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

R. De Lange[1], J. Kleine[2], F. Hampe[3], P. Asselman[1], C. Manz[4], E. De Crop[1], L. Delgat[1,5], S. Adamčík[6,7,*], A. Verbeken[1]

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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

[1] Ghent University, Department of Biology, Research Group Mycology, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium.
[2] Am Lindenhof 9, 04277 Leipzig, Germany.
[3] Wetzlarer Straße 1, 35510 Butzbach, Germany.
[4] Goethe University, Faculty of Biological Sciences, Research Group Mycology, Max-von-Laue-Str. 13, 60438 Frankfurt am Main, Germany.
[5] Meise Botanic Garden, Research Department, Nieuwelaan 38, 1860 Meise, Belgium.
[6] Slovak Academy of Sciences, Plant Science and Biodiversity Centre, Institute of Botany, Dúbravská cesta 9, 845 23 Bratislava, Slovakia.
[7] Comenius University Bratislava, Faculty of Natural Sciences, Department of Botany, Révová 39, 81102 Bratislava, Slovakia.
* Corresponding author e-mail: Slavomir.Adamcik@savba.sk.

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

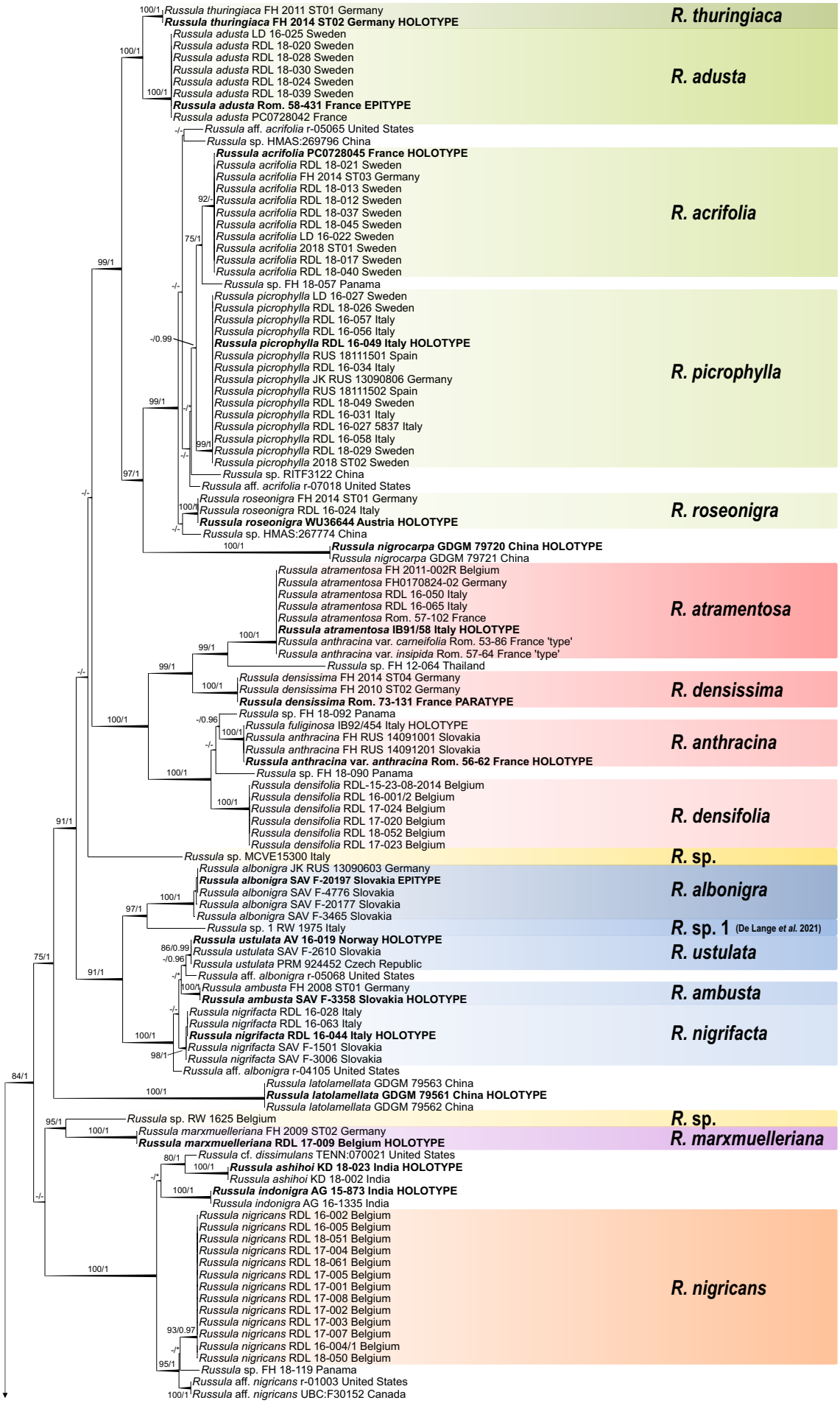


Fig. 1 Maximum Likelihood (ML) tree of *Russula* subg. *Compactae*, based on concatenated ITS, LSU, *RPB2* and *EF-1α* sequence data. ML bootstrap values ≥ 75 and BI posterior probabilities ≥ 0.95 are shown; * missing branch.

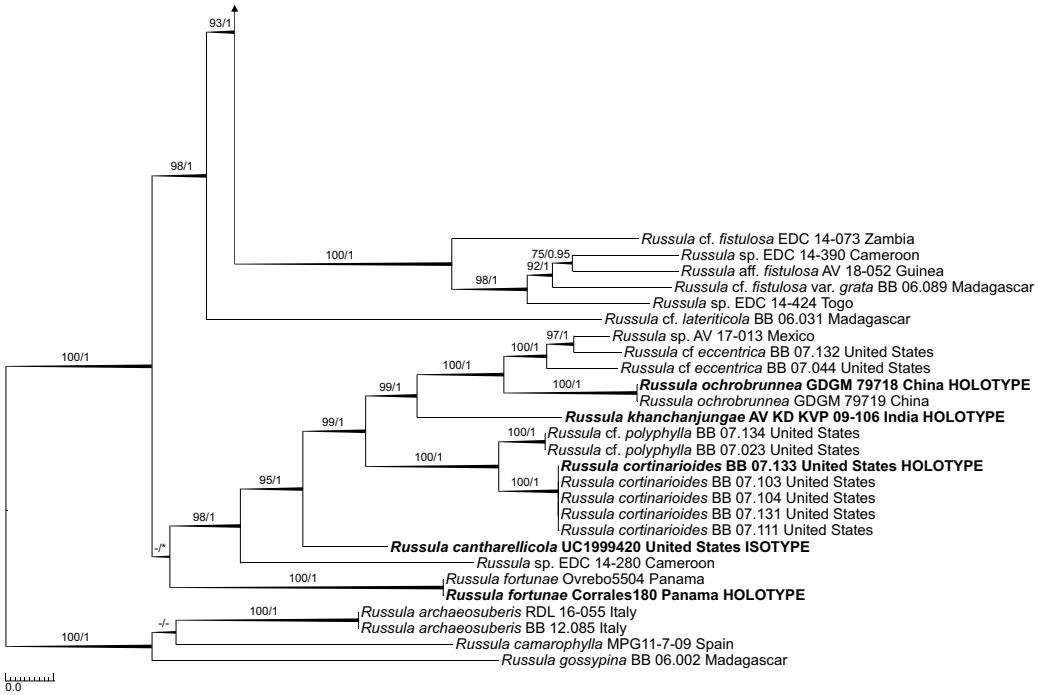


Fig. 1 (cont.)

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

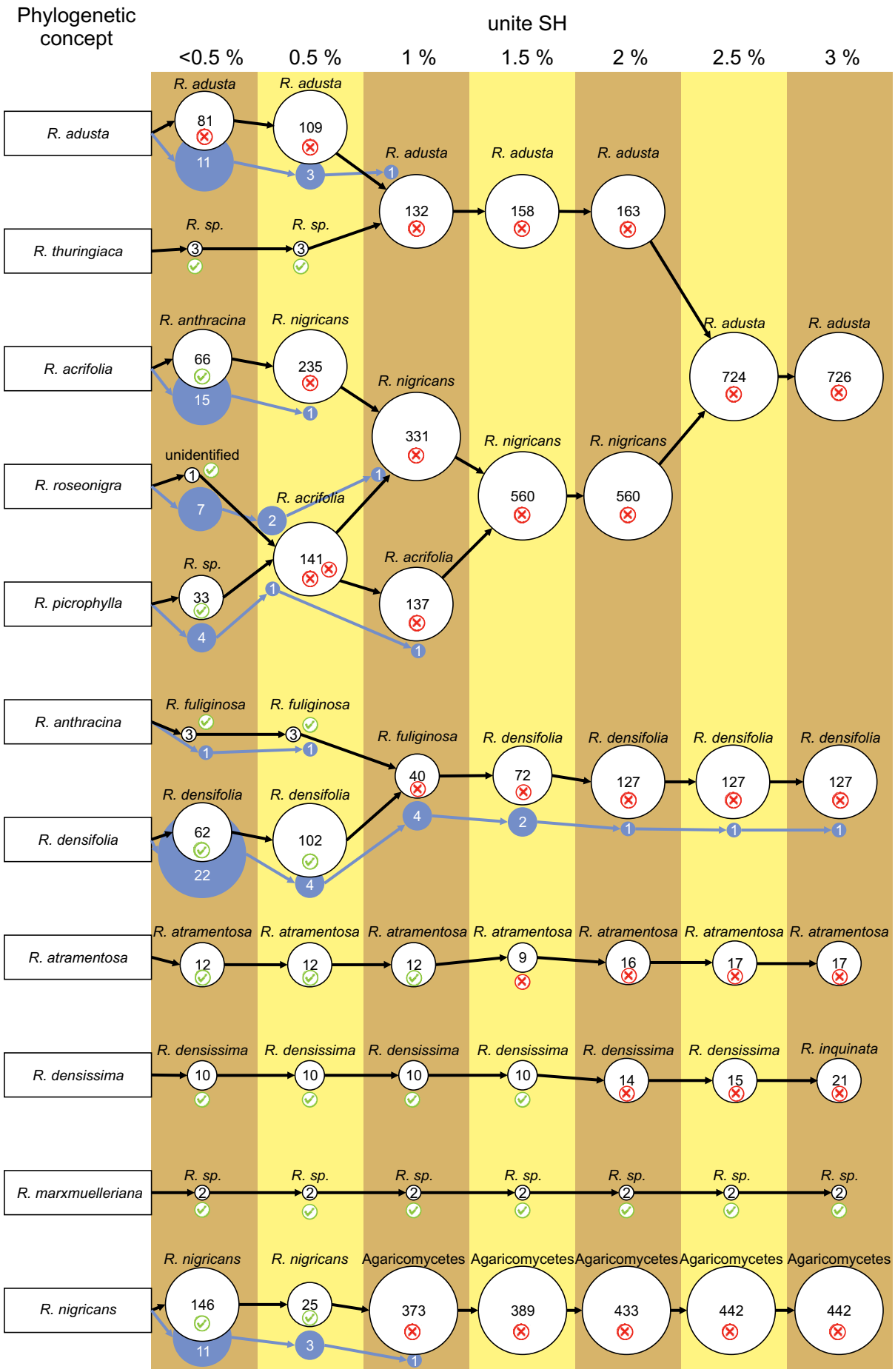


Fig. 2 Representation of the eleven studied *Compactae* species in the UNITE database at different distance thresholds. White circles give information about sequence numbers of the species hypothesis (SH) with the best match, the names above them are adopted from UNITE. Blue circles give information 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-

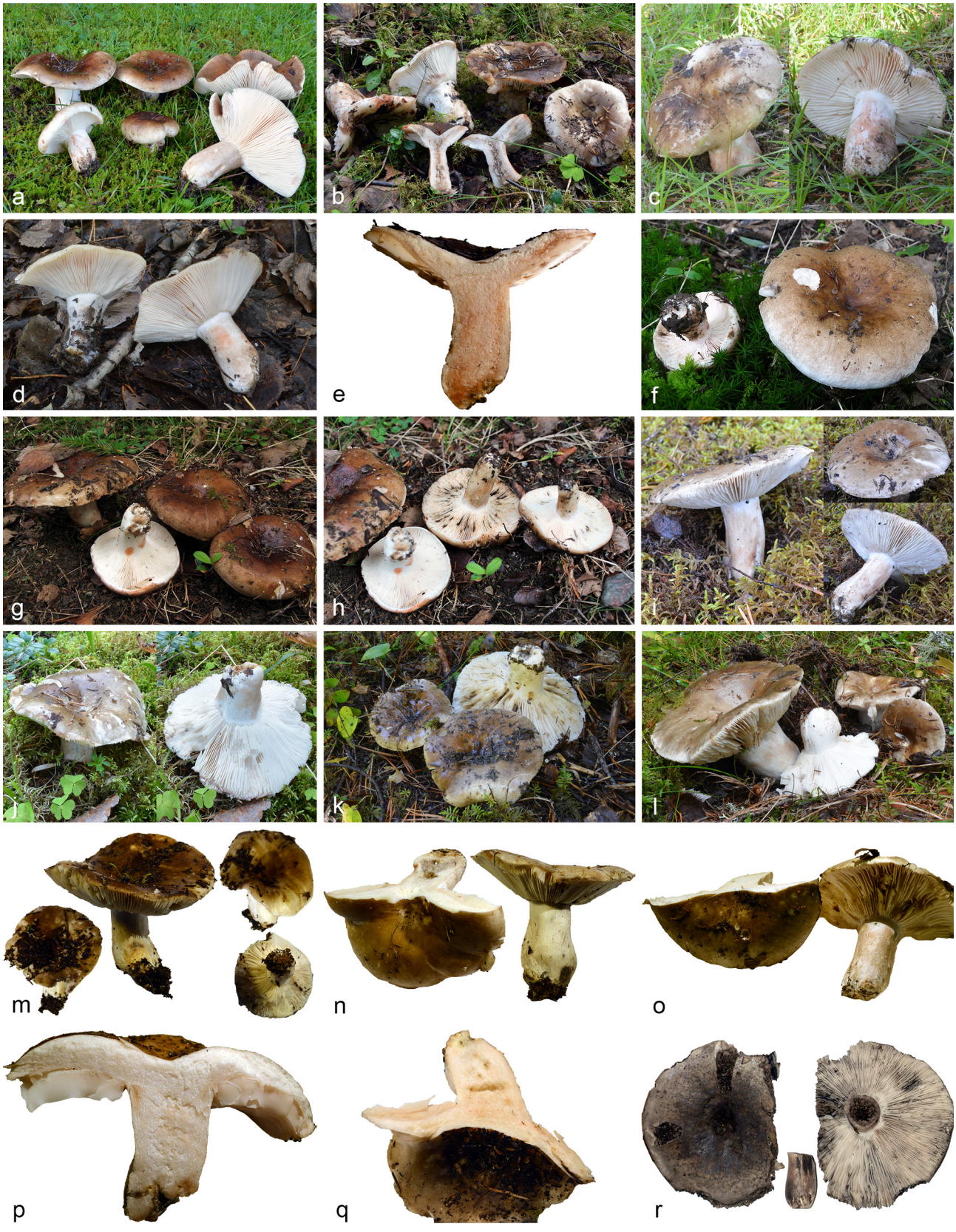


Fig. 3 Basidiomata. a–h. *Russula acrifolia* (a. RDL 18-037; b. RDL 18-021; c. RDL 18-040; d–e. RDL 18-045; f. FH 2014 ST03; g–h. 2018 ST01). — i–q. *Russula adusta* (i. RDL 18-033; j. RDL 18-020; k. RDL 18-039; l. RDL 18-028; m. RDL 18-034; n. RDL 18-035; o. RDL 18-024; p. RDL 18-031; q. RDL 18-030). — 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.

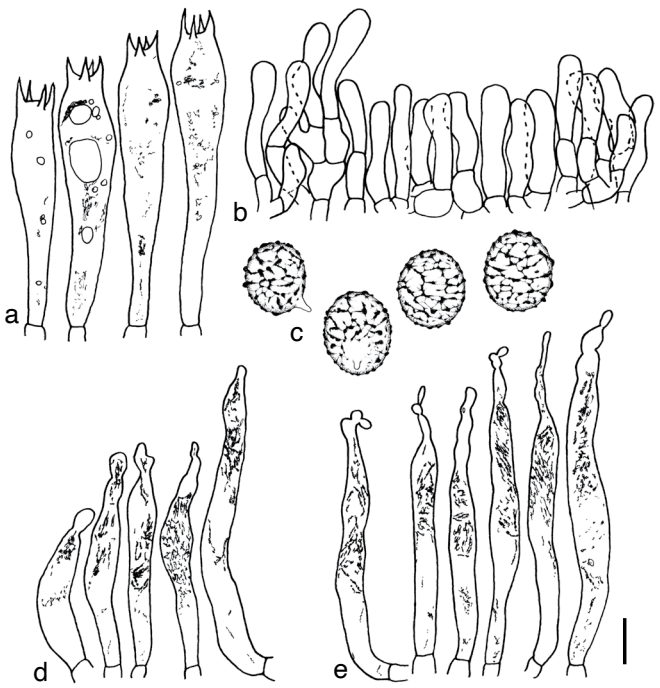


Fig. 4 *Russula acrifolia*, micromorphology of the hymenium. a. Basidia (RDL 18-013); b. marginal cells (RDL 18-012); c. basidiospores (RDL 18-037); d. cystidia near lamellae edges (RDL 18-012); e. cystidia on lamellae sides (RDL 18-013). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

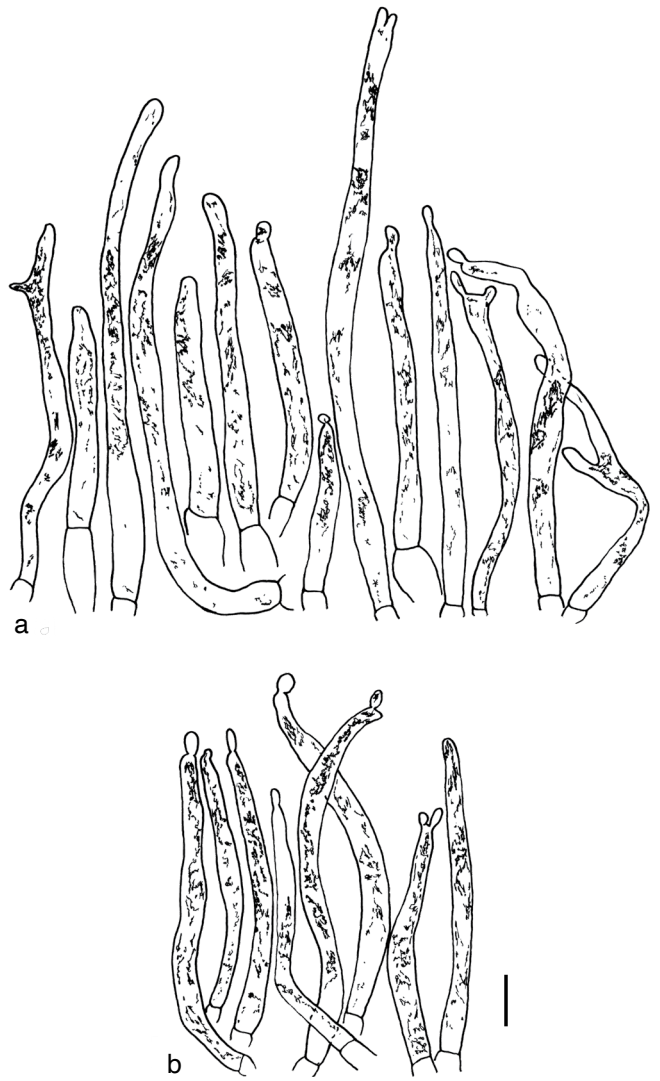


Fig. 6 *Russula acrifolia*, pileocystidia. a. Near the pileus margin (RDL 18-037); b. near the pileus centre (RDL 18-012, RDL 18-013, RDL 18-037). — Scale bar = 10 µm.

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.

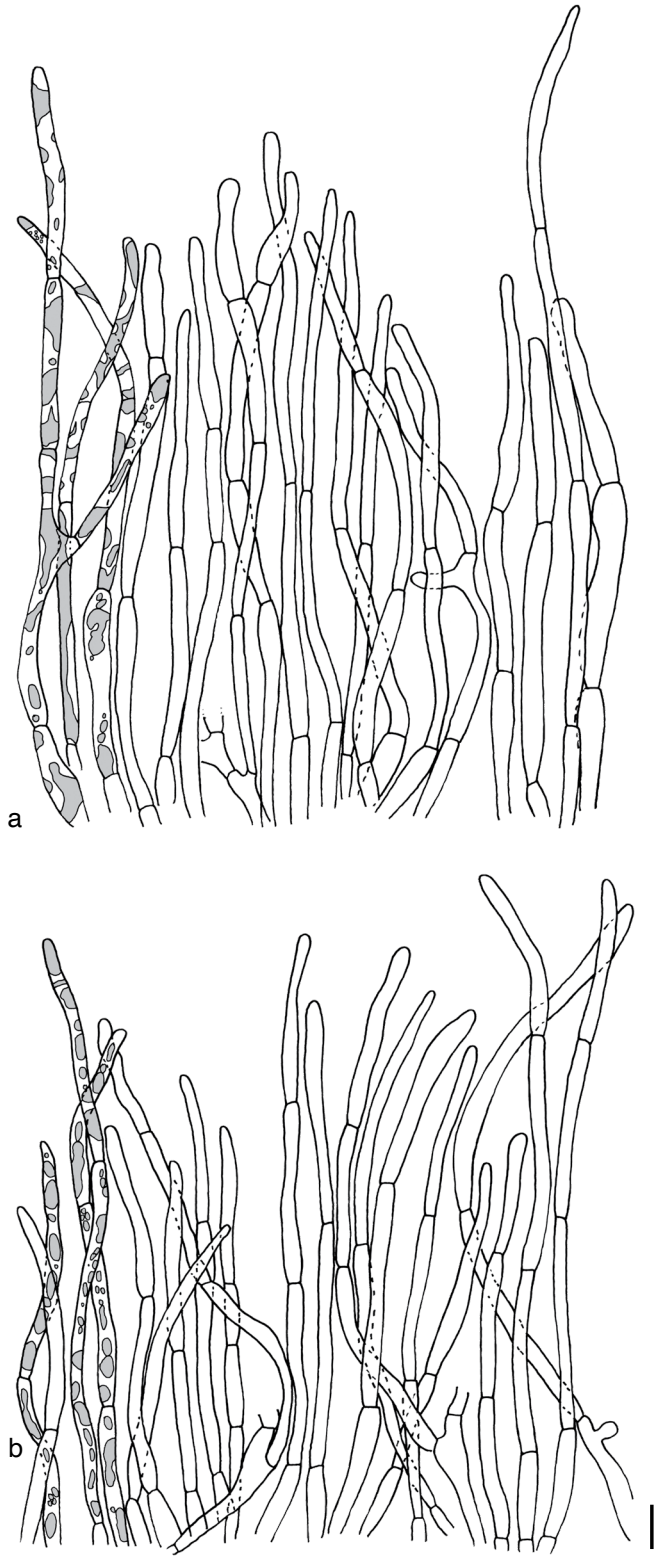


Fig. 5 *Russula acrifolia*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 18-037); b. near the pileus centre (RDL 18-037). — Scale bar = 10 µm.

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.

