Estonia, France, Germany, Italy, Norway, Slovakia	–
R. densifolia	Belgium, Czech Republic, Denmark, Estonia, France, Germany, Italy, Norway, Poland, Portugal, Slovakia, Slovenia, Spain, Switzerland, United Kingdom	*Abies alba*, *Fagus sylvatica*, *Halimium lasianthum*, *Picea abies*, *Pinus pinaster*, *Pinus sylvestris*, *Quercus*, *Quercus robur*, *Quercus suber*
R. densissima	France, Germany, Hungary, Italy, Switzerland	*Fagus sylvatica*, *Quercus*, *Quercus petraea*
R. marxmuelleriana	Belgium, France, Germany	*Quercus robur*
R. nigricans	Austria, Belgium, Czech Republic, Denmark, Estonia, France, Germany, Hungary, Italy, Latvia, Norway, Poland, Serbia, Slovenia, Spain, Sweden, Switzerland, United Kingdom	*Abies alba*, *Fagus sylvatica*, *Halimium lasianthum*, *Picea abies*, *Pinus sylvestris*, *Quercus*, *Quercus petraea*, *Quercus suber*
R. picrophylla	Austria, Czech Republic, Estonia, France, Germany, Hungary, Italy, Latvia, Portugal, Slovenia, Spain, Sweden, Switzerland	*Epipactis helleborine*, *Pinus sylvestris*, *Pyrola rotundifolia*, *Quercus ilex*, *Quercus petraea*, *Quercus rotundifolia*
R. roseonigra	Austria, Bosnia and Herzegovina, Czech Republic, Estonia, France, Germany, Italy, Latvia, Slovenia, Switzerland	*Abies alba*, *Fagus sylvatica*
R. thuringiaca	Germany, Slovakia, Italy, Czech Republic, Switzerland	*Castanea*, *Picea abies*

which seem to be relatively rare species, are so far only known to be associated with deciduous trees. Our UNITE-search strongly suggests that *R. adusta* is exclusively associated with conifers. *Russula densifolia*, *R. nigricans* and *R. picrophylla* were represented also on roots of non-woody plants belonging to the families *Cistaceae*, *Ericaceae* and *Orchidaceae*.

Coalescent-based species delimitation

Both coalescent delimitation methods confirmed the species hypothesis for all 18 European clusters in the multi-locus phylogenetic analysis (Fig. 1). The BP&P analysis recovered the full set of proposed species (i.e., 18 species) as the highest supported species model under each combination of settings, with posterior probabilities ranging from 0.85 to 0.99. Species hypotheses for 14 or less species did not receive any support, species hypotheses for 15 to 17 species received only low support (Fig. S3). The STACEY analysis resulted in the highest probability (posterior probability of 0.99) for 18 minimal clusters (species). The analysis did not support models with less clusters (Fig. S4).

TAXONOMY

Russula acrifolia Romagn., Les Russules d'Europe et d'Afrique du Nord: 203. 1967 — Fig. 3a–h, 4–6

Replaced synonym. *Russula adusta* f. *rubens* Romagn., Bull. Trimestriel Soc. Mycol. France 59: 71. 1943.

Synonyms. *Russula acrifolia* Romagn., Bull. Mens. Soc. Linn. Lyon 31(1): 173. 1962, nom. inval. (ICNafp Arts. 40.1 and 41.5); *Russula acrifolia* Romagn., Doc. Mycol. 26(104): 32. 1997, nom. illeg. (ICNafp Art. 53.1, homotypic synonymy established by Art. 7.5).

Typus. France, Île-de-France/Yvelines, Saint-Nom-la-Bretêche, forêt de Marly, on the path between the Etoile du Pavé and the Etoile du Loup, deciduous forest, 12 Sept. 1943, *H. Romagnesi* (PC0728045/6, holotype).

Pileus large, 40–140 mm diam, plano-convex with shallow depression to infundibuliform; margin straight to inflexed, when young more involute, smooth; pileus surface smooth, shiny, viscid when moist or even slightly slimy, from yellowish white (4A2) to light brown, yellowish brown (5D4–5, 5E4, 5E7, 7D7) to umber, rust brown, liver brown, dark brown (5F8, 6E5–6, 6E8, 6F6–8, 7F4, 7F6, 7F8, 8F5–6). *Lamellae* segmentiform to subventricose, up to 5 mm deep, narrowly adnate, white to pale cream when older, with pinkish tinge; lamellulae numerous, of different lengths in a regular pattern; rarely furcating; moderately distant to moderately dense (5–10 L + 3–6 l/cm at mid-radius); edges even, concolorous. *Stipe* 20–60 × 15–40 mm, cylindrical, firm and fleshy, solid; surface smooth, white, browning when older. *Context* c. up to 8 mm thick at mid-radius of the pileus, firm, white, slowly turning light to moderately orange red, then slowly greying-blackening; surface of pileus and stipe and lamellae strongly reddening when touched, then blackening; turning greenish with $FeSO_4$, sometimes first some slightly orange reaction, greying afterwards, slightly yellowish with KOH, immediately dark blue with guaiac (strong reaction, +++); taste acrid to strongly acrid (rarely the taste is becoming slowly or weakly acrid); odour fruity, slightly musty when old. *Spore print* white (Ia).

Basidiospores (7.0–)7.6–*8.1*–8.6(–9.6) × (5.4–)6.1–*6.6*–7.1 (–7.8) µm, broadly ellipsoid, Q = (1.11–)1.16–*1.24*–1.32 (–1.47); ornamentation of low, very dense ((10–)11–16(–19) in a 3 µm diam circle) amyloid warts, 0.1–0.5 µm high, subreticulate, abundantly fused into chains (4–9(–11) fusions in a 3 µm diam circle), abundantly connected by short, fine line connections ((4–)5–10(–12) in a 3 µm diam circle); suprahilar spot small, not amyloid. *Basidia* (45–)50.6–*55.2*–59.8(–71) × (10–)10.1–*11.0*–11.9(–13) µm, narrowly clavate, 4-spored. *Hymenial cystidia* (45–)55.6–*63.0*–70.4(–77) × (5–)5.8–*6.5*–7.2(–8) µm, cylindrical to narrowly fusiform, flexuous, irregularly tapering towards the top, apically with one to multiple constrictions or an eccentric appendage, thin-walled; content heteromorphous, oily, fragmented in multiple crystalline-like masses, blackening in sulfovanillin; cystidia near the lamellae edges, (33–)39.6–*46.1*–52.6(–64) × (4–)5.2–*6.1*–7.0(–8) µm, narrowly fusiform, rarely narrowly clavate, often slightly flexuous, apically tapering towards the top with constriction or central appendage, thin-walled; content as on lamellae sides. *Lamellae edges* sterile; *marginal cells* (11–)15.6–*19.8*–24.0(–27) × (4–)4.7–*5.4*–6.1(–7) µm, poorly differentiated, cylindrical to narrowly clavate, slightly flexuous, thin-walled. *Pileipellis* orthochromatic in Cresyl Blue, 180–240 µm deep, moderately delimited from trama; subpellis moderately delimited from suprapellis; subpellis 30–60 µm deep, of dense, more parallel horizontal oriented, near trama 3–5 µm wide hyphae; suprapellis 150–175 µm deep, of loose, irregularly oriented hyphae; pigmented in all parts, with some gelatinous matrix, especially near pileus margin. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, slender, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (25–)37.3–*49.3*–61.3(–79) × (3–)3.3–*4.2*–5.1(–6) µm, narrowly cylindrical, on average apically constricted to 3.2 µm; subterminal cells and the cells below similar in length and width, subterminal cells sometimes branched. Hyphal terminations near the pileus centre slightly slenderer and apically hardly attenuated; terminal cells (24–)32.6–*44.1*–55.6(–80) × (2–)2.9–*3.6*–4.3(–6) µm. *Pileocystidia* near the pileus margin widely dispersed, 1-celled, (34–)48.7–*69.7*–90.7(–125) × (4–)4.4–*5.2*–6.0(–8) µm, cylindrical, sometimes slightly subulate or slightly fusiform, sometimes slightly flexuous, apically obtuse or with 1–2 eccentric appendages, rarely bifurcating; content heteromorphous, oily, fragmented in multiple crystalline-like masses, blackening in sulfovanillin; cystidia near the pileus centre rare, 1–2-celled, similar in shape and content; terminal cells (40–)46.2–*57.7*–69.2(–85) × (4–)4.2–*4.9*–5.6(–6) µm (n = 10). Oleiferous hyphae containing brown pigments and cystidioid hyphae present in the trama.

Ecology & Distribution — Most of our collections originated from boreal mixed forests but sequence metadata retrieved from public databases also contains information about association with *Fagus* and *Quercus*, typical trees for temperate European forests. Our material originated from France, Germany and Sweden, but sequence metadata demonstrated that the distribution of the species is much wider and extends from Spain in the west to the Russian federation in the east and from Slovenia in the south to Norway and Sweden in the north.

Additional specimens examined. France, Hauts-de-France/Oise, Ermenonville, 1955, H. Romagnesi, n° 55-164; Auvergne-Rhône-Alpes, Drôme, Gigors-et-Lozeron, Le Savel, 28 Sept. 2010, *H. Marxmüller*, MxM R-010115 (KR-M-0071289). – Germany, Thuringia, Arnstadt, Mühlburg, N50°51'59.45" E10°50'16.99", alt. 375 m, deciduous forest on argillaceous soil over Keuper, 17 Aug. 2014, *J. Girwert*, FH 2014 ST03 (GENT, FH). – Sweden, Västernorrlands län, Sidsjö, N62°43'59.48" E15°8'34.12", alt. 340 m, with *Betula*, *Picea abies* and *Salix*, 28 Aug. 2018, *J. Girwert & F. Hampe* 2018 ST01 (GENT); Västernorrlands län, Dysjöberget, N62°36'21.00" E15°32'39.00", alt. 350–360 m, with *Betula*, *Picea abies*, *Populus tremula* and *Salix*, 30 Aug. 2016, *L. Delgat*, LD 16-022 (GENT); Jämtlands län, Storvålen, N63°1'37.05" E14°45'0.70", alt. 360 m, 27 Aug. 2018, *R. De Lange*, RDL 18-012 (GENT); Tubbobäcken, N62°31'0.32" E16°2'19.55", alt. 155–160 m, with *Picea abies* and *Pinus*, 27 Aug. 2018, *R. De Lange*, RDL 18-013 (GENT); Granbodåsen nature reserve, N62°36'47.00" E15°36'47.00", alt. 360 m, with *Picea abies* and *Pinus*, 27 Aug. 2018, *R. De Lange*, RDL 18-017 (GENT); Bodtjärnsbäcken, N62°43'2.66" E15°25'16.71", alt. 315–320 m, with *Picea abies* and *Pinus*, 28 Aug. 2018, *R. De Lange*, RDL 18-021 (GENT); Ånge NO, Orråsberget North, Husmyrbäcken-Husmyra, N62°34'22.37" E15°47'46.61", alt. 215–220 m, with *Betula*, *Picea abies* and *Populus tremula*, 31 Aug. 2018, *R. De Lange*, RDL 18-037 (GENT); ibid., 31 Aug. 2018, *R. De Lange*, RDL 18-040 (GENT); ibid., 31 Aug. 2018, *R. De Lange*, RDL 18-045 (GENT).

Notes — This species, which has been widely accepted for the last decades, was originally described by Romagnesi (1943) under the name *R. adusta* f. *rubens* based on a single collection (holotype according to ICNafp Art. 9.1 b). In his *Russula* monograph (Romagnesi 1967), Romagnesi validly introduced *R. acrifolia* as a replacement name at species rank. Therefore, the new type designation and validation (Romagnesi 1967, 1997) are superfluous and our concept of *R. acrifolia* is based on the sequence obtained from the isotype specimen of *R. adusta* f. *rubens* (PC0728045). We also extracted DNA from Romagnesi's invalid type (n° 55-164), but we did not get an ITS sequence of sufficient quality. Our microscopic observa-

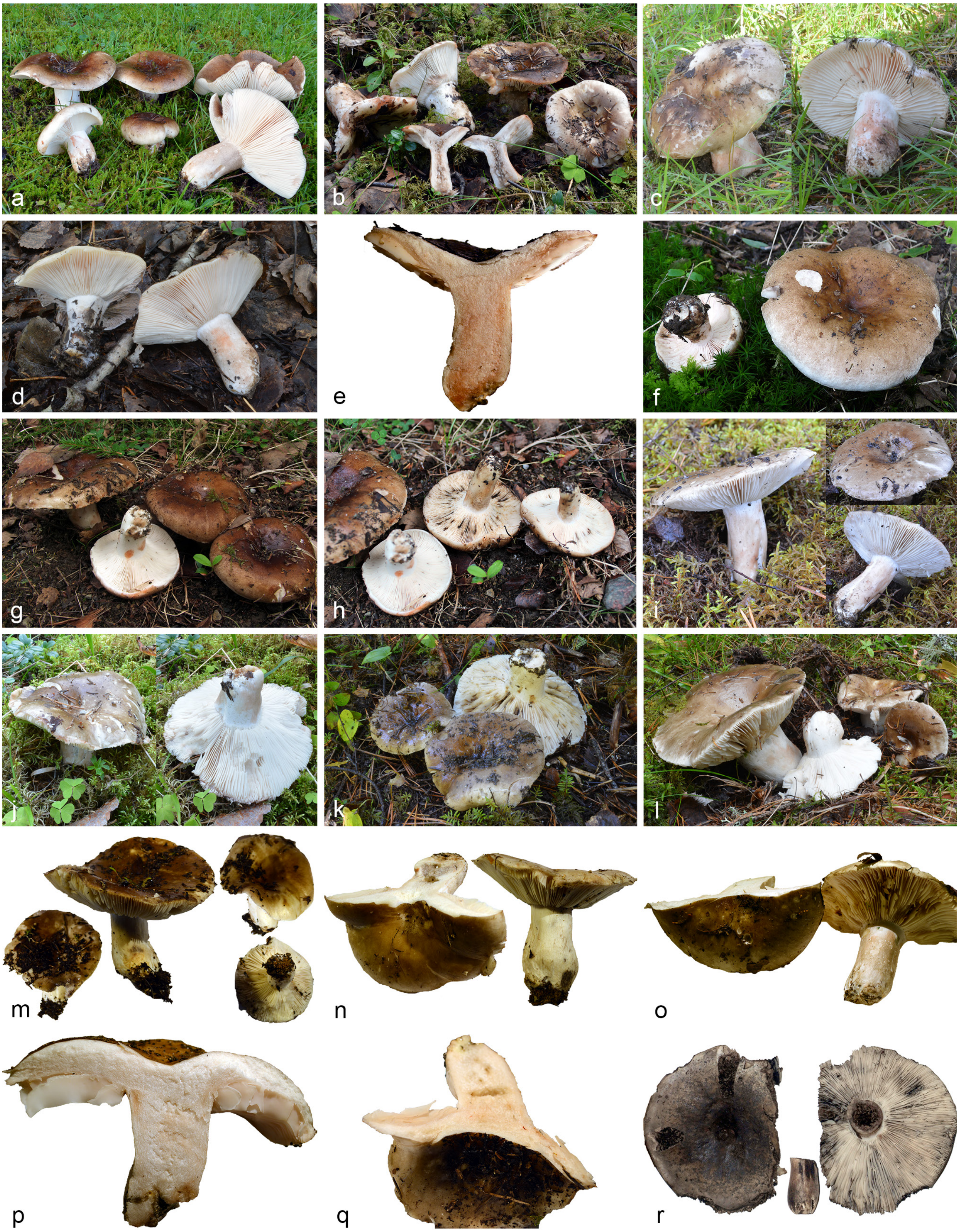

Fig. 3 Basidiomata. a–h. *Russula acrifolia* (a. RDL 18-037; b. RDL 18-021; c. RDL 18-040; d–e. RDL 18-045; f. FH 2014 ST03; g–h. 2018 ST01). — i–q. *Russula adusta* (i. RDL 18-033; j. RDL 18-020; k. RDL 18-039; l. RDL 18-028; m. RDL 18-034; n. RDL 18-035; o. RDL 18-024; p. RDL 18-031; q. RDL 18-030). — r. *Russula anthracina* (FH RUS 14091201). — Photos by: a–e, i–q. R. De Lange; f, h J. Girwert; g F. Hampe; r J. Kleine.

tion of this collection showed a perfect morphological match to the concept of the species adopted in this study based on the actual holotype collection.

According to our phylogenetic study, the traditional and widely accepted concept introduced by Romagnesi refers to a lineage of closely related and morphologically similar taxa including *R. acrifolia*, *R. picrophylla* and *R. roseonigra*. Historical collections identified as *R. acrifolia* need revision using the morphological characters proposed in this study or sequences of the ITS region.

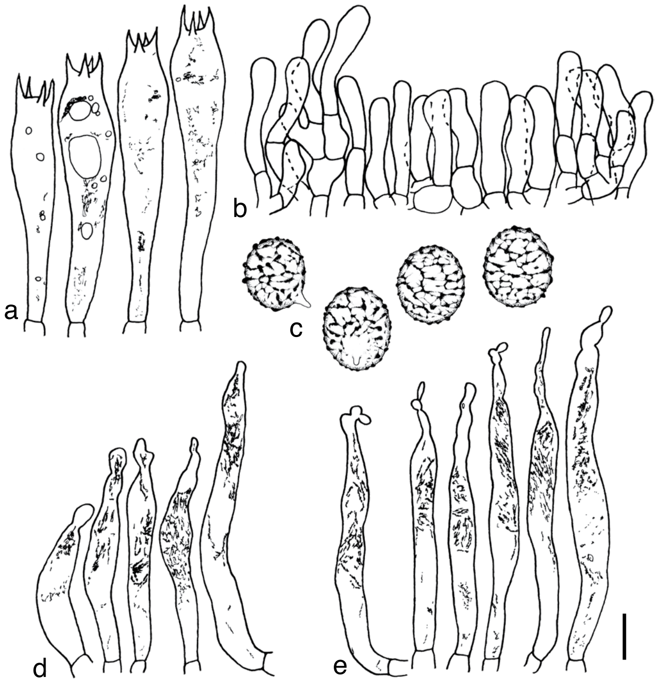

Fig. 4 *Russula acrifolia*, micromorphology of the hymenium. a. Basidia (RDL 18-013); b. marginal cells (RDL 18-012); c. basidiospores (RDL 18-037); d. cystidia near lamellae edges (RDL 18-012); e. cystidia on lamellae sides (RDL 18-013). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

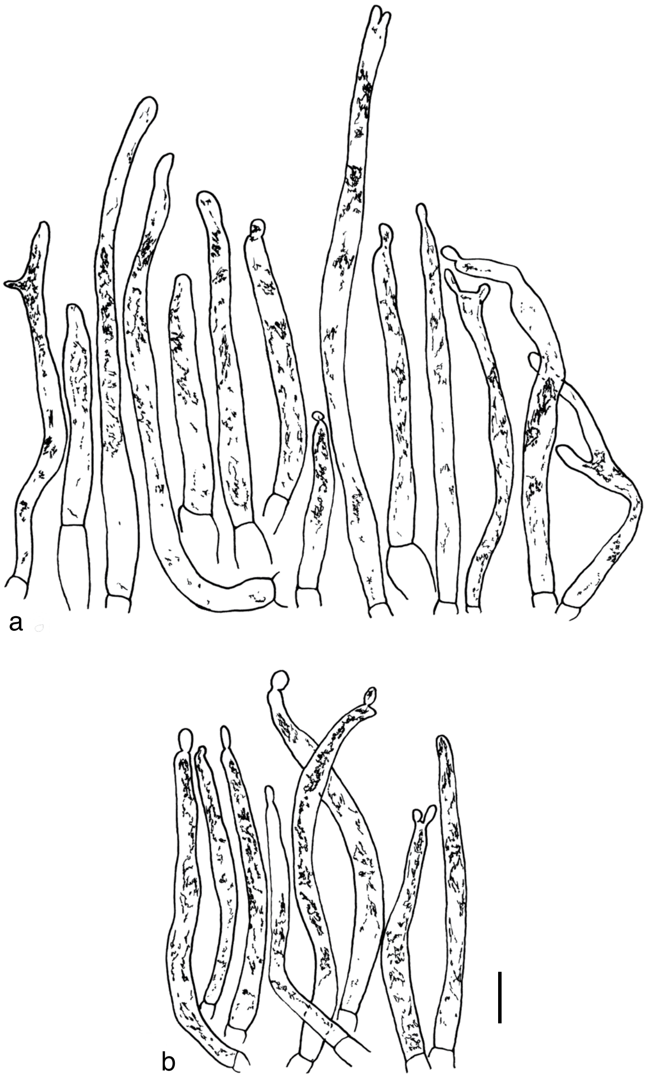

Fig. 6 *Russula acrifolia*, pileocystidia. a. Near the pileus margin (RDL 18-037); b. near the pileus centre (RDL 18-012, RDL 18-013, RDL 18-037). — Scale bar = 10 µm.

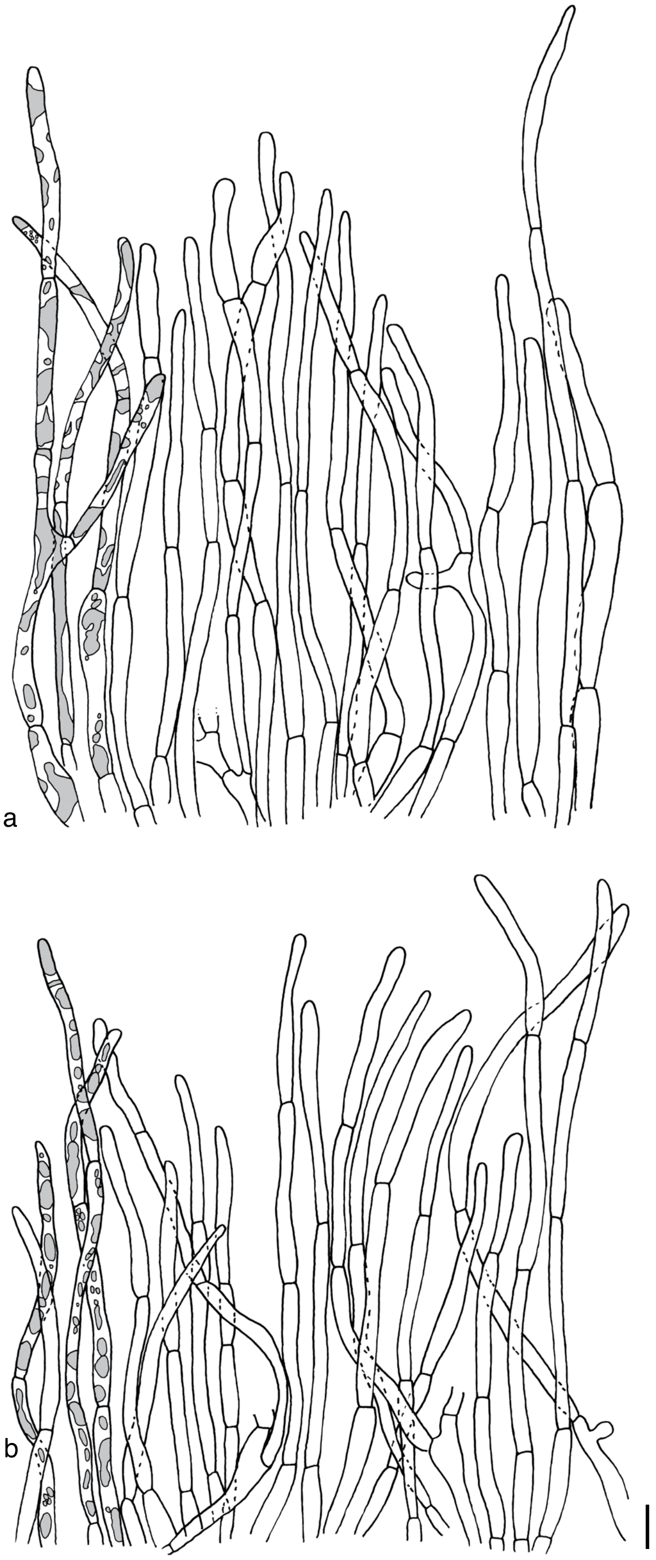

Fig. 5 *Russula acrifolia*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 18-037); b. near the pileus centre (RDL 18-037). — Scale bar = 10 µm.

Russula adusta (Pers.) Fr., Epicr. Syst. Mycol.: 350. 1838 — Fig. 3i–q, 7–9

Basionym. Agaricus adustus Pers., Syn. Meth. Fung. 2: 459. 1801.

Synonym. Russula adusta (Pers.) Fr., Stirp. Agri Fems.: 57. 1825, nom. inval. (ICNafp Arts. 41.1 and 41.3; Art. 38.1).

Typus. Pl. 579 f. II in Bulliard (1793) (lectotype, designated by Sarnari 1998); France, Pays de la Loire/Vendée, south of Les Sables d'Olonne, mixed forest with *Pinus pinaster* and *Quercus ilex* on sandy soil, 10 Nov. 1958, leg. *J. Boiffard* and *A. Leclaire*, herb. H. Romagnesi, n° 58-431 (PC - epitype, designated by Sarnari 1998).

Pileus large, 50–140 mm diam, plano-convex, with shallow depression to depressed, when old more towards slightly infundibuliform; margin straight to inflexed, when young more involute, smooth; pileus surface smooth, shiny, somewhat viscid when moist, from yellowish white, orange white (4A2–3, 5A2) to greyish yellow, greyish orange, orange grey (4B4, 4C4, 5B2–3) to brownish orange (5C3–4) to light brown, café-au-lait (5D4–7, 6D3–4) to yellowish brown, umber, dark brown (5D4–7, 5F8, 6E4–6, 6F6–8), sometimes containing some light yellow (4A5) spots. *Lamellae* rather thin, segmentiform to subventricose, up to 8 mm deep, narrowly adnate, white to pale cream when older, often with some slightly pink tinge, sometimes with brown spots when older; with numerous lamellulae of different lengths in a regular pattern; moderately distant to dense (4–8(–10 in very young specimens) L + 2–5 l/cm at mid-radius); edges even, concolorous. *Stipe* 30–70 × 15–35 mm, cylindrical or slightly tapering up- or downwards, firm and fleshy, solid; surface smooth, white, browning when older. *Context* c. up to 10 mm thick at mid-radius of the pileus, firm, white, slightly reddening (orange red) but mostly very faintly, sometimes only partly, later (but sometimes almost simultaneously) greying but not strongly blackening, when older context mostly already grey; surface of pileus and stipe sometimes also slightly reddening when touched (possibly a little stronger than the context); turning greenish with $FeSO_4$ (sometimes first with a slight orange reaction, but this is probably the start of the normal reddish discoloration of bruised surfaces), slightly yellowish with KOH, immediately dark blue with guaiac (strong reaction, +++); taste mild; odour musty but with some fruity component, like old wine barrels. *Spore print* white (Ia).