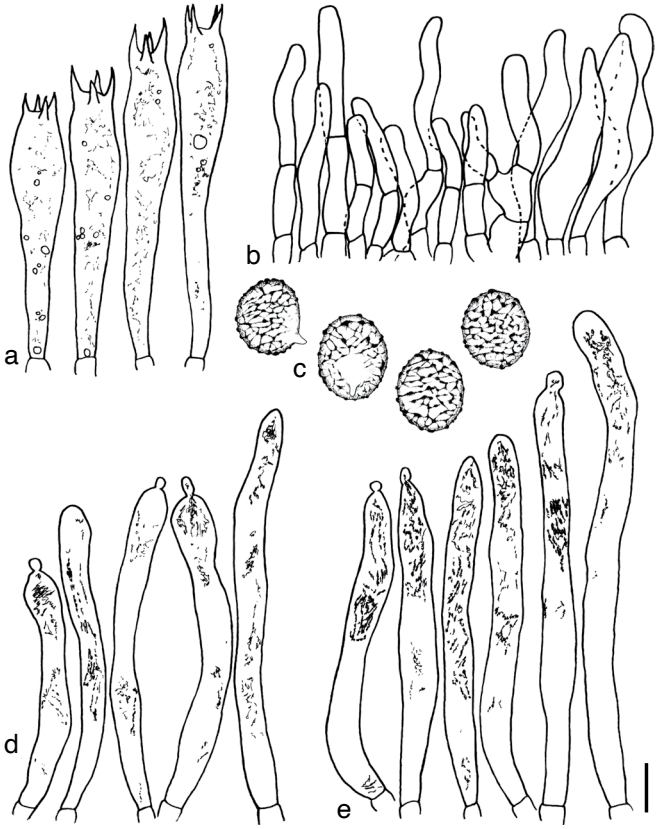


Fig. 7 *Russula adusta*, micromorphology of the hymenium. a. Basidia (RDL 18-028); b. marginal cells (RDL 18-028); c. basidiospores (RDL 18-028); d. cystidia near lamellae edges (RDL 18-028); e. cystidia on lamellae sides (RDL 18-020, RDL 18-028). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

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.,

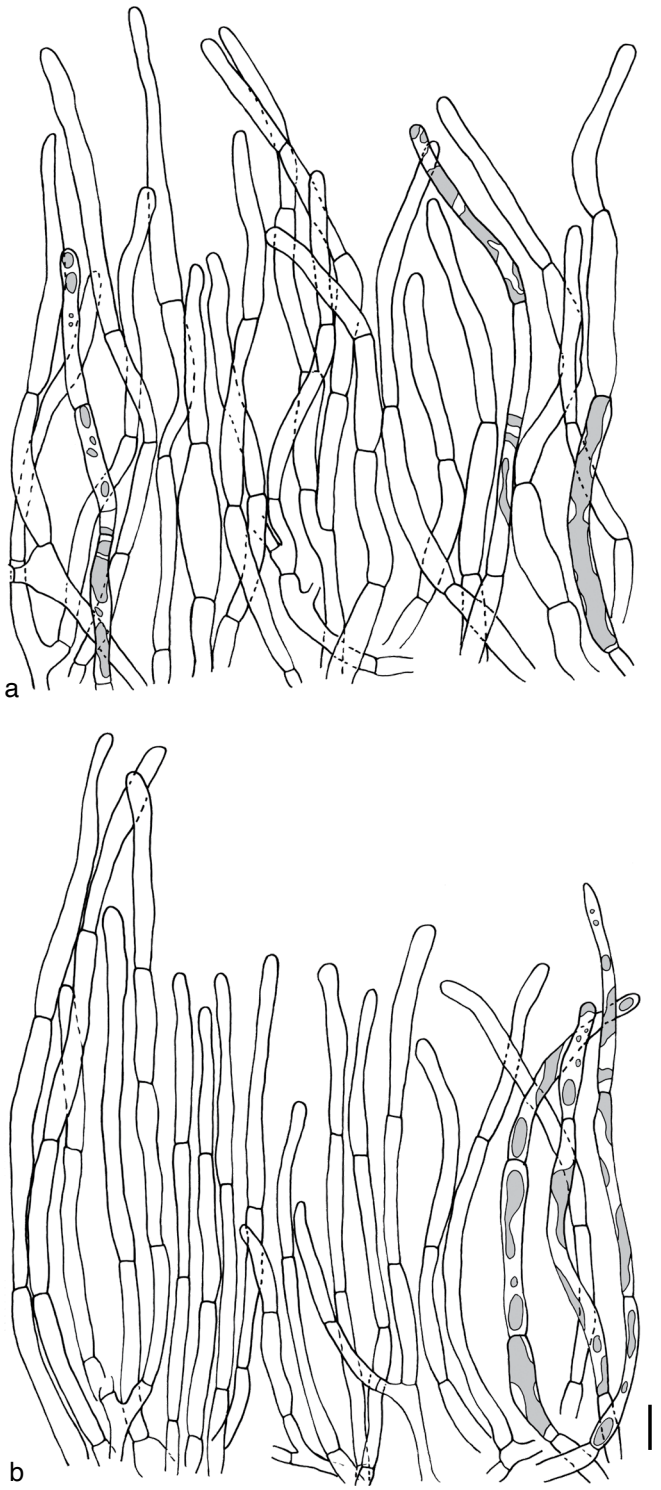


Fig. 8 *Russula adusta*, hyphal terminations of the pileipellis (RDL 18-028). a. Near the pileus margin; b. near the pileus centre (RDL 18-028). — Scale bar = 10 µm.

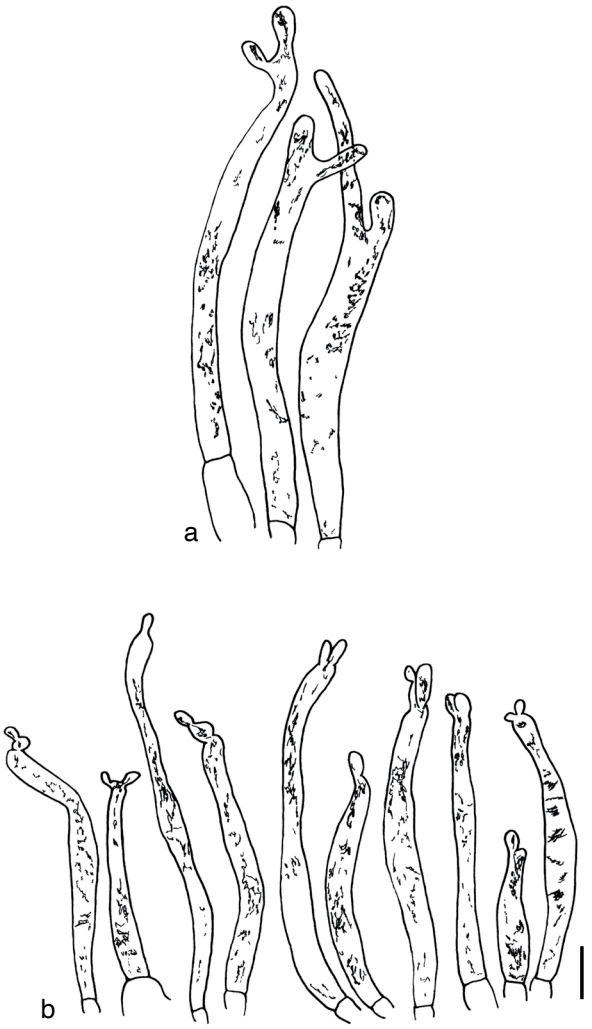


Fig. 9 *Russula adusta*, pileocystidia. a. Near the pileus margin (RDL 18-028); b. near the pileus centre (RDL 18-020, RDL 18-028). — Scale bar = 10 µm.

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).

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).

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.

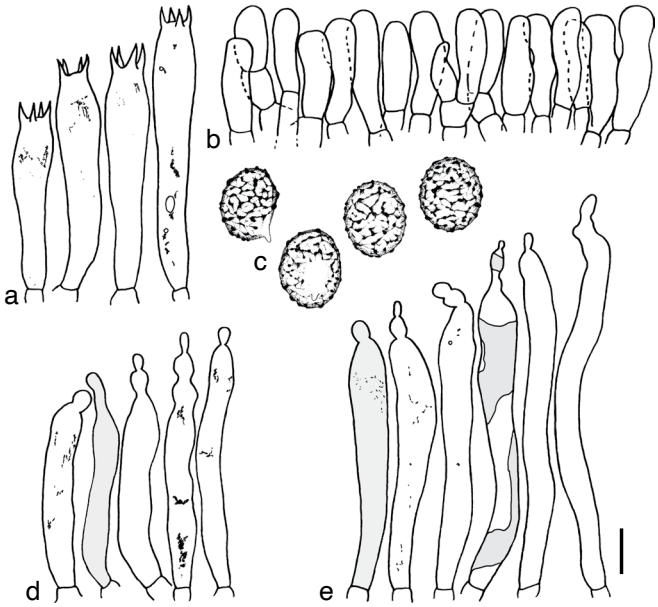


Fig. 10 *Russula anthracina*, micromorphology of the hymenium. a. Basidia (Rom. 56-62, holotype); b. marginal cells (Rom. 56-62); c. basidiospores (Rom. 56-62); d. cystidia near lamellae edges (Rom. 56-62); e. cystidia on lamellae sides (Rom. 56-62). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

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

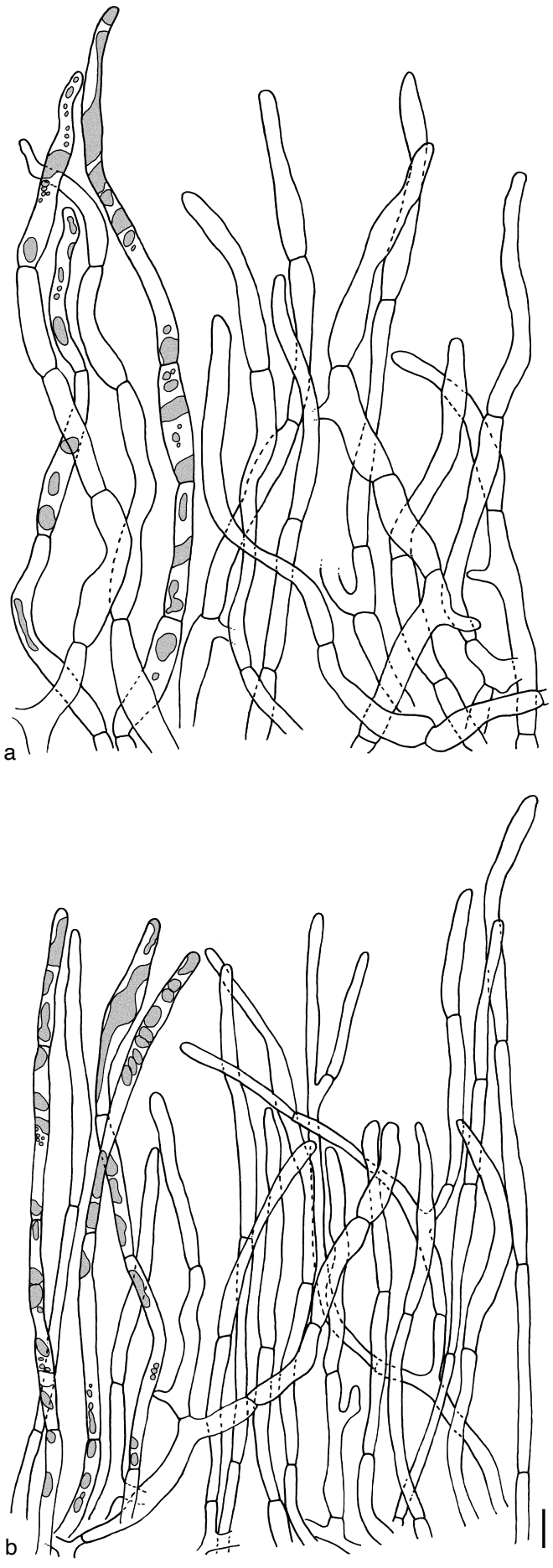


Fig. 11 *Russula anthracina*, hyphal terminations of the pileipellis. a. Near the pileus margin (Rom. 56-62, holotype); b. near the pileus centre (Rom. 56-62). — Scale bar = 10 µm.

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.

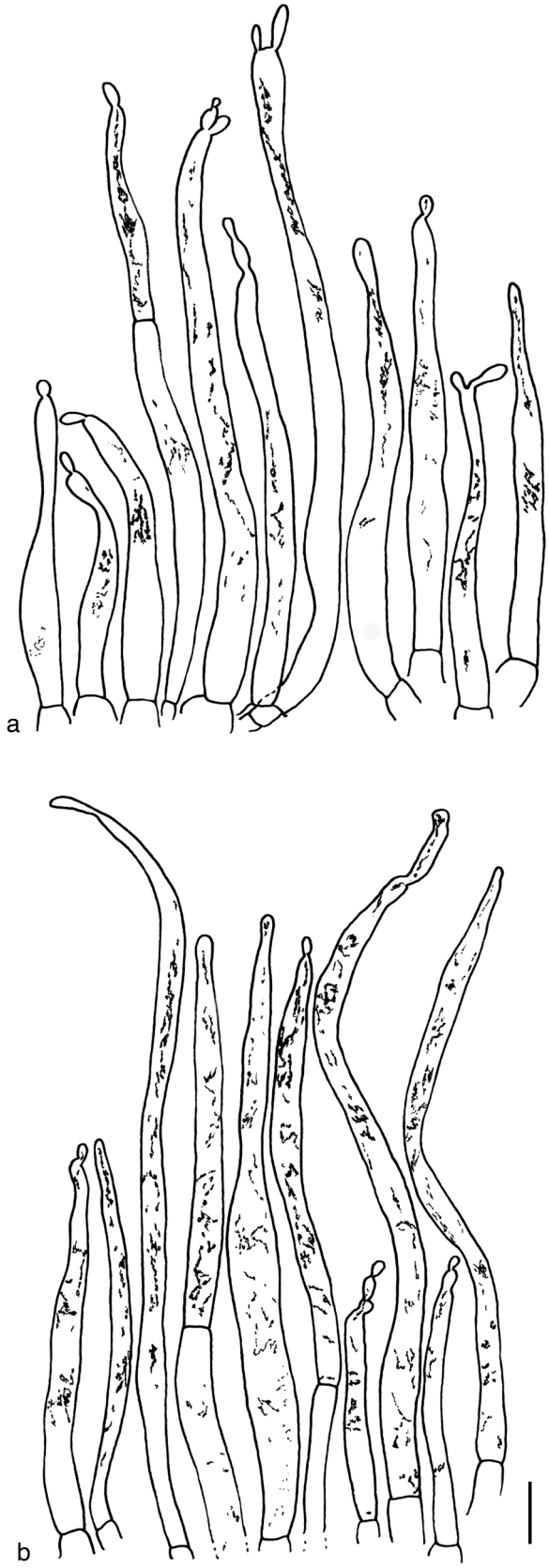


Fig. 12 *Russula anthracina*, pileocystidia. a. Near the pileus margin (Rom. 56-62, holotype); b. near the pileus centre (Rom. 56-62). — Scale bar = 10 µm.

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-

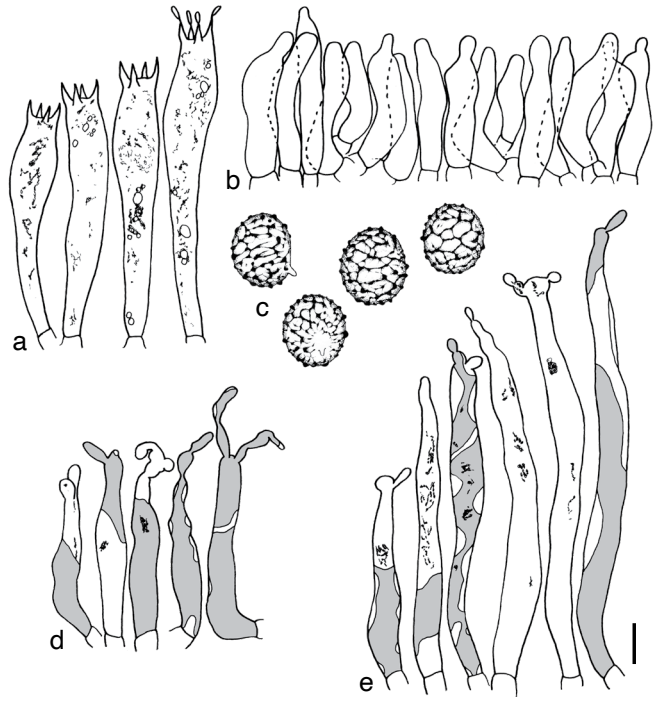


Fig. 14 *Russula atramentosa*, micromorphology of the hymenium. a. Basidia (FH 2011-002R); b. marginal cells (RDL 16-050); c. basidiospores (RDL 16-050); d. cystidia near lamellae edges (RDL 16-050); e. cystidia on lamellae sides (FH 2011-002R). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

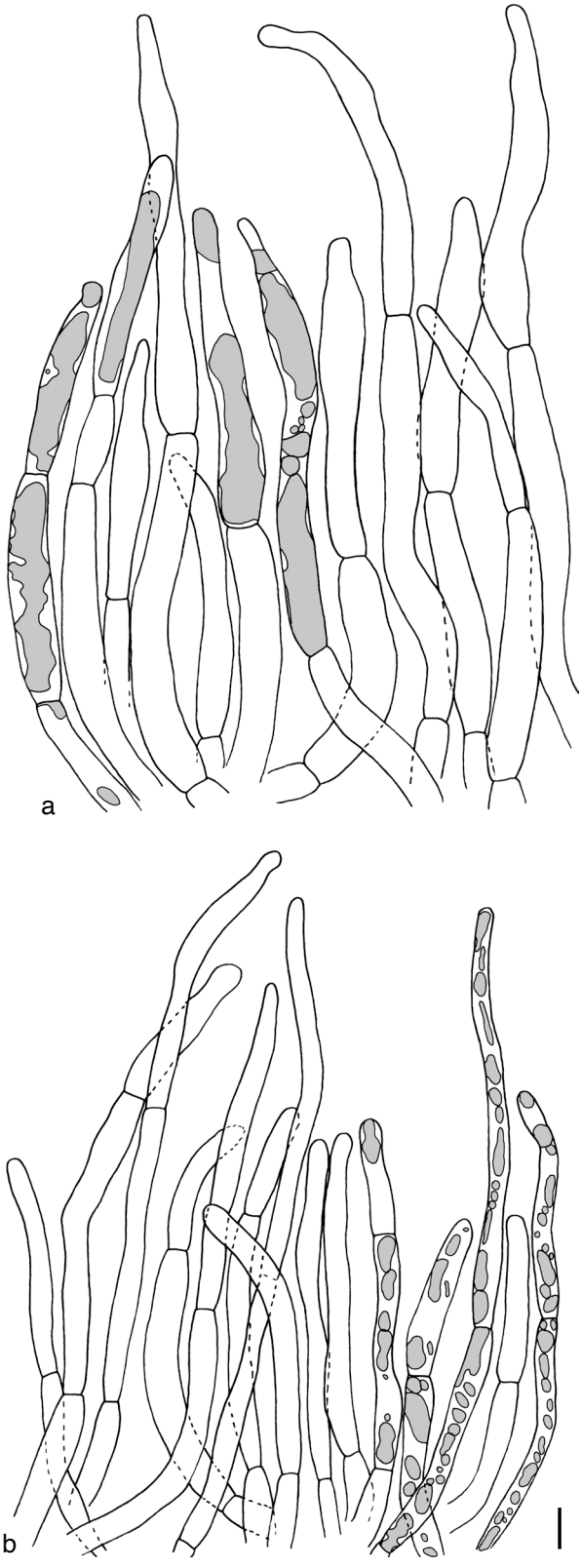


Fig. 15 *Russula atramentosa*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 16-050); b. near the pileus centre (RDL 16-050). — Scale bar = 10 µm.

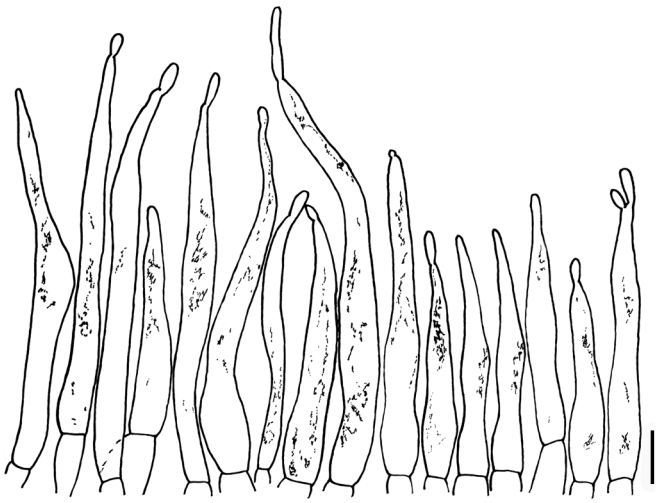


Fig. 16 *Russula atramentosa*, pileocystidia near the pileus centre (JK RUS 16111003). — Scale bar = 10 µm.

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*

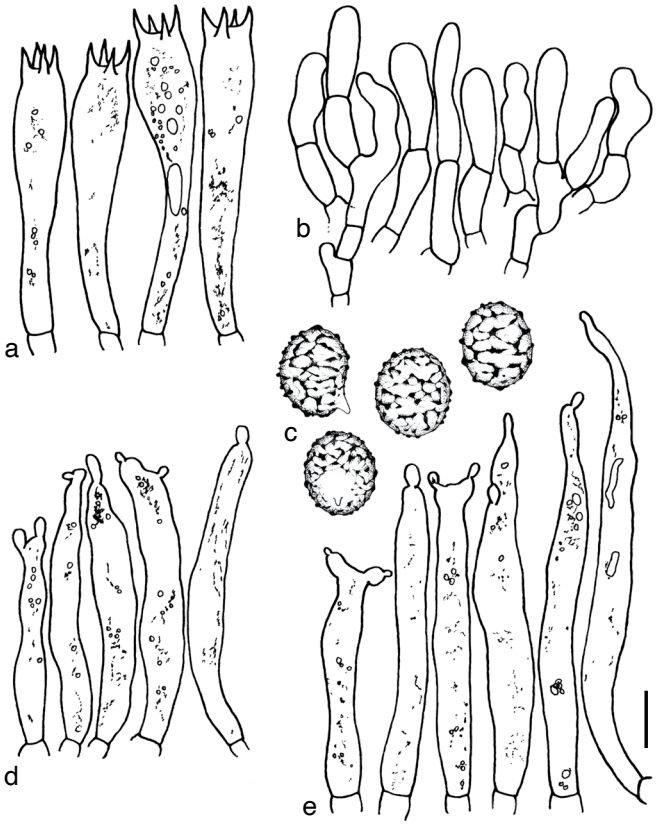


Fig. 18 *Russula densifolia*, micromorphology of the hymenium. a. Basidia (RDL 17-024); b. marginal cells (RDL 17-024); c. basidiospores (RDL 17-024); d. cystidia near lamellae edges (RDL 17-024); e. cystidia on lamellae sides (RDL 17-024). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

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*.

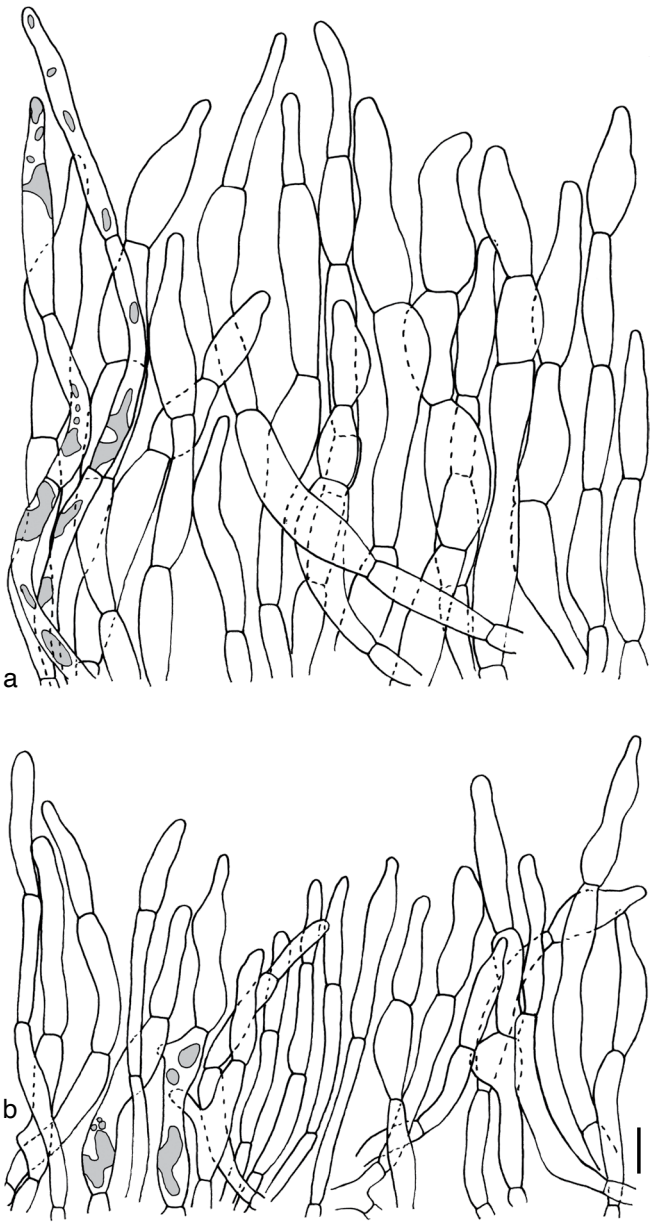


Fig. 19 *Russula densifolia*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 17-024); b. near the pileus centre (RDL 17-024). — Scale bar = 10 µm.

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,

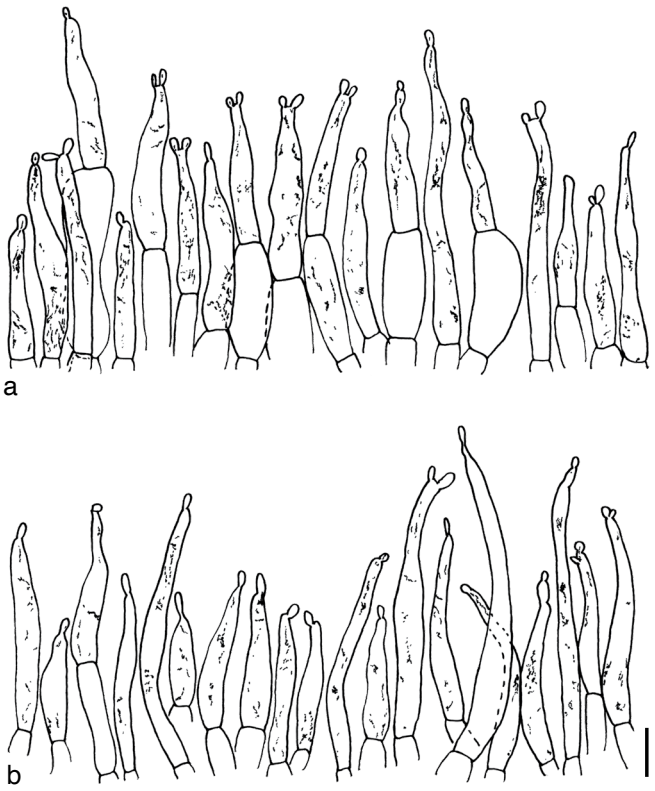


Fig. 20 *Russula densifolia*, pileocystidia. a. Near the pileus margin (RDL 17-024); b. near the pileus centre (RDL 17-024). — Scale bar = 10 µm.

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., Vývrať, 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.

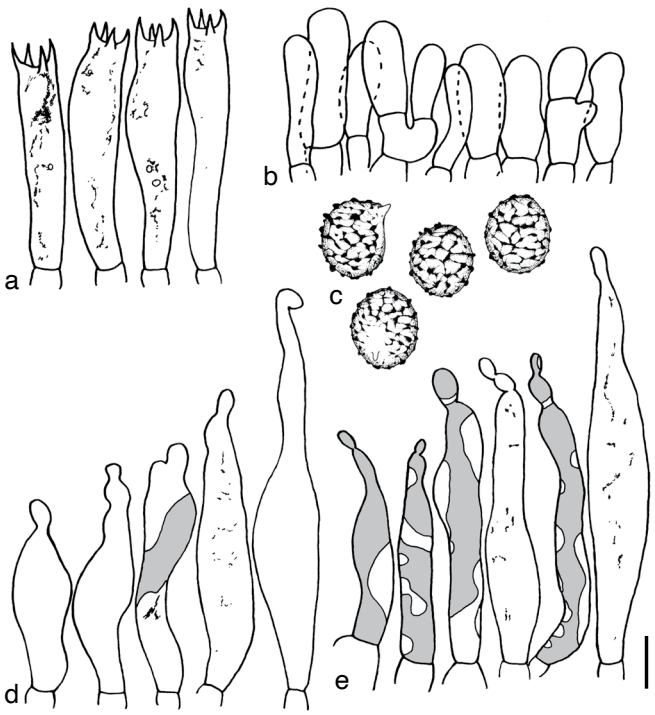


Fig. 22 *Russula densissima*, micromorphology of the hymenium. a. Basidia (Rom. 73-131, paratype); b. marginal cells (FH 2010 ST02); c. basidiospores (Rom. 73-131); d. cystidia near lamellae edges (FH 2010 ST02); e. cystidia on lamellae sides (Rom. 73-131). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

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.

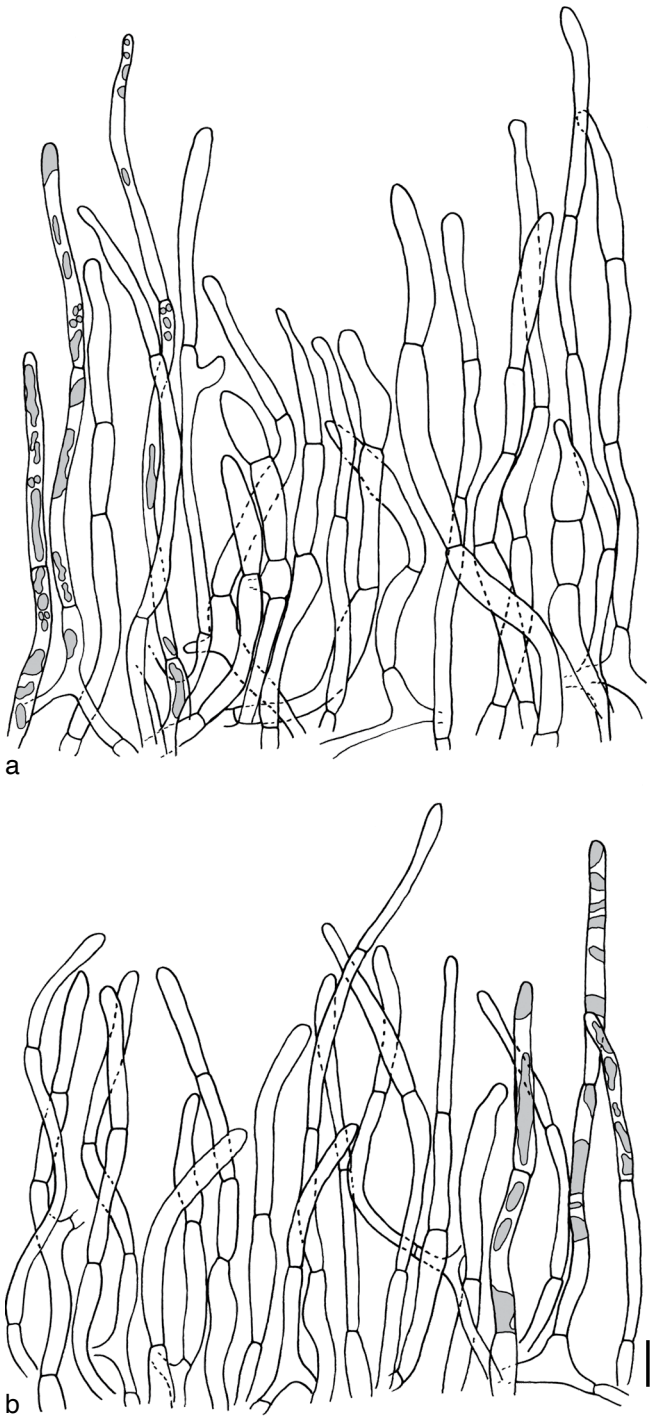


Fig. 23 *Russula densissima*, hyphal terminations of the pileipellis. a. Near the pileus margin (Rom. 73-131, paratype); b. near the pileus centre (FH 2010 ST02). — Scale bar = 10 µm.

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.

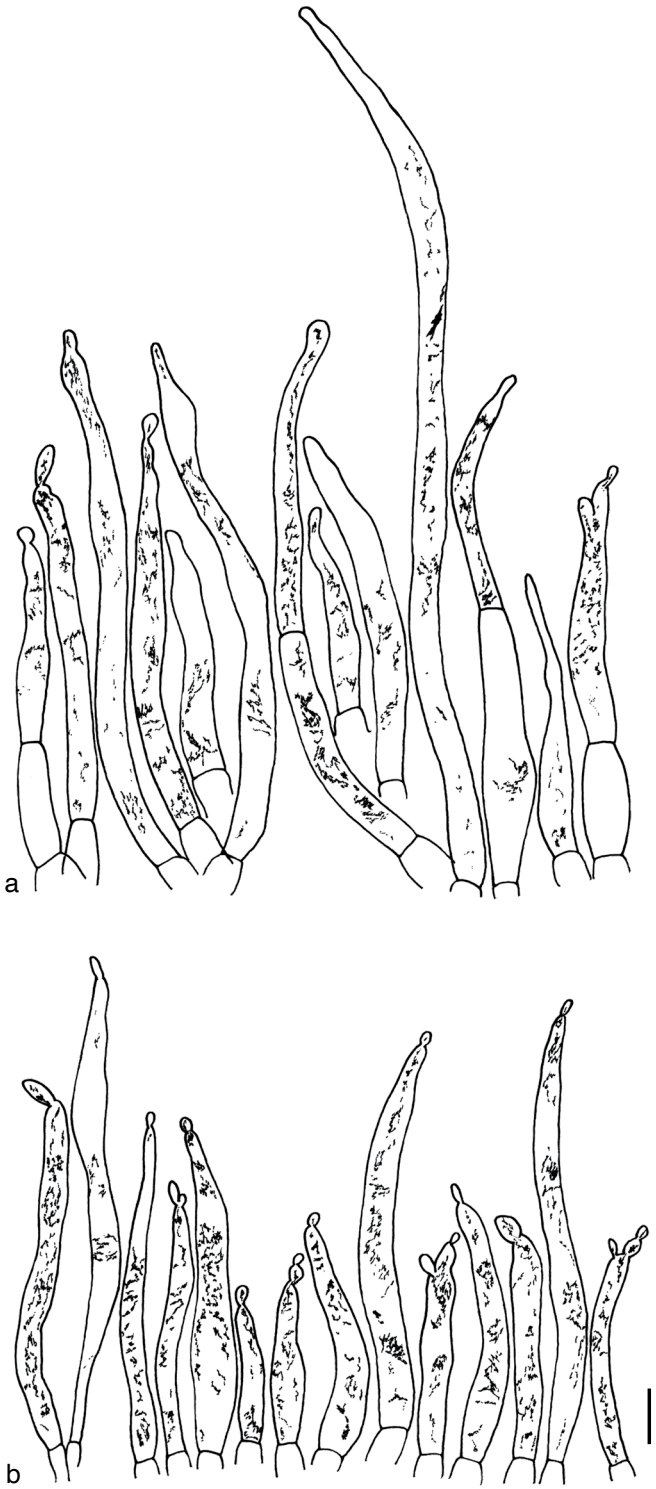


Fig. 24 *Russula densissima*, pileocystidia. a. Near the pileus margin (Rom. 73-131, paratype); b. near the pileus centre (FH 2010 ST02). — Scale bar = 10 µm.

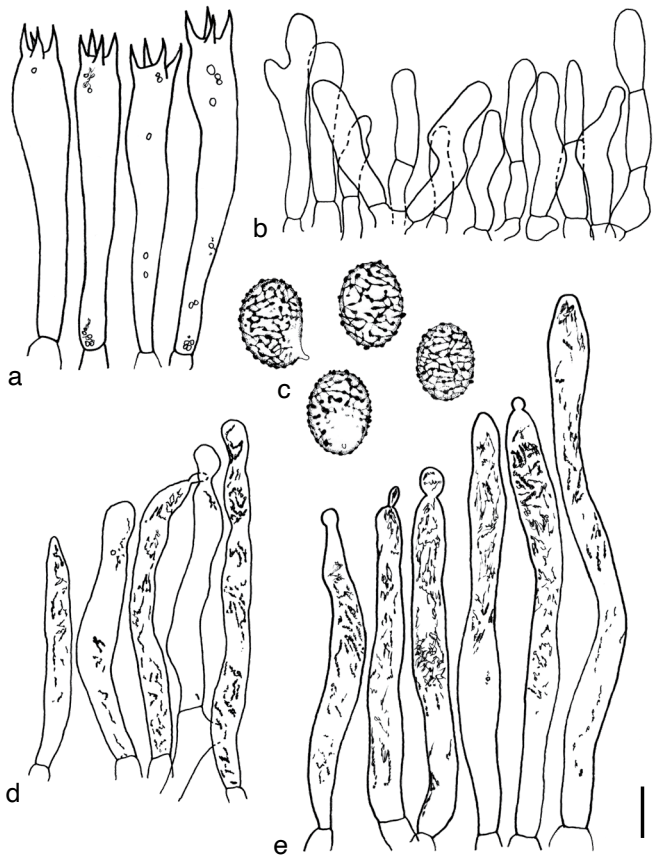


Fig. 25 *Russula marxmuelleriana*, micromorphology of the hymenium. a. Basidia (RDL 17-009, holotype); b. marginal cells (RDL 17-009); c. basidiospores (RDL 17-009); d. cystidia near lamellae edges (FH 2009 ST02); e. cystidia on lamellae sides (RDL 17-009). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

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

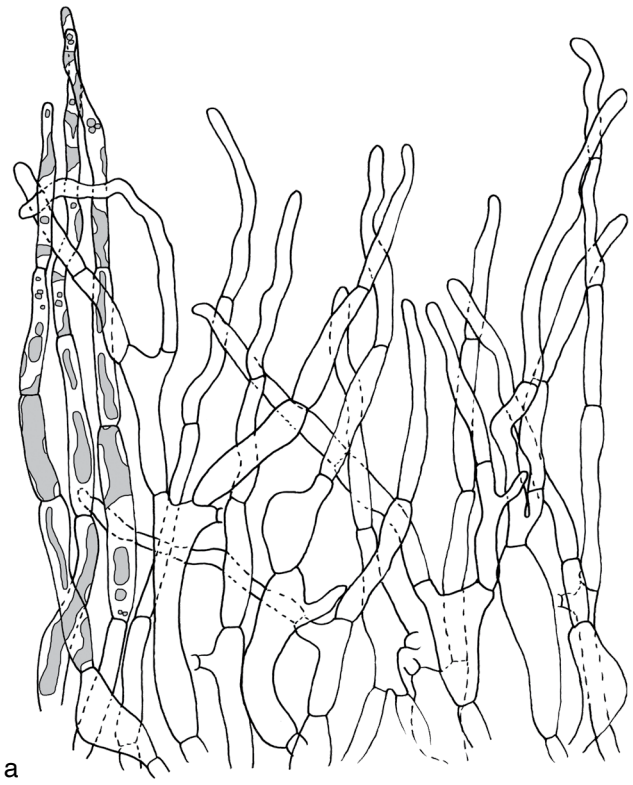
Etymology. In honour of the mycologist Helga Marxmüller, who made important contributions to *Russula* studies.

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-



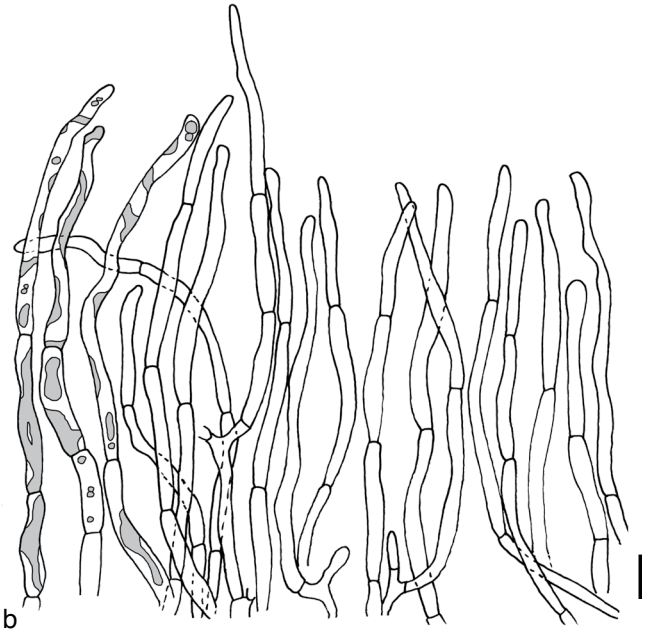


Fig. 26 *Russula marxmuelleriana*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 17-009, holotype); b. near the pileus centre (RDL 17-009). — Scale bar = 10 µm.

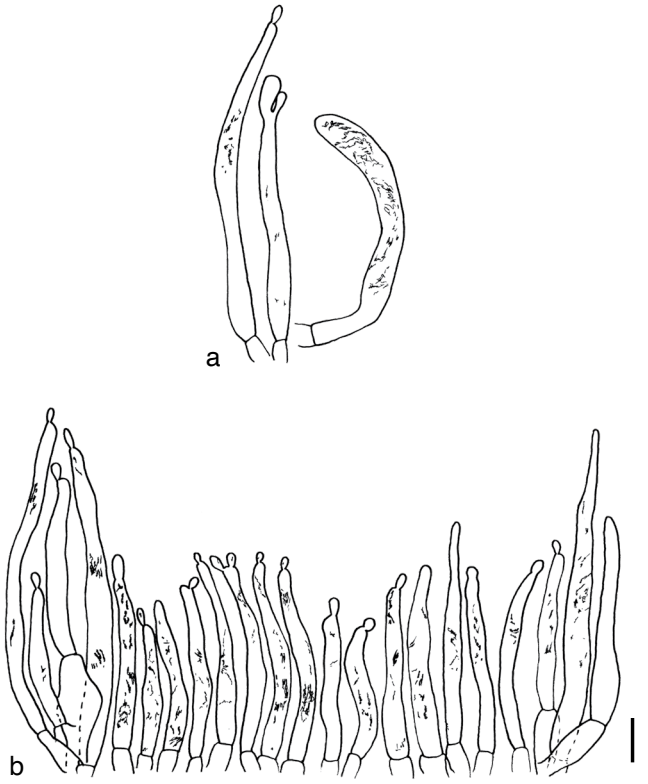


Fig. 27 *Russula marxmuelleriana*, pileocystidia. a. Near the pileus margin (FH 2009 ST02); b. near the pileus centre (RDL 17-009, holotype). — Scale bar = 10 µm.

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-

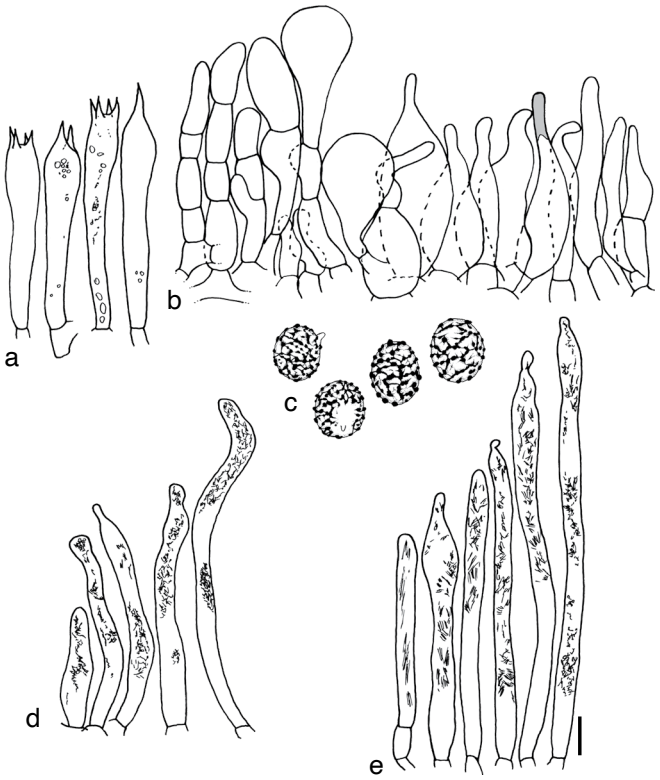


Fig. 28 *Russula nigricans*, micromorphology of the hymenium. a. Basidia (RDL 17-001, RDL 18-061); b. marginal cells (RDL 16-005, RDL 17-002, RDL 17-004, RDL 17-005); c. basidiospores (RDL 17-003, RDL 17-008); d. cystidia near lamellae edges (RDL 16-002); e. cystidia on lamellae sides (RDL 16-004/1).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

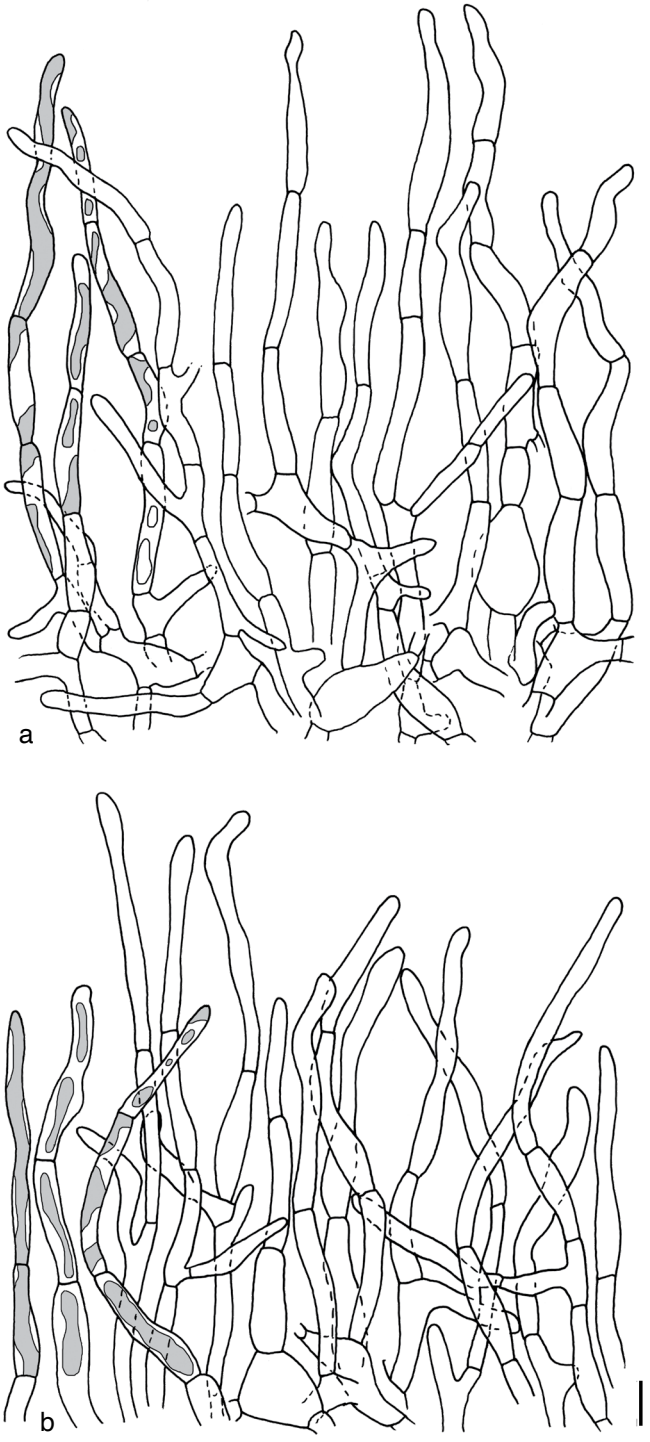


Fig. 29 *Russula nigricans*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 17-003); b. near the pileus centre (RDL 17-001). — Scale bar = 10 µm.

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.