Basidiospores (7.0–)7.4–*7.9*–8.4(–8.9) × (5.5–)5.9–*6.4*–6.9 (–7.5) µm, broadly ellipsoid, Q = (1.13–)1.17–*1.24*–1.31(–1.39); ornamentation of very low, very dense ((11–)13–19(–21) in a 3 µm diam circle) amyloid warts, 0.2–0.3 µm high, subreticulate, abundantly fused into chains (4–10(–12) fusions in a 3 µm diam circle), abundantly connected by short, fine line connections ((5–)6–12(–14) in a 3 µm diam circle); suprahilar spot small, not amyloid. *Basidia* (48–)51.7–*57.1*–62.5(–74) × (10–)10.7–*11.5*–12.3(–14) µm, narrowly clavate, 4-spored. *Hymenial cystidia* (62–)67.7–*81.5*–85.3(–120) × (5–)6.4–*7.1*–7.8(–8) µm, cylindrical to narrowly fusiform to narrowly clavate, sometimes slightly flexuous, apically obtuse or with central appendage, thin-walled; content heteromorphous, oily, fragmented in multiple crystalline-like masses, greying in sulfovanillin; cystidia near the lamellae edges, (43–)53.8–*65.3*–76.8(–90) × (5–)6.1–*7.3*–8.5(–10) µm, similar in shape and content, or slightly more flexuous. *Lamellae edges* fertile, but with only few basidia; *marginal cells* (13–)17.2–*25.4*–33.6(–45) × (4–)4.5–*5.7*–6.9(–9) µm, cylindrical, rarely subulate, flexuous, thin-walled. *Pileipellis* orthochromatic in Cresyl Blue, 125–200 µm deep, gradually passing in trama; subpellis not delimited from suprapellis; hyphae 4–7 µm wide near trama, dense, irregularly oriented, more horizontal near trama and surface; most strongly pigmented near trama, much less near surface, with strong gelatinous matrix. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, slender, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (32–)37.1–*46.3*–55.5(–65) × (4–)4.2–*4.8*–5.4(–6) µm, narrowly cylindrical to subulate; subterminal cells and the cells below similar in length and width or shorter and wider, subterminal cells regularly branched. Hyphal terminations near the pileus centre similar, less flexuous; terminal cells (20–)30.2–*45.1*–60.0(–90) × (3–)3.8–*4.6*–5.4(–6) µm. *Pileocystidia* near the pileus margin very rare, 1-celled, (70–)75.0–*82.2*–89.4 × (6–)6.1–*7.3*–8.5(–10) µm (n = 14), subulate to narrowly fusiform, slightly flexuous, apically bifurcating; content heteromorphous, oily, fragmented in multiple crystalline-like masses, greying in sulfovanillin; cystidia near the pileus centre rare, 1-celled, (29–)38.3–*53.5*–68.7(–92) × 5.0–*5.8*–6.6(–8) µm, subulate to narrowly fusiform, slightly flexuous, apically with 1–2 eccentric appendages or rarely with double appendage. Oleiferous hyphae containing brown pigments and cystidioid hyphae present in the trama.

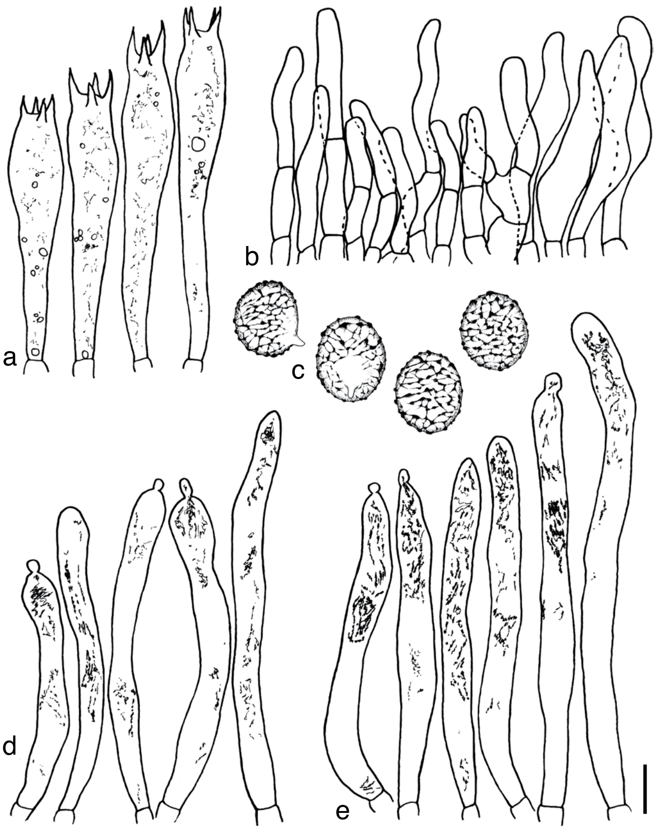

Fig. 7 *Russula adusta*, micromorphology of the hymenium. a. Basidia (RDL 18-028); b. marginal cells (RDL 18-028); c. basidiospores (RDL 18-028); d. cystidia near lamellae edges (RDL 18-028); e. cystidia on lamellae sides (RDL 18-020, RDL 18-028). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

Ecology & Distribution — Apart from the epitype, all material used in this study originates from Sweden, but we retrieved publicly available sequence data originating from distant areas ranging from the United Kingdom and the Russian federation in the west-east direction and Italy and Finland in the south-north direction. Our experience and published data clearly suggest that this species is typically (but not exclusively) boreal/montane and all retrieved data from ectomycorrhizal root tips are from conifers, suggesting it grows in coniferous and mixed forests with coniferous hosts preferably on nutrient poor soils (sandy soils, podzols).

Additional specimens examined. Sweden, Västernorrlands län, Varsjön lake, N62°00'00.00" E15°00'00.00", alt. 370–375 m, 31 Aug. 2016, *L. Delgat*, LD 16-025 (GENT); Granbodäsen nature reserve, N62°36'47.00" E15°36'47.00", alt. 360 m, with *Picea abies*, 02 Sept. 2016, *L. Delgat*, LD 16-029 (GENT); Tubbobäcken, N62°31'0.32" E16°2'19.55", with *Picea abies* and *Pinus*, 27 Aug. 2018, *R. De Lange*, RDL 18-014 (GENT); ibid.,

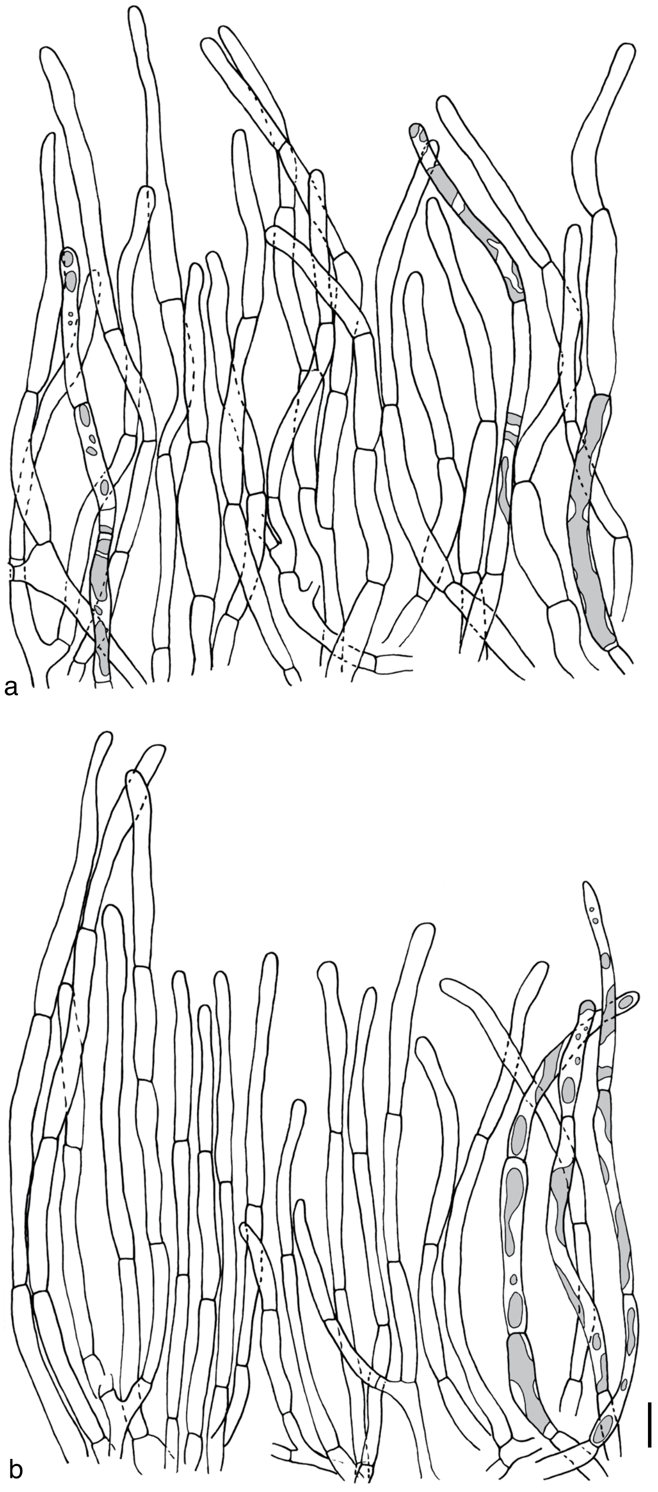

Fig. 8 *Russula adusta*, hyphal terminations of the pileipellis (RDL 18-028). a. Near the pileus margin; b. near the pileus centre (RDL 18-028). — Scale bar = 10 µm.

27 Aug. 2018, *R. De Lange*, RDL 18-015 (GENT); Granbodåsen nature reserve, N62°36'47.00" E15°36'47.00", alt. 360 m, with *Picea abies* and *Pinus*, 27 Aug. 2018, *R. De Lange*, RDL 18-016 (GENT); Sidsjö, Stuguberget, N62°44'4.14" E15°8'39.21", alt. 355–360 m, with *Betula*, *Picea abies* and *Pinus*, 28 Aug. 2018, *R. De Lange*, RDL 18-020 (GENT); ibid., 28 Aug. 2018, *R. De Lange*, RDL 18-024 (GENT); Borgsjö, N62°32'29.89" E15°54'6.13", alt. 115 m, with *Picea abies* and *Pinus*, 29 Aug. 2018, *R. De Lange*, RDL 18-025 (GENT); Ormberget, N62°30'55.29" E15°53'55.20", alt 170–175 m, 29 Aug. 2018, *R. De Lange*, RDL 18-028 (GENT); Nedertjärnen, Balbodbäcken, N62°35'57.01" E15°47'45.95", alt. 261 m, with *Betula*, *Picea abies* and *Pinus*, 29 Aug. 2018, *R. De Lange*, RDL 18-030 (GENT); Borgsjö, N62°32'29.89" E15°54'6.13", alt. 115 m, with *Picea abies* and *Pinus*, 29 Aug. 2018, *R. De Lange*, RDL 18-031 (GENT); Svarttjärn, Jämtgaveln nature reserve, N62°41'28.12" E15°52'29.93", alt. 410–414 m, with *Betula* and *Pinus*, 30 Aug. 2018, *R. De Lange*, RDL 18-033 (GENT); ibid., 30 Aug. 2018, *R. De Lange*, RDL 18-034 (GENT); ibid., 30 Aug. 2018, *R. De Lange*, RDL 18-035 (GENT); Medelpad, Borgsjö parish, Sodra Sillre, N62°31'20.58" E15°57'4.51", alt. 120–125 m, with *Betula*, *Picea abies* and *Populus tremula*, 31 Aug. 2018, *R. De Lange*, RDL 18-039 (GENT); ibid., 31 Aug. 2018, *R. De Lange*, RDL 18-048 (GENT).

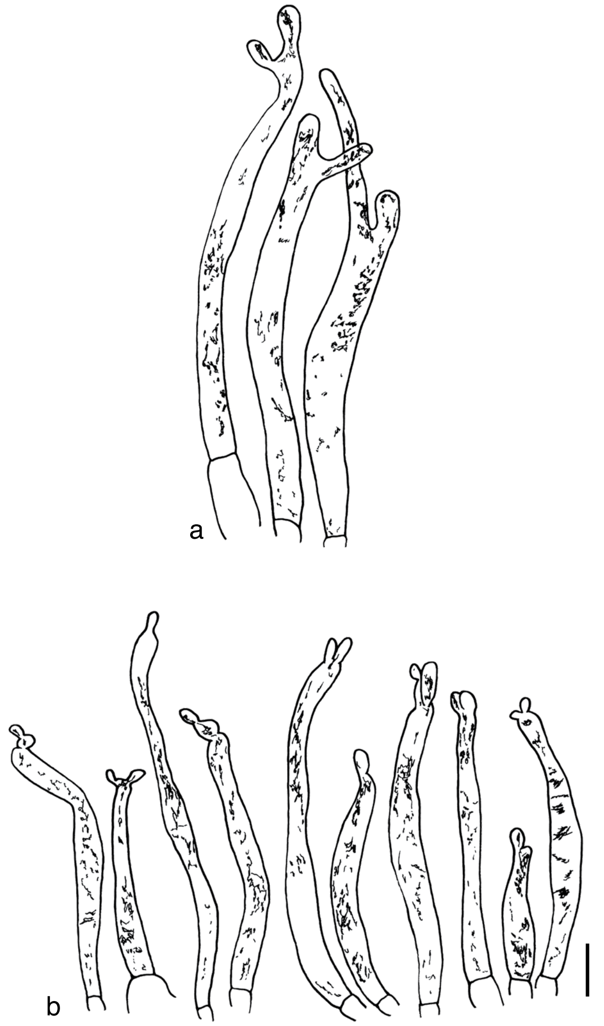

Fig. 9 *Russula adusta*, pileocystidia. a. Near the pileus margin (RDL 18-028); b. near the pileus centre (RDL 18-020, RDL 18-028). — Scale bar = 10 µm.

Notes — *Russula adusta* can be recognised in the field with relatively high confidence based on the weak context discoloration that never turns black. Weak reddening and blackening may also be exhibited by other European *Compactae*, but *R. adusta* can be distinguished by the low spore ornamentation. *Russula thuringiaca* may be similar, but is usually distinguished by a very conspicuous pinkish tinge of the lamellae.

The intricate nomenclatural histories of both *R. adusta* and *R. nigricans* have been addressed by various recent authors (Kuyper & Van Vuure 1985, Sarnari 1998, Maffert 2021, Melot 2021a, b). Following Melot (2021a, b), we consider *Agaricus adustus* as the name of a new taxon rather than a replacement name for *Agaricus nigricans*.

Russula anthracina Romagn., Les Russules d'Europe et d'Afrique du Nord: 209-212, 930. 1967 — Fig. 3r, 10–12

Synonyms. *Russula anthracina* Romagn., Bull. Mens. Soc. Linn. Lyon 31(1): 173. 1962, nom. inval. (ICNafp Art. 40.1); *Russula fuliginosa* Sarnari, Rivista Micol. 36(1): 37–41. 1993.

Typus. France, Île-de-France, Val d'Oise, Forêt de Carnelle, 05 Aug. 1956, herb. H. Romagnesi, n° 56-62 (PC - holotype).

Pileus large, 50–110 mm diam, plano-convex, irregularly expanded, depressed, when young more convex and somewhat subumbilicate; margin straight to inflexed, more involute for a long time, smooth; pileus surface smooth, viscid when moist, somewhat matt when dry, cuticle hardly peeling, pale for a very long time, yellowish white (3A2, 4A2) to sand-coloured (4B3), later dark blond (5D4), with some yellowish brown, light brown (5E4–7) and few patches of umber (5F8), in general becoming more sooty, greyish brown (5D–F3) when older. *Lamellae* narrow, segmentiform to subventricose, up to 7 mm deep, narrowly adnate, white, occasionally with a slight pinkish tinge, blackening when bruised; with numerous lamellulae of different lengths in a regular pattern; sometimes locally anastomosing or furcating; dense to very dense (11–16 L + 6–10 l/cm at mid-radius); edges even, concolorous. *Stipe* 30–60 × 15–28 mm, cylindrical or slightly tapering up or even a little swollen at the base, firm and fleshy, smooth, possibly with some folds or crevices at the base or a little wrinkled under the lamellae, solid; surface white, greying/blackening when older. *Context* c. up to 8 mm thick at mid-radius of the pileus, firm, white, slowly blackening but strong in the end, without intermediate reddening or very diffuse and more locally; surface of pileus and stipe also blackening when touched or with age; context turning orange with $FeSO_4$, immediately dark blue with guaiac (strong reaction, +++), bright orange with formalin; taste acrid/peppery in the lamellae but mild or only slightly acrid in the context; odour sometimes weak, sometimes more clear, not distinct, somewhat musty with slightly fruity component as in most species of the subgenus. *Spore print* white (Ia).

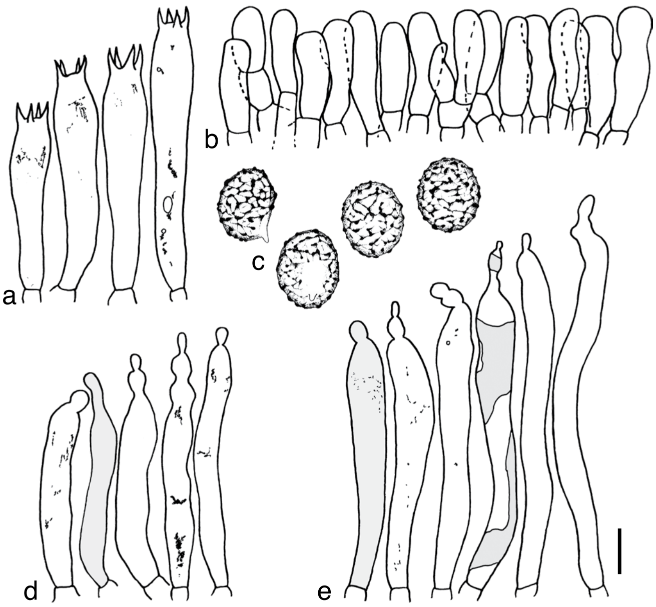

Fig. 10 *Russula anthracina*, micromorphology of the hymenium. a. Basidia (Rom. 56-62, holotype); b. marginal cells (Rom. 56-62); c. basidiospores (Rom. 56-62); d. cystidia near lamellae edges (Rom. 56-62); e. cystidia on lamellae sides (Rom. 56-62). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

Basidiospores (6.7–)7.0–*7.3*–7.6(–7.9) × (4.6–)5.3–*5.7*–6.1 (–6.6) µm, broadly ellipsoid to ellipsoid, Q = (1.17–)1.21–*1.28*–1.35(–1.41); ornamentation of low, very dense (8–14(–16) in a 3 µm diam circle) amyloid warts, 0.1–0.4 µm high, subreticulate, abundantly fused into chains ((2–)3–7(–8) fusions in a 3 µm diam circle), abundantly connected by short, fine line connections (3–8(–9) in a 3 µm diam circle); suprahilar spot medium-sized, not amyloid. *Basidia* (38–)45.1–*50.0*–54.9 (–64) × 8.9–*9.6*–10.3(–11) µm, narrowly clavate, 4-spored. *Hymenial cystidia* (59–)62.1–*68.5*–74.9(–85) × (6–)6.8–*7.7*–8.6(–9) µm, cylindrical to narrowly fusiform to narrowly clavate, flexuous, apically with central appendage or sometimes double appendage or double constriction, thin-walled; content hyaline, hardly any visible, with some brown pigmentation but mostly completely faded, sometimes very few and very small oily masses visible, greying in sulfovanillin, oily masses even slightly blackening, hard to observe; cystidia near the lamellae edges, (40–)45.1–*50.1*–55.1(–57) × (5–)6.2–*7.1*–8.0(–9) µm, similar in shape and content, apically often with more constrictions. *Lamellae edges* sterile; *marginal cells* (12–)15.6–*20.3*–25.0(–29) × (5–)5.7–*6.7*–7.7(–8) µm, poorly differentiated, cylindrical to narrowly clavate, thin-walled. Generally, a lot of brown pigmentation within the elements of the hymenium. *Pileipellis* orthochromatic in Cresyl Blue, 150–250 µm deep, gradually passing in trama; subpellis not delimited from suprapellis; pellis of intermediately dense, irregularly oriented, near trama 4–7 µm wide hyphae; more strongly pigmented towards the surface, with some gelatinous coating, stronger in centre. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, slender, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (37–)43.9–*57.3*–70.7(–92) × (5–)5.4–*6.5*–7.6(–9) µm, narrowly cylindrical to subulate, on average apically constricted to 3.8 µm (average difference of 2.6 µm between maximum width and width of the tips), flexuous; subterminal cells and the cells below mostly slightly shorter but can be similar in length or larger, gradually wider, regularly branched. Hyphal terminations near the pileus centre slightly slenderer, less flexuous; terminal cells (22–)45.0–*62.8*–80.6(–91) × 3.9–*4.9*–5.9(–7) µm, less attenuated. *Pileocystidia* near the pileus margin dispersed, hard to find, 1–2-celled, (38–)45.7–*74.0*–102.3(–148) × (4–)4.8–*5.8*–6.8(–7) µm, subulate to narrowly fusiform, slightly flexuous, apically with 1–2 eccentric appendages or tapering towards the top; content heteromorphous, oily, fragmented in multiple crystalline-like masses, greying to blackening in sulfovanillin; cystidia near the pileus centre rare, 1–2-celled, 34.7–*88.9*–143.1(–235) × (4–)4.4–*5.4*–6.4(–8) µm (n = 12), subulate to narrowly fusiform, slightly flexuous, apically with 1 eccentric or central appendage or tapering towards the top. Oleiferous hyphae containing brown pigments and cystidioid hyphae present in the trama.

Ecology & Distribution — Our material is limited to the types of *Russula anthracina* and *R. fuliginosa* from France and Italy, respectively, and to our collections from oak forests in Slovakia. This suggests that this species prefers thermophilous Mediterranean and Pannonian oak forests. It is probably widely distributed in Northern, Central and Southern Europe, but rare.

Additional specimens examined. Italy, Umbria, near Camerata, deciduous forest with *Quercus cerris*, 25 June 1992, *M. Sarnari*, n° 92/454 (IB) (holotype of *R. fuliginosa*). – Slovakia, Žuhračka, N48°19'34.81" E18°38'54.51", alt. 400 m, deciduous forest with *Quercus cerris* and *Carpinus betulus*, 10 Sept. 2014, *F. Hampe*, FH RUS 14091001 (GENT, JK); Lovce, N48°27'3.91" E18°20'49.26”, alt. 340 m, deciduous forest with *Quercus cerris* and *Quercus petraea*, 11 Sept. 2014, *P. Marstad*, FH RUS 14091201 (GENT, JK).

Notes — *Russula anthracina* has been a poorly understood species since its first (invalid) description in 1962 and according to our findings the name has been frequently misapplied to *R. atramentosa*. While the type of *R. anthracina* var. *anthracina* represents the same taxon as the type of the younger name *R. fuliginosa* (Fig. 1, S2), the types of the other two varieties described by Romagnesi (1962), var. *carneifolia* nom. inval. and var. *insipida* nom. inval., clearly represent the same taxon as *R. atramentosa*. *Russula anthracina* has no wide or inflated terminal cells in the pileipellis which distinguishes it from the similar *R. atramentosa*. It has the field appearance of the species within the *R. albonigra* complex with the context directly turning grey or black and a mild or weakly acrid taste in the stipe context, but a distinctly acrid taste in the lamellae. It seems that the narrow pileocystidia (4.4–6.8 µm) with a distinct sulfovanillin reaction (grey to black) distinguish *R. anthracina* from the *R. albonigra* complex.

In our ITS tree, there is a single Estonian soil sample sequence retrieved from UNITE that is placed close to (sister) *R. anthracina*, but also shows some differences from our sequences and may represent a separate European taxon.

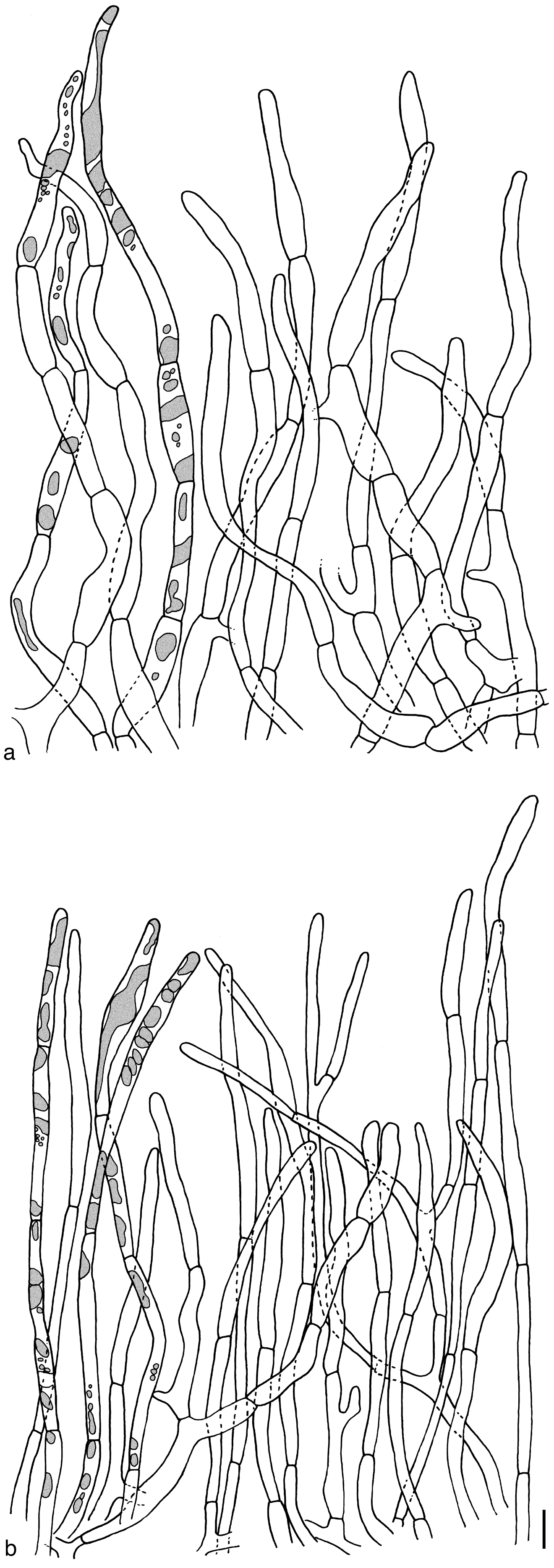

Fig. 11 *Russula anthracina*, hyphal terminations of the pileipellis. a. Near the pileus margin (Rom. 56-62, holotype); b. near the pileus centre (Rom. 56-62). — Scale bar = 10 µm.

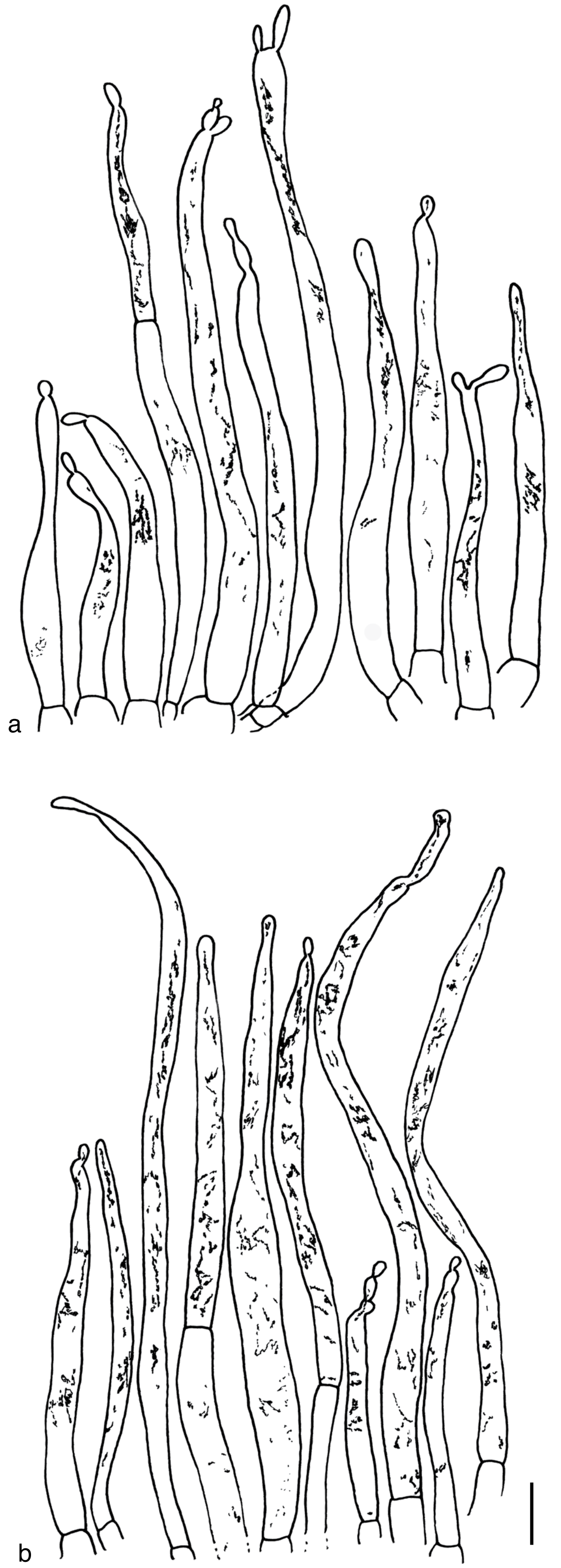

Fig. 12 *Russula anthracina*, pileocystidia. a. Near the pileus margin (Rom. 56-62, holotype); b. near the pileus centre (Rom. 56-62). — Scale bar = 10 µm.

Fig. 13 Basidiomata. a–h. *Russula atramentosa* (a. FH0170824-02; b. FH 2010 ST03; c–d. JK RUS 16111003; e. FH 21-004; f. FH 2011-002R; g. RDL 16-050; h. JK RUS 14091101). — i–r. *Russula densifolia* (i. FH RUS 15101001; j. FH RUS 15101002; k. FH 2014 ST06; l. RDL 16-001; m. RDL 17-024; n. RDL 17-023; o. RDL 18-052; p. RDL-15-23-08-2014; q–r. FH 2006 ST02). — Photos by: a, f, i–j F. Hampe; b, k, q–r J. Girwert; c–d, h J. Kleine; e J. Ehrich; g, l–o R. De Lange; p Mycolim.

Russula atramentosa Sarnari, Boll. Assoc. Micol. Ecol. Romana 26: 32. 1992 — Fig. 13a–h, 14–16

Synonyms. *Russula anthracina* var. *carneifolia* Romagn., Bull. Mens. Soc. Linn. Lyon 31(1): 173. 1962, nom. inval. (ICNafp Art. 40.1: no type indicated; cited as a synonym of *R. anthracina* when the type was indicated in Romagnesi 1967: 930, ICNafp Art. 36.1 (b)); *Russula anthracina* var. *insipida* Romagn., Bull. Mens. Soc. Linn. Lyon 31(1): 173. 1962, nom. inval. (ICNafp Art. 40.1: no type indicated, type indication in Romagnesi 1967 without full and direct reference to the Latin description, ICNafp Art. 38.13).

Typus. ITALY, Tuscany, near Capalbio, evergreen oak forest (*Quercus ilex*), 18 Oct. 1991, *M. Sarnari*, n° 91/58 (IB - holotype).

Pileus large, 40–120 mm diam, plano-convex, depressed, to slightly infundibuliform, when young more convex and subumbilicate; margin straight to inflexed, when young more involute, smooth; pileus surface smooth, dull, dry, even somewhat finely velvety, cuticle only slightly peeling (max. up to 2/5 of the radius), from yellowish white, cream, ivory (4A2) to orange grey (5B3) to café-au-lait, dark blond (5D4, 6D3) to coffee brown (5F7), already soon with more greyish components of the colours. *Lamellae* rather narrow, segmentiform to subventricose, up to 8 mm deep, narrowly adnate; white to cream when older to even somewhat pale café-au-lait, conspicuously blackening, a pinkish or salmon tinge is possible and can even be very strong; lamellulae numerous, of different lengths in a regular pattern; sometimes very locally slightly anastomosing, rarely furcating; dense (6–10 L + 6–9 l/cm at mid-radius); edges even, concolorous, blackening. *Stipe* 30–70 × 10–30 mm, cylindrical, firm and fleshy, solid; surface smooth, white, browning when older. *Context* c. up to 10 mm thick at mid-radius of the pileus, firm, white, at most faintly reddening, later greying and blackening, when older sometimes with an already blackening reaction before cutting; surface of pileus and stipe also strongly and rapidly blackening when touched or bruised; turning greenish with $FeSO_4$ (but possibly first somewhat orange like reaction), slightly yellowish with KOH, immediately dark blue with guaiac (strong reaction, +++), more or less bright red with formalin; taste mild, but sometimes slightly refreshing or acrid in the lamellae; odour fruity, not always very clear, but when strong it can resemble apple or ripe pear, but also with a musty component. *Spore print* white (Ia).

Basidiospores (7.4–)7.9–*8.4*–8.9(–9.4) × (5.7–)6.3–*6.9*–7.5 (–7.8) µm, broadly ellipsoid, Q = (1.10–)1.16–*1.20*–1.24(–1.26); ornamentation of low, dense ((5–)6–10(–13) in a 3 µm diam circle) amyloid warts, 0.1–0.6 µm high, subreticulate, abundantly fused into chains ((1–)2–5(–6) fusions in a 3 µm diam circle), abundantly connected by short, fine line connections (3–6(–9) in a 3 µm diam circle); suprahilar spot small, not amy-

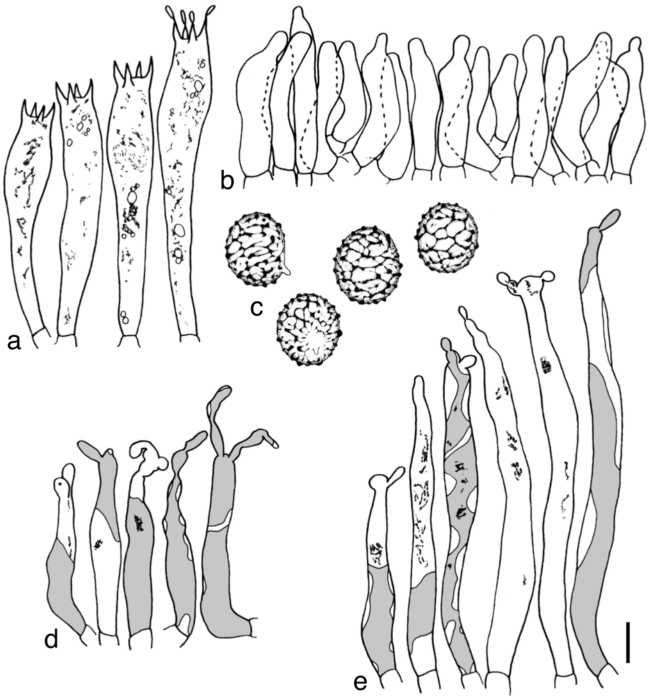

Fig. 14 *Russula atramentosa*, micromorphology of the hymenium. a. Basidia (FH 2011-002R); b. marginal cells (RDL 16-050); c. basidiospores (RDL 16-050); d. cystidia near lamellae edges (RDL 16-050); e. cystidia on lamellae sides (FH 2011-002R). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

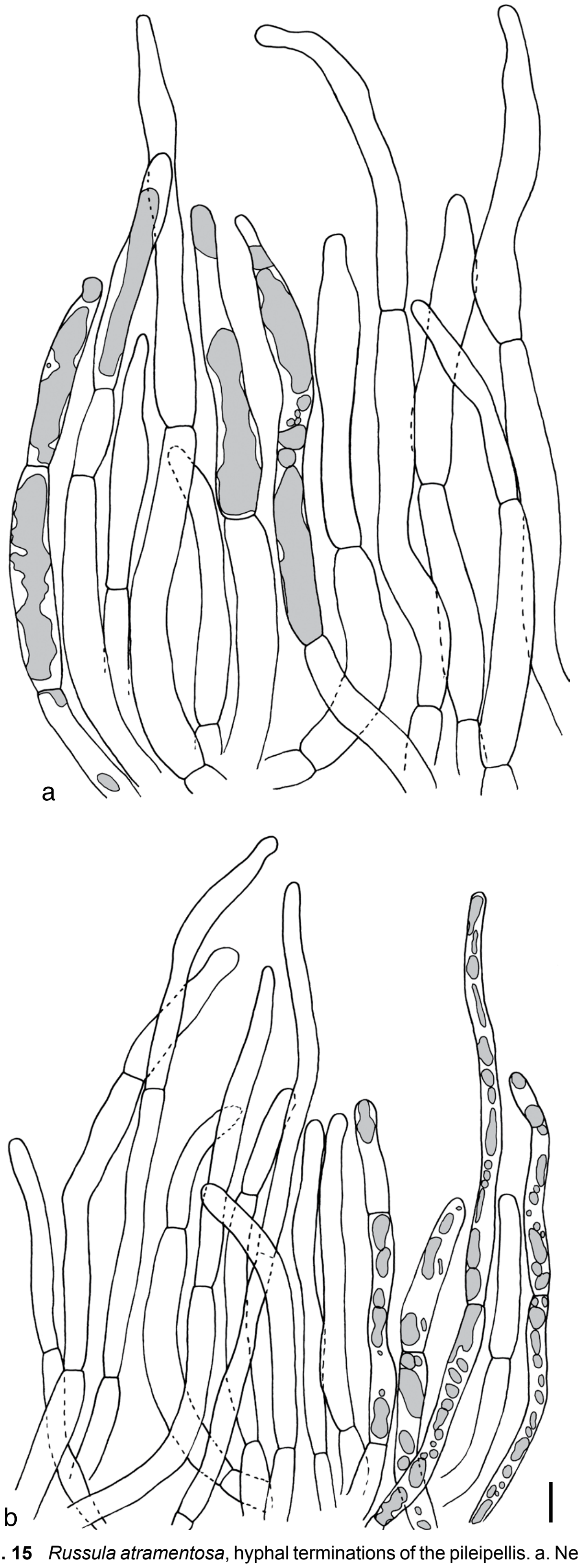

Fig. 15 *Russula atramentosa*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 16-050); b. near the pileus centre (RDL 16-050). — Scale bar = 10 µm.

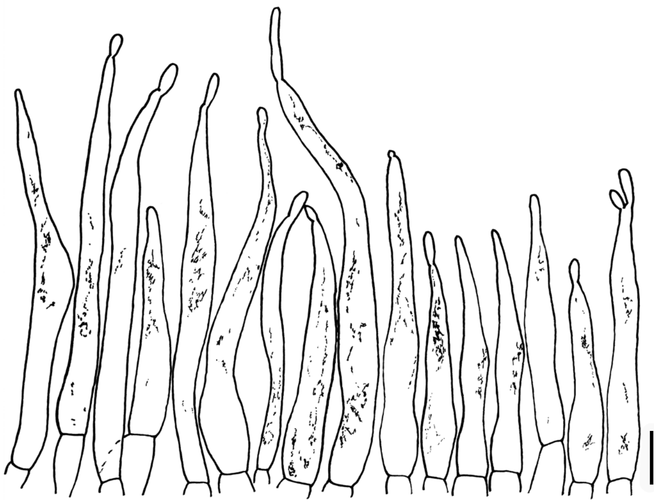

Fig. 16 *Russula atramentosa*, pileocystidia near the pileus centre (JK RUS 16111003). — Scale bar = 10 µm.

loid. *Basidia* (50–)53.5–*58.3*–63.1(–72) × (10–)10.6–*11.2*–11.8(–12) µm, narrowly clavate, 4-spored. *Hymenial cystidia* (56–)69.6–*86.8*–104.0(–150) × (7–)7.2–*8.2*–9.2(–11) µm, subulate to narrowly fusiform, slightly flexuous, apically 1–2 or one and double eccentric appendage or one central appendage, thin-walled; partly to almost completely filled with refractive brown pigments, sometimes very few and very small oily masses visible (somewhat granulose), reaction in sulfovanillin not clear due to brown pigmentation, brown pigment in general turning somewhat more greyish brown; cystidia near the lamellae edges, (33–)41.4–*50.2*–59.0(–70) × (5–)6.2–*7.7*–9.2(–12) µm, similar in shape but more irregular, often with multiple constrictions, appendages often stretched; content as on lamellae sides. *Lamellae edges* sterile; *marginal cells* (11–)23.0–*30.4*–37.8(–45) × (5–)5.9–*7.2*–8.5(–10) µm, cylindrical to narrowly fusiform or subulate, flexuous, thin-walled. *Pileipellis* orthochromatic in Cresyl Blue, 50–150 µm deep, gradually passing in trama; subpellis not delimited from suprapellis; hyphae 4–8 µm wide near trama, dense, more horizontal near trama and surface, more irregular in between; pigmented in all parts, some gelatinous matter can be present. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, broad, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (47–)58.5–*76.7*–94.9(–112) × (6–)7.2–*9.2*–11.2(–14) µm, subulate to narrowly fusiform, on average apically constricted to 4.8 µm (average difference of 4.4 µm between maximum width and width of the tips), slightly flexuous; subterminal cells and the cells below variable in length, similar in width, never branched. Hyphal terminations near the pileus centre slenderer and less attenuated; terminal cells (28–)41.0–*58.5*–76.0(–100) × 5.0–*6.0*–7.0(–9) µm. *Pileocystidia* usually absent; or extremely rare near centre (observed in only two collections), 1-celled, (42–)44.5–*60.9*–77.3(–91) × (5–)6.0–*7.1*–8.2(–9) µm (n = 14), subulate to narrowly fusiform, apically with one central or 1–2 eccentric appendages or tapering towards the top; content mostly scattered, heteromorphous, oily, fragmented in multiple masses. Oleiferous hyphae containing brown pigments present in the trama, cystidioid hyphae not observed.

Ecology & Distribution — Our material was collected in Belgium, France, Germany, Italy and Slovakia, but we also retrieved sequence data originating from Austria, Estonia and Norway. There is no information about plant hosts available from ectomycorrhizal root tips sequencing. Our material originated from various types of forests suggesting that the species has a broad ecological amplitude and grows in temperate to boreal/montane forests with both conifers and deciduous trees.

Additional specimens examined. Belgium, Wallonië, Mariembourg, N50°2'31.79" E4°34'35.60", alt. 400 m, with *Fagus sylvatica* on calcareous soil, 02 Oct. 2011, *F. Hampe*, FH 2011-002R (GENT, FH). – France, Hauts-de-France, Oise, forêt de la Haute-Pommeraie near Apremont, 15 July 1953, *H. Romagnesi*, Rom. 53-86 (in Romagnesi 1967 as *R. anthracina* var. *carneifolia*); Hauts-de-France, Oise, Villers-Saint-Frambourg, forest with prevalent *Fagus sylvatica*, 14 Sept. 1954, *H. Romagnesi*, Rom. 54-235 (PC0735191) (in Romagnesi 1967 as *R. anthracina*); Hauts-de-France, Oise, forêt de Ermenonville, bois de Ver-sur-Launette, with *Corylus*, *Carpinus betulus* and *Quercus* on muddy, somewhat acidic soil, 14 Aug. 1957, *H. Romagnesi*, Rom. 57-64 (in Romagnesi 1967 as *R. anthracina* var. *insipida*); Île-de-France, Val-d'Oise, forêt de Carnelle, 25 Aug. 1957, *H. Romagnesi*, Rom. 57-102 (in Romagnesi 1967 as *R. anthracina* var. *insipida*). – Germany, Thuringia, Hayn near Erfurt, N50°42'39.03" E11°9'28.90", alt. 350 m, deciduous forest with prevalent *Fagus sylvatica* on calcareous soil, 21 Aug. 2010, *J. Girwert*, FH-2010-ST03 (GENT, FH); Baden-Württemberg, Rottweil, Schramberg, Gifizenmoos, N48°12'21.82" E8°26'59.92", alt. 750 m, coniferous forest with *Abies alba* and *Picea abies* on neutral soil; 24 Aug. 2017, *F. Hampe*, FH170824-02 (GENT, FH); Lower Saxony, Seesen, Kurpark, N51°53'3.60" E10°12'33.15", alt. 270 m, park with *Fagus sylvatica*, *Quercus* spp., *Tilia* spp., *Picea abies*, *Pseudotsuga menziesii*, 04 Sept. 2021, *F. Hampe* & *J. Ehrich*, FH 21-004 (GENT, FH). – Italy, Tuscany, Montioni, Nature reserve Parco naturale di Montioni, N43°02'48.00" E10°43'47.00", alt. 45–80 m, 09 Nov. 2016, *R. De Lange*, RDL 16-050 (GENT); Tuscany, Batani, St. Quirico, N42°58'35.00" E10°30'02.00", alt. 120–190 m, 11 Nov. 2016, *R. De Lange*, RDL 16-065 (GENT); Tuscany, Montioni, Nature reserve Parco naturale di Montioni, N43°02'48.00" E10°43'47.00", alt. 45–80 m, in broadleaf forest with prevalent *Quercus cerris*, 10 Nov. 2016, *J. Kleine*, JK RUS 16111003 (hb. Jesko Kleine). – Slovakia, Tríbeč Mts., Jelenec, around the autocamp, in deciduous forest associated with *Carpinus betulus* and *Quercus* sp., N48°24'4.00" E18°12'26.00", alt. 230–250 m, 11 Sept. 2014, *S. Adamčík*, JK RUS 14091101 (hb. Jesko Kleine); Malé Karpaty Mts., Modranská skala near Kuchyňa, N48°24'6.00" E17°11'28.00", alt. 320–400 m, with *Fagus sylvatica*, 14 July 1998, *S. Adamčík*, (SAV F-1810); Spišská Magura Mts., Dlhá hora, south slope, N49°15'37.00" E20°24'42.92", alt. 780–850 m, with *Abies alba* and *Picea abies*, 26 Aug. 2014, *S. Adamčík*, (SAV F-4236).

Notes — This species covers partly the concept of *R. anthracina* as defined by Romagnesi (1962, 1967). Our type sequencing confirmed that two varieties described by Romagnesi are synonyms of *R. atramentosa* (see note on *R. anthracina*). The species has a field aspect similar to several European *Compactae* and a good character to distinguish it are the voluminous and wide hyphal terminations near the pileus margin.

Russula densifolia Gillet, Hyménomycètes: 231. 1874 — Fig. 13i–r; 17–20

Synonym. *Agaricus adustus densifolius* Secr., Mycogr. Suisse: 476 s. 1833, nom. inval. (ICNafp Art. 34.1).

Typus. France, Hauts-de-France/Oise, Ermenonville, Bois de Montlognon, near the crossroad la Croix-Marchande, 26 Aug. 1955, *H. Romagnesi*, n° 55-165 (PC - neotype, designated in Romagnesi 1967).

Pileus medium-sized to large, 25–100 mm diam, plano-convex, with depression; margin straight to inflexed, when young more involute, smooth; pileus surface smooth, viscid when moist, from yellowish white, yellowish grey (3A2, 4B2) to brownish grey, greyish brown (5D2, 5E3) to brownish orange (5C4) to yellowish brown, light brown (5E7–8), with local patches of umber, dark brown (5F8), often containing some olive tinges from khaki (4D3) to (dark) olive brown (4E7, 4F8). *Lamellae* very narrow, segmentiform to subventricose, up to 6 mm deep, narrowly adnate, white to pale cream when older, reddening (orange red) when bruised, then blackening; with numerous lamellulae of different lengths in a regular pattern; rarely somewhat anastomosing, rarely furcating; very dense (10–20 L + 5–10 l/cm at mid-radius); edges even, concolorous. *Stipe* 20–50 × 5–20 mm, cylindrical or slightly tapering upwards, firm and fleshy, solid; surface smooth, white. *Context* c. up to 10 mm thick at mid-radius of the pileus, firm, white, clearly reddening (orange red) but often slowly, later blackening, surface of pileus and stipe also reddening when touched; turning greenish with

Fig. 17 Aquarelle of *Russula densifolia* collection MxM R-9407/KR-M-0070924 (KR). — Reproduced from Marxmüller 2014 with permission from the author.

$FeSO_4$ (sometimes first an orange reaction can be present, but this is probably the start of the normal reddening reaction from touching), slightly yellowish with KOH, immediately dark blue with guaiac (strong reaction, +++); taste mild, or slightly to moderately (when young) acrid in the lamellae only, but not too strong; odour not distinct, slightly fruity, slightly musty. *Spore print* white (Ia).

Basidiospores (6.3–)6.6–*6.9*–7.2(–7.5) × (4.8–)5.3–*5.6*–5.9 (–6.2) µm, broadly ellipsoid, Q = (1.14–)1.18–*1.24*–1.30 (–1.42); ornamentation of low, very dense ((8–)9–13(–15) in a 3 µm diam circle) amyloid warts, 0.1–0.4 µm high, subreticulate, abundantly fused into chains (3–7(–9) fusions in a 3 µm diam circle), abundantly connected by short, fine line connections ((4–)5–10(–11) in a 3 µm diam circle); suprahilar spot small, not amyloid. *Basidia* (40–)44.1–*47.7*–51.3(–55) × (9–)9.9–*10.6*–11.3(–12) µm, narrowly clavate, 4-spored. *Hymenial cystidia* (40–)52.8–*62.9*–73.0(–85) × (5–)6.1–*7.0*–7.9(–9) µm, subulate to narrowly fusiform or narrowly cylindrical, slightly flexuous, apically tapering towards the top or with one central or 1–2 eccentric appendages, thin-walled; content scattered, heteromorphous, oily, fragmented in multiple very small masses to somewhat granulose and oily hyaline refractive guttules, greying in sulfovanillin; cystidia near the lamellae edges, (21–) 35.5–*42.0*–48.5(–54) × (5–)5.6–*6.5*–7.4(–8) µm, similar in shape, sometimes with one and double eccentric appendages; content as on lamellae sides. *Lamellae edges* sterile; *marginal*

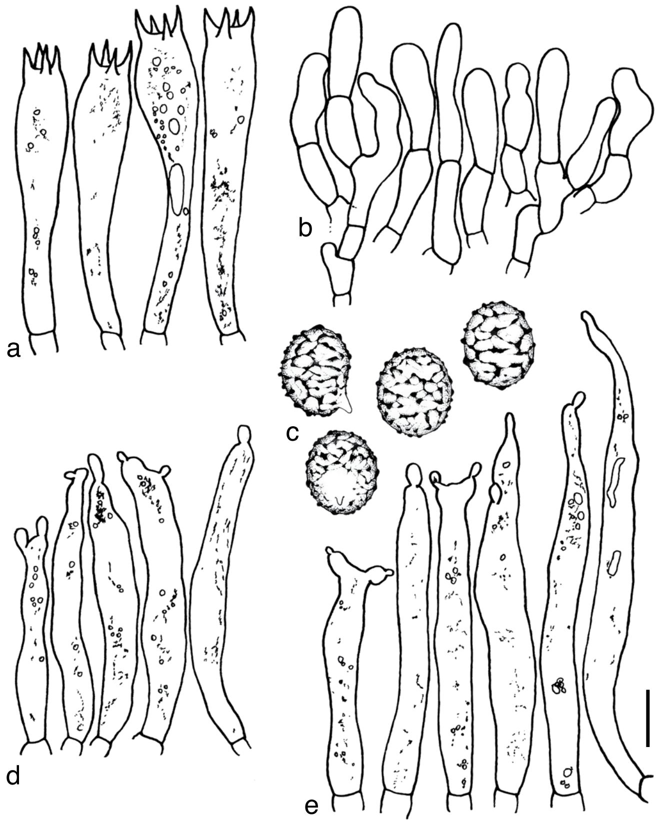

Fig. 18 *Russula densifolia*, micromorphology of the hymenium. a. Basidia (RDL 17-024); b. marginal cells (RDL 17-024); c. basidiospores (RDL 17-024); d. cystidia near lamellae edges (RDL 17-024); e. cystidia on lamellae sides (RDL 17-024). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

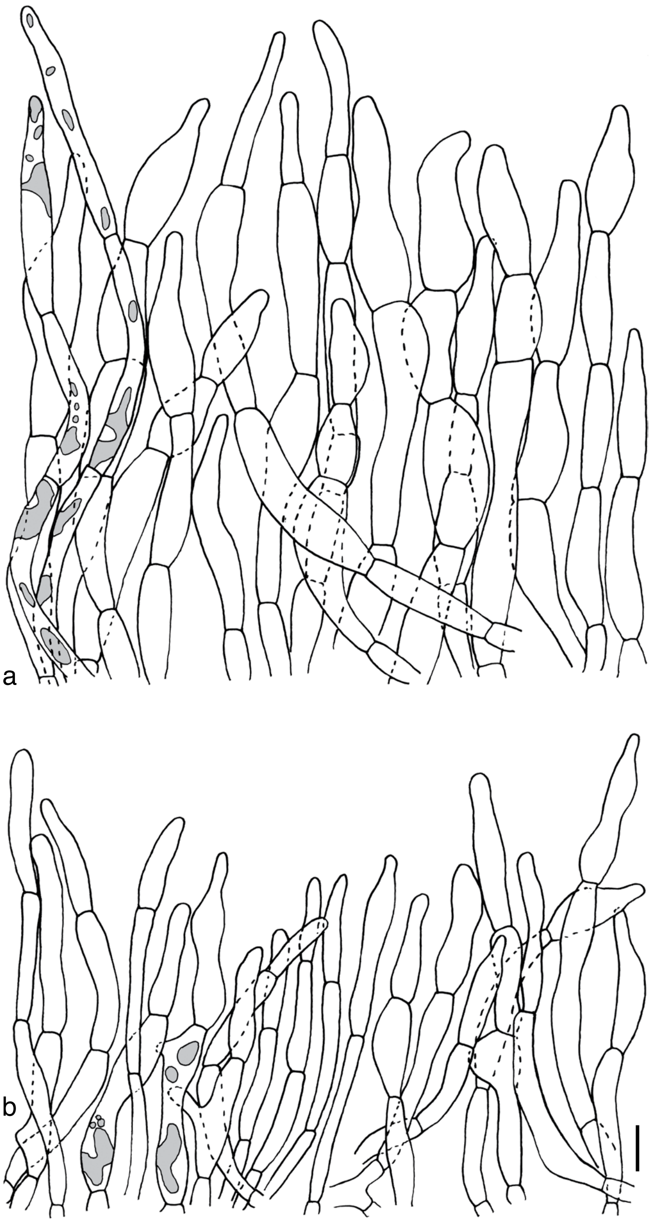

Fig. 19 *Russula densifolia*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 17-024); b. near the pileus centre (RDL 17-024). — Scale bar = 10 µm.

cells (11–)13.6–*17.6*–21.6(–26) × (4–)4.8–*5.6*–6.4(–8) µm, poorly differentiated, cylindrical to narrowly clavate, slightly flexuous, thin-walled. *Pileipellis* orthochromatic in Cresyl Blue, 200–275 µm deep, clearly delimited from trama; subpellis not delimited from suprapellis; of intermediately dense, irregularly oriented, near trama 4–6 µm wide hyphae; pigmented in all parts, without gelatinous coating. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, with multiple septa, composed out of short and very broad elements, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (12–)24.0–*35.2*–46.4 (–65) × (4–)6.4–*9.3*–12.2(–16) µm, subulate, on average apically constricted to 4.4 µm (average difference of 4.9 µm between maximum width and width of the tips); subterminal cells and the cells below similar in length, often gradually wider, subterminal cells never branched. Hyphal terminations near the pileus centre much shorter, slenderer and apically less attenuated; terminal cells (15–)20.7–*29.8*–38.9(–55) × (5–)5.4–*7.5*–9.6(–14) µm, narrowly subulate, flexuous, subterminal cells and cells below similar in length and width, sometimes branched. *Pileocystidia* near the pileus margin numerous to abundant, 1-celled, (18–)28.5–*42.2*–55.9(–88) × (5–)5.2–*6.6*–8.0 (–13) µm, subulate, sometimes slightly flexuous, apically with one central or 1–2 eccentric appendages; content scattered, heteromorphous, oily, fragmented in multiple masses, greying in sulfovanillin; near the pileus centre very abundant, (20–)29.8–*42.0*–54.2(–85) × (4–)4.9–*6.2*–7.5(–12) µm, similar in shape and content. Oleiferous hyphae containing brown pigments and cystidioid hyphae present in the trama.