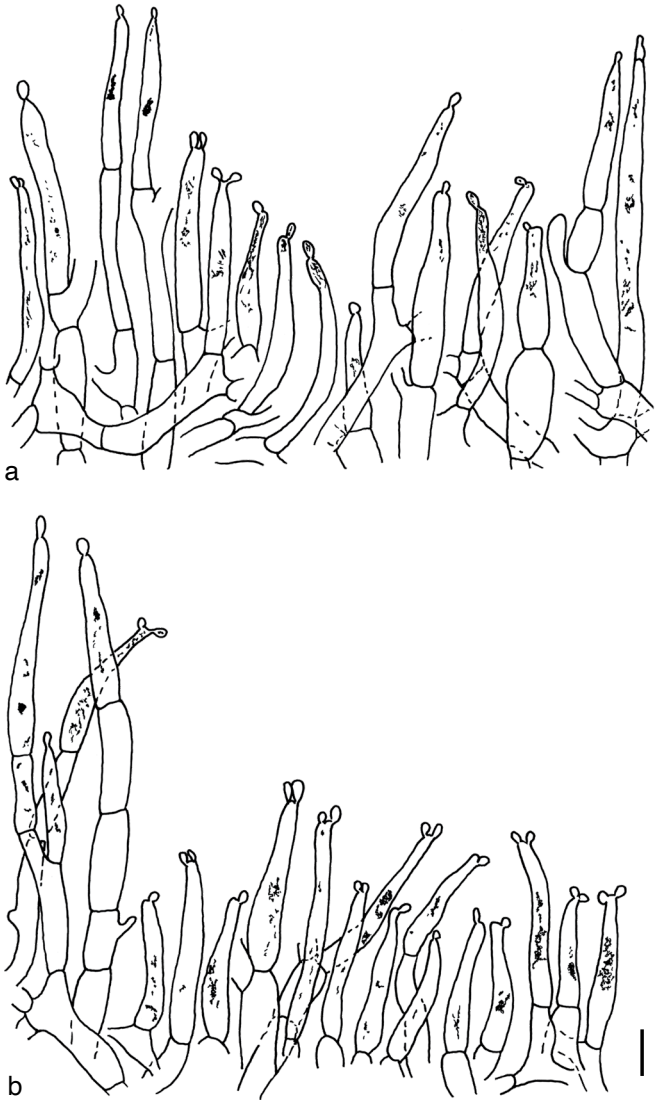


Fig. 30 *Russula nigricans*, pileocystidia. a. Near the pileus margin (RDL 17-008); b. near the pileus centre (RDL 17-008). — Scale bar = 10 µm.

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.

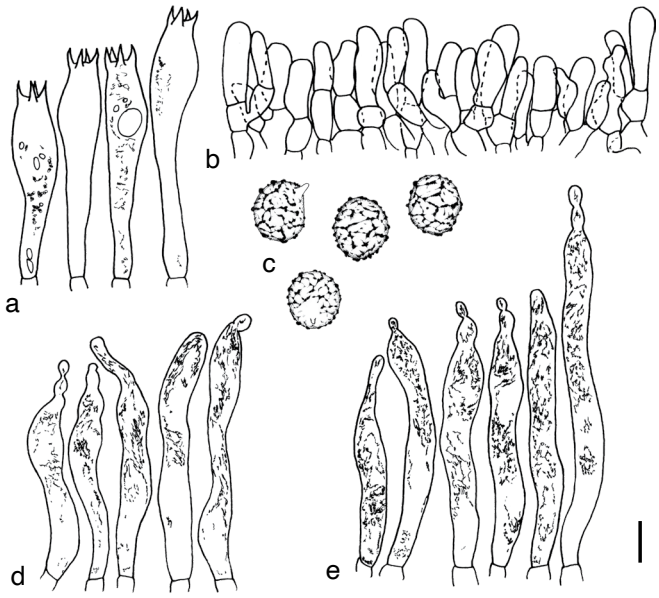


Fig. 33 *Russula picrophylla*, micromorphology of the hymenium. a. Basidia (RDL 16-049); b. marginal cells (RDL 16-049); c. basidiospores (RDL 16-049); d. cystidia near lamellae edges (RDL 16-049, RDL 18-029); e. cystidia on lamellae sides (RDL 16-031, RDL 16-049). — Scale bar: a–b, d–e = 10 µm; c =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

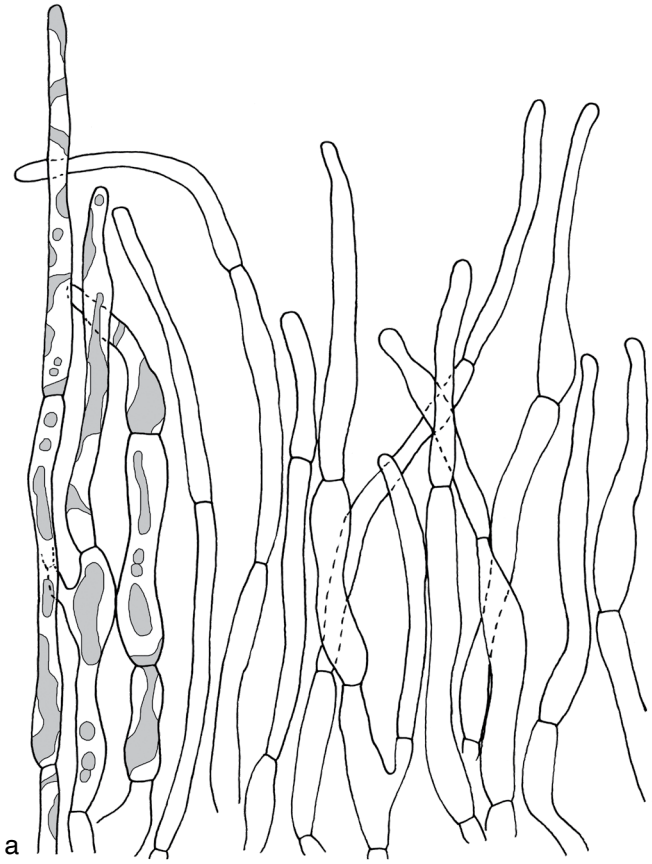


Fig. 34 *Russula picrophylla*, hyphal terminations of the pileipellis. a. Near the pileus margin (RDL 16-049); b. near the pileus centre (RDL 16-049). — Scale bar = 10 µm.

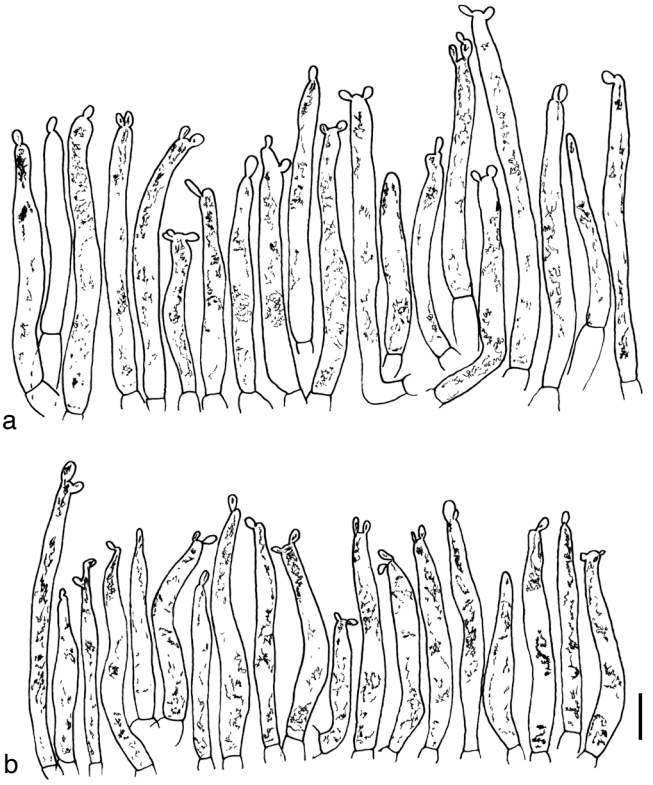


Fig. 35 *Russula picrophylla*, pileocystidia. a. Near the pileus margin (RDL 16-049); b. near the pileus centre (RDL 16-049). — Scale bar = 10 µm.

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

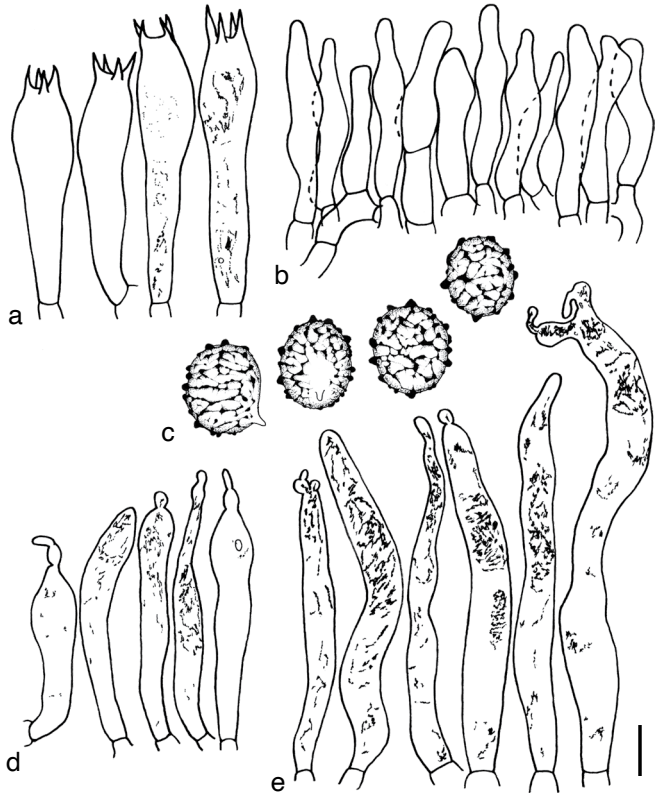


Fig. 37 *Russula roseonigra*, micromorphology of the hymenium. a. Basidia (WU36644, holotype); b. marginal cells (WU36644); c. basidiospores (WU36644); d. cystidia near lamellae edges (WU36644); e. cystidia on lamellae sides (RDL 16-024, WU36644). — Scale bar: a–b, d–e = 10 µm; c = 5 µm.

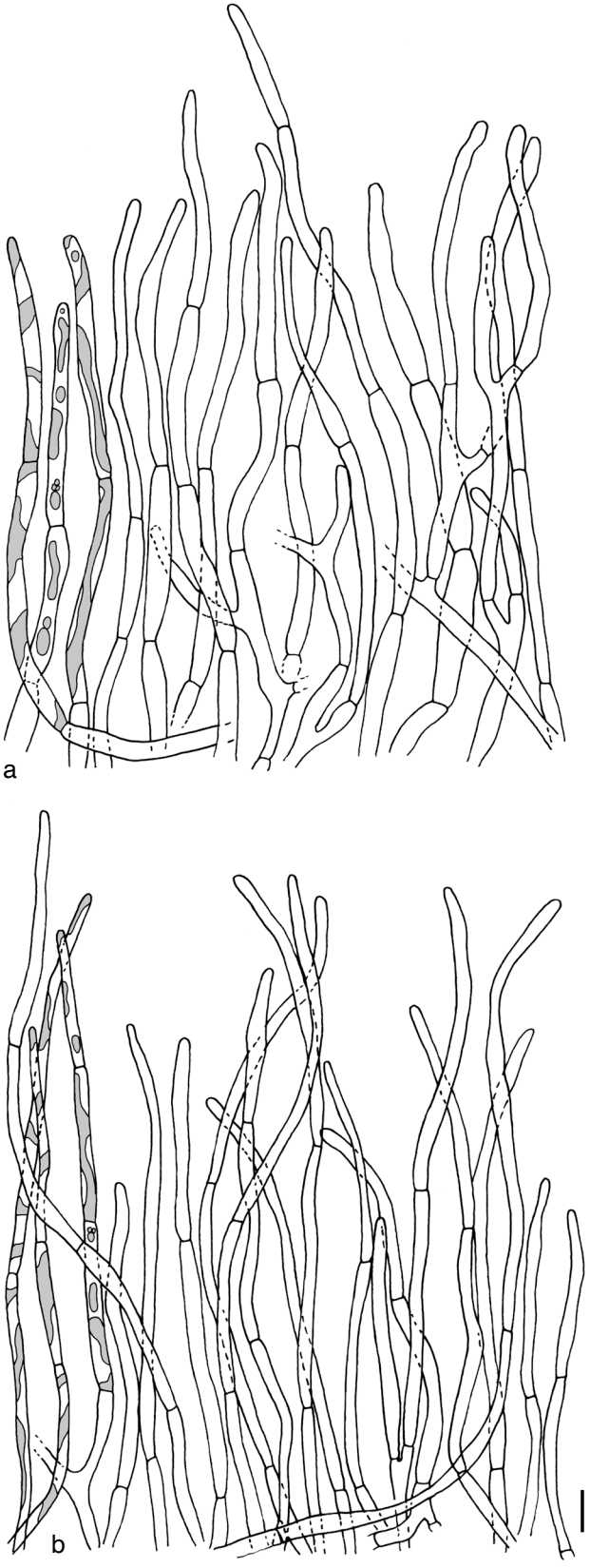


Fig. 38 *Russula roseonigra*, hyphal terminations of the pileipellis. a. Near the pileus margin (WU36644, holotype); b. near the pileus centre (WU36644, holotype). — Scale bar = 10 µm.

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.

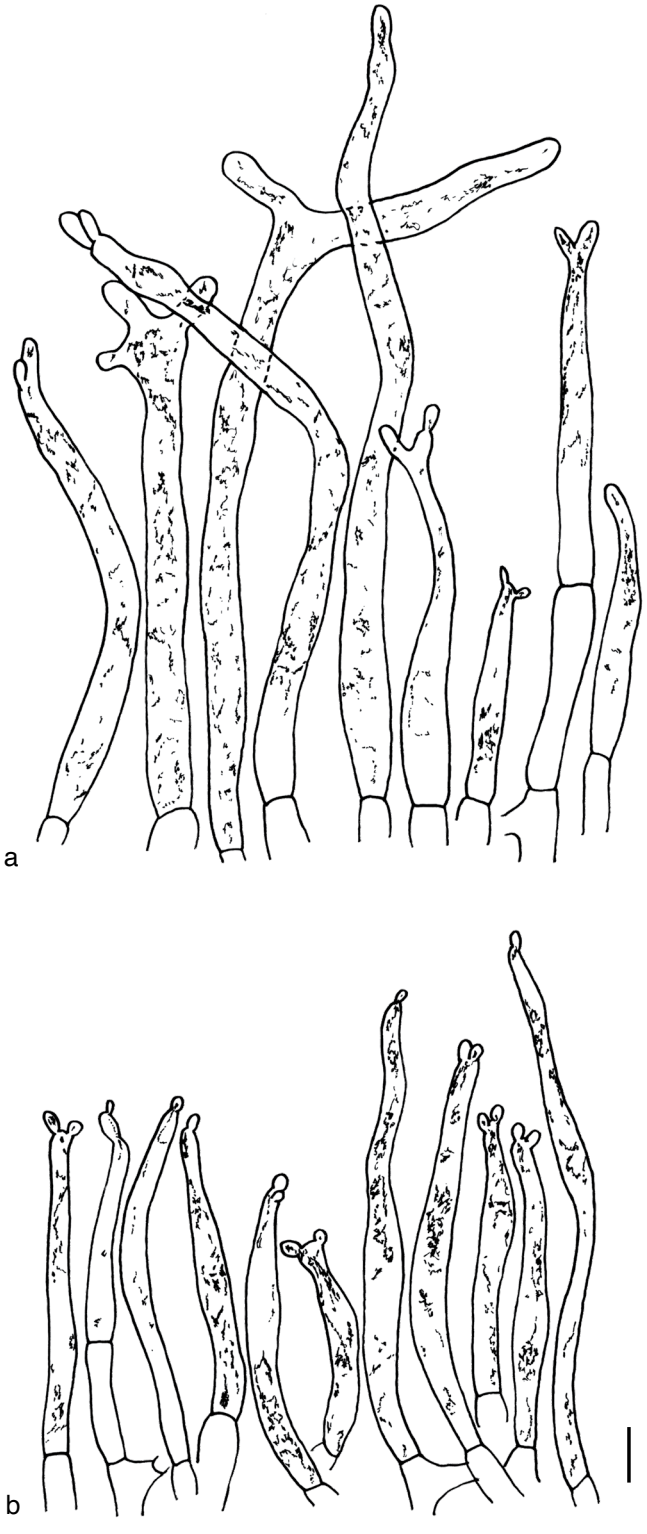


Fig. 39 *Russula roseonigra*, pileocystidia. a. Near the pileus margin (WU36644, holotype); b. near the pileus centre (WU36644, holotype). — Scale bar = 10 µm.

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

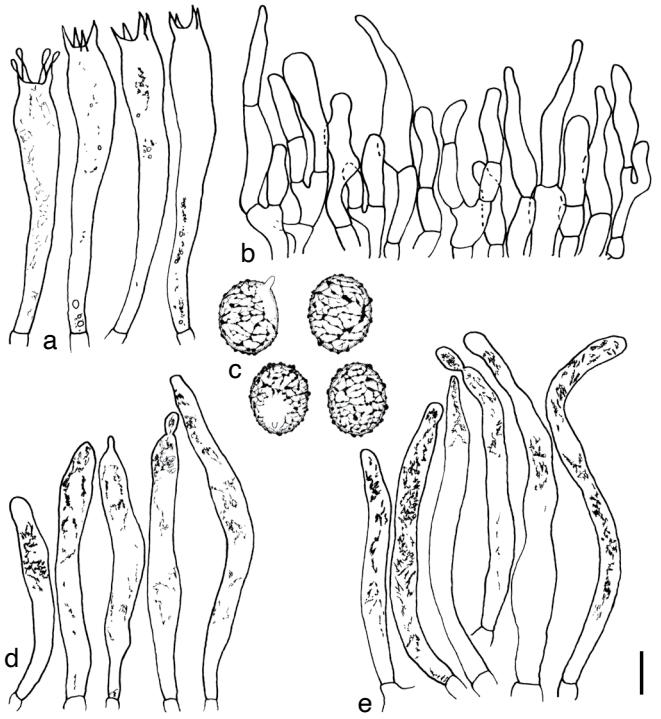


Fig. 40 *Russula thuringiaca*, micromorphology of the hymenium. a. Basidia (FH 2010 ST06); b. marginal cells (FH 2008 ST02, FH 2014 ST02, holotype); c. basidiospores (FH 2010 ST06); d. cystidia near lamellae edges (FH 2008 ST02); e. cystidia on lamellae sides (FH 2010 ST06). — Scale bar: a–b, d–e = 10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

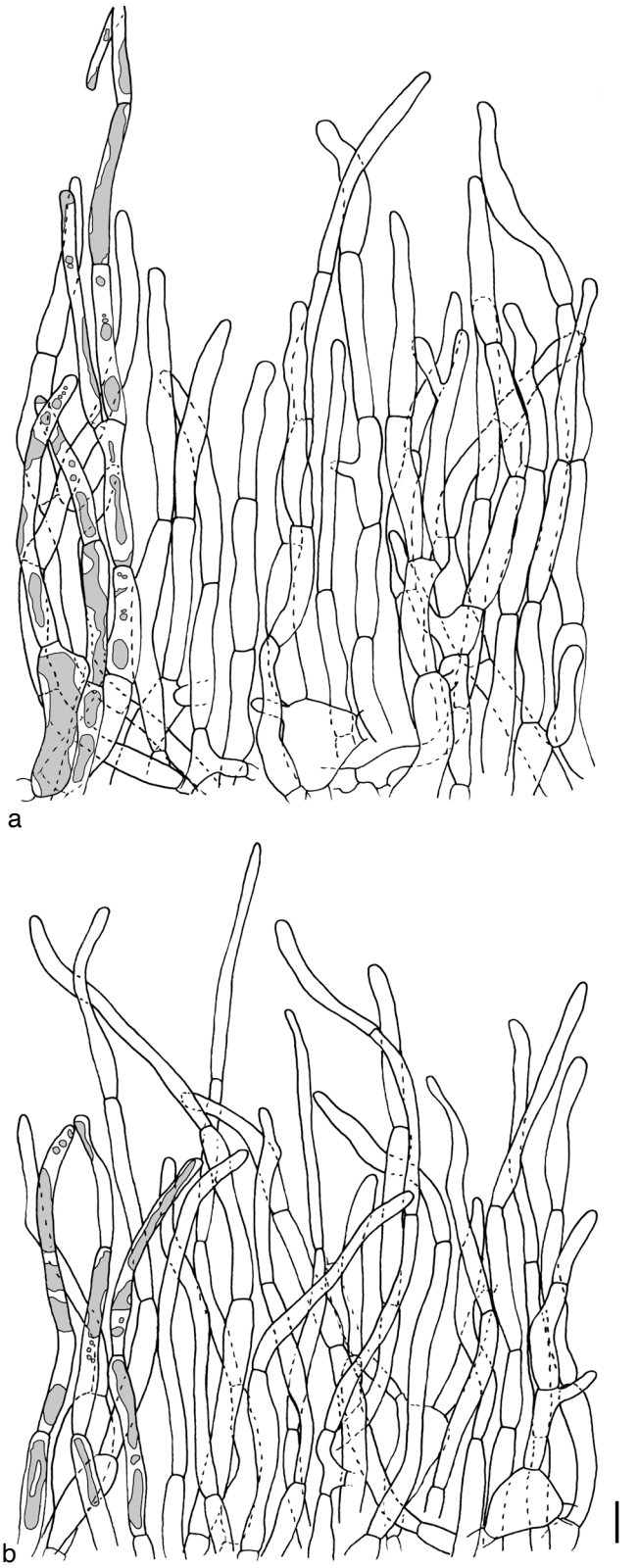


Fig. 41 *Russula thuringiaca*, hyphal terminations of the pileipellis. a. Near the pileus margin (FH 2010 ST06); b. near the pileus centre (FH 2010 ST06). — Scale bar = 10 µm.

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*.

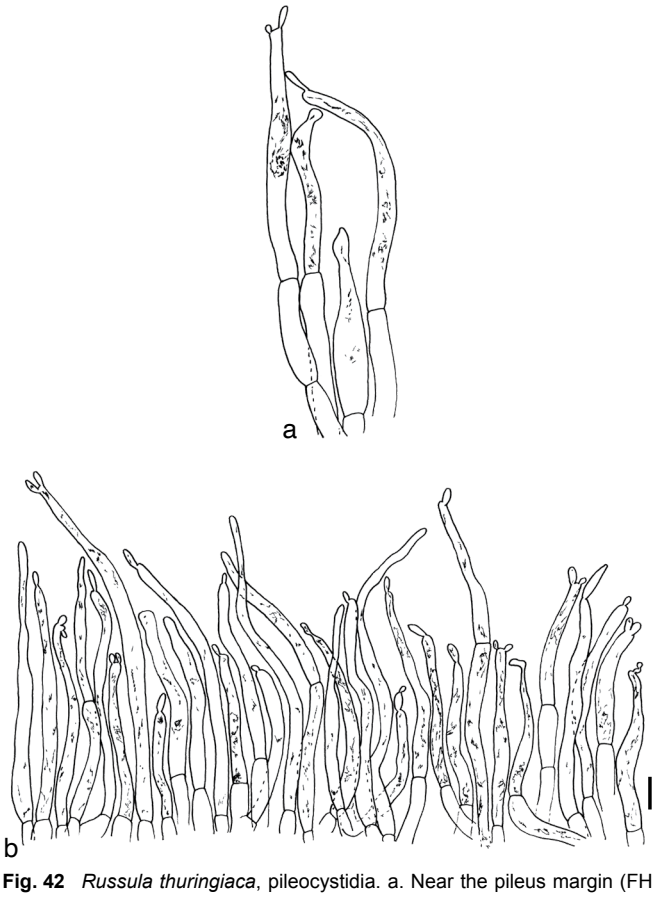


Fig. 42 *Russula thuringiaca*, pileocystidia. a. Near the pileus margin (FH 2010 ST06); b. near the pileus centre (FH 2008 ST02, FH 2014 ST02, holotype). — Scale bar = 10 µm.