Ecology & Distribution — Our material originated from Central and Western Europe, but we also retrieved sequence data from the United Kingdom, Iberian Peninsula, Denmark and Estonia. The UNITE data suggests that this species is, together with *R. nigricans*, the most common European member of the *Compactae*. To our experience, the species typically grows in deciduous forests, but UNITE data from ectomycorrhizal root tips report in addition to *Fagus* and *Quercus* also *Picea*, *Pinus* and *Abies* as partner trees. The species is also reported to be associated with Mediterranean woody plants such as *Pinus pinaster* and *Halimium lasianthum*.

Additional specimens examined. Belgium, Limburg, Diepenbeek/Kortessem, Netelbroekstraat, Nietelbroeken, N50°53'2.00" E05°22'40.00", alt. 50 m, in old broadleaf forest stand with *Populus canescens* and *Quercus robur*, 23 Aug. 2014, *R. De Lange*, RDL-15-23-08-2014 (GENT); Limburg, Vliermaalroot (Kortessem), Jongenbos, N50°52'45.00" E05°26'21.00", alt. 56 m, in old deciduous forest with *Corylus avellana*, *Betula*, *Populus alba*, *Populus tremula* and *Quercus robur*, 27 Oct. 2016, *R. De Lange*, RDL 16-001/2 (GENT); ibid., in old deciduous forest with *Betula*, *Populus alba*, *Populus tremula* and *Quercus robur*, 26 Sept. 2017, *R. De Lange*, RDL 17-014 (GENT); Namen, Viroinval, Bois de Frasnes, N50°39'03.6" E3°40'10.6", alt. 115–120 m, with *Picea abies* and *Abies alba*, 30 Sept. 2017, *R. De Lange*, RDL 17-020 (GENT); ibid., 30 Sept. 2017, *R. De Lange*, RDL 17-023 (GENT); ibid., 30 Sept. 2017, *R. De Lange*, RDL 17-024 (GENT); Namen, Viroinval, Nismes, with *Betula* and *Picea abies*, 29 Sept. 2018, *R. De Lange*, RDL 18-052 (GENT). – France, Bourgogne-Franche-Comté, Yonne, Foret d'Herreau et Val de la Nef, 29 Aug. 1994, *M. Waldteufel*, MxM R-9407 (KR-M-0070924) (in Marxmüller 2014 as *R. densissima*); Hauts-de-France, Oise,

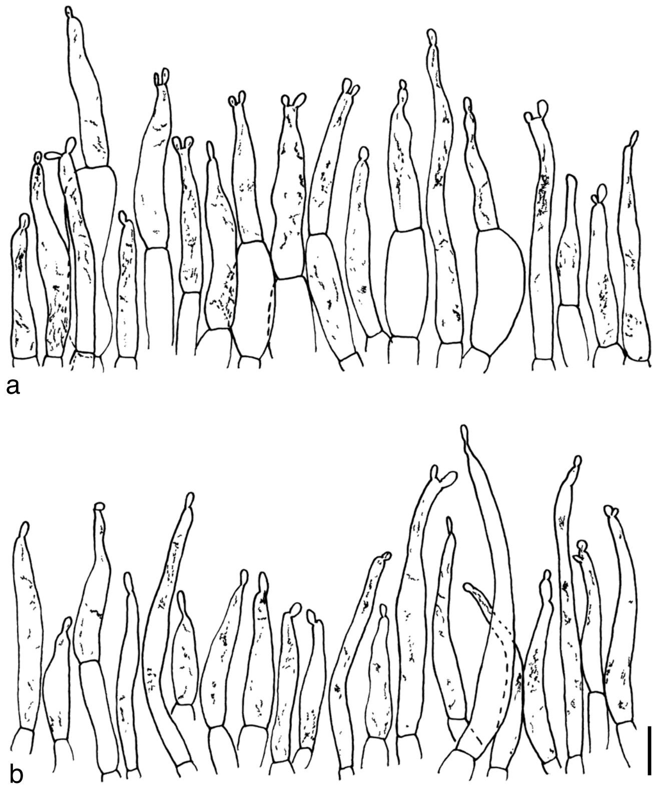

Fig. 20 *Russula densifolia*, pileocystidia. a. Near the pileus margin (RDL 17-024); b. near the pileus centre (RDL 17-024). — Scale bar = 10 µm.

Tracy-le-Mont, Forêt de Laigue, N49°27'34.00" E02°56'16.00", alt. 55 m, siliceous beech forest, 25 Aug. 1963, *H. Romagnesi*, Rom. 63-131 (PC); Hauts-de-France, Oise, Thury, La Neuville-en-Hez, Forêt de Hez-Froidmont, N49°23'09.00" E02°19'31.00", alt. 150 m, deciduous forest, 12 Aug. 1971, *H. Romagnesi*, Rom. 71-150 (PC). – Germany, Thuringia, Paulinzella near Stadtilm, N50°56'7.37" E11°6'12.84", alt. 430 m, plantation with *Picea abies* on acidic soil over sandstone, 15 Aug. 2006, *J. Girwert*, FH 2006 ST02 (GENT, FH); Thuringia, Schellroda, Aspenbusch, N50°54'46.84" E11°5'42.29", alt. 435 m, plantation with *Picea abies* over calcareous bedrock, 20 Oct. 2006, *J. Girwert*, FH 2006 ST03 (GENT, FH); Thuringia, Stadtilm, Wüllersleben, Großes Sperlingsholz, N50°48'16.35" E11°5'34.22", alt. 460 m, plantation with *Picea abies* and single deciduous trees over calcareous bedrock, 20 Aug. 2014, *J. Girwert*, FH 2014 ST05 (GENT, FH); Thuringia, Neustadt am Harz, N51°33'45.79" E10°50'24.87", alt. 300 m, mixed forest with *Picea abies* and *Quercus robur* on acidic soil over rhyolitic bedrock, 30 Aug. 2014, *J. Girwert*, FH 2014 ST06 (GENT, FH); Thuringia, Bücheloh near Ilmenau, N50°43'38.12" E10°59'14.39", alt. 465 m, coniferous forest with *Picea abies* and *Pinus sylvestris* on acidic soil over sandstone, 10 Oct. 2015, *F. Hampe*, FH RUS 15101001 (GENT, FH); Thuringia, Frankenhain, Windberg, N50°44'54.62" E10°47'4.03", alt. 520 m; mixed forest with *Fagus sylvatica* and *Picea abies* on acidic soil over sandstone, 10 Oct. 2015, *F. Hampe*, FH RUS 15101002 (GENT, FH). – Slovakia, Tríbeč Mts., Gáborka, vicinity of the spring, N48°21'29.00" E18°8'51.00", alt. 370–450 m, with *Quercus* and *Fagus sylvatica*, 02 Sept. 2010, *S. Adamčík*, (SAV F-3162); Malé Karpaty Mts., Vývrat', Janková, west slope of the hill, N48°25'39.40" E17°11'24.63", alt. 310–320 m, with *Quercus*, 06 July 2011, *T. Christiansen*, (SAV F- 3372); Malé Karpaty Mts., Lozorno, Bukovina, N48°19'34.77" E17°5'31.60", alt. 295 m, with *Fagus sylvatica*, 07 July 2011, *S. Adamčík*, (SAV F- 3386).

Notes — *Russula densifolia* is characterised by dense lamellae, context with a usually distinct reddish discoloration and a mild taste in the stipe, and a dry pileus surface. This combination of characters together with the common occurrence of the species offers a relatively high chance to correctly identify it already in the field. However, we recommend also to check the presence of short inflated cells in the pileipellis (near the pileus margin) to identify the species, as was already proposed by Romagnesi (1967).

Gillet's 'Pl. 173' (Gillet 1878), proposed as lectotype by Sarnari (1998), was actually published after the protologue of the species (Gillet 1874) and should not be considered to represent original material (ICNafp Art. 9.4). Gillet's original publication (1874) did neither include nor specifically refer to any illustration. Gillet's plates are undated and were published only from 1878 onward. Therefore, the specimen indicated by Romagnesi (1967) as 'type' is a validly designated neotype. Since sequencing of some of the *R. densifolia* collections from Romagnesi (PC) was not successful, our species concept is based on microscopic examination of the neotype.

Russula densissima Romagn., Bull. Soc. Mycol. France 96 (3): 297. 1980 — Fig. 21a–b, 22–24

Typus. France, Normandy, Manche, near La Pernelle, Bois de Pépinvast, among grasses on a muddy path under deciduous trees with conifers nearby, on acidic soil, 19 Aug. 1977, *H. Romagnesi*, n° 77-131 (PC - holotype).

Pileus medium-sized, 30–80 mm diam, plano-convex, depressed, margin straight to inflexed, when young more involute, smooth; pileus surface smooth, rarely somewhat rugose, viscid when moist, rather shiny, from yellowish white (4A2) to yellowish brown (5D–E4) to umber, dark brown (6F6), with olive brown, nutria patches (5F3). *Lamellae* narrow to very narrow, segmentiform to subventricose, up to 5 mm deep, narrowly adnate to subdecurrent, white to ivory, pale cream when older, blackening when bruised; with numerous lamellulae of different lengths in a regular pattern; rarely furcating; dense to very dense (6–15 L + 5–8 l/cm at mid-radius); edges even, concolorous, sometimes blackening. *Stipe* 20–30 × 5–16 mm, cylindrical or slightly tapering upwards, firm and fleshy, solid; surface smooth, white, browning/blackening when older. *Context* c. up to 6 mm thick at mid-radius of the pileus, firm, white, first greying, then blackening, without any reddening, surface of pileus and stipe also not reddening but only blackening when touched; immediately dark blue with guaiac (strong reaction, +++); taste acrid in the lamellae but the context is mild; odour not distinct. *Spore print* white (Ia).

Basidiospores (5.7–)6.3–*6.7*–7.1(–7.6) × (4.7–)5.1–*5.5*–5.9 (–6.3) µm, broadly ellipsoid, Q = (1.12–)1.18–*1.23*–1.28(–1.32); ornamentation of low, very dense ((7–)9–14 in a 3 µm diam circle) amyloid warts, 0.1–0.5 µm high, subreticulate, abundantly fused into chains (3–8(–10) fusions in a 3 µm diam circle), abundantly connected by short, fine line connections ((3–)4–8(–10) in a 3 µm diam circle); suprahilar spot medium-sized, not amyloid. *Basidia* (41–)45.1–*49.0*–52.9(–55) × (8–) 9.0–*9.6*–10.2(–11) µm, narrowly clavate, 4-spored. *Hymenial cystidia* (37–)44.6–*55.9*–67.2(–80) × (5–)6.5–*8.2*–9.9 (–10) µm, subulate to narrowly fusiform, apically tapering towards the top or with one or double constriction or appendage, thin-walled; content hyaline, heteromorphous, oily, sometimes filled with refractive brown pigments, greying in sulfovanillin; cystidia near the lamellae edges, (38–)41.8–*52.7*–63.6(–75) × (7–)7.7–*9.8*–11.9(–14) µm, similar in shape; content as on lamellae sides. *Lamellae edges* sterile; *marginal cells* (12–)15.8–*19.5*–23.2(–27) × (5–)5.6–*7.0*–8.4(–9) µm, poorly differentiated, cylindrical, thin-walled. *Pileipellis* orthochromatic in Cresyl Blue, 150–205 µm deep, gradually passing into trama; subpellis not delimited from suprapellis; of intermediately dense, irregularly oriented, near trama 3–7 µm wide hyphae; pigmented in all parts, with gelatinous matrix. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, slender, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (18–)27.8–*38.9*–50.0(–61) × (3–)3.7–*5.2*–6.7(–8) µm, narrowly cylindrical, on average apically constricted to 4.1 µm; subterminal cells and the cells below similar in length and width, subterminal cells and cells below regularly branched, especially at the bases. Hyphal terminations near the pileus

Fig. 21 Basidiomata. a–b. *Russula densissima* (a. FH 2010 ST02; b. FH 2014 ST04). — c–d. *Russula marxmuelleriana* (c. RDL 17-009, holotype; d. FH 2009 ST02). — e–u. *Russula nigricans* (e. RDL 16-007; f. RDL 16-009; g. RDL 17-007; h. RDL 17-003; i. RDL 17-005; j. RDL 17-001; k. RDL 17-004; l. RDL 18-050; m. RDL 17-008; n. RDL 18-061; o. RDL 16-004; p. RDL 16-002; q. RDL 16-005; r–s. RDL 18-051, t. FH 20-066; u. RDL 16-011). — Photos by: a–b, d J. Girwert; c, e–s, u R. De Lange; t F. Hampe.

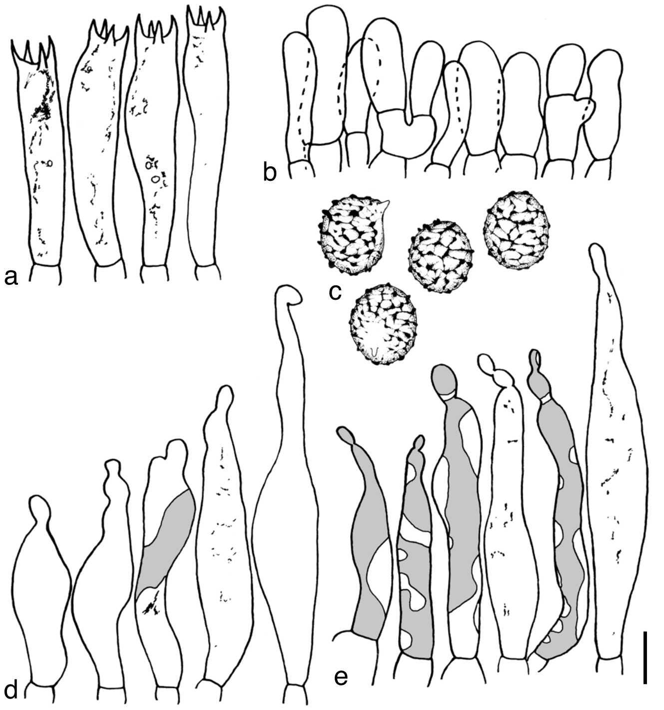

Fig. 22 *Russula densissima*, micromorphology of the hymenium. a. Basidia (Rom. 73-131, paratype); b. marginal cells (FH 2010 ST02); c. basidiospores (Rom. 73-131); d. cystidia near lamellae edges (FH 2010 ST02); e. cystidia on lamellae sides (Rom. 73-131). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

centre similar; terminal cells (25–)29.5–*36.8*–44.1(–52) × (3–)3.5–*4.3*–5.1(–6) µm, narrowly cylindrical, subterminal cells and cells below similar in length and width, subterminal cells never branched, cells below regularly branched. *Pileocystidia* near the pileus margin dispersed, 1-celled, (35–)38.6–*68.4*–98.2(–168) × 5.8–*6.7*–7.6(–8) µm, cylindrical to subulate, apically tapering towards the top or with small constriction or with 1–2 eccentric appendages; content heteromorphous, oily, fragmented in multiple masses, greying in sulfovanillin; cystidia near the pileus centre dispersed, (30–)36.8–*51.2*–65.6(–88) × (4–)4.8–*6.0*–7.2(–9) µm, similar in shape and content, apically sometimes with double constriction or one and double eccentric appendages. Oleiferous hyphae containing brown pigments and cystidioid hyphae present in the trama.

Ecology & Distribution — All our collections of the species originate from Germany, and we also studied the paratype from France. The UNITE search resulted in retrieving additional sequences from Hungary, Italy and Switzerland, and confirmed that it is associated with *Fagus sylvatica* and *Quercus (Quercus petraea* and *Quercus* sp.). This species seems to be relatively rare and our limited data also suggests it can form mycorrhizae with conifers (collection FH 2014 ST04 from a forest dominated by *Picea abies*).

Specimens examined. France, Normandy, Manche, near La Pernelle, Bois de Pépinvast, among grasses on a moist path, on acidic soil, 21 Aug. 1973, *H. Romagnesi*, Rom. 73-131 (PC) (paratype). – Germany, Thuringia, Friedrichsdorf near Erfurt, N51°1'14.99" E10°53'57.53", alt. 345 m, deciduous forest with prevalent *Quercus petraea* over calcareous bedrock, 18 Aug. 2010, *J. Girwert*, FH 2010 ST02 (GENT, FH); Thuringia, Stadtilm, Wüllersleben, Großes Sperlingsholz, N50°48'16.35" E11°5'34.22", alt. 460 m, plantation with *Picea abies* and single deciduous trees over calcareous bedrock, 20 Aug. 2014, *J. Girwert*, FH 2014 ST04 (GENT, FH).

Notes — The field aspect of *R. densissima* reminds *R. anthracina* or other species with a dry pileus cuticle and weak or absent context reddening. Morphological identification of this species requires microscopic observations: it has subulate, sulfovanillin positive hymenial cystidia and a pileipellis with a mixture of long narrow and short inflated terminal cells near the pileus margin.

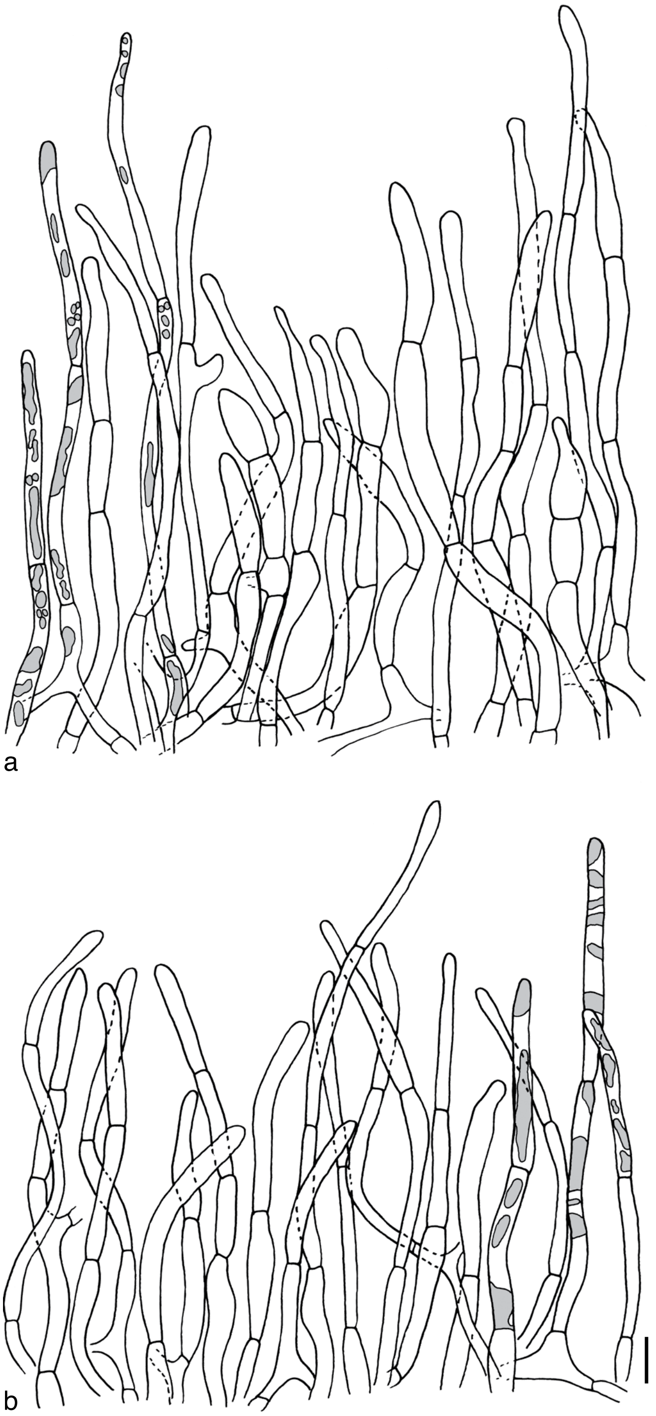

Fig. 23 *Russula densissima*, hyphal terminations of the pileipellis. a. Near the pileus margin (Rom. 73-131, paratype); b. near the pileus centre (FH 2010 ST02). — Scale bar = 10 µm.

Despite the contradictory statements in the original publication (including incorrect author citation and a reference to an invalid basionym), *R. densissima* is a valid and legitimate name of a new taxon described by Romagnesi (1980). Our concept of the species is based on the paratype collected a few years earlier in the type locality, because DNA extraction of the holotype specimen failed.

The name *Russula densissima* (Jul. Schäff.) J. Blum appeared in earlier literature (Blum 1962) as combination of the invalid name *R. densifolia* f. *densissima* Jul. Schäff., nom. inval. (Schäffer 1952), but it is uncertain if this interpretation represents the same taxon as Romagnesi's species.

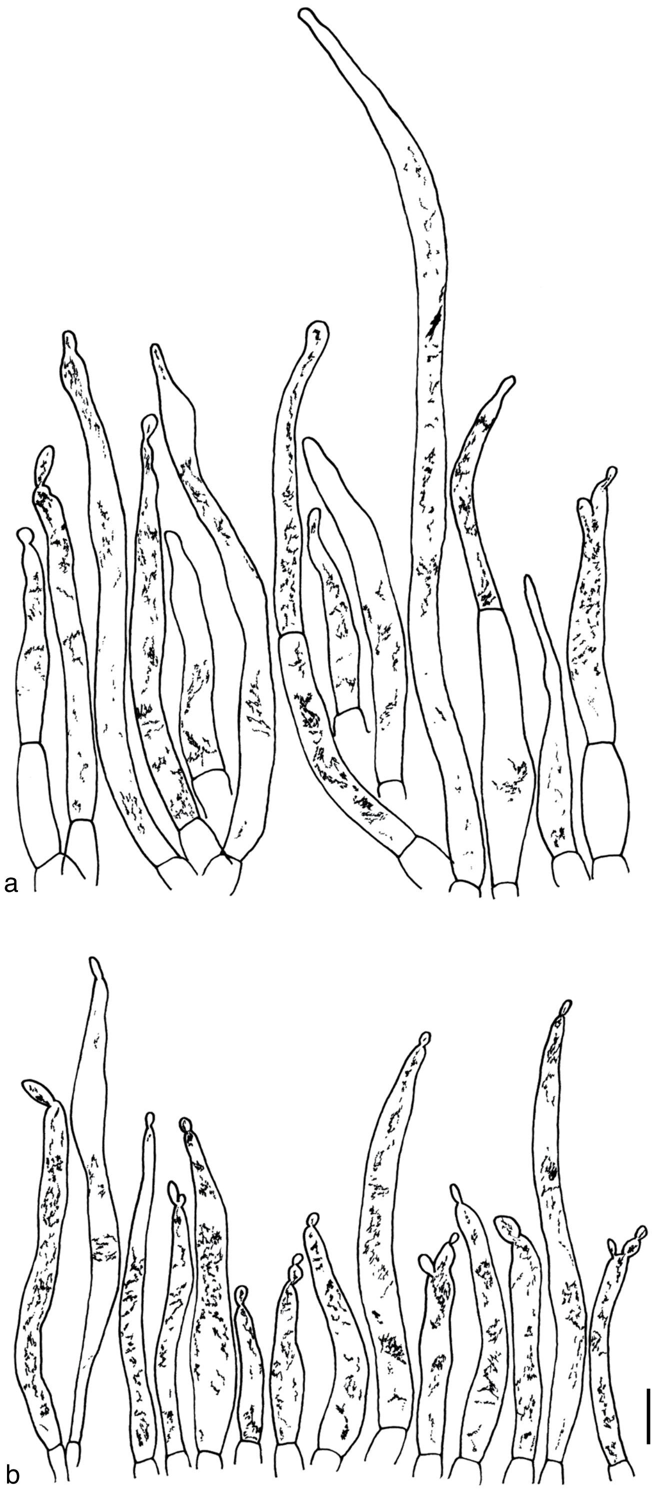

Fig. 24 *Russula densissima*, pileocystidia. a. Near the pileus margin (Rom. 73-131, paratype); b. near the pileus centre (FH 2010 ST02). — Scale bar = 10 µm.

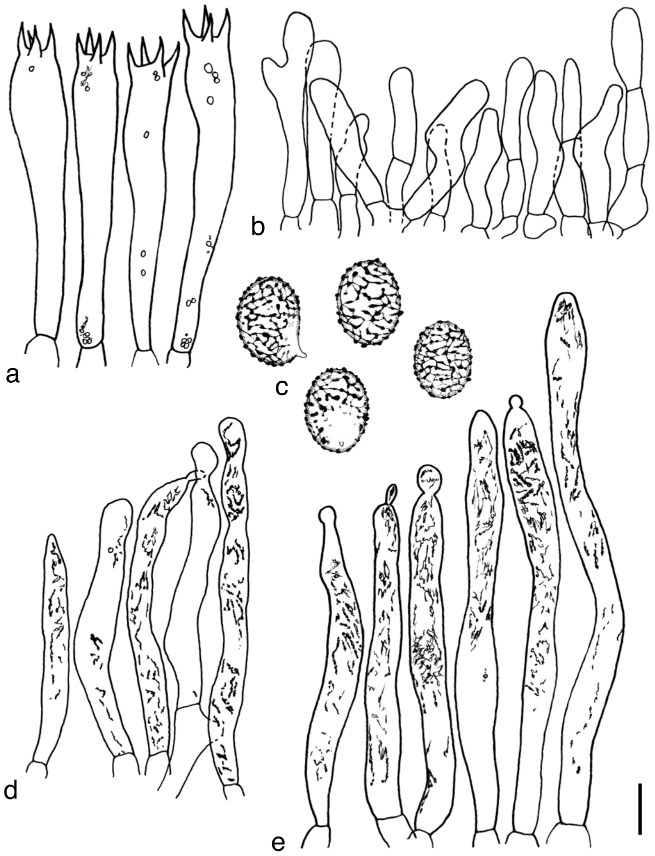

Fig. 25 *Russula marxmuelleriana*, micromorphology of the hymenium. a. Basidia (RDL 17-009, holotype); b. marginal cells (RDL 17-009); c. basidiospores (RDL 17-009); d. cystidia near lamellae edges (FH 2009 ST02); e. cystidia on lamellae sides (RDL 17-009). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

Russula marxmuelleriana De Lange, Girwert & F. Hampe, *sp. nov.* — MycoBank MB 847331; Fig. 21c–d, 25–27

Etymology. In honour of the mycologist Helga Marxmüller, who made important contributions to *Russula* studies.

Typus. Belgium, Limburg, Vliermaalroot (Kortessem), Jongenbos, N50°52'45.00" E5°26"21.00", alt. 55 m, deciduous forest on sandy/loamy soil, 26 Sept. 2017, *R. De Lange*, RDL 17-009 (GENT - holotype).

Diagnosis — *Russula marxmuelleriana* can be easily distinguished from the other European species of *R.* subg. *Compactae* by its narrowly ellipsoid spore shape. In the field it may resemble *R. nigricans* or *R. thuringiaca*. *Russula nigricans* has even more widely spaced and thicker lamellae, and a strong reddening of the context where *R. marxmuelleriana* shows at most a slight reddish discoloration. *Russula thuringiaca* has a greasy shiny pileus cuticle whereas *R. marxmuelleriana* has a dry, matt pileus cuticle.

Pileus small to medium-sized, 30–100 mm diam, plano-convex with depressed centre; margin inflexed, long involuted, not striated, smooth; pileus surface smooth, dry, matt, cuticle peeling up to 1/2 of the radius, from sand coloured (4B3) at the margin to yellowish brown (5E6) or dark brown, chocolate brown (6F4) at the centre. Cap centre sometimes with a white powdery coating. *Lamellae* segmentiform to subventricose, up to 4 mm deep, narrowly adnate, white to somewhat creme or with yellowish spots when older, sometimes with a slight (but distinct) pinkish tinge; lamellulae not very abundant and not in a clear regular pattern; often strongly anastomosing; moderately distant (6–7 L + 1–3 l/cm at mid-radius); edges even, concolorous (rarely blackening with age). *Stipe* 15–32 × 12–20 mm, cylindrical, firm and fleshy, solid; surface smooth, white when young, strongly darkening to reddish blonde, brownish orange (5C3) when older. *Context* c. 5–7 mm thick at mid-radius of the pileus, firm; white, hardly to only slightly and slowly reddening before greying and blackening (medium), surface of pileus and stipe sometimes also slightly reddening; turning salmon pink (orange reaction) with $FeSO_4$ (but can be quickly darkening), immediately dark blue with guaiac (strong reaction, +++), negative or slightly yellowing with KOH, quickly reddish brown with phenol; taste mild; odour not distinct, musty or somewhat bread-like. *Spore print* white (Ia-Ib).

Basidiospores (7.0–)7.6–*8.1*–8.6(–9.2) × (4.7–)5.3–*5.7*–6.1 (–6.6) µm, ellipsoid to narrowly ellipsoid, Q = (1.20–)1.32–*1.42*–1.52(–1.62); ornamentation of low, very dense ((8–)9–14(–15) in a 3 µm diam circle) amyloid warts, 0.2–0.5 µm high, subreticulate, abundantly fused into chains ((1–)2–5(–7) fu-

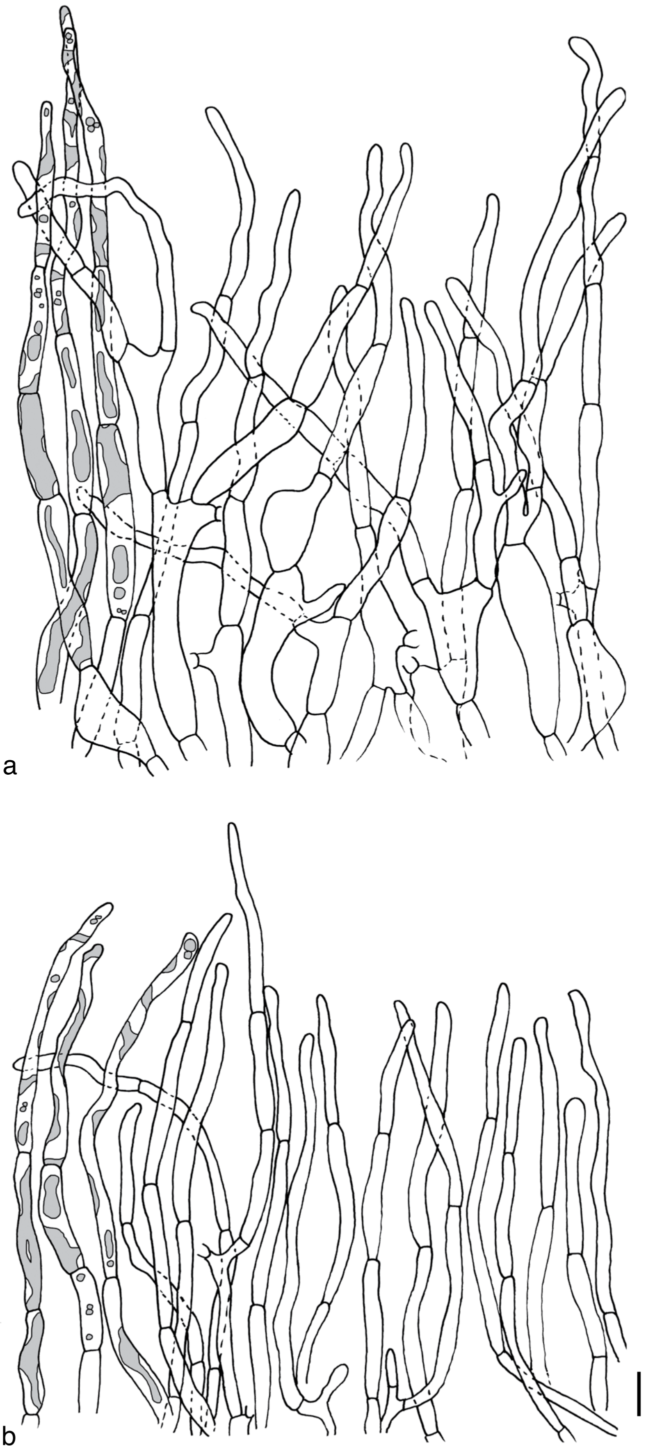

Fig. 26 *Russula marxmuelleriana*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 17-009, holotype); b. near the pileus centre (RDL 17-009). — Scale bar = 10 µm.

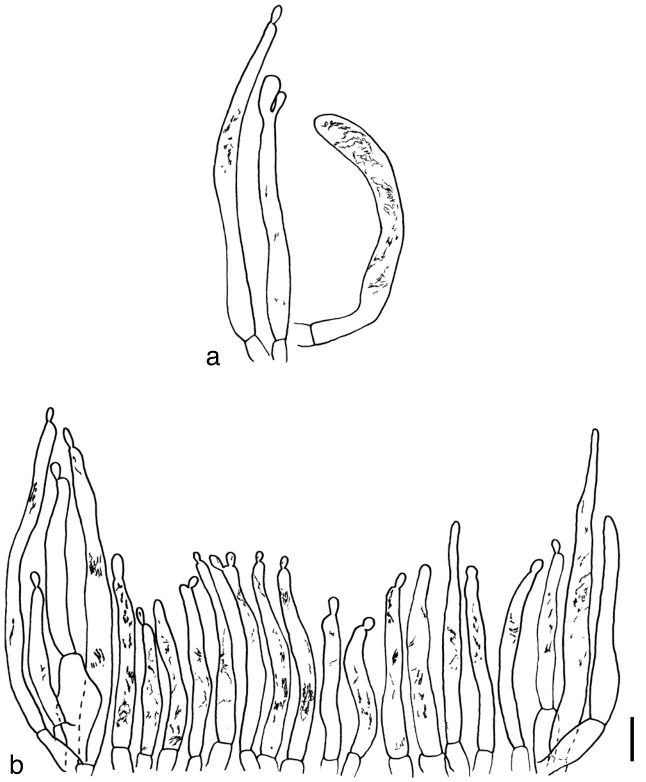

Fig. 27 *Russula marxmuelleriana*, pileocystidia. a. Near the pileus margin (FH 2009 ST02); b. near the pileus centre (RDL 17-009, holotype). — Scale bar = 10 µm.

sions in a 3 µm diam circle), abundantly connected by short, fine line connections ((1–)2–7(–8) in a 3 µm diam circle); suprahilar spot large, not amyloid. *Basidia* (50–)52.4–*56.7*–61.0(–66) × (8–)9.1–*9.7*–10.3 µm, narrowly clavate, 4-spored. *Hymenial cystidia* (50–)60.6–*77.3*–94.0(–140) × (6–)6.4–*7.2*–8.0 µm, cylindrical to narrowly fusiform, sometimes slightly flexuous, apically obtuse or with central or eccentric appendage, thin-walled; content heteromorphous, oily, fragmented in multiple crystalline-like masses to somewhat granulose, slightly greying in sulfovanillin; cystidia near the lamellae edges, (36–)41.7–*51.1*–60.5(–72) × (6–)5.9–*6.6*–7.3(–8) µm, cylindrical to narrowly fusiform, rarely narrowly clavate, often slightly flexuous, more irregular in shape, apically obtuse or with constriction, sometimes with appendage or slightly tapering towards the top, thin-walled; content as on lamellae sides. *Lamellae edges* sterile; *marginal cells* (10–)15.8–*23.4*–31.0(–40) × (5–) 5.1–*5.8*–6.5(–7) µm, poorly differentiated, cylindrical to narrowly clavate, flexuous, thin-walled. *Pileipellis* orthochromatic in Cresyl Blue, 80–140 µm deep, sharply delimited from trama; subpellis moderately delimited from suprapellis; subpellis 20–40 µm deep, of dense, parallel and horizontal, near trama 4–6 µm wide hyphae; suprapellis 50–120 µm deep, of moderately dense to dense, irregularly oriented hyphae; pigmented in all parts, without gelatinous coating. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, slender, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (22–)35.2–*49.0*–62.8(–75) × (3–)3.7–*4.7*–5.7(–7) µm, narrowly cylindrical, on average apically constricted to 3.1 µm; subterminal cells and the cells below slightly shorter and broader, regularly branched and containing somewhat inflated cells. Hyphal terminations near the pileus centre similar; terminal cells (25–)33.2–*52.9*–72.6(–91) × (3–)3.3–*4.2*–5.1(–6) µm, subterminal cells and cells below less often branched and without inflated cells. *Pileocystidia* near the pileus margin extremely rare, 1-celled, 56.3–*65.0*–73.7(–75) × 4.3–*6.0*–7.7(–8) µm (n = 3), subulate to narrowly fusiform, apically obtuse or with 1–2 eccentric appendages; content mostly scattered, heteromorphous, oily, fragmented in multiple crystalline-like masses; cystidia near the pileus centre dispersed, 1-celled, (30–)32.7–*45.2*–57.7(–77) × (3–)4.0–*5.0*–6.0(–7) µm, subulate to narrowly fusiform, slightly flexuous, apically slightly tapering towards the top or with one central or 1–2 eccentric appendages; content mostly scattered, heteromorphous, oily, fragmented in multiple crystalline-like masses, slightly greying in sulfovanillin but inconspicuous. Oleiferous hyphae, sometimes containing brown pigments, and cystidioid hyphae present in the trama.

Ecology & Distribution — In deciduous temperate forests of Central and Western Europe; our two collections originate from Belgium and Germany and were associated with various deciduous trees, we also retrieved sequence data originating from *Quercus robur* root tips collected in France; to understand the ecology of this species more data is needed.

Additional specimen examined. Germany, Thuringia, south of Erfurt, Schellroda, Aspenbusch, near the motorway A4, N50°55'1.20" E11°6'11.29", alt. 425 m, deciduous forest with *Alnus glutinosa*, *Fagus sylvatica*, *Fraxinus excelsior* and *Quercus robur* on clayey black soil/loess over calcareous bedrock (Muschelkalk), 04 Aug 2009, *J. Girwert*, FH 2009 ST02 (GENT, FH).

Notes — Phylogenetically, *R. marxmuelleriana* occupies an isolated position among the European representatives of subg. *Compactae*. Although the narrowly ellipsoid spore shape seems to be a good distinguishing character, our studied material was limited and this needs further confirmation by observations on future collections. According to our data and sequence search, *R. marxmuelleriana* is an uncommon species. This might explain why this taxon escaped the attention of previous authors.

Russula nigricans Fr., Epicr. Syst. Mycol.: 350. 1838 — Fig. 21e–u, 28–30

Replaced synonym. *Agaricus nigricans* Bull., Herb. France (5): pl. 212. 1785 (non *Agaricus nigricans* O.F. Müll. 1782).

Synonyms. ?*Agaricus nigrescens* Dubois, Meth. Eprouv.: 168. 1803; *Agaricus nigrescens* Bull. & Vent., Hist. Champ. France (2): 587. 1812, nom. illeg. (ICNafp Art. 53.1).

Typus. Pl. 212 in Bulliard (1785) (lectotype of *Agaricus nigricans* Bull., designated by Sarnari 1998); France, Normandy, Orne, forêt de Bellême, 05 Oct. 2007, leg. *B. Buyck*, BB 07.342 (PC 0124713 - epitype, designated by Melot 2021a).

Pileus large to very large, 38–200 mm diam, plano-convex, with shallow depression to depressed, margin straight to inflexed, when young more involute, smooth; pileus surface smooth, dry, cuticle peeling up to 1/3–1/2 of the pileus radius, from dark brown, brownish grey, chocolate brown to umber, bronze brown, yellowish brown, dark blond with paler spots of orange grey (4B2, 5B2, 5C3, 5D4, 5E4–5, 5F2, 5F8, 6E4, 6F4, 6F8, 7F4). *Lamellae* thick to very thick, sturdy but brittle, segmentiform to subventricose, up to 10 mm deep, narrowly adnate, white to pale cream when older, reddening when bruised, rarely with a pinkish or orange tinge; with numerous lamellulae of different lengths in a regular pattern; rarely somewhat anastomosing, rarely furcating; widely spaced (2–5 L + 2–10 l/cm at mid-radius); edges even, concolorous, can be blackening. *Stipe* 17–60 × 11–25 mm, cylindrical or slightly tapering up- or downwards, firm and fleshy, stout, solid; surface smooth, white, browning when older. *Context* c. up to 10 mm thick at mid-radius of the pileus, firm, white, strongly and relatively rapidly reddening, later blackening (turning completely black), when old colour change can be slower, surface of pileus and stipe can also be redden-

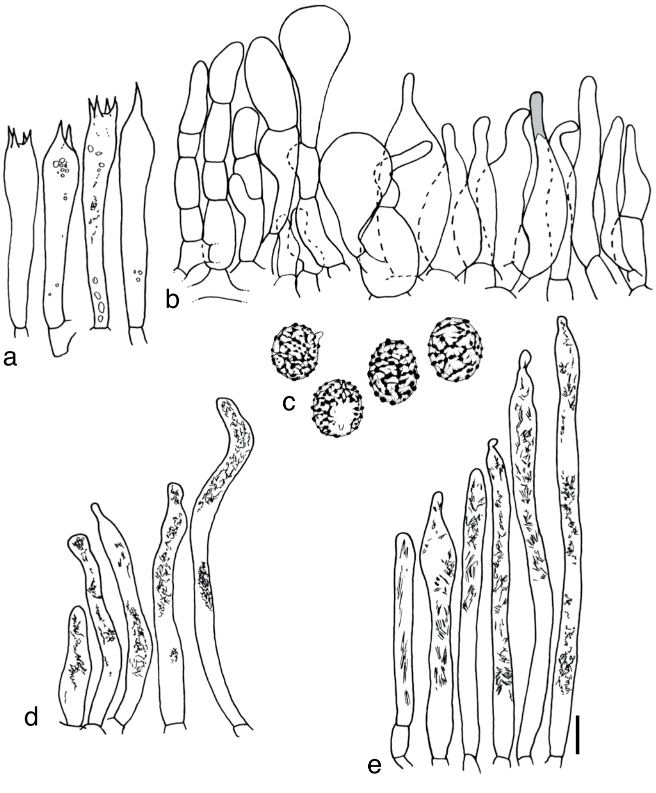

Fig. 28 *Russula nigricans*, micromorphology of the hymenium. a. Basidia (RDL 17-001, RDL 18-061); b. marginal cells (RDL 16-005, RDL 17-002, RDL 17-004, RDL 17-005); c. basidiospores (RDL 17-003, RDL 17-008); d. cystidia near lamellae edges (RDL 16-002); e. cystidia on lamellae sides (RDL 16-004/1). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

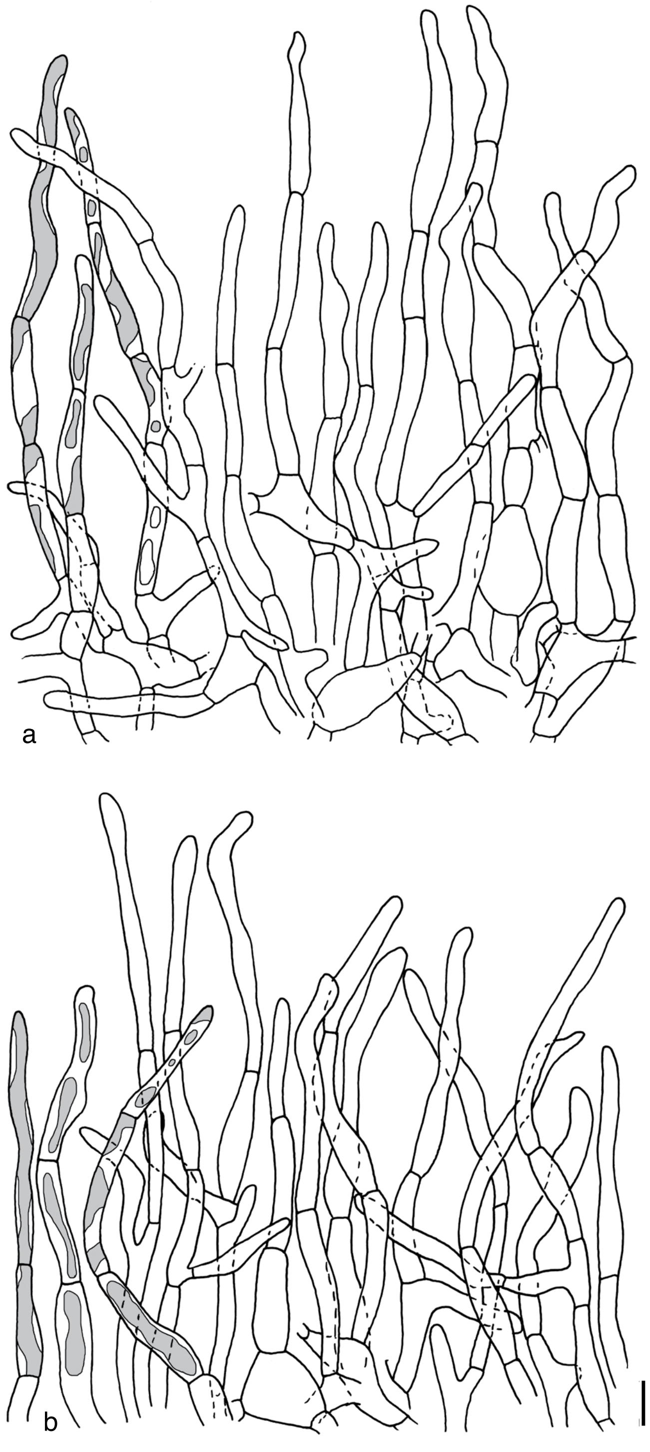

Fig. 29 *Russula nigricans*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 17-003); b. near the pileus centre (RDL 17-001). — Scale bar = 10 µm.

ing when touched; turning greenish with $FeSO_4$ (sometimes first an orange reaction can be present, but this is probably the start of the normal reddening reaction from touching), slightly yellowish with KOH, immediately dark blue with guaiac (strong reaction, +++); taste mild; odour not distinct, musty, sometimes somewhat unagreeable (sweaty feet), when young there can be a slightly fruity component. *Spore print* white (Ia). Very old basidiomes remain for a long time, completely pitch black, looking as if mummified.

Basidiospores (5.7–)6.5–*7.0*–7.5(–8.6) × (4.5–)5.2–*5.7*–6.2 (–7.5) µm, broadly ellipsoid, Q = (1.02–)1.15–*1.23*–1.31(–1.43); ornamentation of low, dense to very dense ((5–)7–13(–19) in a 3 µm diam circle) amyloid warts, 0.1–0.5 µm high, subreticulate, abundantly fused into chains ((0–)2–7(–11) fusions in a 3 µm diam circle), abundantly connected by short, fine line connections ((0–)2–7(–11) in a 3 µm diam circle); suprahilar spot medium-sized, not amyloid. *Basidia* (43–)49.6–*53.7*–57.8(–64) × (7–)8.2–*9.0*–9.8(–12) µm, narrowly clavate, 4-spored, 1- and 2-spored basidia can be present and abundant or absent. *Hymenial cystidia* (48–)57.9–*74.6*–91.3(–125) × (5–)5.3–*6.3*–7.3(–10) µm, cylindrical to narrowly fusiform or narrowly clavate, flexuous, apically mainly obtuse or with central appendage, thin-walled; content heteromorphous, oily, fragmented in multiple fine crystalline-like masses to banded, blackening in sulfovanillin; cystidia near the lamellae edges, (21–)44.7–*57.1*–69.5(–85) × (5–)5.1–*5.9*–6.7(–9) µm, similar in shape and content as on lamellae sides, apically obtuse. *Lamellae edges* sterile; *marginal cells* (13–)25.2–*35.5*–45.8(–62) × (4–)5.2–*9.5*–13.8(–29) µm, well differentiated, variable in shape, clavate to broadly clavate, or cylindrical to broadly cylindrical or broadly subulate and flexuous, thin-walled; sometimes containing brown pigments when old. *Pileipellis* orthochromatic in Cresyl Blue, 90–190 µm deep, moderately delimited from trama; subpellis not delimited from suprapellis; hyphae 4–7 µm wide near trama, moderately dense, irregularly oriented, somewhat more parallel towards the trama; pigmented in all parts, without gelatinous coating. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, slender, with multiple septa, often branched at the bases, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (23–)38.6–*50.5*–62.4(–81) × (3–)4.2–*5.2*–6.2(–8) µm, narrowly cylindrical to subulate, on average apically constricted to 3.6 µm; subterminal cells and the cells below often shorter, often gradually broader, sometimes slightly inflated, subterminal cells sometimes branched, cells below regularly branched. Hyphal terminations near the pileus centre slightly slenderer; terminal cells (20–)33.2–*49.8*–66.4(–87) × (3–)3.5–*4.4*–5.3(–7) µm, subterminal cells and cells below not gradually wider like near pileus margin. *Pileocystidia* near the pileus margin very rare to widely dispersed, inconspicuous, usually 1-celled but rarely 2-celled, (26–)37.8–*48.8*–59.8(–83) × (4–)4.6–*5.4*–6.2(–8) µm, subulate to narrowly fusiform, sometimes slightly flexuous, apically with 1–2 eccentric appendages, rarely without appendages and only tapering towards the top; content very scattered, heteromorphous, oily, fragmented in multiple fine masses to banded, blackening or greying in sulfovanillin but hard to observe due to limited content; cystidia near the pileus centre rare to dispersed, similar as near pileus margin, (24–)30.5–*40.5*–50.5(–80) × (4–)4.2–*4.9*–5.6(–7) µm. Oleiferous hyphae containing brown pigments and cystidioid hyphae present in the trama.