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 recom-

mendable 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*,

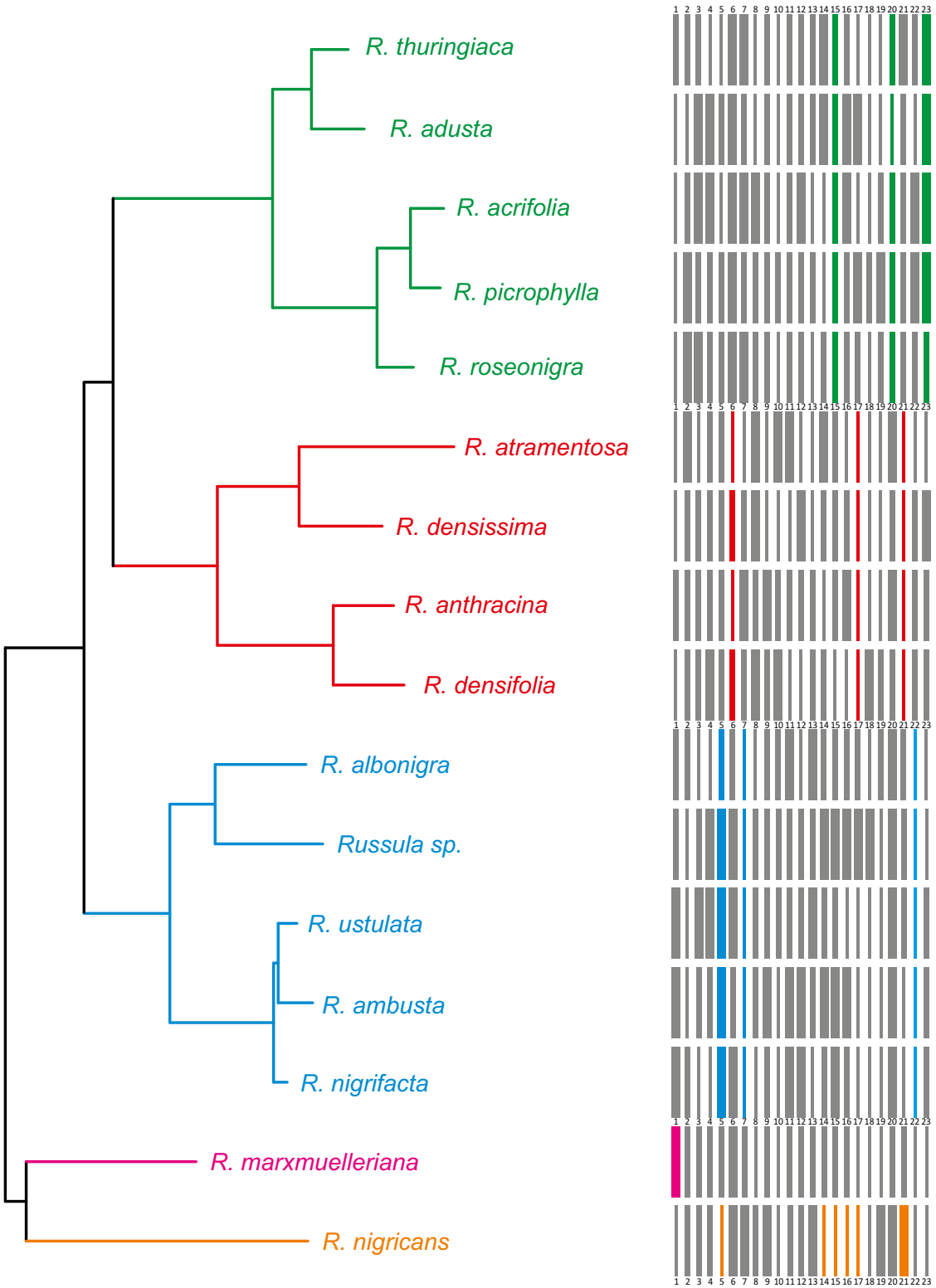


Fig. 43 Simplified phylogenetic tree of the studied European *Compactae* members with a morphological barcode based on 23 characters coded to three categories, represented by different bar thicknesses. Selected characters typical for individual lineages are labelled by corresponding colours. Details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

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.

Species	Information	Unite SH						
		<0.5 %	0.5 %	1 %	1.5 %	2 %	2.5 %	3 %
R. adusta	SH best blast match	SH2310086.08FU	SH1961373.08FU	SH1740691.08FU	SH1569597.08FU	SH1425814.08FU	SH1300488.08FU	SH1188800.08FU
	Unite identification	R. adusta	R. adusta	R. adusta	R. adusta	R. adusta	R. adusta	R. adusta
	representative sequence	HM044555	MN992514	HM069440	UDB0101857 but short sequence	AY969758	UDB0315418 but short sequence	EU711745
	seq no.	81	109	132	158	163	724	726
	remarks	this is the best match for the European species, but it contains also a neighbouring clade with samples from North America and China	includes 5 more SH at <0.5 % ; species from North America and China	includes 9 more SH at <0.5 % ; R. thuringiaca + species from North America and China	includes 12 more SH at <0.5 % and 2 more at 0.5 %; R. thuringiaca + species from North America and China	includes 12 more SH at <0.5 % and 3 more at 0.5 %; R. thuringiaca + species from North America and China	includes 2 SH at 2%; sequences of R. acrifolia, R. picrophylla, R. roseonigra and R. thuringiaca + Asian and North American species	includes 2 SH at 2%; sequences of R. acrifolia, R. picrophylla, R. roseonigra and R. thuringiaca + Asian and North American species
	(other) SH under this name	/	SH2079866.08FU, SH1961388.08FU, SH1961390.08FU, SH1961393.08FU, SH1961494.08FU, SH1961510.08FU, SH3616768.08FU	SH1740701.08FU, SH1740703.08FU, SH1740705.08FU, SH1740796.08FU	SH1569606.08FU, SH1569610.08FU	SH1425822.08FU	SH1300498.08FU	SH1188811.08FU
	other SH with pylogenetically matching sequences	SH3011803.08FU, SH3025952.08FU, SH3130880.08FU, SH3810417.08FU, SH3810320.08FU, SH3812148.08FU, SH2310232.08FU, SH2930315.08FU, SH2310304.08FU, SH3027569.08FU, SH2310419.08FU	SH2820480.08FU, SH1961494.08FU, SH1961550.08FU	SH1740807.08FU				
	remarks	single sequences	good match	good match				
	countries	Austria, Estonia, Finland, France, Italy, Netherlands, Poland, Russian Federation, Sweden, United Kingdom						
	ECM hosts	Larix decidua, Picea abies, Pinus cembra, Pinus koraiensis, Pinus sylvestris						
R. thuringiaca	SH best blast match	SH2310352.08FU	SH1961516.08FU	SH1740691.08FU	SH1569597.08FU	SH1425814.08FU	SH1300488.08FU	SH1188800.08FU
	Unite identification	Russula sp.	Russula sp.	R. adusta	R. adusta	R. adusta	R. adusta	R. adusta
	representative sequence	DQ990850	DQ990850	HM069440	UDB0101857 but short sequence	AY969758	UDB0315418 but short sequence	EU711745
	seq no.	3	3	132	158	163	724	726
	remarks	good match	good match	includes 9 more SH at <0.5 %; R. adusta + species from North America and China	includes 12 more SH at <0.5 % and 2 more at 0.5 %; R. adusta + species from North America and China	includes 12 more SH at <0.5 % and 3 more at 0.5 %; R. adusta + species from North America and China	includes 2 SH at 2%; sequences of R. acrifolia, R. picrophylla, R. roseonigra and R. thuringiaca + Asian and North American species	includes 2 SH at 2%; sequences of R. acrifolia, R. picrophylla, R. roseonigra and R. thuringiaca + Asian and North American species
	(other) SH under this name	/	/	/	/	/	/	/
	other SH with pylogenetically matching sequences	/	/	/	/	/	/	/
	countries	Germany, Slovakia, Italy, Czech Republic, Switzerland						
	ECM hosts	Castanea, Picea abies						

Fig. S1 (cont.)

Species	Information	Unite SH						
		<0.5 %	0.5 %	1 %	1.5 %	2 %	2.5 %	3 %
R. acrifolia	SH best blast match	SH2310119.08FU	SH1961379.08FU	SH1740690.08FU	SH1569596.08FU	SH1425813.08FU	SH1300488.08FU	SH1188800.08FU
	Unite identification	R. anthracina	R. nigricans	R. nigricans	R. nigricans	R. nigricans	R. adusta	R. adusta
	representative sequence	UDB0346705	AB507016	AB507016	UDB0122694	UDB0375918	UDB0315418	EU711745
	seq no.	66	235	331	553	560	724	726
	remarks	good match	includes 15 SH at <0,5%; species from Asia and North America	includes 22 SH at <0,5%; sequences of R. picrophylla and R. roseonigra + species from Asia and North America	includes 4 SH at 1%; sequences of R. picrophylla and R. roseonigra + Asian and North American species	includes 4 SH at 1%; sequences of R. picrophylla and R. roseonigra + Asian and North American species	includes 2 SH at 2%; sequences of R. adusta, R. picrophylla, R. roseonigra and R. thuringiaca + Asian and North American species	includes 2 SH at 2%; sequences of R. adusta, R. picrophylla, R. roseonigra and R. thuringiaca + Asian and North American species
	(other) SH under this name	/	SH1961378.08FU, SH1961391.08FU, SH1961450.08FU, SH1961485.08FU, SH1961543.08FU	SH1740695.08FU, SH1740724.08FU	no SH	no SH	no SH	no SH
	other SH with pylogenetically matching sequences	SH2310131.08FU, SH2310387.08FU, SH2932153.08FU, SH3017589.08FU, SH3026738.08FU, SH3044373.08FU, SH3778099.08FU, SH3778103.08FU, SH3778112.08FU, SH3794059.08FU, SH2310131.08FU, SH3778099.08FU, SH3811172.08FU, SH3812483.08FU, SH3640538.08FU	SH3616768.08FU	SH1740796.08FU				
	remarks	good macth, SH3640538.08FU is a single sequence from the Russian Federation	single sequence from the Russian Federation	Species from North America and Asia + sequence from the Russian Federation				
	countries	Estonia, France, Germany, Italy, Latvia, Russian Federation, Slovenia, Spain, Sweden, Switzerland						
	ECM hosts	Fagus sylvatica, Picea abies, Pinus sylvestris, Quercus						

Fig. S1 (cont.)

Species	Information	Unite SH						
		<0.5 %	0.5 %	1 %	1.5 %	2 %	2.5 %	3 %
R. picrophylla	SH best blast match	SH2310313.08FU	SH1961391.08FU	SH1740695.08FU	SH1569596.08FU	SH1425813.08FU	SH1300488.08FU	SH1188800.08FU
	Unite identification	Russula sp.	R. acrifolia	R. acrifolia	R. nigricans	R. nigricans	R. adusta	R. adusta
	representative sequence	UDB0162904	UDB0162904	UDB0162904	UDB0122694	UDB0375918	UDB0315418 but short sequence	EU711745
	seq no.	33	141	137	553	560	724	726
	remarks	?	includes 7 more SH at <0.5 %; sequences of R. roseonigra + Asian species	includes 7 more SH at <0.5 %; sequences of R. roseonigra + Asian species	includes 4 SH at 1%; sequences of R. acrifolia and R. roseonigra + Asian and North American species	includes 4 SH at 1%; sequences of R. acrifolia and R. roseonigra + Asian and North American species	includes 2 SH at 2%; sequences of R. acrifolia, R. adusta, R. roseonigra and R. thuringiaca + Asian and North American species	includes 2 SH at 2%; sequences of R. acrifolia, R. adusta, R. roseonigra and R. thuringiaca + Asian and North American species
	(other) SH under this name	/	/	/	/	/	/	/
	other SH with pylogenetically matching sequences	SH2310108.08FU, SH2310112.08FU, SH3056293.08FU, SH3671922.08FU	SH1961383.08FU	SH1740690.08FU				
	remarks	good matches	good match	includes 7 SH at 0,5%; sequences of R. acrifolia and R. roseonigra + Asian and North American species				
	countries	Austria, Czech Republic, Estonia, France, Germany, Hungary, Italy, Latvia, Portugal, Slovenia, Spain, Sweden, Switzerland						
	ECM hosts	Epipactis helleborine, Pinus sylvestris, Pyrola rotundifolia, Quercus ilex, Quercus petraea, Quercus rotundifolia						

Fig. S1 (cont.)

Species	Information	Unite SH						
		<0.5 %	0.5 %	1 %	1.5 %	2 %	2.5 %	3 %
R. roseonigra	SH best blast match	SH3807839.08FU	SH1961391.08FU	SH1740690.08FU	SH1569596.08FU	SH1425813.08FU	SH1300488.08FU	SH1188800.08FU
	Unite identification	unidentified	R. acrifolia	R. nigricans	R. nigricans	R. nigricans	R. adusta	R. adusta
	representative sequence	UDB0784090	UDB0162904	AB507016	UDB0122694	UDB0375918	UDB0315418 but short sequence	EU711745
	seq no.	1	141	331	553	560	724	726
	remarks		includes 7 SH at <0,5%, sequences of R. picrophylla + Asian species	includes 22 SH at <0,5% and 6 SH at 0,5%; sequences of R. acrifolia and R. picrophylla + species from Asia and North America	includes 4 SH at 1%; sequences of R. acrifolia and R. picrophylla + Asian and North American species	includes 4 SH at 1%; sequences of R. acrifolia and R. picrophylla + Asian and North American species	includes 2 SH at 2%; sequences of R. acrifolia, R. adusta, R. picrophylla and R. thuringiaca + Asian and North American species	includes 2 SH at 2%; sequences of R. acrifolia, R. adusta, R. picrophylla and R. thuringiaca + Asian and North American species
	(other) SH under this name	no SH	no SH	no SH	no SH	no SH	no SH	no SH
	other SH with pylogenetically matching sequences	SH2310179.08FU, SH3807855.08FU, SH3808324.08FU, SH3808362.08FU, SH2310279.08FU, SH3010295.08FU, SH3044181.08FU	SH1961450.08FU, SH1961485.08FU	SH1740695.08FU				
	remarks	good matches, SH2310179.08FU contains sequences from De Lange et al. 2021	good matches, contain overlapping SH at <0,5% with eachother and SHSH1961391.08FU	good match, overlapping SH at <0,5% (SH2310179.08FU) with SH1740690.08FU				
	countries	Austria, Bosnia and Herzegovina, Czech Republic, Estonia, France, Germany, Italy, Latvia, Slovenia, Switzerland						
	ECM hosts	Abies alba, Fagus sylvatica						
R. anthracina	SH best blast match	SH2310293.08FU	SH1961489.08FU	SH1740780.08FU	SH1569674.08FU	SH1425816.08FU	SH1300491.08FU	SH1188803.08FU
	Unite identification	R. fuliginosa	R. fuliginosa	R. fuliginosa	R. densifolia	R. densifolia	R. densifolia	R. densifolia
	representative sequence	HG798529	HG798529	UDB0788149	UDB0788159	MT278176	MT278176	MT278176
	seq no.	3	3	40	72	127	127	127
	remarks	good match	good match	includes 1 more SH at <0.5 % and 0.5 %; includes SH's matching R. densifolia	includes 2 more SH at <0.5 %	includes 9 more SH at <0.5 % and one more at 1 %	includes 9 more SH at <0.5 % and one more at 1 %	includes 9 more SH at <0.5 % and one more at 1 %
	(other) SH under this name	/	SH1961396.08FU	no SH	SH1569618.08FU	no SH	no SH	no SH
	other SH with pylogenetically matching sequences	SH3067284.08FU	SH2884977.08FU	SH2794198.08FU				
	remarks	good match	good match	contains sequences of R. densifolia and a Japanese species				
	countries	Estonia, France, Italy, Slovakia						
	ECM hosts	/						

Fig. S1 (cont.)

Species	Information	Unite SH						
		<0.5 %	0.5 %	1 %	1.5 %	2 %	2.5 %	3 %
R. densifolia	SH best blast match	SH2310093.08FU	SH1961374.08FU	SH1740780.08FU	SH1569674.08FU	SH1425816.08FU	SH1300491.08FU	SH1188803.08FU
	Unite identification	R. densifolia	R. densifolia	R-. fuliginosa	R. densifolia	R. densifolia	R. densifolia	R. densifolia
	representative sequence	UDB0788149	MT278178	UDB0788149	UDB0788159	MT278176	MT278176	MT278176
	seq no.	62	102	40	72	127	127	127
	remarks	?	includes 5 more SH at <0.5 %	includes 1 more SH at <0.5 % and 0.5 %; includes SH's matching R. anthracina	includes 2 more SH at <0.5 %	includes 9 more SH at <0.5 % and one more at 1 %	includes 9 more SH at <0.5 % and one more at 1 %	includes 9 more SH at <0.5 % and one more at 1 %
	(other) SH under this name	/	SH2880348.08FU, SH2834844.08FU, SH2845277.08FU, SH2839591.08FU, SH1961376.08FU, SH1961381.08FU, SH1961383.08FU, SH1961399.08FU, SH1961401.08FU, SH1961413.08FU, SH1961414.08FU, SH1961430.08FU, SH1961436.08FU, SH1961511.08FU, SH3620187.08FU, SH3621238.08FU, SH3621511.08FU, SH3621519.08FU, SH3762702.08FU, SH3768897.08FU, SH3768910.08FU	SH1669098.08FU, SH1740692.08FU, SH1740693.08FU, SH1740702.08FU, SH1740707.08FU, SH1740712.08FU, SH1740733.08FU, SH1740740.08FU, SH1740778.08FU, SH2764199.08FU, SH2768025.08FU, SH2794198.08FU, SH2791260.08FU, SH3603968.08FU, SH3604642.08FU, SH3604815.08FU, SH3746829.08FU	SH1569598.08FU, SH1569599.08FU, SH1569608.08FU, SH1569609.08FU, SH1569617.08FU, SH1569641.08FU, SH1569673.08FU, SH1509964.08FU, SH2700213.08FU, SH2709095.08FU, SH3592447.08FU, SH3731650.08FU	SH1373645.08FU, SH1425815.08FU, SH1425825.08FU, SH1425826.08FU, SH1425831.08FU, SH1425851.08FU, SH1425878.08FU, SH2657244.08FU, SH2664694.08FU, SH3581503.08FU, SH3582447.08FU	SH1253573.08FU, SH1300501.08FU, SH1300502.08FU, SH1300503.08FU, SH1300542.08FU, SH1300490.08FU, SH2620594.08FU, SH2627031.08FU, SH3573189.08FU, SH3574002.08FU	SH1145758.08FU, SH1188802.08FU, SH1188814.08FU, SH1188815.08FU, SH1188816.08FU, SH1188848.08FU, SH2588561.08FU, SH2594295.08FU, SH3565942.08FU, SH3566669.08FU
	other SH with pylogenetically matching sequences	SH2310090.08FU, SH2310152.08FU, SH2310402.08FU, SH3649494.08FU, SH2310189.08FU, SH2310212.08FU, SH2310295.08FU, SH3032079.08FU, SH3033575.08FU, SH3649495.08FU, SH3806647.08FU, SH3806686.08FU, SH3807794.08FU, SH3808111.08FU, SH3809219.08FU, SH3809277.08FU, SH3810018.08FU, SH3810050.08FU, SH3649482.08FU, SH3054168.08FU, SH3797820.08FU, SH3649471.08FU	SH3621519.08FU, SH2880348.08FU, SH3762702.08FU, SH3621511.08FU	SH1740693.08FU, SH2791260.08FU, SH2794198.08FU, SH3604815.08FU	SH1569599.08FU, SH3592447.08FU	SH3582447.08FU	SH3574002.08FU	SH3566669.08FU
	remarks	good match	good match	SH1740693.08FU and SH2794198.08FU contain other species	SH1569599.08FU contains others species	single sequence	single sequence	single sequence
	countries	Belgium, Czech Republic, Denmark, Estonia, France, Germany, Italy, Norway, Poland, Portugal, Slovakia, Slovenia, Spain, Switzerland, United Kingdom						
	ECM hosts	Abies alba, Fagus sylvatica, Halimium lasianthum, Picea abies, Pinus pinaster, Pinus sylvestris, Quercus, Quercus robur, Quercus suber						

Fig. S1 (cont.)

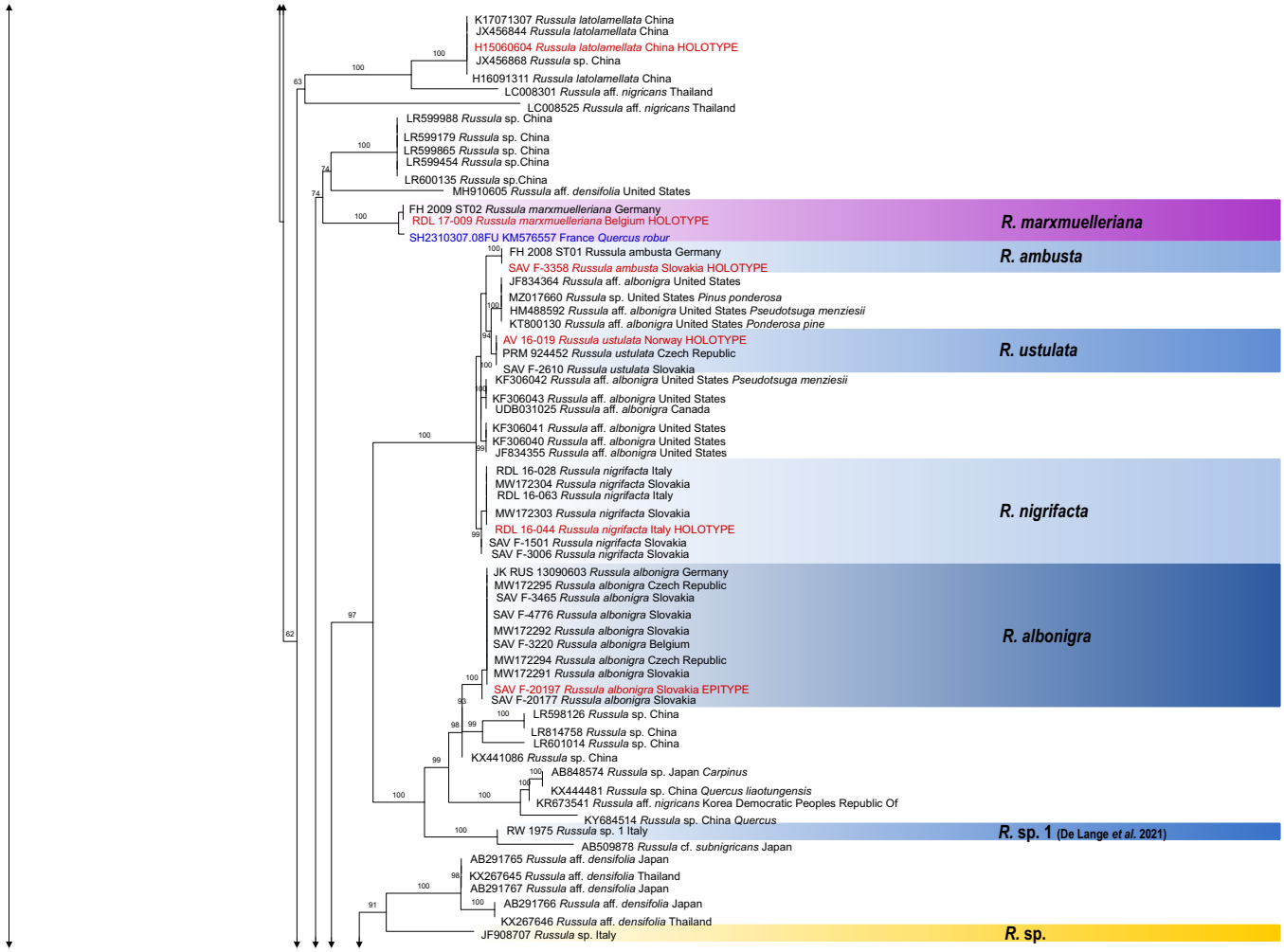
Species	Information	Unite SH						
		<0.5 %	0.5 %	1 %	1.5 %	2 %	2.5 %	3 %
R. atramentosa	SH best blast match	SH2310098.08FU	SH1961400.08FU	SH1740713.08FU	SH1569618.08FU	SH1425823.08FU	SH1300500.08FU	SH1188812.08FU
	Unite identification	R. atramentosa	R. atramentosa	R. atramentosa	R. anthracina	R. atramentosa	R. atramentosa	R. atramentosa
	representative sequence	UDB0219641	UDB0219641	UDB0219641	FM999656	FM999656	FM999656	FM999656
	seq no.	12	12	12	9	16	17	17
	remarks	good match	good match	good match	includes 1 more SH at 1 % (only US sequences)	includes 1 more SH at 1 % (only US sequences)	includes 1 more SH at 1 % (only US sequences)	includes 1 more SH at 1 % (only US sequences)
	(other) SH under this name	/	no additional SH	no additional SH	SH1569619.08FU	no additional SH	no additional SH	no additional SH
	other SH with pylogenetically matching sequences	/	/	/	/	/	/	/
	countries	Austria, Belgium, Estonia, France, Germany, Italy, Norway, Slovakia						
	ECM hosts	/						
R. densisssima	SH best blast match	SH2310117.08FU	SH1961416.08FU	SH1740727.08FU	SH1569629.08FU	SH1425824.08FU	SH1300499.08FU	SH1188807.08FU
	Unite identification	R. densissima	R. densissima	R. densissima	R. densissima	R. densissima	R. densissima	R. inquinata
	representative sequence	UDB0784080	UDB0784080	UDB0784080	UDB0784080	UDB0784080	UDB0784080	UDB0784080
	seq no.	10	10	10	10	14	15	21
	remarks	good match	good match	good match	good match	includes 3 more SH at <0.5 % (non-EU)	includes 4 more SH at <0.5 % (non-EU)	includes 8 more SH at <0.5 % and two more at 2,5 % (non-EU)
	(other) SH under this name	/	SH1961416.08FU	SH1740727.08FU	SH1569629.08FU	SH1425824.08FU	SH1300499.08FU	no SH
	other SH with pylogenetically matching sequences	/	/	/	/	/	/	/
	countries	France, Germany, Hungary, Italy, Switzerland						
	ECM hosts	Fagus sylvatica, Quercus, Quercus petraea						
R. marxmuelleriana	SH best blast match	SH2310307.08FU	SH1961497.08FU	SH1740786.08FU	SH1569679.08FU	SH1425883.08FU	SH1300547.08FU	SH1188852.08FU
	Unite identification	Russula sp.	Russula sp.	Russula sp.	Russula sp.	Russula sp.	Russula sp.	Russula sp.
	representative sequence	KM576557	KM576557	KM576557	KM576557	KM576557	KM576557	KM576557
	seq no.	2	2	2	2	2	2	2
	remarks	yes	yes	yes	yes	yes	yes	yes
	(other) SH under this name	/	/	/	/	/	/	/
	other SH with pylogenetically matching sequences	/	/	/	/	/	/	/
	countries	Belgium, France, Germany						
	ECM hosts	Quercus robur						

Fig. S1 (cont.)

Species	Information	Unite SH						
		<0.5 %	0.5 %	1 %	1.5 %	2 %	2.5 %	3 %
R. nigricans	SH best blast match	SH2310087.08FU	SH1961375.08FU	SH1740689.08FU	SH1569595.08FU	SH1425812.08FU	SH1300489.08FU	SH1188801.08FU
	Unite identification	R. nigricans	R. nigricans	Agaricomycetes	Agaricomycetes	Agaricomycetes	Agaricomycetes	Agaricomycetes
	representative sequence	UDB0781551	KX168665	UDB071490	UDB0787769	UDB0787769	UDB0787769	UDB0787769
	seq no.	146	25	373	389	433	442	442
	remarks	good match	good match, includes 1 more SH at <0.5 %	includes 10 SH at <0.5 %; also North American species	includes 2 SH at 1%	includes 3 additional SH at 1,5% (non-EU)	includes 2 additional SH at 1,5% (Asian)	matching SH1300489.08FU
	(other) SH under this name	/	SH2112750.08FU, SH2831629.08FU, SH2833985.08FU, SH1961377.08FU, SH1961379.08FU, SH1961386.08FU, SH1961429.08FU, SH1961432.08FU, SH1961441.08FU, SH1961443.08FU, SH1961453.08FU, SH1961460.08FU, SH1961472.08FU, SH1961473.08FU, SH1961477.08FU, SH1961484.08FU, SH1961487.08FU, SH1961499.08FU, SH1961500.08FU, SH1961503.08FU, SH1961525.08FU, SH1961541.08FU, SH3621687.08FU, SH3755217.08FU, SH3755218.08FU, SH3762002.08FU	SH1848837.08FU, SH1740690.08FU, SH1740696.08FU, SH1740721.08FU, SH1740735.08FU, SH1740737.08FU, SH1740745.08FU, SH1740752.08FU, SH1740756.08FU, SH1740765.08FU, SH1740766.08FU, SH1740770.08FU, SH1740777.08FU, SH2760477.08FU, SH2782985.08FU, SH3604920.08FU, SH3738200.08FU, SH3742716.08FU	SH1569596.08FU, SH1569601.08FU, SH1569607.08FU, SH1569626.08FU, SH1569637.08FU, SH1569638.08FU, SH1569646.08FU, SH1569650.08FU, SH1569654.08FU, SH1569662.08FU, SH1569663.08FU, SH1569666.08FU, SH1655628.08FU, SH2706248.08FU, SH2723911.08FU, SH3592526.08FU, SH3725056.08FU, SH3728643.08FU	SH1497967.08FU, SH1425813.08FU, SH1425817.08FU, SH1425838.08FU, SH1425840.08FU, SH1425849.08FU, SH1425857.08FU, SH1425861.08FU, SH1425867.08FU, SH1425868.08FU, SH1425871.08FU, SH2677045.08FU, SH3582514.08FU, SH3713999.08FU, SH3717088.08FU	SH1300511.08FU, SH1300521.08FU, SH1300528.08FU, SH1300533.08FU, SH1300534.08FU, SH1300537.08FU, SH1300492.08FU, SH1362641.08FU, SH2637732.08FU, SH3574059.08FU, SH3704363.08FU	SH1243364.08FU, SH1188804.08FU, SH1188823.08FU, SH1188831.08FU, SH1188835.08FU, SH1188840.08FU, SH1188841.08FU, SH1188843.08FU, SH2603726.08FU, SH3566717.08FU, SH3695696.08FU
	other SH with pylogenetically matching sequences	SH2310088.08FU, SH2310136.08FU, SH2310294.08FU, SH3030988.08FU, SH3808471.08FU, SH3014642.08FU, SH2310144.08FU, SH2310087.08FU, SH2310088.08FU, SH2310316.08FU, SH2986848.08FU	SH1961372.08FU, SH1961386.08FU, SH1961544.08FU	SH1740803.08FU				
	remarks	good matches	SH1961372.08FU contains also a species from North America; SH1961372.08FU, SH1961375.08FU and SH1961544.08FU have overlapping SH at <0,5%	good match; has overlapping SH with SH1740689.08FU				
	countries	Austria, Belgium, Czech Republic, Denmark, Estonia, France, Germany, Hungary, Italy, Latvia, Norway, Poland, Serbia, Slovenia, Spain, Sweden, Switzerland, United Kingdom						
	ECM hosts	Abies alba, Fagus sylvatica, Halimium lasianthum, Picea abies, Pinus sylvestris, Quercus, Quercus petraea, Quercus suber						

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. S2 (cont.)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JX456844 Russula latolamellata China
H15060604 Russula latolamellata China HOLOTYPE
JX456868 Russula sp. China
H16091311 Russula latolamellata China
LC008301 Russula aff. nigricans Thailand
LC008525 Russula aff. nigricans Thailand
LR599988 Russula sp. China
LR599179 Russula sp. China
LR599865 Russula sp. China
LR599454 Russula sp.China
LR600135 Russula sp.China
MH910605 Russula aff. densifolia United States
FH 2009 ST02 Russula marxmuelleriana Germany
RDL 17-009 Russula marxmuelleriana Belgium HOLOTYPE
SH2310307.08FU KM576557 France Quercus robur
R. marxmuelleriana
FH 2008 ST01 Russula ambusta Germany
SAV F-3358 Russula ambusta Slovakia HOLOTYPE
R. ambusta
JF834364 Russula aff. albonigra United States
MZ017660 Russula sp. United States Pinus ponderosa
HM488592 Russula aff. albonigra United States Pseudotsuga menziesii
KT800130 Russula aff. albonigra United States Ponderosa pine
AV 16-019 Russula ustulata Norway HOLOTYPE
PRM 924452 Russula ustulata Czech Republic
SAV F-2610 Russula ustulata Slovakia
R. ustulata
KF306042 Russula aff. albonigra United States Pseudotsuga menziesii
KF306043 Russula aff. albonigra United States
UDB031025 Russula aff. albonigra Canada
KF306041 Russula aff. albonigra United States
KF306040 Russula aff. albonigra United States
JF834355 Russula aff. albonigra United States
RDL 16-028 Russula nigrifacta Italy
MW172304 Russula nigrifacta Slovakia
RDL 16-063 Russula nigrifacta Italy
MW172303 Russula nigrifacta Slovakia
RDL 16-044 Russula nigrifacta Italy HOLOTYPE
SAV F-1501 Russula nigrifacta Slovakia
SAV F-3006 Russula nigrifacta Slovakia
R. nigrifacta
JK RUS 13090603 Russula albonigra Germany
MW172295 Russula albonigra Czech Republic
SAV F-3465 Russula albonigra Slovakia
SAV F-4776 Russula albonigra Slovakia
MW172292 Russula albonigra Slovakia
SAV F-3220 Russula albonigra Belgium
MW172294 Russula albonigra Czech Republic
MW172291 Russula albonigra Slovakia
SAV F-20197 Russula albonigra Slovakia EPITYPE
SAV F-20177 Russula albonigra Slovakia
R. albonigra
LR598126 Russula sp. China
LR814758 Russula sp. China
LR601014 Russula sp. China
KX441086 Russula sp. China
AB848574 Russula sp. Japan Carpinus
KX444481 Russula sp. China Quercus liaotungensis
KR673541 Russula aff. nigricans Korea Democratic Peoples Republic Of
KY684514 Russula sp. China Quercus
RW 1975 Russula sp. 1 Italy
AB509878 Russula cf. subnigricans Japan
R. sp. 1 (De Lange et al. 2021)
AB291765 Russula aff. densifolia Japan
KX267645 Russula aff. densifolia Thailand
AB291767 Russula aff. densifolia Japan
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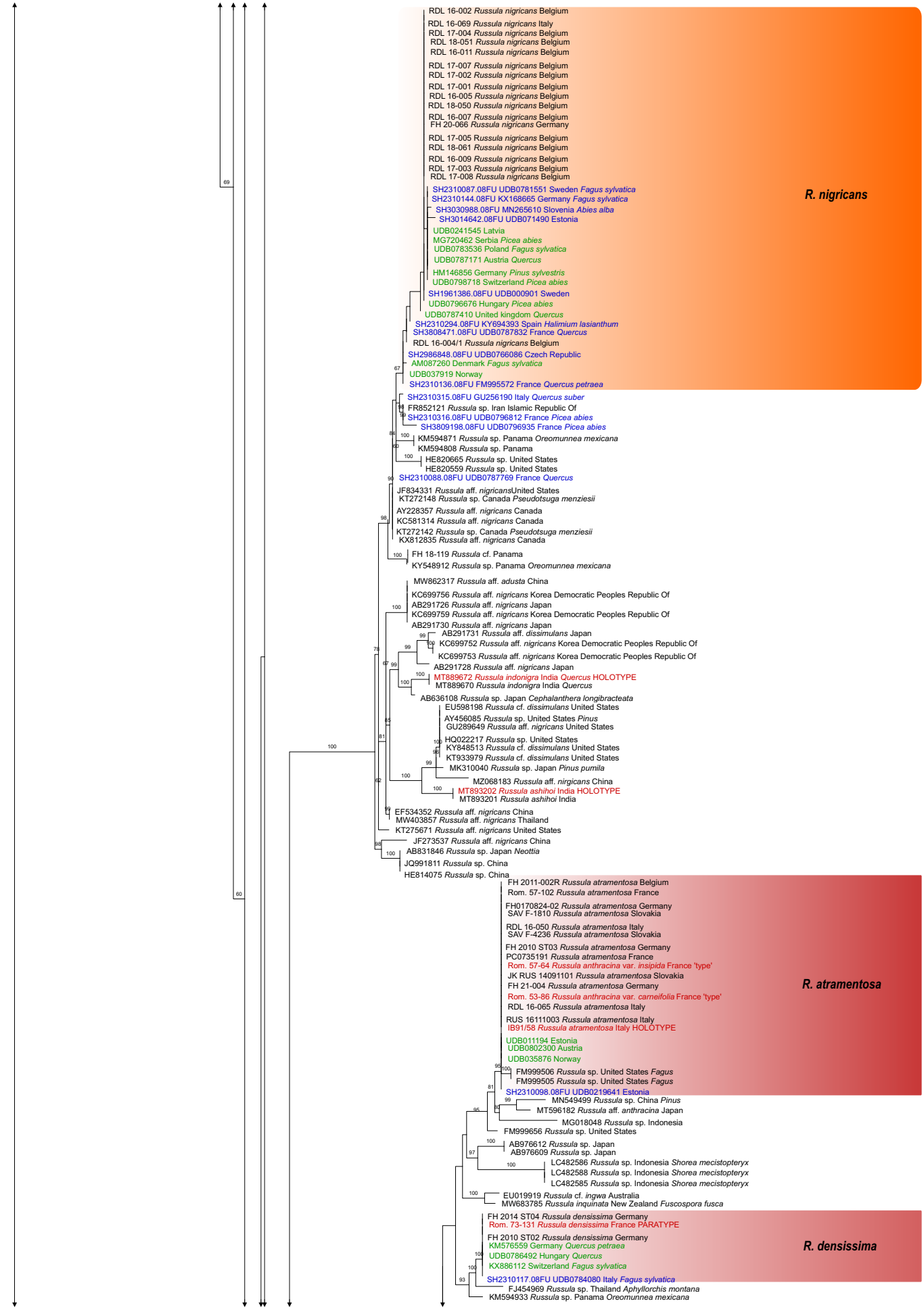
KX267646 Russula aff. densifolia Thailand
JF908707 Russula sp. Italy
R. sp.

Fig. S2 (cont.)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RDL 16-069 Russula nigricans Italy
RDL 17-004 Russula nigricans Belgium
RDL 18-051 Russula nigricans Belgium
RDL 16-011 Russula nigricans Belgium
RDL 17-007 Russula nigricans Belgium
RDL 17-002 Russula nigricans Belgium
RDL 17-001 Russula nigricans Belgium
RDL 16-005 Russula nigricans Belgium
RDL 18-050 Russula nigricans Belgium
RDL 16-007 Russula nigricans Belgium
FH 20-066 Russula nigricans Germany
RDL 17-005 Russula nigricans Belgium
RDL 18-061 Russula nigricans Belgium
RDL 16-009 Russula nigricans Belgium
RDL 17-003 Russula nigricans Belgium
RDL 17-008 Russula nigricans Belgium
SH2310087.08FU UDB0781551 Sweden Fagus sylvatica
SH2310144.08FU KX168665 Germany Fagus sylvatica
SH3030988.08FU MN265610 Slovenia Abies alba
SH3014642.08FU UDB071490 Estonia
UDB0241545 Latvia
MG720462 Serbia Picea abies
UDB0783536 Poland Fagus sylvatica
UDB0787171 Austria Quercus
HM146856 Germany Pinus sylvestris
UDB0798718 Switzerland Picea abies
SH1961386.08FU UDB000901 Sweden
UDB0796676 Hungary Picea abies
UDB0787410 United kingdom Quercus
SH2310294.08FU KY694393 Spain Halimium lasianthum
SH3808471.08FU UDB0787832 France Quercus
RDL 16-004/1 Russula nigricans Belgium
SH2986848.08FU UDB0766086 Czech Republic
AM087260 Denmark Fagus sylvatica
UDB037919 Norway
SH2310136.08FU FM995572 France Quercus petraea
R. nigricans
SH2310315.08FU GU256190 Italy Quercus suber
FR852121 Russula sp. Iran Islamic Republic Of
SH2310316.08FU UDB0796812 France Picea abies
SH3809198.08FU UDB0796935 France Picea abies
KM594871 Russula sp. Panama Oreomunnea mexicana
KM594808 Russula sp. Panama
HE820665 Russula sp. United States
HE820559 Russula sp. United States
SH2310088.08FU UDB0787769 France Quercus
JF834331 Russula aff. nigricansUnited States
KT272148 Russula sp. Canada Pseudotsuga menziesii
AY228357 Russula aff. nigricans Canada
KC581314 Russula aff. nigricans Canada
KT272142 Russula sp. Canada Pseudotsuga menziesii
KX812835 Russula aff. nigricans Canada
FH 18-119 Russula cf. Panama
KY548912 Russula sp. Panama Oreomunnea mexicana
MW862317 Russula aff. adusta China
KC699756 Russula aff. nigricans Korea Democratic Peoples Republic Of
AB291726 Russula aff. nigricans Japan
KC699759 Russula aff. nigricans Korea Democratic Peoples Republic Of
AB291730 Russula aff. nigricans Japan
AB291731 Russula aff. dissimulans Japan
KC699752 Russula aff. nigricans Korea Democratic Peoples Republic Of
KC699753 Russula aff. nigricans Korea Democratic Peoples Republic Of
AB291728 Russula aff. nigricans Japan
MT889672 Russula indonigra India Quercus HOLOTYPE
MT889670 Russula indonigra India Quercus
AB636108 Russula sp. Japan Cephalanthera longibracteata
EU598198 Russula cf. dissimulans United States
AY456085 Russula sp. United States Pinus
GU289649 Russula aff. nigricans United States
HQ022217 Russula sp. United States
KY848513 Russula cf. dissimulans United States
KT933979 Russula cf. dissimulans United States
MK310040 Russula sp. Japan Pinus pumila
MZ068183 Russula aff. nigricans China
MT893202 Russula ashihoi India HOLOTYPE
MT893201 Russula ashihoi India
EF534352 Russula aff. nigricans China
MW403857 Russula aff. nigricans Thailand
KT275671 Russula aff. nigricans United States
JF273537 Russula aff. nigricans China
AB831846 Russula sp. Japan Neottia
JQ991811 Russula sp. China
HE814075 Russula sp. China
FH 2011-002R Russula atramentosa Belgium
Rom. 57-102 Russula atramentosa France
FH0170824-02 Russula atramentosa Germany
SAV F-1810 Russula atramentosa Slovakia
RDL 16-050 Russula atramentosa Italy
SAV F-4236 Russula atramentosa Slovakia
FH 2010 ST03 Russula atramentosa Germany
PC0735191 Russula atramentosa France
Rom. 57-64 Russula anthracina var. insipida France 'type'
JK RUS 14091101 Russula atramentosa Slovakia
FH 21-004 Russula atramentosa Germany
Rom. 53-86 Russula anthracina var. carneifolia France 'type'
RDL 16-065 Russula atramentosa Italy
RUS 16111003 Russula atramentosa Italy
IB91/58 Russula atramentosa Italy HOLOTYPE
UDB011194 Estonia
UDB0802300 Austria
UDB035876 Norway
FM999506 Russula sp. United States Fagus
FM999505 Russula sp. United States Fagus
SH2310098.08FU UDB0219641 Estonia
R. atramentosa
MN549499 Russula sp. China Pinus
MT596182 Russula aff. anthracina Japan
MG018048 Russula sp. Indonesia
FM999656 Russula sp. United States
AB976612 Russula sp. Japan
AB976609 Russula sp. Japan
LC482586 Russula sp. Indonesia Shorea mecistopteryx
LC482588 Russula sp. Indonesia Shorea mecistopteryx
LC482585 Russula sp. Indonesia Shorea mecistopteryx
EU019919 Russula cf. ingwa Australia
MW683785 Russula inquinata New Zealand Fuscospora fusca
FH 2014 ST04 Russula densissima Germany
Rom. 73-131 Russula densissima France PARATYPE
FH 2010 ST02 Russula densissima Germany
KM576559 Germany Quercus petraea
UDB0786492 Hungary Quercus
KX886112 Switzerland Fagus sylvatica
SH2310117.08FU UDB0784080 Italy Fagus sylvatica
R. densissima
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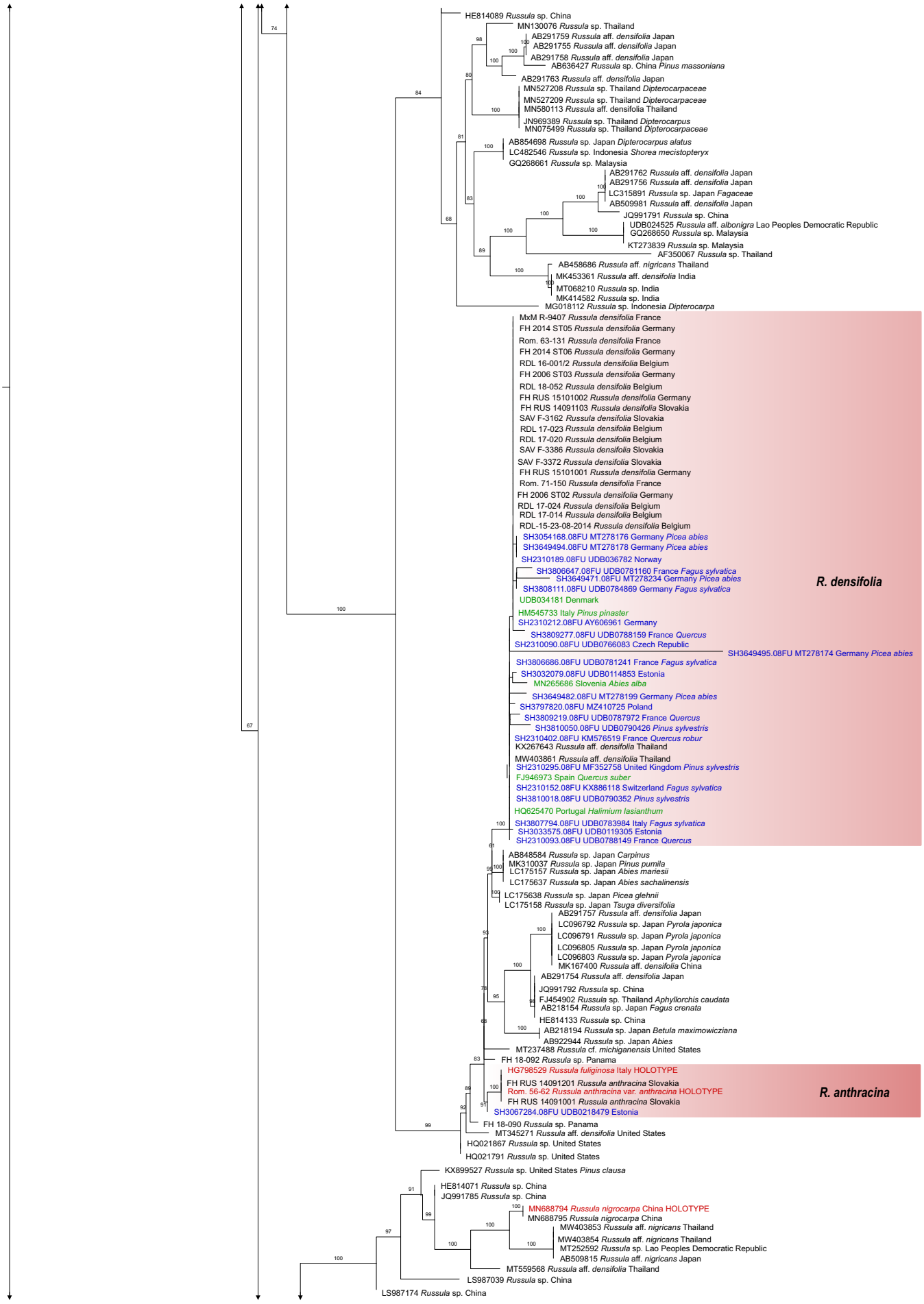
KM594933 Russula sp. Panama Oreomunnea mexicana