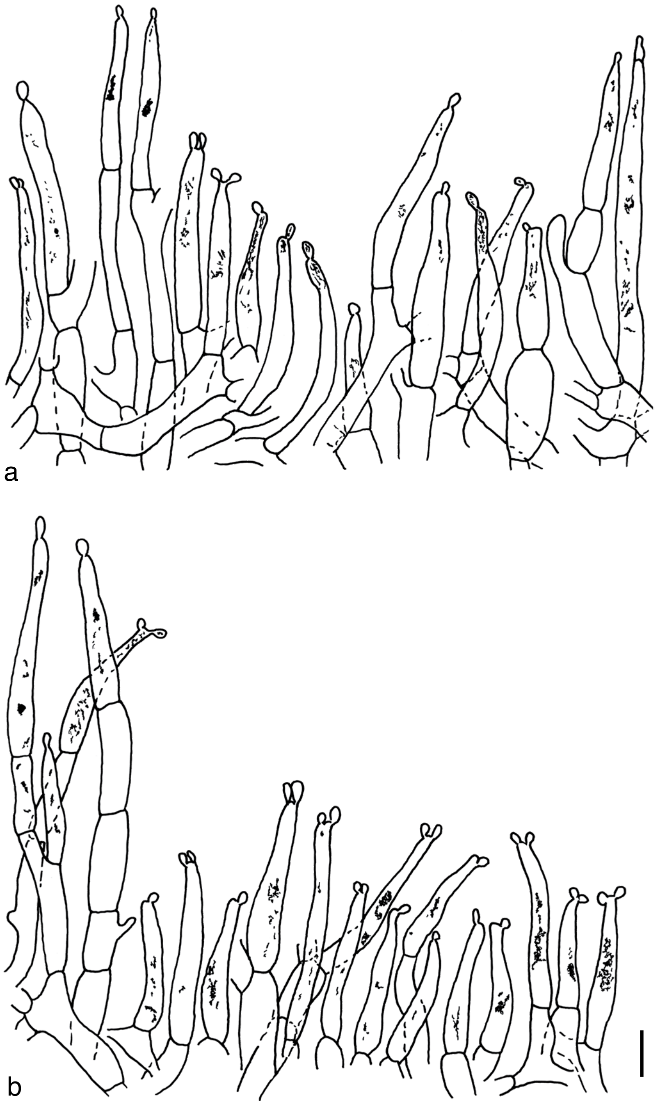

Fig. 30 *Russula nigricans*, pileocystidia. a. Near the pileus margin (RDL 17-008); b. near the pileus centre (RDL 17-008). — Scale bar = 10 µm.

Ecology & Distribution — This is probably the most common European *Compactae* species, fruitbodies of the species appear not only frequently but also in high numbers in various types of forests. Based on our data and our UNITE search, the species is distributed in Western, Central and Eastern Europe, the Iberian and Apennine Peninsulas, Scandinavia, the Baltic countries and the British Islands. It forms ectomycorrhizae with conifers and deciduous trees in temperate and hemiboreal/submontane areas. It is also detected from ectomycorrhizal root tips of Mediterranean woody plants such as *Quercus suber* and *Halimium lasianthum*.

Specimens examined. Belgium, Limburg, Vliermaalroot (Kortessem), Jongenbos, N50°52'45.00" E05°26'21.00", alt. 56 m, in old deciduous forest with *Betula*, *Populus alba*, *Populus tremula* and *Quercus robur*, 27 Oct. 2016, *R. De Lange*, RDL 16-002 (GENT); ibid., 27 Oct. 2016, *R. De Lange*, RDL 16-004 (GENT); ibid., 27 Oct. 2016, *R. De Lange*, RDL 16-005 (GENT); ibid., *R. De Lange*, RDL 16-007 (GENT); ibid., 27 Oct. 2016, *R. De Lange*, RDL 16-009 (GENT); ibid., 27 Oct. 2016, *R. De Lange*, RDL 16-011 (GENT); Luxemburg, Engreux, with *Abies alba* and *Picea abies*, 16 Sept. 2016, *R. De Lange*, RDL 17-001 (GENT); ibid., with *Fagus sylvatica*, 16 Sept. 2016, *R. De Lange*, RDL 17-002 (GENT); Oost-Vlaanderen, Ronse, Muziekbos, N50°45'48.00" E03°38'24.00", alt. 110–155 m, with *Fagus sylvatica*, 24 Sept. 2017, *R. De Lange*, RDL 17-003 (GENT); ibid., 24 Sept. 2017, *R. De Lange*, RDL 17-004 (GENT); ibid., 24 Sept. 2017, *R. De Lange*, RDL 17-005 (GENT); ibid., 24 Sept. 2017, *R. De Lange*, RDL 17-007 (GENT); Limburg, Vliermaalroot (Kortessem), Jongenbos, N50°52'45.00" E05°26'21.00", alt. 56 m, in old deciduous forest with *Alnus glutinosa*, *Betula*, *Carpinus betulus*, *Corylus avellana*, *Fagus sylvatica*, *Populus canescens*, *Populus tremula*, *Quercus robur*, *Quercus rubra* and *Tilia*, 26 Sept. 2017, *R. De Lange*, RDL 17-008 (GENT); Oost-Vlaanderen, Ronse, Sint-Pietersbos, N50°45'56.00" E03°38'05.00", alt. 100–130 m, with *Fagus sylvatica*, 08 Sept. 2018, *R. De Lange*, RDL 18-050 (GENT); ibid., 08 Sept. 2018, *R. De Lange*, RDL 18-051 (GENT); Limburg, Vliermaalroot (Kortessem), Jongenbos, N50°52'45.00" E05°26'21.00", alt. 56 m, in old deciduous forest with *Populus alba* and *Populus tremula*, 07 Nov. 2018, *R. De Lange*, RDL 18-061 (GENT). – Germany, Thuringia, Ilmenau, Oberpörlitz, N50°42'32.63" E10°54'5.61", alt. 550 m, coniferous forest with *Picea abies* and *Pinus sylvestris* on acidic, sandy soil over sandstone bedrock, 07 Sept. 2020, *F. Hampe* & *C. Manz* FH 20-066 (GENT, FH). – ITALY, Tuscany, Montioni, Nature reserve Parco naturale di Montioni, N43°02'48.00" E10°43'47.00", alt. 45–80 m, 11 Nov. 2016, *R. De Lange*, RDL 16-069 (GENT).

Notes — *Russula nigricans* is probably the most common and best known representative of *Russula* subg. *Compactae* in Europe. It has a very typical field appearance with the large sturdy basidiomata, intense reddish context discoloration before strongly blackening and distant, thick lamellae. It can be confused in the field with *R. thuringiaca*, but the latter has a distinct salmon pinkish tinge in the lamellae and larger pileocystidia. The epitype (Melot 2021a) was not included in our phylogenetic analyses (Fig. 1) because of a missing ITS sequence, but the available *RPB2* and *EF-1α* sequences have a perfect match with other European samples of *R. nigricans* included in our study. Regarding nomenclature, see the notes on *R. adusta* and the references provided there.

Russula picrophylla De Lange & Kleine, *sp. nov.* — MycoBank MB 847332; Fig. 31–35

Etymology. Named after the burning acrid taste in the lamellae.

Typus. ITALY, Tuscany, Livorno, Montioni, Nature reserve Parco naturale di Montioni, N43°02'48.00" E10°43'47.00", alt. 45–80 m, with *Quercus cerris* and *Quercus ilex*, 09 Nov. 2016, *R. De Lange*, RDL 16-049 (GENT - holotype).

Diagnosis — *Russula picrophylla* has a similar field aspect to *R. acrifolia*, characterised by the viscid and somewhat greasy appearance of the pileus surface, the reddish discoloration of the whole context and the basidiomata surfaces, and the distinctly acrid taste even in the stipe which distinguishes it from the other European species within *R.* subg. *Compactae*. It can be distinguished from *R. acrifolia* by microscopic characters: it has smaller spores, abundant pileocystidia at the pileus centre and larger, partly subulate/attenuated hyphal terminations near the pileus margin. *Russula*

Fig. 31 Basidiomata of *Russula picrophylla* (a. 2018 ST02; b. FH 2005 ST02; c–d. FH 2008 ST03; e. FH RUS 14081335; f–g. RDL 16-031; h–i. RDL 16-034; j. JK RUS 13090806; k. RDL 16-049, holotype; l. RUS 18111501; m. RUS 18111502; n. RDL 18-023; o. RDL 18-029). — Photos by: a–b J. Girwert; c–e, m F. Hampe; f–i, k, n–o R. De Lange; j, l J. Kleine.

roseonigra is another macroscopically similar species, which has more prominent spore ornamentation and usually a less acrid taste.

Pileus large, 45–135 mm diam, plano-convex to infundibuliform, depressed, margin straight to inflexed, when young more involute, smooth; pileus surface smooth, viscid when moist, cuticle only peeling at the margin, from yellowish white, sand coloured (4A2, 4B3) to greyish orange, orange grey, brownish grey (5B2–3, 6C2) to café-au-lait, light brown (5D4–6, 6C2) to yellowish brown, bronze brown (5E4–5, 5E8) to umber, dark brown, chocolate (5F8, 6E4–6, 6F4, 6F6). *Lamellae* segmentiform to subventricose, up to 4 mm deep, narrowly adnate, white to pale cream when older, with pinkish tinge, reddening and finally blackening where bruised or injured, sometimes containing yellowish spots when old; with numerous lamellulae of different lengths in a regular pattern; moderately distant to dense (4–10 L + 4–8 l/cm at mid-radius); edges even, concolorous. *Stipe* 20–65 × 13–35 mm, cylindrical to tapering downwards, firm and fleshy, solid; surface smooth, white, browning when older. *Context* c. up to 8 mm thick at mid-radius of the pileus, firm, white, turning moderately to strongly orange red, later blackening (greying), when old colour change possibly slower, surface of pileus and stipe reddening when bruised; turning greenish with $FeSO_4$ (sometimes first some orange reaction), slightly yellowish with KOH, immediately dark blue with guaiac (strong reaction, +++), red with formalin; taste very acrid (burning acrid); odour fruity. *Spore print* white (Ia).

Basidiospores (5.8–)6.6–*7.1*–7.6(–8.3) × (4.6–)5.2–*5.7*–6.3(–7.1) µm, broadly ellipsoid, Q = (1.12–)1.17–*1.24*–1.31(–1.44); ornamentation of low, very dense ((9–)10–13(–14) in a 3 µm diam circle) amyloid warts, 0.2–0.6 µm high, subreticulate, abundantly fused into chains ((2–)3–6(–7) fusions in a 3 µm diam circle), abundantly connected by short, fine line connections ((1–)2–7(–8) in a 3 µm diam circle); suprahilar spot small, not amyloid. *Basidia* (45–)48.4–*52.2*–56.0(–62) × 9.6–*10.5*–11.1(–12) µm, narrowly clavate, 4-spored. *Hymenial cystidia* (50–)59.7–*70.2*–80.7(–100) × (6–)6.7–*7.2*–7.7(–8) µm, narrowly fusiform, flexuous, apically tapering towards the top or with one or double constriction, thin-walled; content heteromorphous, oily, fragmented in multiple crystalline-like masses, weakly blackening in sulfovanillin; cystidia near the lamellae edges, (33–)45.0–*51.7*–58.4(–65) × 6.5–*7.4*–8.3(–11) µm, cylindrical to narrowly fusiform, flexuous, more irregular in shape, apically tapering towards the top with one or double constriction, thin-walled; content as on lamellae sides. *Lamellae edges* fertile, but with only few basidia; *marginal cells* (10–)13.4–*16.8*–20.2(–25) × (4–)4.4–*5.2*–6.0(–7) µm, poorly differentiated, cylindrical to narrowly clavate, sometimes flexuous, thin-walled. *Pileipellis* orthochromatic in Cresyl Blue, 110–300 µm deep, clearly delimited from trama; subpellis not delimited from suprapellis; hyphae 3–5 µm wide near trama, dense near trama, gradually less dense to intermediate towards surface, parallel and horizontal near trama, irregular near surface; pigmented in all parts, some gelatinous matter can be present. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, slender, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (27–)47.1–*61.3*–75.5(–92) × (4–)4.8–*6.1*–7.4(–9) µm, narrowly cylindrical to subulate, on average apically constricted to 3.8 µm (average difference of 2.3 µm between maximum width and width of the tips); subterminal cells and the cells below similar in length or larger, rarely shorter, broader, subterminal cells sometimes branched. Hyphal terminations near the pileus centre slenderer and apically hardly attenuated; terminal cells (29–)42.3–*57.5*–72.7(–95) × (3–)3.2–*3.9*–4.6(–6) µm, narrowly cylindrical, subterminal cells and cells below similar in length and width, rarely branched. *Pileocystidia* near the pileus margin moderately numerous, 1-celled, (36–)47.1–*63.2*–79.3(–100) × (4–)4.7–*5.6*–6.5(–9) µm, cylindrical to subulate, rarely fusiform, sometimes slightly flexuous, apically with one central or 1–3 eccentric appendages, sometimes even with double appendages, rarely obtuse or

Fig. 32 Aquarelle of *Russula picrophylla* collection MxM R-9154 (KR-M-0071292). — Reproduced from Marxmüller 2014 with permission from the author.

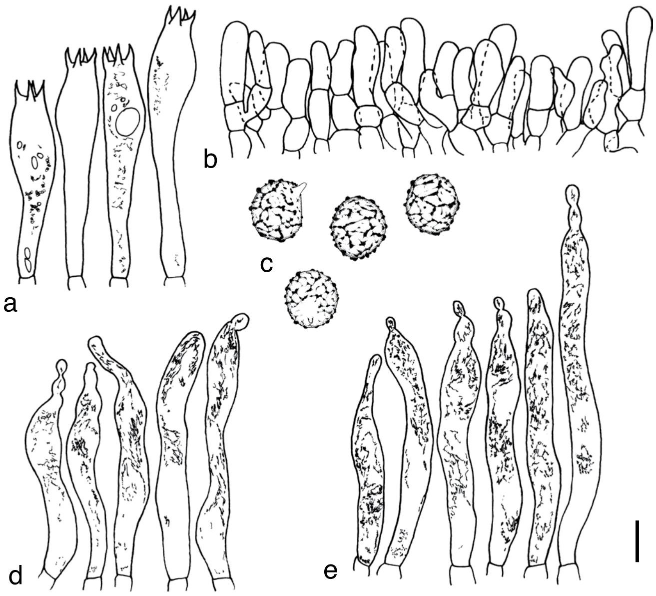

Fig. 33 *Russula picrophylla*, micromorphology of the hymenium. a. Basidia (RDL 16-049); b. marginal cells (RDL 16-049); c. basidiospores (RDL 16-049); d. cystidia near lamellae edges (RDL 16-049, RDL 18-029); e. cystidia on lamellae sides (RDL 16-031, RDL 16-049). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

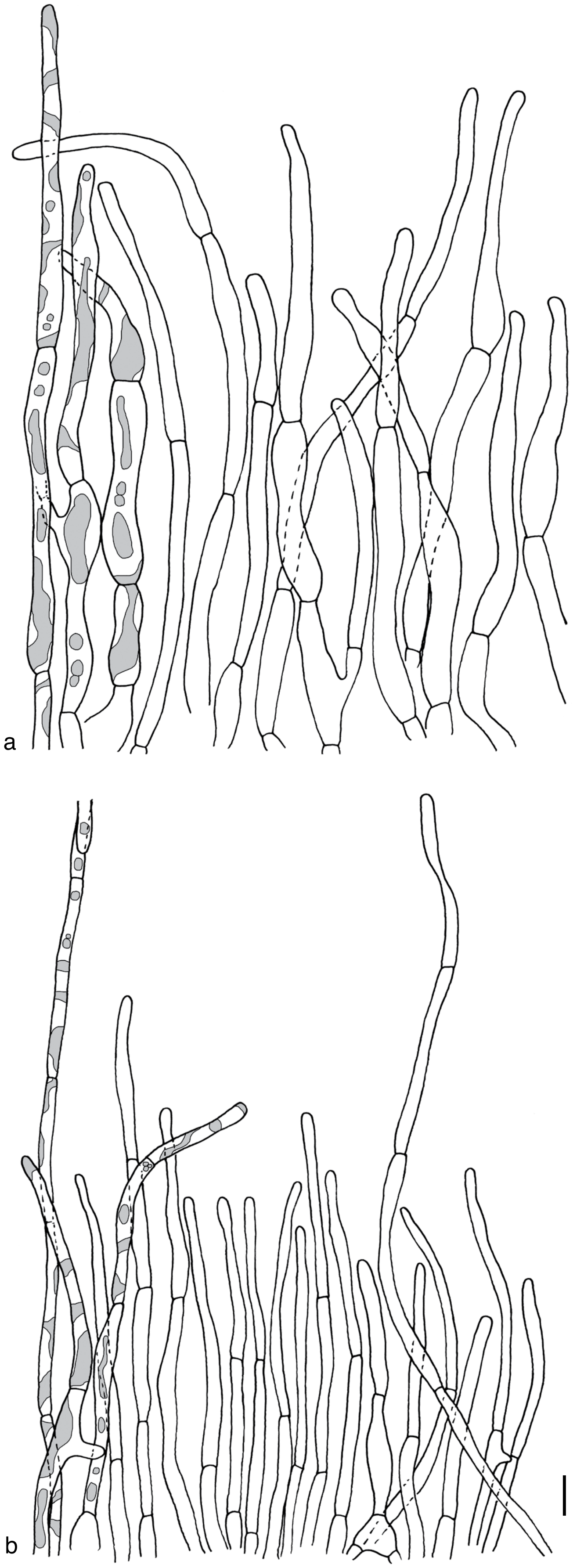

Fig. 34 *Russula picrophylla*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 16-049); b. near the pileus centre (RDL 16-049). — Scale bar = 10 µm.

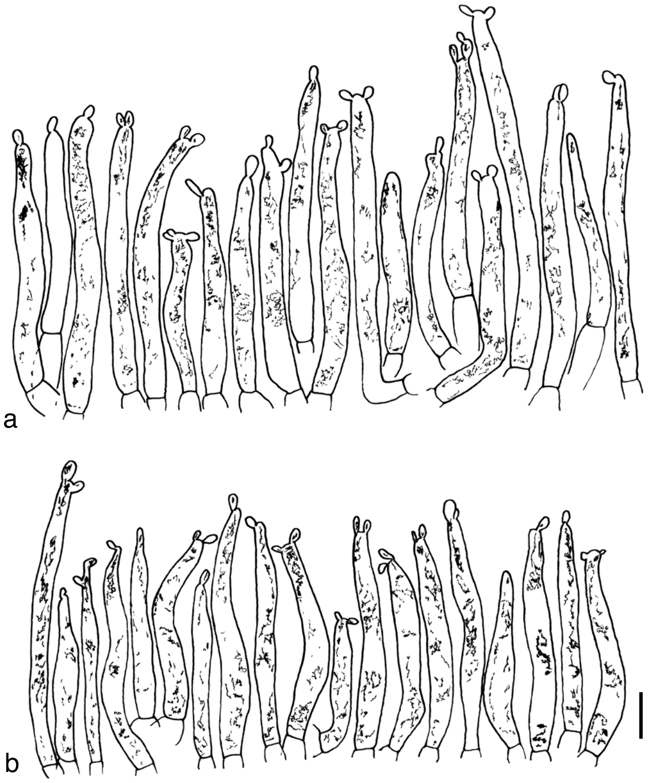

Fig. 35 *Russula picrophylla*, pileocystidia. a. Near the pileus margin (RDL 16-049); b. near the pileus centre (RDL 16-049). — Scale bar = 10 µm.

slightly tapering towards the top; content heteromorphous, oily, fragmented in multiple masses, weakly blackening in sulfovanillin but hard to observe due to limited content; cystidia near the pileus centre numerous, (30–)39.4–*49.8*–60.2(–97) × (4–)4.5–*5.3*–6.1(–7) µm, similar in shape and content. Oleiferous hyphae containing brown pigments and cystidioid hyphae present in the trama.

Ecology & Distribution — In Mediterranean, temperate to boreal or montane deciduous and coniferous forests, possibly with a certain preference for calcareous soils. Our collections originated from five European countries and seven more countries are represented in public sequence data. It seems that the species has a wide host range, among the confirmed plants from ectomycorrhizal sequences are *Pinus sylvestris*, Mediterranean evergreen and temperate deciduous oak species, heterotrophic plants and orchids (Table 2).

Additional specimens examined. FRANCE, Île-de-France, Yvelines, Saint-Nom-la-Bretèche, Forêt de Marly, N48°51'35.74" E2°2'46.02", alt. 101–182 m, deciduous forest, 01 Sept. 1994, *H. Marxmüller & H. Romagnesi*, MxM R-01091994 (KR-M-0071188); Auvergne-Rhône-Alpes, Drôme, Gigors-et-Lozeron, Le Savel, mixed forest with *Pinus sylvestris* and *Quercus pubescens* on sandy soil, 04 Nov. 1991, *H. Marxmüller*, MxM R-9154 (KR-M-0070921) (in Marxmüller 2014 as *R. acrifolia*). – GERMANY, Thuringia, Klettbach south of Erfurt, N50°54'42.73" E11°9'47.14", alt. 390 m, deciduous forest on loamy soil over calcareous bedrock (Muschelkalk), 30 Aug. 2005, *J. Girwert*, FH 2005 ST02 (GENT, FH); Thuringia, Klettbach south of Erfurt, Stiefelburg, N50°54'5.83" E11°10'49.39", alt. 455 m, mixed forest with *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris* on loamy soil over calcareous bedrock (Muschelkalk), 27 Sept. 2008, *F. Hampe & J. Girwert*, FH 2008 ST03 (GENT, FH); Thuringia, Erfurt, Rohda-Haarberg, Büssleber-Holz, N50°56'2.80" E11°8'38.63", alt. 380 m, deciduous forest with *Carpinus betulus*, *Quercus robur* and *Quercus petraea* on calcareous soil, 13 Aug. 2013, *F. Hampe*, FH RUS 14081335 (GENT, FH); Bavaria, Oberallgäu, Reichenbach bei Oberstdorf, N47°26'19.9" E10°18'5.3", alt. 950 m, montane mixed forest with *Fagus sylvatica* and *Picea abies* on calcareous soil, 08 Sept. 2013, *J. Kleine*, JK RUS 13090806 (hb. Jesko Kleine). – ITALY, Tuscany, Livorno, Piombino, with *Quercus ilex* and *Quercus suber*, 07 Nov. 2016, *R. De Lange*, RDL 16-027 (GENT); Tuscany, Livorno, Sughereta della Lattaia, N42°58'40.00" E11°6'3.00", alt. 20–40 m, with *Quercus suber*, 08

Nov. 2016, *R. De Lange*, RDL 16-031 (GENT); ibid., 08 Nov. 2016, *R. De Lange*, RDL 16-034 (GENT); Montioni, Nature reserve Parco naturale di Montioni, N43°02'48.00" E10°43'47.00", alt. 45–80 m, 09 Nov. 2016, *R. De Lange*, RDL 16-056 (GENT); ibid., 09 Nov. 2016, *R. De Lange*, RDL 16-057 (GENT); ibid., 09 Nov. 2016, *R. De Lange*, RDL 16-058 (GENT). – Spain, Mallorca, north of Banyalbufar, N39°41'1.3" E2°32'23.7", 300 m a.s.l., mixed forest with *Quercus ilex* s.lat. and *Pinus halepensis*, on calcareous soil, 15 Nov. 2018, *F. Hampe* & *J. Kleine*, RUS 18111501 (hb. Jesko Kleine, GENT); ibid., 15 Nov. 2018, *F. Hampe* & *J. Kleine*, RUS 18111502 (hb. Jesko Kleine, GENT); Morella, Pereroles, Ombria del Pi Rois, associated with *Pinus nigra* and *Quercus ilex*, 18 Oct. 2010, *S. Adamčík*, (SAV F-3234). – Sweden, Ånge NO, Balbodbäcken west of Nedertjärnen, N62°35'57.00" E15°47'46.00", alt. 261 m, with *Betula*, *Picea abies and Pinus*, 29 Aug. 2018, *J. Girwert*, FH-2018-ST02 (GENT); Tunsved, N62°57'17" E15°4'44", alt. 320 m, with *Picea abies*, 01 Sept. 2016, *L. Delgat*, LD 16-026 (GENT); ibid., 01 Sept. 2016, *L. Delgat*, LD 16-027 (GENT); Ånge NO, East of Långberget, habitat protection area, N62°32'26.4" E16°04'17.6", alt. 150 m, with *Picea abies*, 28 Aug. 2018, *R. De Lange*, RDL 18-023 (GENT); ibid., with *Betula* and *Picea abies*, 28 Aug. 2018, *R. De Lange*, RDL 18-026 (GENT); Ånge NO, Orråsberget North, Husmyrbäcken-Husmyra, N62°34'22.37" E15°47'46.61", alt. 218 m, 29 Aug. 2018, *R. De Lange*, RDL 18-029 (GENT); ibid., 31 Aug. 2018, *R. De Lange*, RDL 18-049 (GENT).

Notes — Both *R. picrophylla* and the closely related and very similar *R. acrifolia* are apparently very common and part of the historical data of the well-known *R. acrifolia* probably refers to *R. picrophylla* (e.g., Marxmüller 2014).

Russula roseonigra Pidlich-Aigner, Österr. Z. Pilzk. 24: 76. 2015 — Fig. 36a–f, 37–39

Typus. Austria, Niederösterreich, Pottenstein, Herrgottskreuz, Totenkopf, N47°58'30.00" E16°07'30.00", alt. 380 m, in mixed forest with *Carpinus betulus*, *Fagus sylvatica*, *Picea abies*, *Pinus* and *Quercus*, 29 Aug. 2010, *H. Pidlich-Aigner*, (WU36644 - holotype).

Pileus large, 40–105 mm diam, convex when young, plano-convex, depressed when older, margin straight to inflexed, when young more involute, smooth to slightly undate; pileus surface smooth, when dry dull, when moist viscid, cuticle hardly peeling, often with paler, sand coloured (4B3) marginal zone, darker towards the centre, from orange grey, brownish grey, brownish

Fig. 36 Basidiomata. a–f. *Russula roseonigra* (a. RDL 16-024; b–c. FH RUS 14091311; d. FH 2014 ST01; e–f. WU36644, holotype). — g–o. *Russula thuringiaca* (g–h. FH 20-056; i. FH 2011 ST01; j–k. FH 2014 ST02, holotype; l–m. FH 2010 ST06; n. FH 2008 ST02; o. FH 19-032). — Photos by: a R. De Lange; b–c, g–i, n–o F. Hampe; d, j–m J. Girwert. — e–f Reproduced from Pidlich-Aigner (2015) with permission from the editor.

orange, dark blonde (5B2, 5C2–5, 5D4) to light brown, yellowish brown, sod brown (5D5, 5E5, 5F5). *Lamellae* segmentiform to subventricose, up to 5 mm deep, narrowly adnate, white to pale cream when older; with numerous lamellulae of different lengths in a more or less regular pattern; locally anastomosing, sometimes furcating; moderately distant to moderately dense (6–9 L + 5–7 l/cm at mid-radius); edges even, concolorous. *Stipe* 30–60 × 10–25 mm, cylindrical or slightly tapering downwards, firm and fleshy, solid; surface smooth to somewhat pruinose, white, browning when older. *Context* c. up to 10 mm thick at mid-radius of the pileus, moderately firm, white, slowly reddening, later slowly blackening (first more greying), surface of pileus and stipe and lamellae can also be reddening when touched; turning slowly dirty orange with $FeSO_4$, slightly yellowish with KOH, immediately dark blue with guaiac (strong reaction, +++), relatively quickly brown with phenol; taste slightly acrid, stronger in the lamellae; odour slightly fruity. *Spore print* white (Ia).

Basidiospores (7.1–)7.4–*7.9*–8.3(–9.2) × (5.8–)6.0–*6.4*–6.8(–7.4) µm, broadly ellipsoid, Q = (1.14–)1.19–*1.24*–1.29(–1.40); ornamentation of low to normal, very dense ((8–)10–17(–19) in a 3 µm diam circle) amyloid warts, 0.2–0.8(–1) µm high, many warts reaching at least 0.5 µm, subreticulate, abundantly fused into chains ((3–)4–10(–12) fusions in a 3 µm diam circle), abundantly connected by short, fine line connections ((2–)2–8(–11) in a 3 µm diam circle); suprahilar spot medium-sized, not amyloid. *Basidia* (39–)42.8–*47.2*–51.6(–56) × (9–)10.0–*10.9*–11.8(–12) µm, narrowly clavate, 4-spored. *Hymenial cystidia* (55–)58.3–*69.1*–79.9(–98) × (6–)6.5–*7.4*–8.3(–9) µm, cylindrical to narrowly fusiform, sometimes slightly flexuous, apically with one central appendage or constriction, rarely with double appendage or somewhat bifurcating or tapering towards the top, thin-walled; content heteromorphous, oily, fragmented in multiple crystalline-like masses, blackening in sulfovanillin; cystidia near the lamellae edges, (33–)38.7–*44.5*–50.3(–55) × (5–)6.2–*7.4*–8.6(–9) µm, cylindrical to narrowly fusiform or narrowly clavate, flexuous, apically obtuse or with one central or eccentric appendage or with double constriction, thin-walled; content as on lamellae sides but sometimes very scattered. *Lamellae edges* sterile; *marginal cells* (27–)27.9–*32.4*–36.9(–40) × (5–)5.7–*6.9*–8.1(–9) µm, narrowly fusiform to subulate, flexuous, thin-walled. *Pileipellis* orthochromatic in Cresyl

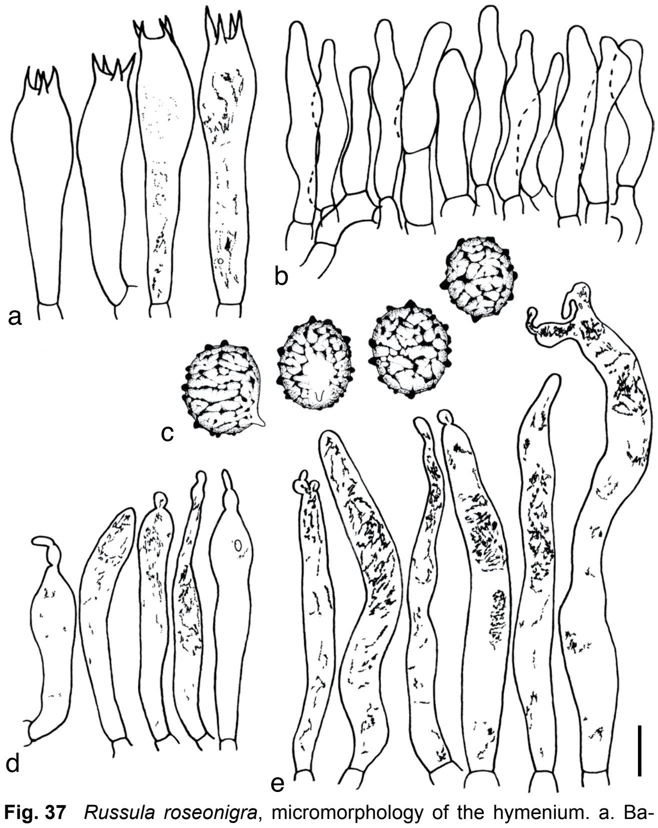

Fig. 37 *Russula roseonigra*, micromorphology of the hymenium. a. Basidia (WU36644, holotype); b. marginal cells (WU36644); c. basidiospores (WU36644); d. cystidia near lamellae edges (WU36644); e. cystidia on lamellae sides (RDL 16-024, WU36644). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

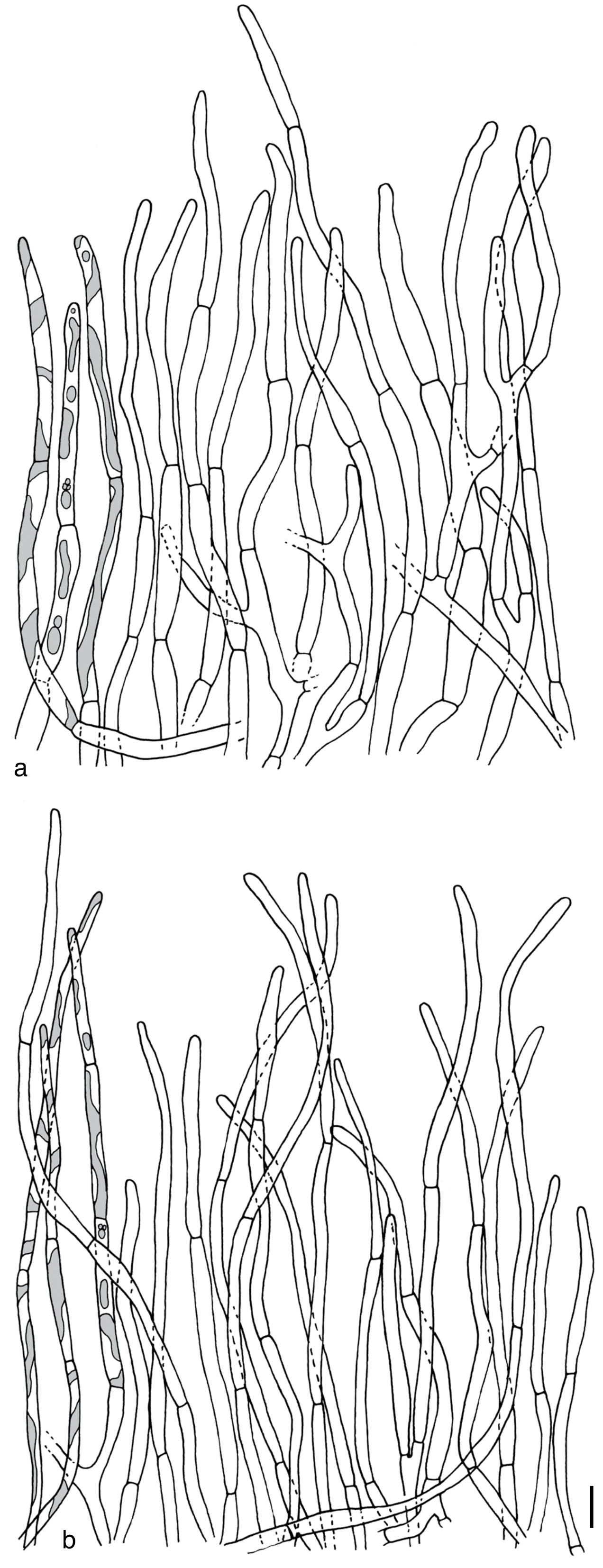

Fig. 38 *Russula roseonigra*, hyphal terminations of the pileipellis. a. Near the pileus margin (WU36644, holotype); b. near the pileus centre (WU36644, holotype). — Scale bar = 10 µm.

Blue, 100–150 µm deep, moderately delimited from trama; subpellis not delimited from suprapellis; hyphae 3–5 µm wide near trama, dense near trama and surface, moderately dense to loose in between, more parallel and horizontal near trama and surface, irregularly oriented in between; pigmented in all parts, some gelatinous matter can be present. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, slender, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (32–)43.8–*57.6*–71.4(–90) × (4–)4.3–*5.3*–6.3(–7) µm, narrowly cylindrical, on average apically constricted to 3.5 µm; subterminal cells and the cells below similar in length and width, subterminal cells regularly branched. Hyphal terminations near the pileus centre slightly slenderer and apically hardly attenuated; terminal cells (32–)39.8–*60.9*–82.0(–115) × (2–)3.0–*3.7*–4.4(–5) µm, narrowly cylindrical, subterminal cells and cells below similar in length and width, less branched. *Pileocystidia* near the pileus margin rare, 1-celled, (36–)44.7–*77.3*–109.9(–123) × (5–)5.7–*7.0*–8.3(–8) µm (n = 9), cylindrical to subulate, slightly flexuous, apically with 1–3 eccentric appendages or one and double eccentric appendage, sometimes tapering towards the top or even bifurcating; content heteromorphous, oily, fragmented in multiple masses, greying in sulfovanillin; cystidia near the pileus centre rare to widely dispersed, (35–)38.3–*50.3*–62.3(–85) × (4–)4.5–*5.2*–5.9(–6) µm, similar in shape and content, apically with 1–2 eccentric appendages. Oleiferous hyphae containing brown pigments and cystidioid hyphae present in the trama.

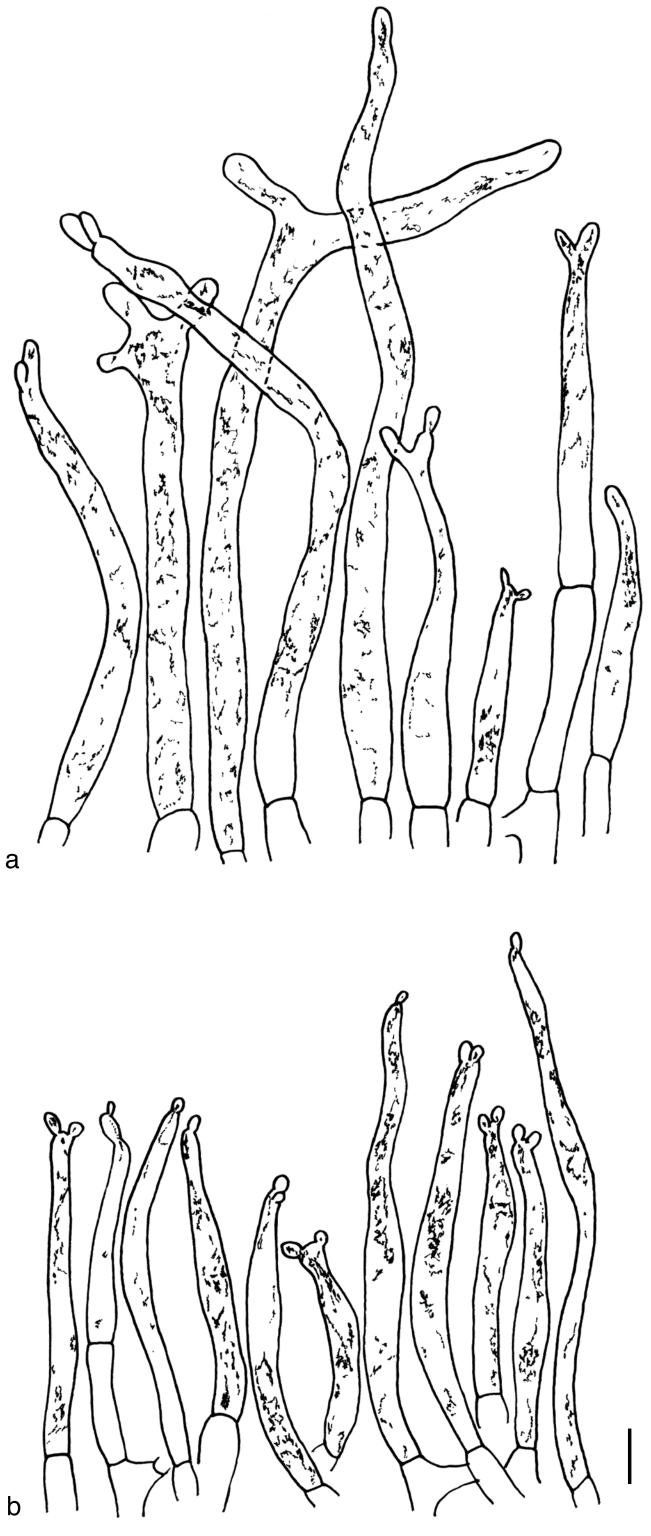

Fig. 39 *Russula roseonigra*, pileocystidia. a. Near the pileus margin (WU36644, holotype); b. near the pileus centre (WU36644, holotype). — Scale bar = 10 µm.

Ecology & Distribution — This species was described relatively recently from Austria (Pidlich-Aigner 2015), but our collections expand the known distribution to Czech Republic, France, Germany and Italy, and the UNITE search reveals also its occurrence in Estonia, Hungary, Latvia, Portugal, Slovenia, Spain, Sweden and Switzerland. Sequences from ectomycorrhizal root tips show its association with *Pinus* and *Quercus*, but we also retrieved sequences from roots of orchids and heterotrophic plants.

Additional specimens examined. Czech Republic, Southern Moravia, Okres Břeclav, Miloviká stráň, N48°50'52.30" E16°41'38.00", alt. 230 m, in broadleaf forest with prevalent *Quercus pubescens* and *Sorbus torminalis*, 13 Sept. 2014, *F. Hampe* & *J. Kleine*, FH RUS 14091311 (hb. Jesko Kleine). – France, Auvergne-Rhône-Alpes, Drôme, Gigors-et-Lozeron, Le Savel, with *Pinus* sp., 20 July 1993, *H. Marxmüller*, MxM R-9308 (KR-M-0042973). – Germany, Thuringia, Nauendorf near Erfurt, N50°54'4.67" E11°10'6.34", alt. 365 m, mixed forest with *Quercus petraea*, *Carpinus betulus* and *Picea abies* over calcareous bedrock, 30 July 2014, *J. Girwert*, FH 2014 ST01 (GENT, FH). – Italy, Tuscany, Livorno, Piombino, with *Quercus ilex* and *Quercus suber*, 07 Nov. 2016, *R. De Lange*, RDL 16-024 (GENT).

Notes — *Russula roseonigra* is closely related to *R. acrifolia* and shares its field aspect with the characteristic viscid pileus cuticle, distinct reddening of the context and acrid taste at least in the lamellae. It is distinguished from the other members of the *R. acrifolia* lineage by its more prominent spore ornamentation.

Russula thuringiaca De Lange, F. Hampe & Girwert, *sp. nov.* — MycoBank MB 847333; Fig. 36g–o, 40–42

Etymology. Named after the German Free State of Thuringia, because this species was first only found in this region.

Typus. Germany, Thuringia, south of Erfurt, Schellroda, Aspenbusch, N50°54'55.51" E11°6'15.54", alt. 440 m, deciduous forest with *Fagus sylvatica* on clayey black soil/loess over calcareous bedrock (Muschelkalk), 10 Aug. 2014, *J. Girwert*, FH 2014 ST02 (GENT - holotype).

Diagnosis — The field aspect of *R. thuringiaca* is characterised by the stout habit of the often large-sized basidiomata and the distant lamellae resembling *R. nigricans*. It can be distinguished from the latter by a conspicuous salmon to orange tinge of the lamellae. The only other species with rather strong pinkish or orange tinges of the lamellae is *R. atramentosa*, which differs in the larger hyphal terminations near the pileus margin.

Pileus large, 45–150 mm diam, plano-convex but irregular, centrally depressed, when young more convex, margin straight to inflexed, when young more involute, smooth; pileus surface smooth, (slightly) greasy, shiny, from dark brown, rust brown, cacao brown (7F8, 7F4, 6F8, 6F6, 6E8, 6E6) or grey brown (7F3) to light brown, camel brown, bronze brown, yellowish brown (6D8, 6D–E4, 5E5) to orange grey, yellowish white (5B2, 4A2), sometimes almost completely dark brown, when young sometimes lacking the darker tones. *Lamellae* segmentiform to subventricose, up to 7 mm deep, narrowly adnate, white to pale cream, with a clear and strong pinkish orange (salmon) tinge (on dried specimens often with a strong orange tint); with lamellulae of different lengths; sometimes somewhat locally anastomosing, rarely furcating near the stipe; rather distant to moderately distant (4–7 L + 3–5 l/cm at mid-radius); edges even, concolorous. *Stipe* 35–75 × 20–50 mm, cylindrical or slightly tapering up- or downwards or somewhat inflated at the base, firm and fleshy, stout, solid; surface smooth, white. *Context* c. up to 7 mm thick at mid-radius of the pileus, firm, white, (very) slowly and slightly/weakly reddening (orange red), mostly at first inconspicuous, sometimes only starting after 20–30 min, later slowly greying (or more towards blackening but no strong dark blackening), sometimes greying simultaneously with reddening, surface of the stipe sometimes also slightly/weakly reddening; with $FeSO_4$ variable, turning orange or brown orange, later greying, sometimes green mottling or even planar grey-green reaction, no reaction with KOH, immediately dark blue with guaiac (strong reaction, +++), red/orange on stipe with formalin; taste mild in the context, in the lamellae mild or slightly to moderately acrid; odour not distinct (one fruitbody with iodine smell). *Spore print* white (Ia–b).

Basidiospores (6.9–)7.3–*7.7*–8.1(–9.3) × (5.0–)5.6–*6.0*–6.4 (–7.3) µm, broadly ellipsoid to ellipsoid, Q = (1.18–)1.23–*1.29*–1.35(–1.47); ornamentation of low, very dense ((7–)8–13(–14) in a 3 µm diam circle) amyloid warts, 0.2–0.4 µm high, incomplete reticulum, abundantly fused into chains ((2–)3–7(–9) fusions in a 3 µm diam circle), frequently connected by short, fine line connections (1–5(–7) in a 3 µm diam circle); suprahilar spot medium-sized, not amyloid. *Basidia* (55–)58.9–*64.4*–69.9(–76) × (10–)10.1–*10.8*–11.5(–13) µm, narrowly clavate, 4-spored. *Hymenial cystidia* (55–)65.8–*76.1*–86.4(–93) × (5–)5.5–*6.7*–7.9(–11) µm, cylindrical to narrowly fusiform, rarely subulate, slightly flexuous, apically obtuse, tapering towards the top or with constriction to slightly mucronate, thin-walled; content heteromorphous, oily, fragmented in multiple crystalline-like masses, blackening in sulfovanillin; cystidia near the lamellae edges, (23–)38.2–*51.2*–64.2(–78) × (5–)6.1–*6.9*–7.7(–8) µm, cylindrical to narrowly fusiform, sometimes narrowly clavate, slightly flexuous, more irregular in shape, apically obtuse or with central appendage, or even slightly mucronate, thin-walled; content as on lamellae sides. *Lamellae edges* fertile, but with only few basidia; *marginal cells* (10–)15.9–*24.2*–32.5(–43) × (4–)4.9–*5.8*–6.7(–8) µm, cylindrical to subulate, flexuous, thin-walled. *Pileipellis* orthochromatic in Cresyl Blue, 75–125 µm deep, gradually passing in trama; subpellis not delimited from suprapellis; of moderately dense, irregularly oriented, near

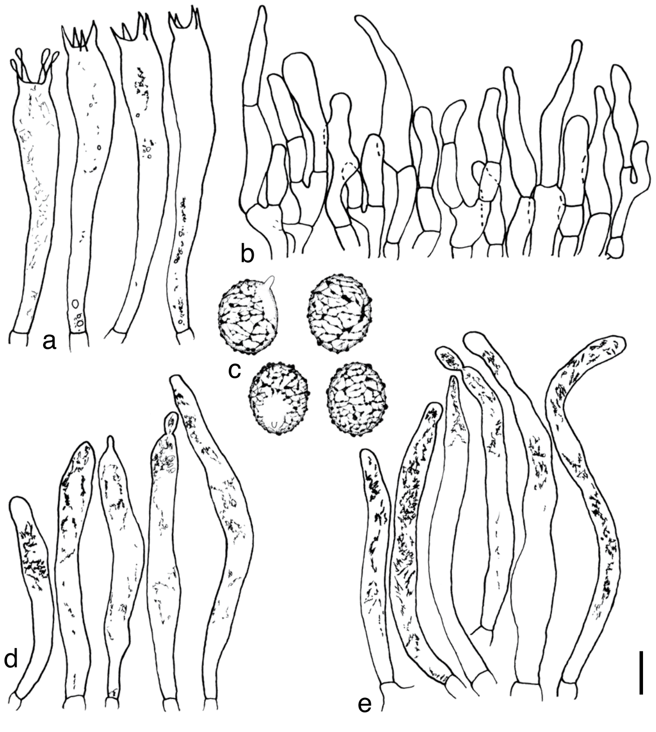

Fig. 40 *Russula thuringiaca*, micromorphology of the hymenium. a. Basidia (FH 2010 ST06); b. marginal cells (FH 2008 ST02, FH 2014 ST02, holotype); c. basidiospores (FH 2010 ST06); d. cystidia near lamellae edges (FH 2008 ST02); e. cystidia on lamellae sides (FH 2010 ST06). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

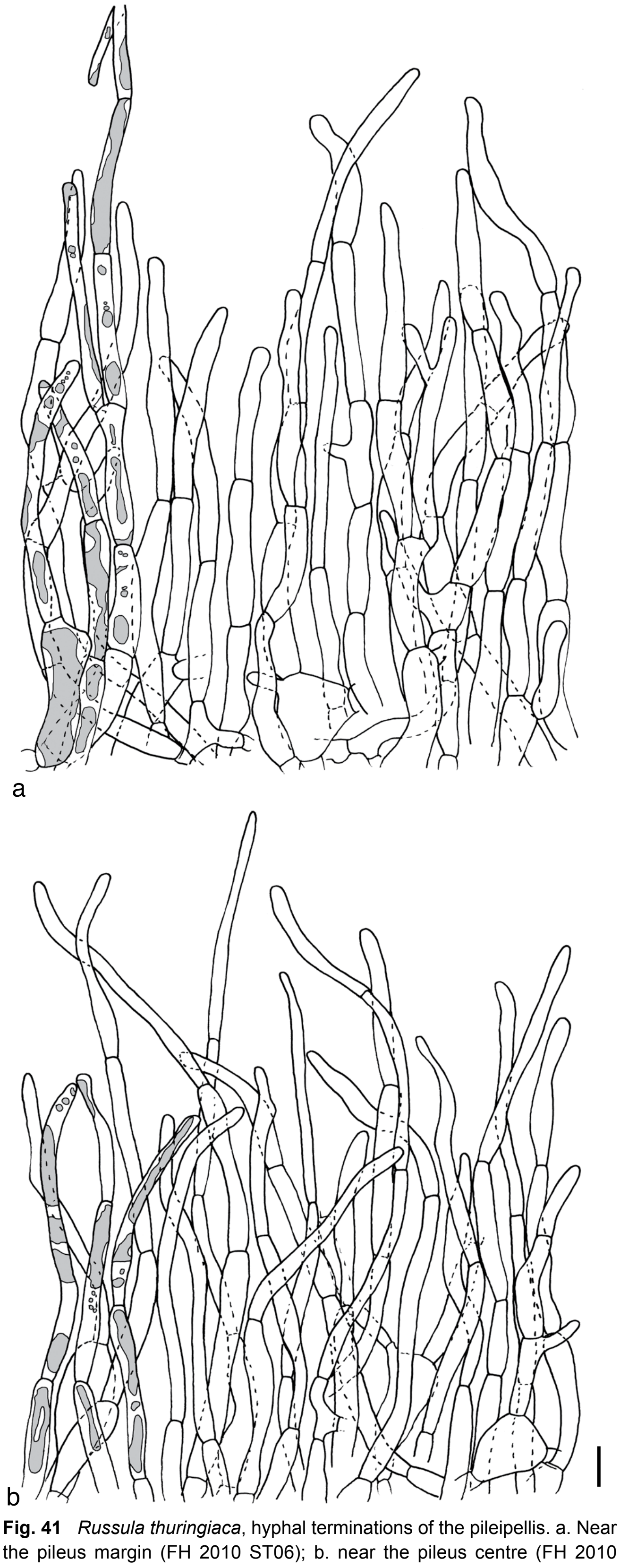

Fig. 41 *Russula thuringiaca*, hyphal terminations of the pileipellis. a. Near the pileus margin (FH 2010 ST06); b. near the pileus centre (FH 2010 ST06). — Scale bar = 10 µm.

trama 4–8 µm wide hyphae; pigmented in all parts, without gelatinous coating. *Acid-resistant incrustations* absent. *Hyphal terminations* near the pileus margin long, slender, with multiple septa, flexuous, thin-walled, filled with irregular refractive bodies containing brown pigments; terminal cells (28–)38.3–*49.3*–60.3(–83) × (4–)4.7–*5.8*–6.9(–8) µm, narrowly cylindrical to subulate, on average apically constricted to 3.7 µm (average difference of 2.1 µm between maximum width and width of the tips); subterminal cells and the cells below usually slightly shorter and broader, subterminal cells sometimes branched but deep in the suprapellis, some inflated cells can be observed deeper in the pileipellis. Hyphal terminations near the pileus centre slightly slender and apically less attenuated; terminal cells larger (31–)43.6–*60.0*–76.4(–105) × 3.9–*4.6*–5.3(–7) µm, subterminal cells less branched, some inflated cells can be observed as near the pileus margin. *Pileocystidia* near the pileus margin extremely rare, 1-celled, (50–)50.9–*68.8*–86.7 × (6–)6.1–*7.8*–9.5(–10) µm (n = 4), cylindrical to subulate, slightly flexuous, apically with constriction or 1–2 eccentric appendages; cystidia near the pileus centre dispersed, 1–2-celled, (39–)43.7–*61.6*–79.5(–114) × (4–)4.5–*5.3*–6.1(–7) µm, cylindrical to subulate, sometimes narrowly fusiform, apically rarely obtuse, or tapering towards the top, mostly with one central or 1–2 eccentric appendages; content scattered, heteromorphous, oily, fragmented in multiple masses, blackening in sulfovanillin but inconspicuous. Oleiferous hyphae and cystidioid hyphae present in the trama.