Fig. S2 (cont.)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AB636427 Russula sp. China Pinus massoniana
AB291763 Russula aff. densifolia Japan
MN527208 Russula sp. Thailand Dipterocarpaceae
MN527209 Russula sp. Thailand Dipterocarpaceae
MN580113 Russula aff. densifolia Thailand
JN969389 Russula sp. Thailand Dipterocarpus
MN075499 Russula sp. Thailand Dipterocarpaceae
AB854698 Russula sp. Japan Dipterocarpus alatus
LC482546 Russula sp. Indonesia Shorea mecistopteryx
GQ268661 Russula sp. Malaysia
AB291762 Russula aff. densifolia Japan
AB291756 Russula aff. densifolia Japan
LC315891 Russula sp. Japan Fagaceae
AB509981 Russula aff. densifolia Japan
JQ991791 Russula sp. China
UDB024525 Russula aff. albonigra Lao Peoples Democratic Republic
GQ268650 Russula sp. Malaysia
KT273839 Russula sp. Malaysia
AF350067 Russula sp. Thailand
AB458686 Russula aff. nigricans Thailand
MK453361 Russula aff. densifolia India
MT068210 Russula sp. India
MK414582 Russula sp. India
MG018112 Russula sp. Indonesia Dipterocarpa
MxM R-9407 Russula densifolia France
FH 2014 ST05 Russula densifolia Germany
Rom. 63-131 Russula densifolia France
FH 2014 ST06 Russula densifolia Germany
RDL 16-001/2 Russula densifolia Belgium
FH 2006 ST03 Russula densifolia Germany
RDL 18-052 Russula densifolia Belgium
FH RUS 15101002 Russula densifolia Germany
FH RUS 14091103 Russula densifolia Slovakia
SAV F-3162 Russula densifolia Slovakia
RDL 17-023 Russula densifolia Belgium
RDL 17-020 Russula densifolia Belgium
SAV F-3386 Russula densifolia Slovakia
SAV F-3372 Russula densifolia Slovakia
FH RUS 15101001 Russula densifolia Germany
Rom. 71-150 Russula densifolia France
FH 2006 ST02 Russula densifolia Germany
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SH3649494.08FU MT278178 Germany Picea abies
SH2310189.08FU UDB036782 Norway
SH3806647.08FU UDB0781160 France Fagus sylvatica
SH3649471.08FU MT278234 Germany Picea abies
SH3808111.08FU UDB0784869 Germany Fagus sylvatica
UDB034181 Denmark
HM545733 Italy Pinus pinaster
SH2310212.08FU AY606961 Germany
SH3809277.08FU UDB0788159 France Quercus
SH2310090.08FU UDB0766083 Czech Republic
SH3649495.08FU MT278174 Germany Picea abies
SH3806686.08FU UDB0781241 France Fagus sylvatica
SH3032079.08FU UDB0114853 Estonia
MN265686 Slovenia Abies alba
SH3649482.08FU MT278199 Germany Picea abies
SH3797820.08FU MZ410725 Poland
SH3809219.08FU UDB0787972 France Quercus
SH3810050.08FU UDB0790426 Pinus sylvestris
SH2310402.08FU KM576519 France Quercus robur
KX267643 Russula aff. densifolia Thailand
MW403861 Russula aff. densifolia Thailand
SH2310295.08FU MF352758 United Kingdom Pinus sylvestris
FJ946973 Spain Quercus suber
SH2310152.08FU KX886118 Switzerland Fagus sylvatica
SH3810018.08FU UDB0790352 Pinus sylvestris
HQ625470 Portugal Halimium lasianthum
SH3807794.08FU UDB0783984 Italy Fagus sylvatica
SH3033575.08FU UDB0119305 Estonia
SH2310093.08FU UDB0788149 France Quercus
R. densifolia
AB848584 Russula sp. Japan Carpinus
MK310037 Russula sp. Japan Pinus pumila
LC175157 Russula sp. Japan Abies mariesii
LC175637 Russula sp. Japan Abies sachalinensis
LC175638 Russula sp. Japan Picea glehnii
LC175158 Russula sp. Japan Tsuga diversifolia
AB291757 Russula aff. densifolia Japan
LC096792 Russula sp. Japan Pyrola japonica
LC096791 Russula sp. Japan Pyrola japonica
LC096805 Russula sp. Japan Pyrola japonica
LC096803 Russula sp. Japan Pyrola japonica
MK167400 Russula aff. densifolia China
AB291754 Russula aff. densifolia Japan
JQ991792 Russula sp. China
FJ454902 Russula sp. Thailand Aphyllorchis caudata
AB218154 Russula sp. Japan Fagus crenata
HE814133 Russula sp. China
AB218194 Russula sp. Japan Betula maximowicziana
AB922944 Russula sp. Japan Abies
MT237488 Russula cf. michiganensis United States
FH 18-092 Russula sp. Panama
HG798529 Russula fuliginosa Italy HOLOTYPE
FH RUS 14091201 Russula anthracina Slovakia
Rom. 56-62 Russula anthracina var. anthracina HOLOTYPE
FH RUS 14091001 Russula anthracina Slovakia
SH3067284.08FU UDB0218479 Estonia
R. anthracina
FH 18-090 Russula sp. Panama
MT345271 Russula aff. densifolia United States
HQ021867 Russula sp. United States
HQ021791 Russula sp. United States
KX899527 Russula sp. United States Pinus clausa
HE814071 Russula sp. China
JQ991785 Russula sp. China
MN688794 Russula nigrocarpa China HOLOTYPE
MN688795 Russula nigrocarpa China
MW403853 Russula aff. nigricans Thailand
MW403854 Russula aff. nigricans Thailand
MT252592 Russula sp. Lao Peoples Democratic Republic
AB509815 Russula aff. nigricans Japan
MT559568 Russula aff. densifolia Thailand
LS987039 Russula sp. China
LS987174 Russula sp. China

Fig. S2 (cont.)

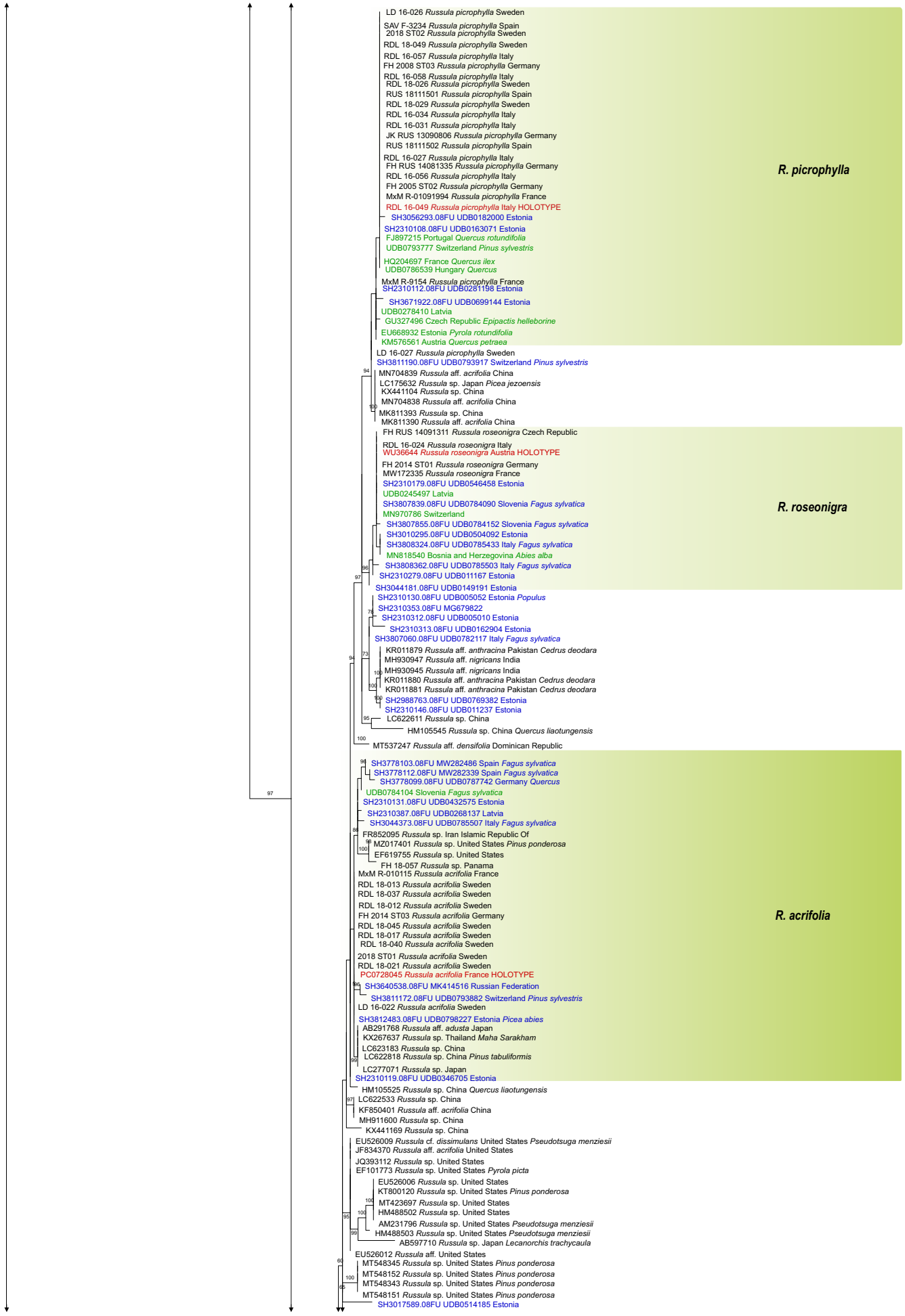
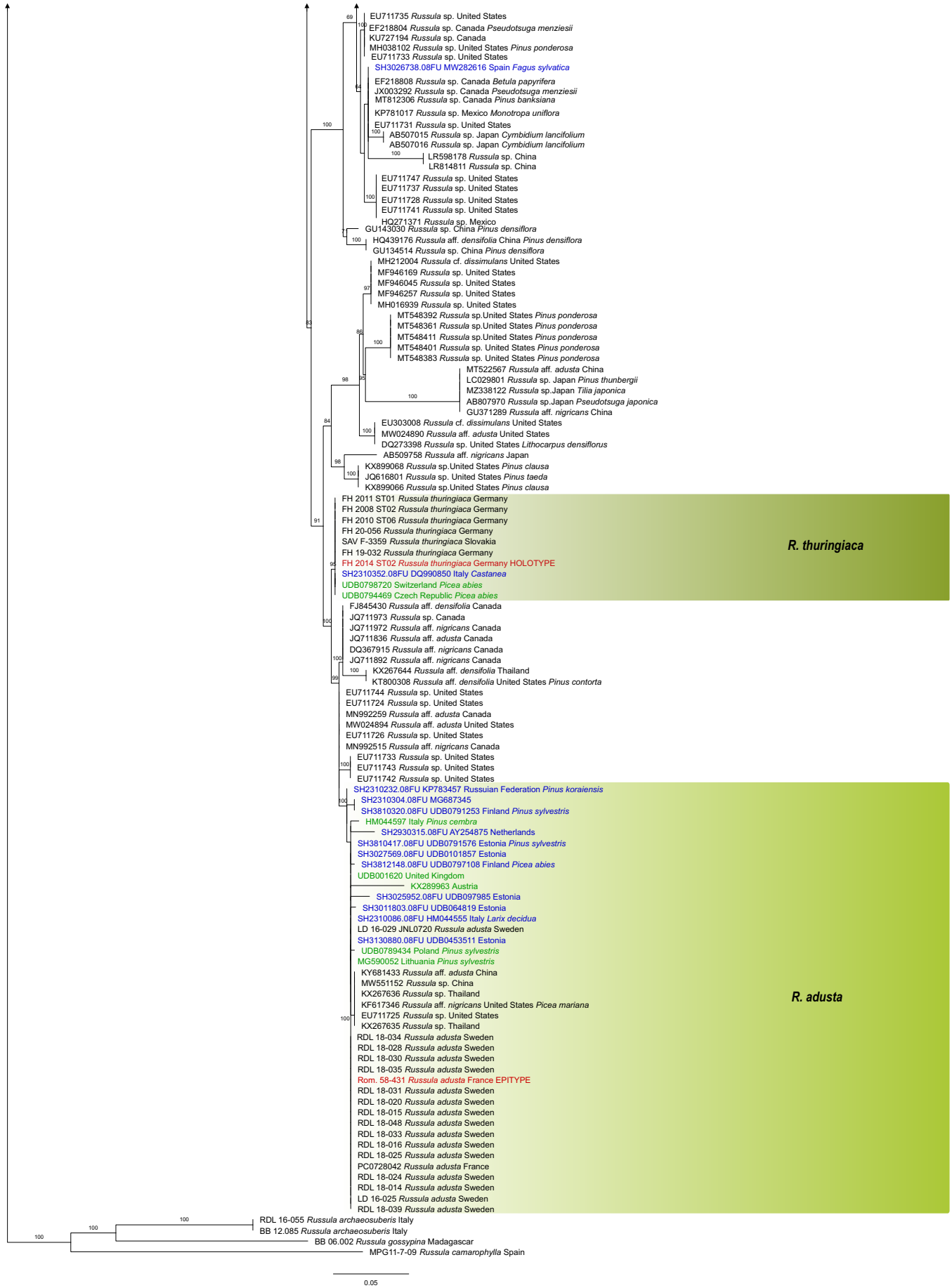


Fig. S2 (cont.)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EF218804 Russula sp. Canada Pseudotsuga menziesii
KU727194 Russula sp. Canada
MH038102 Russula sp. United States Pinus ponderosa
EU711733 Russula sp. United States
SH3026738.08FU MW282616 Spain Fagus sylvatica
EF218808 Russula sp. Canada Betula papyrifera
JX003292 Russula sp. Canada Pseudotsuga menziesii
MT812306 Russula sp. Canada Pinus banksiana
KP781017 Russula sp. Mexico Monotropa uniflora
EU711731 Russula sp. United States
AB507015 Russula sp. Japan Cymbidium lancifolium
AB507016 Russula sp. Japan Cymbidium lancifolium
LR598178 Russula sp. China
LR814811 Russula sp. China
EU711747 Russula sp. United States
EU711737 Russula sp. United States
EU711728 Russula sp. United States
EU711741 Russula sp. United States
HQ271371 Russula sp. Mexico
GU143030 Russula sp. China Pinus densiflora
HQ439176 Russula aff. densifolia China Pinus densiflora
GU134514 Russula sp. China Pinus densiflora
MH212004 Russula cf. dissimulans United States
MF946169 Russula sp. United States
MF946045 Russula sp. United States
MF946257 Russula sp. United States
MH016939 Russula sp. United States
MT548392 Russula sp.United States Pinus ponderosa
MT548361 Russula sp.United States Pinus ponderosa
MT548411 Russula sp.United States Pinus ponderosa
MT548401 Russula sp. United States Pinus ponderosa
MT548383 Russula sp. United States Pinus ponderosa
MT522567 Russula aff. adusta China
LC029801 Russula sp. Japan Pinus thunbergii
MZ338122 Russula sp.Japan Tilia japonica
AB807970 Russula sp.Japan Pseudotsuga japonica
GU371289 Russula aff. nigricans China
EU303008 Russula cf. dissimulans United States
MW024890 Russula aff. adusta United States
DQ273398 Russula sp. United States Lithocarpus densiflorus
AB509758 Russula aff. nigricans Japan
KX899068 Russula sp.United States Pinus clausa
JQ616801 Russula sp. United States Pinus taeda
KX899066 Russula sp.United States Pinus clausa
FH 2011 ST01 Russula thuringiaca Germany
FH 2008 ST02 Russula thuringiaca Germany
FH 2010 ST06 Russula thuringiaca Germany
FH 20-056 Russula thuringiaca Germany
SAV F-3359 Russula thuringiaca Slovakia
FH 19-032 Russula thuringiaca Germany
FH 2014 ST02 Russula thuringiaca Germany HOLOTYPE
SH2310352.08FU DQ990850 Italy Castanea
UDB0798720 Switzerland Picea abies
UDB0794469 Czech Republic Picea abies
R. thuringiaca
FJ845430 Russula aff. densifolia Canada
JQ711973 Russula sp. Canada
JQ711972 Russula aff. nigricans Canada
JQ711836 Russula aff. adusta Canada
DQ367915 Russula aff. nigricans Canada
JQ711892 Russula aff. nigricans Canada
KX267644 Russula aff. densifolia Thailand
KT800308 Russula aff. densifolia United States Pinus contorta
EU711744 Russula sp. United States
EU711724 Russula sp. United States
MN992259 Russula aff. adusta Canada
MW024894 Russula aff. adusta United States
EU711726 Russula sp. United States
MN992515 Russula aff. nigricans Canada
EU711733 Russula sp. United States
EU711743 Russula sp. United States
EU711742 Russula sp. United States
SH2310232.08FU KP783457 Russuian Federation Pinus koraiensis
SH2310304.08FU MG687345
SH3810320.08FU UDB0791253 Finland Pinus sylvestris
HM044597 Italy Pinus cembra
SH2930315.08FU AY254875 Netherlands
SH3810417.08FU UDB0791576 Estonia Pinus sylvestris
SH3027569.08FU UDB0101857 Estonia
SH3812148.08FU UDB0797108 Finland Picea abies
UDB001620 United Kingdom
KX289963 Austria
SH3025952.08FU UDB097985 Estonia
SH3011803.08FU UDB064819 Estonia
SH2310086.08FU HM044555 Italy Larix decidua
LD 16-029 JNL0720 Russula adusta Sweden
SH3130880.08FU UDB0453511 Estonia
UDB0789434 Poland Pinus sylvestris
MG590052 Lithuania Pinus sylvestris
KY681433 Russula aff. adusta China
MW551152 Russula sp. China
KX267636 Russula sp. Thailand
KF617346 Russula aff. nigricans United States Picea mariana
EU711725 Russula sp. United States
KX267635 Russula sp. Thailand
RDL 18-034 Russula adusta Sweden
RDL 18-028 Russula adusta Sweden
RDL 18-030 Russula adusta Sweden
RDL 18-035 Russula adusta Sweden
Rom. 58-431 Russula adusta France EPITYPE
RDL 18-031 Russula adusta Sweden
RDL 18-020 Russula adusta Sweden
RDL 18-015 Russula adusta Sweden
RDL 18-048 Russula adusta Sweden
RDL 18-033 Russula adusta Sweden
RDL 18-016 Russula adusta Sweden
RDL 18-025 Russula adusta Sweden
PC0728042 Russula adusta France
RDL 18-024 Russula adusta Sweden
RDL 18-014 Russula adusta Sweden
LD 16-025 Russula adusta Sweden
RDL 18-039 Russula adusta Sweden
R. adusta
RDL 16-055 Russula archaeosuberis Italy
BB 12.085 Russula archaeosuberis Italy
BB 06.002 Russula gossypina Madagascar
MPG11-7-09 Russula camarophylla Spain
0.05

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

θ ~ IG(3,0.002) and τ ~ IG(3,0.002)								
# species	**PP ε=2, r1**	**PP ε=2, r2**	**PP ε=5, r1**	**PP ε=5, r2**	**PP ε=10, r1**	**PP ε=10, r2**	**PP ε=20, r1**	**PP ε=20, r2**
1–15	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
16	0.000000	0.000000	0.000010	0.000000	0.000000	0.000000	0.000000	0.000000
17	0.000530	0.000485	0.003110	0.000665	0.000875	0.000510	0.000540	0.000675
18	0.999470	0.999515	0.996880	0.999335	0.999125	0.999490	0.999460	0.999325
θ ~ IG(3,0.02) and τ ~ IG(3,0.02)								
# species	**PP ε=2, r1**	**PP ε=2, r2**	**PP ε=5, r1**	**PP ε=5, r2**	**PP ε=10, r1**	**PP ε=10, r2**	**PP ε=20, r1**	**PP ε=20, r2**
1–14	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
15	0.000000	0.000000	0.000000	0.000000	0.000030	0.000045	0.000000	0.000005
16	0.001965	0.001725	0.001795	0.001100	0.002245	0.001715	0.001695	0.001700
17	0.144205	0.143840	0.142625	0.142125	0.138185	0.138280	0.143055	0.138305
18	0.853830	0.854435	0.855580	0.856775	0.859540	0.859960	0.855250	0.859990
θ ~ IG(3,0.02) and τ ~ IG(3,0.002)								
# species	**PP ε=2, r1**	**PP ε=2, r2**	**PP ε=5, r1**	**PP ε=5, r2**	**PP ε=10, r1**	**PP ε=10, r2**	**PP ε=20, r1**	**PP ε=20, r2**
1–14	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000
15	0.000000	0.000000	0.000040	0.000005	0.000030	0.000000	0.000000	0.000010
16	0.001690	0.001110	0.001625	0.001560	0.001565	0.002055	0.001800	0.001615
17	0.138740	0.139735	0.135205	0.142585	0.134715	0.138470	0.141765	0.135010
18	0.859570	0.859155	0.863130	0.855850	0.863690	0.859475	0.856435	0.863365

Fig. S4 Output file of the STACEY analysis.