Ecology & Distribution — In temperate deciduous and coniferous forests on different soil types, our collections originated from Germany and Slovakia and our field observations suggest that it forms ectomycorrhizae with a wide spectrum of trees; based on retrieved sequence information it was also collected in Czech Republic, Italy and Switzerland and is associated with *Castanea sativa* and *Picea abies*.

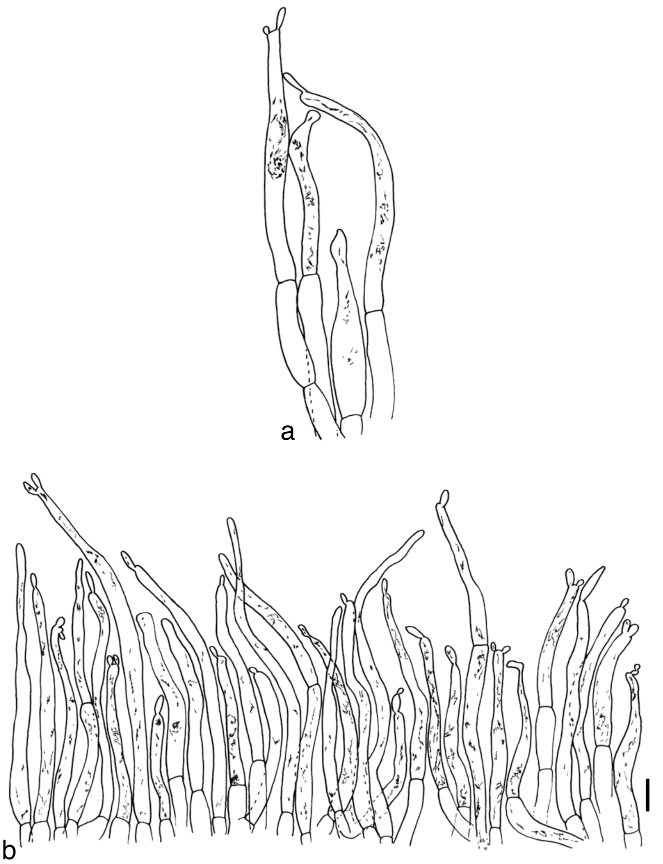

Fig. 42 *Russula thuringiaca*, pileocystidia. a. Near the pileus margin (FH 2010 ST06); b. near the pileus centre (FH 2008 ST02, FH 2014 ST02, holotype). — Scale bar = 10 µm.

Additional specimens examined. Germany, Thuringia, Ilmenau-East, N50°41'47.42" E10°57'44.64", alt. 540 m, coniferous forest with *Picea abies*, *Pinus nigra* and *Pinus sylvestris* on acidic soil (sandstone), 15 July 2008, *F. Hampe*, FH 2008 ST02 (GENT, FH); Thuringia, Schellroda south of Erfurt, Aspenbusch, north of the motorway A4, N50°55'11.35" E11°5'39.65", alt. 410 m, deciduous forest with *Fagus sylvatica* on black soil/loess over calcareous bedrock (Muschelkalk), 02 Aug. 2010, *J. Girwert*, FH 2010 ST06 (GENT, FH); Thuringia, Weimarer Land, Troistedt, N50°55'24.88" E11°15'29.43", alt. 410 m, deciduous forest with *Fagus sylvatica* on clayey/black soil/loess over calcareous bedrock (Muschelkalk), 27 June 2011, *F. Hampe*, FH 2011 ST01 (GENT, FH); Baden-Wuerttemberg, Rottweil, Schramberg, Sulgen, Black Forest, Beschenhof, N48°13'16.39" E8°26'46.46", alt. 705 m, coniferous forest with *Abies alba* and *Picea abies* on neutral to slightly alkaline soil, 06 Sept. 2019, *F. Hampe* & *B. Wergen*, FH 19-032 (GENT, FH); Thuringia, Bücheloh near Ilmenau, N50°43'37.16" E10°59'6.75", alt. 480 m, coniferous forest with *Picea abies*, *Pinus nigra* and *Pinus sylvestris* on acidic soil (sandstone), 11 Sept. 2020, *F. Hampe* & *C. Manz*, FH 20-056 (GENT, FH). – Slovakia, Malé Karpaty Mts, Vývrať, Bučková, west slopes of the hill, N48°25'24.45" E17°11'37.23", alt. 350–430 m, associated with *Quercus*, 06 July 2011, *S. Adamčík* (SAV F-3359).

Notes — Our collections from Germany suggest that this species is at least locally common, but only three collections retrieved from public databases rather indicate its rareness.

KEY TO THE EUROPEAN SPECIES OF RUSSULA SUBG. COMPACTAE

Note — Beside the species presented in the taxonomic part, the key also includes the taxa belonging to the *R. albonigra* complex treated in De Lange et al. (2021). To avoid misidentifications we recommend to use fresh basidiomata. A comprehensive comparison of selected morphological characters is presented in Fig. S5.

1. Lamellae thick, distant; context and surface rapidly and strongly discolouring red . . . . *R. nigricans*
1. Lamellae very narrow to medium, crowded; if lamellae thick and distant then usually with a conspicuous salmon or orange tinge and the reddish discoloration of context and surfaces absent or slow and weak 2

2. Context slowly and faintly discolouring reddish and greyish, not turning black, taste mild or almost so, spore ornamentation very low (≈ 0.25 µm) and dense; usually associated with conifers in boreal forests on nutrient-poor soils . *R. adusta*
2. Context turning dark black (with or without reddening), and/or spore ornamentation higher than 0.3 µm, with broad-leaved or coniferous host trees 3

3. Terminal cells of hyphae near the pileus margin on average > 7.5 µm wide 4
3. Terminal cells near the pileus margin on average < 7.5 µm wide 5

4. Terminal cells of hyphae near the pileus margin relatively short (av. length < 50 µm); hymenial cystidia with dispersed oily inclusions, context distinctly reddening before turning black . . . . *R. densifolia*
4. Terminal cells of hyphae near the pileus margin on av. longer (> 60 µm), hymenial cystidia partly to almost completely filled with refractive brown pigment, context at most weakly reddening or directly turning black . . . . *R. atramentosa*

5. Hymenial cystidia with hardly any content, hyaline, with some brown pigmentation but mostly completely faded, at most very few and very small oily masses visible, pileocystidia on average up to 6 µm wide, context at most weakly reddening or directly turning black . . . . *R. anthracina*
5. Hymenial cystidia with distinct oily, granulose or crystalline contents, if pileocystidia on average narrower than 6 µm then context with distinct reddish discoloration 6

6\. Surface of the basidiomata intensely blackening with a strong contrast between the blackened and the paler, almost white areas; taste in the lamellae mild, often perceived as refreshing or menthol-like; pileus cuticle dry, hymenial cystidia not reacting in sulfovanillin (*R. albonigra* complex) 7

6\. Surface of the basidiomata moderately blackening or taste acrid at least in the lamellae; pileus cuticle dry or viscid; hymenial cystidia usually distinctly turning grey or black in sulfovanillin 11

7\. Hymenial cystidia and pileocystidia with oily guttulate content . . . . *R. albonigra*

7\. Content of cystidia different 8

8\. In boreal/montane forests with conifers; pileocystidia extremely rare near the pileus margin, absent near the centre . . . . *R. ustulata*

8\. In thermophilous/mesophilous deciduous forests or with conifers; pileocystidia at least widely dispersed and observable on the whole pileus surface 9

9\. Pileocystidia never with appendages or bifurcations . . . . *R. nigrifacta*

9\. At least some pileocystidia with appendages and/or bifurcations 10

10\. Pileocystidia numerous, very long (some exceeding 200 µm), with appendages and bifurcations; part of hyphal terminations in the pileipellis inflated . . . . . *Russula* sp. 1 . . . . (De Lange et al. 2021)

10\. Pileocystidia widely dispersed, never exceeding 160 µm, lacking bifurcations; hyphal terminations in the pileipellis without inflated cells . . . . *R. ambusta*

11\. Hyphal terminations in pileipellis near margin heteromorphous, with a mixture of narrow, cylindrical hyphal terminations and short-septate inflated elements . *R. densissima*

11\. Hyphal terminations in pileipellis near margin more or less uniform, with only cylindrical or narrowly subulate hyphal terminations 12

12\. Spore ornamentation exceeds 0.5 µm; context slightly acrid . . . . *R. roseonigra*

12\. Spore ornamentation up to 0.5 µm or context distinctly acrid 13

13\. Context acrid in all parts, especially strong in lamellae, usually distinctly reddening; pileus cuticle viscid or greasy and shiny when wet 14

13\. Context mild or slightly acrid in lamellae, weakly and locally reddening 15

14\. Average spore length > 7.7 µm, average spore width > 6.2 µm; pileocystidia near the pileus centre rare; hyphal terminations near the pileus margin narrowly cylindrical, on average shorter than 55 µm and narrower than 5.2 µm . . . . *R. acrifolia*

14\. Average spore length < 7.7 µm, average spore width < 6.2 µm; pileocystidia near the pileus centre abundant; hyphal terminations near the pileus margin partly subulate/attenuated, larger (av. length > 55 µm, av. width > 5.2 µm) . . . . *R. picrophylla*

15\. Spores with average Q > 1.35 . . . . . *R. marxmuelleriana*

15\. Spores with average Q < 1.35 . . . . *R. thuringiaca*

DISCUSSION

Phylogeny of European Compactae members

Russula subg. *Compactae* is well-defined and forms a well-supported clade in the *Russula* phylogeny, but the relations within the subgenus are less studied. The group was outlined for the first time in the multi-locus phylogeny by Looney et al. (2016) as the 'nigricans' lineage. More recently, several multi-locus phylogenies (e.g., Buyck et al. 2020) confirmed *R.* subg. *Compactae* as a phylogenetically and morphologically well-supported group. Buyck et al. (2018, 2020) recognised several lineages within the subgenus with a geographical pattern. One of them is a European lineage, there are two African lineages and one lineage of mainly North American species that also includes a single collection from New Caledonia. Our multi-locus phylogeny (Fig. 1) supports the delimitation of *R.* subg. *Compactae* as defined by recent studies, and the individual *Compactae* lineages are characterized by a limited distribution, although we revealed more exceptions in the distribution pattern than previously assumed. It is likely that the *Compactae* evolved in Latin America, because in our study *R. fortunae* described from Panama (Adamčík et al. 2019) is in a basal position within *R.* subg. *Compactae* in the multi-locus tree (Fig. 1) (but this position is only supported by BI, not by ML). Our larger tree (Fig. S2), which includes additional individual ITS sequences from available global *Compactae* data, suggests that *R. fortunae* might be a member of a widely spread lineage represented by samples of *R. subnigricans* from Japan and a singleton collection from Madagascar. However, this broader ITS-based dataset also suggests that there is a triplet of sequences with Latin American origin that may represent the most basal *Compactae* group, but this needs more proof with multi-locus data. All European sequences and studied samples are included in a single monophyletic clade in both our phylogenies (Fig. 1, S2), and this clade also contains samples from Asia, North America and Latin America. This clade and two other large clades recognised in our multi-locus phylogeny may correspond to three sections mentioned by Buyck et al. (2018). The clade with European members corresponds to *R.* sect. *Nigricantinae* typified by *R. nigricans* (Sarnari 1998). Its sister clade represented in our phylogenies strictly by African members corresponds to *R.* sect. *Fistulosae* typified by *R. fistulosa* (Buyck 1993). And the large clade consisting mainly of American representatives corresponds to *R.* sect. *Polyphyllae*, typified by *R. polyphylla* (Das et al. 2017). *Russula fortunae* and potentially also other underrepresented clusters in the ITS-tree (Fig. S2) probably form additional unrecognised section-ranked clades that require better sampling and sequence data to be defined.

Global Compactae diversity and habitat adaptation

This is probably not the final phase of the *Nigricantinae* or *Compactae* research in Europe. The presence of two undescribed singleton sequences in our multi-locus tree suggests that there is more diversity to be discovered in this well-explored continent. More taxonomic attention is also required for *R. densifolia* and *R. nigricans*, which have high ITS haplotype diversity and may represent some complexes of low rank taxa or populations with specific ecological adaptations shaped by their phylogenetic origin and geographical location (Rúa et al. 2016). *Russula adusta* also needs special attention, it has ITS MOTU clustering at very high similarity levels and may represent a complex taxon with a hemi-boreal distribution pattern similar to other alpine and boreal taxa of the Northern Hemisphere (Caboň et al. 2019, Noffsinger & Cripps 2021). The European samples of *R.* subg. *Compactae* are all placed in *R.* sect. *Nigricantinae*, but this group also contains samples from different areas of Asia, North and Central America. It seems that this group diversified relatively recently in the Northern Hemisphere, but to locate the place of the section's origin, more global *Compactae* data are needed (Looney et al. 2020). *Nigricantinae* members appear to be distributed from the boreal areas of the Northern Hemisphere (*R. adusta*), to the subtropical and tropical areas of Southeast Asia (Adamčík et al. 2019, Zhou et al. 2020) and Central America (see our Panamanian samples included in Fig. 1). The centre of the known diversity of the group with the highest number of species seems to be the temperate areas of the Northern Hemisphere (Adamčík & Buyck 2014, Das et al. 2020). Our data suggests that the species within *R.* subg. *Compactae* do not have an intercontinental distribution across Europe, Asia and North America as was previously also demonstrated by De Lange et al. (2021) in the case of the *R. albonigra* lineage. The majority of *Russula* species reported (based on molecular studies) from multiple continents are boreal-arctic taxa, occurring in Europe, Asia and North America (Adamčík et al. 2016, Bazzicalupo et al. 2017, Caboň et al. 2019, Noffsinger & Cripps 2021). It was believed for a long time that European *Russula* species are also present in East Asia (Hongo 1960), but our data proves this would be a rather rare phenomenon within *R.* subg. *Compactae.* Both common hypotheses on distribution patterns (i.e., boreal-arctic taxa and Eurasian taxa) are, together with the very high genetic similarity (at least in the ITS-region) between closely related taxa on different continents, a source of frequent and continuous misapplications of European species names to non-European taxa (Buyck 2007, Wang et al. 2009, Avis 2012, Buyck & Adamčík 2013, Cao et al. 2013, Li et al. 2015, Bazzicalupo et al. 2017). This can be easily observed by a simple name search for European taxa in public sequence databases, which results in a high amount of non-European samples. The high genetic similarity is important to take into account, especially when it comes to molecular identification and ecological studies (e.g., on species distribution and conservation). On a global scale *R.* subg. *Compactae* is a species diverse subgenus with at least 194 species and we expect this to be a major underestimation as there is still limited data available for some largely undersampled regions (e.g., Africa, Australia and Latin America). The high number of North American species clades as opposed to the number of available names (Adamčík & Buyck 2014), and the high number of Asian species clades in Fig. S2 show that a similar study as this study is needed for other continents as well.

As demonstrated by the results of our UNITE search for sequences from ectomycorrhizae, *Nigricantinae* mostly do not show specific host preferences. With the exception of *R. adusta* with its prevalently boreal distribution pattern, all other species seem to inhabit temperate deciduous forest types in general, but there is probably some climate and soil niche specialisation as suggested for some species in the *R. albonigra* lineage (De Lange et al. 2021). Interestingly, the association of *R. densifolia* and *R. nigricans* with *Halimium lasianthum* (*Cistaceae*), a shrub known to be ectomycorrhizal (Leonardi et al. 2020), is a further proof of their broad ecological range. *Russula* species are typical ectomycorrhizal colonisers in the late stage of forest succession (Wang et al. 2015), but a number of them are typically found in urban environments, e.g., *R. recondita* (Melera et al. 2017). In our study, we cannot confirm a single collection of *Nigricantinae* from urban or anthropogenic habitats and several species may have a conservation value.

Phylogenetic signal of morphological characters

Our study did not confirm a pseudocryptic diversity to an extent like the previous study by De Lange et al. (2021) that recognised within the traditional concept of *R. albonigra* a species complex with four undescribed species. Two new species are within the *R. acrifolia* lineage (*R. picrophylla* and *R. thuringiaca*) and *R. marxmuelleriana* is a species with unresolved relationships (Fig. 1). In the simplified multi-locus tree we labelled the *R. acrifolia* lineage in green, the *R. densifolia* lineage in red and the *R. albonigra* lineage in blue (Fig. 43). *Russula nigricans* and *R. marxmuelleriana* are not grouped together with a support and they are labelled with different colours as separate lineages. We defined 23 morphological characters that show differences between species and coded each character for each species in one of three categories (Fig. S5). Based on these categories we constructed a barcode tree to better trace differences between species. The *R. acrifolia* lineage (green) is defined by a moderately to very viscid pileus cuticle, weakly to intermediately blackening of the context and always moderately long pileocystidia near the pileus margin (between 60–90 µm long). The *R. densifolia* lineage (red) is defined by dense lamellae in the hymenophore, rare or absent bifurcations on the pileocystidia near the pileus margin and weakly defined or oily contents in the hymenial cystidia. The *R. albonigra* lineage (blue) is defined by a mild taste of the context and hymenial cystidia with abundant crystalline or oily contents that do not react in sulfovanillin. *Russula marxmuelleriana* has the most elongated spores of all studied species. *Russula nigricans* has typically distant, thick lamellae, very inconspicuous pileocystidia and narrow hymenial cystidia. These characters seem to correspond with its basal position within *R.* sect. *Nigricantinae* and may be ancestral. To trace ancestral states of the morphological characters, information about non-European members of other groups within *R.* subg. *Compactae* is needed (Caboň et al. 2017), but such complex information is not currently available and this group is in its initial stage of discovery outside of Europe (Buyck et al. 2020). It is possible that these morphological characters represent ecological and climatic adaptations (Looney et al. 2020).

Looking back to history

Unlike the other *Russula* groups characterised by a more colourful field aspect and used as edible fungi, the *Compactae* received relatively little attention, but they have a long taxonomic tradition in Europe starting from the description of *Agaricus nigricans* (Bulliard 1785) and the explicit recognition of at least two *Nigricantinae* taxa distinguished by thickness and distance of the lamellae (Otto 1816). Looking at the brief descriptions of the earlier studies, it is very likely that names like *R. adusta* or *R. densifolia* were used collectively covering larger groups of *Nigricantinae* recognised in our study. The monograph of Romagnesi (1967) defined relatively well the most common European *Compactae* members and more recent studies added only three additional species confirmed by our phylogeny (Romagnesi 1980, Sarnari 1998, Pidlich-Aigner 2015). While all European *Compactae* taxa accepted in Romagnesi's monograph are covered by our study, there are still some names with an uncertain taxonomic concept.

We have never observed bluish discoloration of the context very rarely reported for some taxa that seem to be mysterious. Among these, *R. cyanescens* was originally described as a russuloid fungus with a white pileus, white lamellae and a bluish discoloration of the context and considered by some authors as belonging to *R.* subg. *Compactae* (Singer 1923, Reumaux et al. 1996). In rare occasions, *Compactae* specimens showing bluish tints on the pileus surface and a somewhat bluish discoloration of the context (with or without contemporaneous reddish discolorations) seem to have been encountered (Blum 1962) sub "*R. caerulescens* Sing." (see also *R. adusta* var. *coerulescens*). Unfortunately, the type specimen of the relatively recently described *R. cyanescens* var. *subrubescens* (Reumaux et al. 1996), with presence of bluish context discoloration, was not made available for sequencing to confirm the taxonomic significance of this character.

Furthermore, our study does not contain any new data about the older Friesian names *R. elephantina* and *R. semicrema*, that are both currently not in use. The first name has been considered as a potential synonym of *R. nigricans* (Sarnari 1998), but Bolton's original description and plate are difficult to interpret and possibly do not even represent a *Compactae* species. If, nevertheless, synonymy with *R. nigricans* should be established through epitypification, it would seem recommendable to ensure nomenclatural stability by conservation of the latter name. *Russula semicremea* (Fries 1838) is described as a *Compactae* species from deciduous woods with a persistently white pileus, crowded, decurrent lamellae, a blackening stipe and a persistently white context (“Caro ... immutabilis”!). The original description is vague and does not match the field aspect of any of the taxa accepted here, therefore we have not interpreted it in this study.

We were also unable to sequence the type of another taxon described by Reumaux et al. (1996), *R. clementinae*. However, Dagron (1999), based on a micromorphological study of the type, concluded that it is not specifically different from *R. densifolia* and combined the name at the rank of a form, *R. densifolia* f. *clementinae*. We agree that Dagron's description of the taxon contains inflated cells in the pileipellis typical for *R. densifolia*.

Using the determination keys of Romagnesi (1967) and Sarnari (1998) leads to several misidentifications confirmed later by our phylogenetic analyses and apparently also from the analysis of the UNITE data (Fig. 1, 2). For the new species, some historical data of *R. nigricans* may cover *R. thuringiaca*,

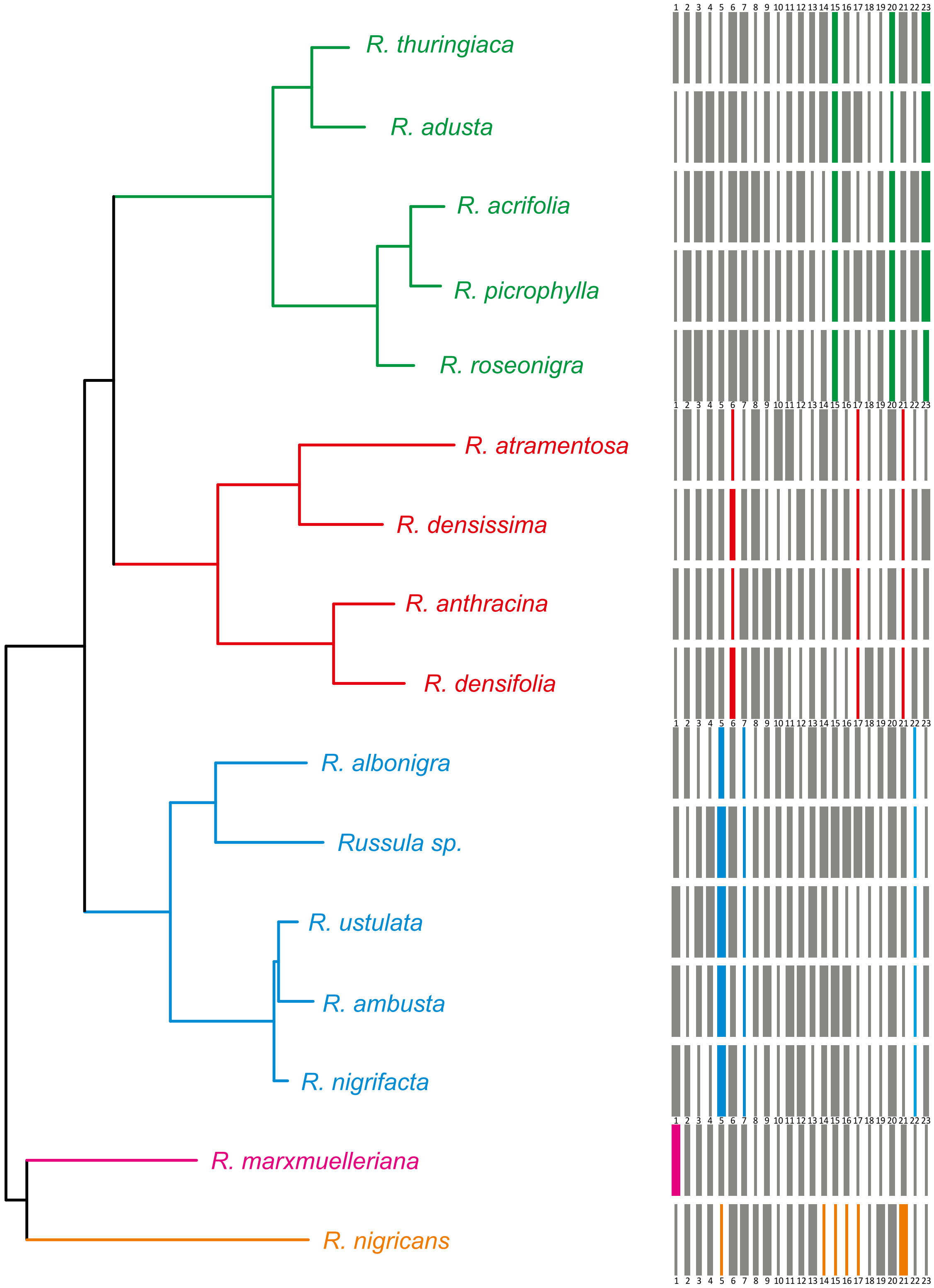

Fig. 43 Simplified phylogenetic tree of the studied European *Compactae* members with a morphological barcode based on 23 characters coded to three categories, represented by different bar thicknesses. Selected characters typical for individual lineages are labelled by corresponding colours. Details about the morphological barcoding are in Fig. S5.

and *R. picrophylla* was usually misidentified as *R. acrifolia*. Our experience with collections previously identified as *R. atramentosa* or *R. anthracina* shows that these species were probably the most frequently confused with each other and with other members of the *Nigricantinae*. Historical data, even of such common and well known species as *R. nigricans* and *R. adusta*, needs to be treated with caution.

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Supplementary material

Fig. S1 Information on UNITE Species Hypotheses (SHs). Sheet 1: details about the best SH match with the phylogenetic concept of the species; Sheet 2: overview of SHs.

Fig. S2 ITS tree. Maximum Likelihood (ML) tree of *Russula* subg. *Compactae*, based on ITS sequence data. ML bootstrap values ≥ 60 are shown. Blue labelled are representative sequences of UNITE SHs; green labelled are additional sequences with informative metadata; red: type sequences.

Fig. S3 Results of the Bayesian Phylogenetics and Phylogeography (BP&P) analyses.

Fig. S4 Output file of the STACEY analysis.

Fig. S5 Comparison of selected morphological characters. Sheet 1: comparison table with average values or prevailing character stages; Sheet 2 explanation of the three character categories and assignment of the codes; Sheet 3: barcode table. PC – pileocystidia, SV – sulfovanillin, TC - terminal cells. Sizes of microscopic elements are in µm.