count	fraction	similarity	nclusters	R	F	I	J	M	H	D	Q	B	N	A	C	K	G	E	P	O	L
3997674	0.9994172507284366	3997674.0	18	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
689	1,72E+12	689.0	17	1	2	3	4	17	5	6	7	8	17	9	10	11	12	13	14	15	16
173	4,32E+10	173.0	17	17	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
156	3,90E+11	156.0	17	17	1	2	3	4	5	6	7	8	9	10	11	12	13	17	14	15	16
114	2,85E+11	114.0	17	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	15	16	17
100	2,50E+11	100.0	17	1	2	3	4	5	6	7	17	8	9	10	11	12	13	17	14	15	16
91	2,27E+11	91.0	17	17	1	2	3	4	5	6	7	8	17	9	10	11	12	13	14	15	16
87	2,17E+11	87.0	17	1	2	3	4	5	6	7	17	8	9	10	11	12	13	14	15	16	17
86	2,15E+11	86.0	17	1	2	3	4	5	6	7	8	9	17	10	11	12	13	14	15	16	17
62	1,55E+10	62.0	17	1	2	3	4	5	6	7	8	9	17	10	11	12	13	17	14	15	16
59	1,47E+11	59.0	17	1	2	3	4	5	6	7	8	9	10	17	11	12	13	14	15	16	17
56	1,40E+11	56.0	17	1	2	3	4	17	5	6	7	8	9	10	11	12	13	14	15	16	17
48	1,20E+10	48.0	17	1	2	3	4	5	6	7	17	8	17	9	10	11	12	13	14	15	16
45	1,12E+11	45.0	17	1	2	3	4	17	5	6	7	8	9	10	11	12	13	17	14	15	16
45	1,12E+11	45.0	17	1	17	2	3	4	5	6	7	8	9	10	11	12	13	17	14	15	16
43	1,07E+11	43.0	17	17	1	2	3	4	5	6	17	7	8	9	10	11	12	13	14	15	16
42	1,05E+11	42.0	17	1	2	3	4	5	6	7	17	8	9	17	10	11	12	13	14	15	16
40	1,00E+10	40.0	17	1	2	3	4	5	6	7	8	9	10	17	11	12	13	17	14	15	16
29	7,25E+09	29.0	17	1	2	3	4	5	6	7	8	9	10	11	17	12	13	14	15	16	17
24	6,00E+09	24.0	17	1	17	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
24	6,00E+09	24.0	17	1	2	3	4	5	6	7	8	9	17	17	10	11	12	13	14	15	16
20	5,00E+09	20.0	17	17	17	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
20	5,00E+09	20.0	17	1	2	3	4	5	6	7	8	9	10	11	17	12	13	17	14	15	16
20	5,00E+09	20.0	17	1	2	3	17	4	5	6	7	8	9	10	11	12	13	14	15	16	17
18	4,50E+09	18.0	17	1	2	3	4	5	6	7	8	9	17	10	17	11	12	13	14	15	16
15	3,75E+10	15.0	17	17	1	2	3	4	5	6	7	8	9	10	17	11	12	13	14	15	16
13	3,25E+10	13.0	17	1	17	2	3	4	5	6	7	8	17	9	10	11	12	13	14	15	16
13	3,25E+10	13.0	17	1	2	3	4	5	6	7	8	9	17	10	11	12	17	13	14	15	16
12	3,00E+10	12.0	17	1	2	3	4	5	6	7	8	9	10	11	12	17	13	14	15	16	17
12	3,00E+10	12.0	17	1	2	3	4	5	6	7	8	9	17	10	11	17	12	13	14	15	16
11	2,75E+10	11.0	17	1	2	3	4	5	6	7	8	9	10	11	12	13	17	14	15	16	17
11	2,75E+10	11.0	16	1	2	3	4	5	6	7	16	8	9	10	11	12	13	16	14	15	16
10	2,50E+09	10.0	17	17	1	2	3	17	4	5	6	7	8	9	10	11	12	13	14	15	16
9	2,25E+10	9.0	17	1	2	3	4	5	6	7	8	9	10	11	12	17	13	17	14	15	16
9	2,25E+10	9.0	17	1	2	3	17	4	5	6	7	8	17	9	10	11	12	13	14	15	16
8	2,00E+09	8.0	17	1	2	3	17	4	5	6	7	8	9	10	11	12	13	17	14	15	16
7	1,75E+10	7.0	17	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	15	17	16
6	1,50E+10	6.0	17	1	2	3	4	5	6	7	8	17	9	10	11	12	13	17	14	15	16
6	1,50E+10	6.0	17	17	1	2	3	4	5	6	7	8	9	17	10	11	12	13	14	15	16
5	1,25E+09	5.0	17	1	17	2	3	4	5	6	7	8	9	17	10	11	12	13	14	15	16
5	1,25E+09	5.0	17	1	2	3	4	5	6	7	8	9	10	11	12	13	17	17	14	15	16
4	1,00E+09	4.0	17	1	2	17	3	4	5	6	7	8	17	9	10	11	12	13	14	15	16
4	1,00E+09	4.0	17	1	2	3	4	17	5	6	7	8	9	17	10	11	12	13	14	15	16
4	1,00E+09	4.0	17	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	17
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3	7,50E+08	3.0	17	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	17	16	17
3	7,50E+08	3.0	17	1	2	17	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
3	7,50E+08	3.0	17	1	2	3	4	5	6	7	8	9	17	10	11	12	13	14	15	17	16
2	5,00E+08	2.0	16	15	1	2	3	16	4	5	6	7	8	9	10	11	12	15	13	14	16
2	5,00E+08	2.0	16	15	16	1	2	3	4	5	6	7	8	9	10	11	12	15	13	14	16
2	5,00E+08	2.0	16	15	1	2	16	3	4	5	6	7	15	8	9	10	11	12	13	14	16
2	5,00E+08	2.0	16	15	1	2	3	4	5	6	7	8	16	9	10	11	12	16	13	14	15
2	5,00E+08	2.0	17	1	2	3	4	5	6	7	8	9	17	10	11	12	13	14	17	15	16
2	5,00E+08	2.0	16	1	2	3	4	5	6	7	8	9	16	10	11	12	13	16	14	15	16
2	5,00E+08	2.0	16	15	1	2	3	4	5	6	16	7	16	8	9	10	11	15	12	13	14
2	5,00E+08	2.0	16	16	1	2	3	4	5	6	7	8	16	9	10	11	12	16	13	14	15
2	5,00E+08	2.0	16	15	1	2	3	4	5	6	15	7	16	8	9	10	11	16	12	13	14
2	5,00E+08	2.0	17	1	2	3	4	5	6	17	7	8	9	10	11	12	13	17	14	15	16
2	5,00E+08	2.0	16	16	1	2	3	4	5	6	7	8	9	10	11	12	13	16	14	15	16
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1	2,50E+08	1.0	16	1	2	3	4	5	6	7	16	8	9	15	10	11	12	16	13	14	15
1	2,50E+08	1.0	16	16	1	2	3	4	5	6	16	7	8	9	10	11	12	16	13	14	15
1	2,50E+08	1.0	16	15	1	2	16	3	4	5	6	7	8	15	9	10	11	16	12	13	14
1	2,50E+08	1.0	16	1	2	3	4	16	5	6	7	8	9	15	10	11	12	15	13	14	16
1	2,50E+08	1.0	16	1	2	3	4	5	6	7	8	9	15	15	10	11	12	16	13	14	16

Fig. S4 (cont.)

count	fraction	similarity	nclusters	R	F	I	J	M	H	D	Q	B	N	A	C	K	G	E	P	O	L
1	2,50E+08	1.0	16	1	2	3	4	5	6	7	8	9	16	15	10	11	12	16	13	14	15
1	2,50E+08	1.0	16	15	1	2	3	4	5	6	16	7	15	8	9	10	11	12	13	14	16
1	2,50E+08	1.0	16	15	1	2	3	4	5	6	7	8	16	16	9	10	11	15	12	13	14
1	2,50E+08	1.0	16	16	1	2	3	4	5	6	16	7	8	9	10	11	12	13	14	15	16
1	2,50E+08	1.0	17	1	2	3	4	17	5	6	17	7	8	9	10	11	12	13	14	15	16
1	2,50E+08	1.0	17	1	2	3	4	5	17	6	7	8	17	9	10	11	12	13	14	15	16
1	2,50E+08	1.0	16	1	2	3	16	4	5	6	7	8	9	10	11	12	13	16	14	15	16
1	2,50E+08	1.0	16	1	16	2	3	4	5	15	6	7	8	9	10	11	12	16	13	14	15
1	2,50E+08	1.0	16	1	2	3	4	5	6	7	8	9	10	16	15	11	12	15	13	14	16
1	2,50E+08	1.0	16	15	1	15	2	3	4	5	16	6	16	7	8	9	10	11	12	13	14
1	2,50E+08	1.0	16	15	1	2	3	4	5	6	7	16	16	8	9	10	11	15	12	13	14
1	2,50E+08	1.0	16	15	1	2	3	4	5	6	15	7	8	9	10	11	16	16	12	13	14
1	2,50E+08	1.0	17	1	2	17	3	4	5	6	7	8	9	10	11	12	13	17	14	15	16
1	2,50E+08	1.0	16	15	1	2	3	4	5	6	16	7	8	9	10	11	12	16	13	14	15
1	2,50E+08	1.0	17	17	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	17	16
1	2,50E+08	1.0	16	15	1	2	3	16	4	5	15	6	7	8	9	10	11	16	12	13	14
1	2,50E+08	1.0	16	15	1	2	3	4	5	6	16	7	8	9	15	10	11	16	12	13	14
1	2,50E+08	1.0	16	15	1	2	3	4	5	6	7	8	9	15	10	11	12	16	13	16	14
1	2,50E+08	1.0	16	1	2	3	4	16	5	6	15	7	15	8	9	10	11	16	12	13	14
1	2,50E+08	1.0	17	1	2	3	4	5	17	6	7	8	9	10	11	12	13	14	15	16	17
1	2,50E+08	1.0	16	1	2	3	4	15	5	6	7	8	9	10	11	16	12	16	13	14	15
1	2,50E+08	1.0	17	1	2	3	4	5	17	6	7	8	9	10	11	12	13	17	14	15	16
1	2,50E+08	1.0	16	1	2	3	4	5	6	7	16	8	15	9	10	11	12	16	13	14	15
1	2,50E+08	1.0	17	1	2	3	4	5	6	17	7	8	9	10	11	12	13	14	15	16	17
1	2,50E+08	1.0	16	15	1	2	3	16	4	5	6	7	15	8	9	10	11	16	12	13	14
1	2,50E+08	1.0	17	17	1	2	3	4	5	17	6	7	8	9	10	11	12	13	14	15	16
1	2,50E+08	1.0	16	1	2	3	4	16	5	6	7	8	9	10	11	12	15	16	13	14	15
1	2,50E+08	1.0	16	15	1	2	3	4	5	6	16	7	8	9	10	11	12	15	13	14	16
1	2,50E+08	1.0	17	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	17	15	16

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.

				R. acrifolia	*R. adusta*	*R. albonigra*	*R. ambusta*	*R. anthracina*	*R. atramentosa*
spores			size	8.1 × 6.6	7.9 × 6.4	8.0 × 6.3	8.2 × 6.0	7.3 × 5.7	8.4 × 6.9
			Q-value	1.24	1.24	1.29	1.38	1.28	1.20
	ornamentation		hight	0.1–0.5	0.2–0.3	0.1–0.4	0.1–0.2	0.1–0.4	0.1–0.6
			w=warts l=lines f=fusions	w=13.4, l=7.9, f=6.8	w=16.5, l=9.4, f=7.3	w=8.4, l=2.2, f=4.8	w=10.2, l=5.4, f=5.1	w=11.1, l=5.6, f=5.1	w=8.1, l=4.4, f=3.7
			suprahilar spot	small	small	medium	medium	medium	small
hymenium	hymenial cystidia at lamellae sides		size	63.0 × 6.5	81.5 × 7.1	85.8 × 8.5	91.9 × 9.8	68.5 × 7.7	86.8 × 8.2
			contents	heteromorphous, oily, fragmented in multiple crystalline-like masses	heteromorphous, oily, fragmented in multiple crystalline-like masses	little, composed of large pale, oily, refringent guttules	heteromorphous, oily, mostly fragmented in multiple crystalline-like masses or slightly granulose	hardly any,hyaline, with some brown pigmentation but mostly completely faded, sometimes very few and very small oily masses visible	partly to almost completely filled with refractive brown pigments, sometimes very few and very small oily masses visible (somewhat granulose)
			SV reaction	blackening	greying	not reacting	not reacting	greying to blackening	not clear
			shape	cylindrical to narrowly fusiform, flexuose, irregularly tapering towards the top, apically with one to multiple constrictions or an eccentric appendage	cylindrical to narrowly fusiform to narrowly clavate, sometimes slightly flexuose, apically obtuse or with central appendage	cylindrical to narrowly fusiform, apically obtuse to mucronate	variable: (1) narrowly fusiform to narrowly clavate, flexuose to even slightly moniliform, apically obtuse or with a constriction or with small appendage to even slightly mucronate; (2) narrowly fusiform to lanceolate, flexuose, tapering towards the top	cylindrical to narrowly fusiform to narrowly clavate, flexuose, apically with central appendage or sometimes double appendage or double constriction	subulate to narrowly fusiform, slightly flexuose, apically 1–2 or one and double eccentric appendage or one central appendage
	hymenial cystidia at lamellae edges		size	46.1 × 6.1	65.3 × 7.3	58.5 × 7.9	63.7 × 8.5	50.1 × 7.1	50.2 × 7.7
	basidia		size	55.2 × 11.0	57.1 × 11.5	55.1 × 10.8	62.6 × 9.5	50.0 × 9.6	58.3 × 11.2
			shape	narrowly clavate	narrowly clavate	narrowly clavate	narrowly clavate	narrowly clavate	narrowly clavate
			N° sterigmata	4	4	4	4	4	4
	marginal cells		size	19.8 × 5.4	25.4 × 5.7	22.1 × 4.9	26.1 × 5.6	20.3 × 6.7	30.4 × 7.2
			shape	poorly differentiated, cylindrical to narrowly clavate, slightly flexuose	cylindrical, flexuose	poorly differentiated, cylindrical, flexuose	undifferentiated, cylindrical to narrowly clavate	undifferentiated, cylindrical to narrowly clavate	cylindrical to narrowly fusiform or subulate, flexuose
Pileipellis	TC margin		size	49.3 × 4.2	46.3 × 4.8	86.6 × 6.6	70.2 × 5.4	57.3 × 6.5	76.7 × 9.2
			shape	narrowly cylindrical	narrowly cylindrical to subulate	narrowly cylindrical to subulate, apically attenuated	narrowly cylindrical, apically slightly attenuated	narrowly cylindrical to subulate, apically attenuated, flexuose	subulate to narrowly fusiform, apically attenuated, slightly flexuose
	TC centre		size	44.1 × 3.6	45.1 × 4.6	72.9 × 6.0	59.8 × 5.0	62.8 × 4.9	58.5 × 6.0
			subterminal cells	similar in length and width, sometimes branching	similar in length and width or shorter and wider, regularly branching	usually shorter and gradually wider	similar in length or slightly shorter, similar in width or gradually slightly wider	mostly slightly shorter but can be similar in length or larger, gradually wider, regularly branching	variable in length, similar in width, never branched
	PC margin		size	69.7 × 5.2	82.2 × 7.3	79.5 × 7.0	110.6 × 7.2	74.0 × 5.8	PC absent
			contents	heteromorphous, oily, fragmented in multiple crystalline-like masses	heteromorphous, oily, fragmented in multiple crystalline-like masses	oily guttulate	heteromorphous, oily content, mostly fragmented in multiple crystalline-like masses or granulose	heteromorphous, oily, fragmented in multiple crystalline-like masses	PC absent
			a= appendages b= bifurcations	a=50%, b=7%	a=0%, b=75%	a=17%, b=17%	a=75%, b=0%	a=90%, b=0%	PC absent
			density	widely dispersed	very rare	widely dispersed	widely dispersed to rare	dispersed	PC absent
	PC centre		size	57.7 × 4.9	53.5 × 5.8	75.2 × 6.8	106.7 × 6.4	88.9 × 5.4	60.9 × 7.1
			contents	heteromorphous, oily, fragmented in multiple crystalline-like masses	heteromorphous, oily, fragmented in multiple crystalline-like masses	oily guttulate	heteromorphous, oily content, mostly fragmented in multiple crystalline-like masses or granulose	heteromorphous, oily, fragmented in multiple crystalline-like masses	few, heteromorphous, oily, fragmented in multiple masses
			a= appendages b= bifurcations	a=75%, b=0%	a=85%, b=0%	a=67%, b=0%	a=100%, b=0%	a=66%, b=0%	a=73%, b=0%
			density	rare	rare	widely dispersed	widely dispersed	rare	PC absent or extremely rare
			depth	180–240	125–200	80–90	175–400	150–250	50–150
			structure	intermediately delimited from trama, subpellis intermediately delimited from suprapellis, subpellis 30–60 µm deep, dense, more parallel horizontal oriented, suprapellis 150–175 µm deep, loose, irregularly oriented	gradually passing in trama, subpellis not delimited from suprapellis, dense, irregularly oriented, more horizontal near trama and surface, with strong gelatinous matrix	not sharply delimited from trama, subpellis not delimited from suprapellis, dense, homogeneous	not sharply delimited from trama, subpellis not delimited from suprapellis, dense near surface and near trama, irregularly oriented, more parallel and horizontal near trama and surface, intricate everywhere	gradually passing in trama, subpellis not delimited from suprapellis, intermediately dense, irregularly oriented	gradually passing in trama, subpellis not delimited from suprapellis, dense, more horizontal near trama and surface, more irregular in between, some gelatinous matter can be present
			pigmentation	throughout the pileipellis	most strongly near trama	only near the surface	only near the surface	more strongly pigmented towards the surface	throughout the pileipellis
trama			cystidioid hyphae	present	present	present	present	present	absent
			oleiferous hyphae	present	present	present	present	present	present

Fig. S5 (cont.)

			R. densifolia	*R. densissima*	*R. marxmuelleriana*	*R. nigricans*	*R. nigrifacta*
spores	ornamentation	size	6.9 × 5.6	6.7 × 5.5	8.1 × 5.7	7.0 × 5.7	8.0 × 6.0
		Q-value	1.24	1.23	1.42	1.23	1.34
		hight	0.1–0.4	0.1–0.5	0.2–0.5	0.1–0.5	0.2–0.4
		w=warts l=lines f=fusions	w=11.1, l=7.4, f=4.8	w=11.3, l=6.1, f=5.9	w=11.5, l=5.0, f=3.9	w=10.1, l=4.5, f=4.2	w=8.6, l=1.4, f=4.6
		suprahilar spot	small	medium	large	medium	small
hymenium	hymenial cystidia at lamellae sides	size	62.9× 7.0	55.9 × 8.2	77.3 × 7.2	74.6 × 6.3	82.6 × 8.9
		contents	few heteromorphous oily content fragmented in multiple very small masses to somewhat granulose and oily hyaline refractive guttules	hyaline heteromorphous oily content, sometimes filled with refractive brown pigments	heteromorphous, oily, fragmented in multiple crystalline-like masses to somewhat granulose	heteromorphous, oily, fragmented in multiple fine crystalline-like masses to banded	heteromorphous, oily, fragmented in multiple crystalline-like masses
		SV reaction	greying	greying	weakly greying	blackening	not reacting
		shape	subulate to narrowly fusiform or narrowly cylindrical, slightly flexuose, apically tapering towards the top or with one central or 1–2 eccentric appendages	subulate to narrowly fusiform, apically tapering towards the top or with one or double constriction or appendage	cylindrical to narrowly fusiform, sometimes slightly flexuose, apically obtuse or with central or eccentric appendage	cylindrical to narrowly fusiform or narrowly clavate, flexuose, apically mainly obtuse or with central appendage	cylindrical to narrowly fusiform to narrowly clavate, sometimes slightly flexuose, apically obtuse or with small appendage
	hymenial cystidia at lamellae edges	size	42.0 × 6.5	52.7 × 9.8	51.1 × 6.6	57.1 × 5.9	69.4 × 9.1
	basidia	size	47.7 × 10.6	49.0 × 9.6	56.7 × 9.7	53.7 × 9.0	62.8 × 9.6
		shape	narrowly clavate	narrowly clavate	narrowly clavate	narrowly clavate	narrowly clavate
		N° sterigmata	4	4	4	1, 2 or 4	4
	marginal cells	size	17.6 × 5.6	19.5 × 7.0	23.4 × 5.8	35.5 × 9.5	22.2 × 5.9
		shape	poorly differentiated, cylindrical to narrowly clavate, slightly flexuose	poorly differentiated, cylindrical	poorly differentiated, cylindrical to narrowly clavate, flexuose	variable, well differentiated, clavate to broadly clavate, or cylindrical to broadly cylindrical or broadly subulate and flexuose	poorly differentiated, cylindrical to narrowly clavate, flexuose
Pileipellis	TC margin	size	35.2 × 9.3	38.9 × 5.2	49.0 × 4.7	50.5 × 5.2	83.5 × 4.9
		shape	subulate	narrowly cylindrical	narrowly cylindrical, apically slightly attenuated	narrowly cylindrical to subulate	narrowly cylindrical
	TC centre	size	29.8 × 7.5	36.8 × 4.3	52.9 × 4.2	49.8 × 4.4	79.6 × 4.6
	subterminal cells		similar in length and width or gradually wider, sometimes branched	similar in length and width, regularly branched, especially at the bases	slightly shorter and broader, regularly branched and containing somewhat inflated cells	often shorter, often gradually broader, sometimes slightly inflated, regularly branched	similar in length or shorter, similar in width
	PC margin	size	42.2 × 6.6	68.4 × 6.7	65.0 × 6.0	48.8 × 5.4	119.5 × 6.7
		contents	few, heteromorphous, oily, fragmented in multiple masses	heteromorphous, oily, fragmented in multiple masses	few, heteromorphous, oily, fragmented in multiple crystalline-like masses	few, heteromorphous, oily, fragmented in multiple fine masses to banded	oily granulose
		a= appendages b= bifurcations	a=95%, b=0%	a=46%, b=0%	a=67%, b=0%	a=93%, b=0%	a=0%, b=0%
		density	numerous to abundant	dispersed	extremely rare	very rare	dispersed
	PC centre	size	42.0 × 6.2	51.2 × 6.0	45.2 × 5.0	40.5 × 4.9	123.0 × 6.0
		contents	few, heteromorphous, oily, fragmented in multiple masses	heteromorphous, oily, fragmented in multiple masses	few, heteromorphous, oily, fragmented in multiple crystalline-like masses	few, heteromorphous, oily, fragmented in multiple fine masses to banded	less, more oily guttulate
		a= appendages b= bifurcations	a=100%, b=0%	a=93%, b=0%	a=77%, b=0%	a=91%, b=0%	a=0%, b=0%
		density	very abundant	dispersed	dispersed	rare to dispersed	dispersed
		depth	200–275	150–205	800–140	90–190	90–136
		structure	clearly delimited from trama, subpellis not delimited from suprapellis, intermediately dense, irregularly oriented	gradually passing into trama, subpellis not delimited from suprapellis, intermediately dense, irregularly oriented, with gelatinous matrix	sharply delimited from trama, subpellis intermediately delimited from suprapellis, subpellis 20–40 µm deep, dense, parallel and horizontal, suprapellis 50–120 µm deep, intermediate to dense, irregularly oriented	intermediately delimited from trama, subpellis not delimited from suprapellis, intermediately dense, irregularly oriented, somewhat more parallel towards the trama	not sharply delimited from trama, subpellis not well delimited from suprapellis, dense near surface and near trama, irregularly oriented, more parallel and horizontal near trama
		pigmentation	throughout the pileipellis	throughout the pileipellis	throughout the pileipellis	throughout the pileipellis	throughout the pileipellis
trama		cystidioid hyphae	present	present	present	present	present
		oleiferous hyphae	present	present	present	present	present

Fig. S5 (cont.)

				R. picrophylla	*R. roseonigra*	*R. thuringiaca*	*R. ustulata*	*R.* **sp. 1**
spores			size	7.1 × 5.7	7.9 × 6.4	7.7 × 6.0	8.5 × 6.3	7.9 × 6.3
			Q-value	1.24	1.24	1.29	1.36	1.26
	ornamentation		hight	0.2–0.6	0.2–0.8(–1)	0.2–0.4	0.1–0.2	0.1–0.3
			w=warts l=lines f=fusions	w=11.5, l=4.5, f=4.6	w=13.2, l=5.4, f=6.7	w=10.6, l=3.0, f=5.0	w=12.4, l=9.2, f=5.4	w=12.0, l=10.4, f=4.6
			suprahilar spot	small	medium	medium	large	medium
hymenium	hymenial cystidia at lamellae sides		size	70.2 × 7.2	69.1 × 7.4	76.1 × 6.7	106.6 × 9.1	83.6 × 8.7
			contents	heteromorphous, oily, fragmented in multiple crystalline-like masses	heteromorphous, oily, fragmented in multiple crystalline-like masses	heteromorphous, oily, fragmented in multiple crystalline-like masses	heteromorphous, oily, fragmented in multiple masses to needle-like crystalline	heteromorphous, oily, fragmented in multiple crystalline-like masses
			SV reaction	weakly blackening	blackening	blackening	not reacting	not reacting
			shape	narrowly fusiform, flexuose, apically tapering towards the top or with one or double constriction	cylindrical to narrowly fusiform, sometimes slightly flexuose, apically with one central appendage or constriction, rarely with double appendage or somewhat bifurcating or tapering towards the top	cylindrical to narrowly fusiform, rarely subulate, slightly flexuose, apically obtuse, tapering towards the top or with constriction to slightly mucronate	cylindrical to narrowly fusiform, apically obtuse with small appendage or slightly tapering towards the top	cylindrical to narrowly fusiform, often slightly moniliform and flexuose, apically obtuse or with double constriction or small appendage
	hymenial cystidia at lamellae edges		size	51.7 × 7.4	44.5 × 7.4	51.2 × 6.9	82.9 × 9.5	62.3 × 7.8
	basidia		size	52.2 × 10.5	47.2 × 10.9	64.4 × 10.8	67.3 × 9.2	60.9 × 9.9
			shape	narrowly clavate	narrowly clavate	narrowly clavate	narrowly clavate to cylindrical	narrowly clavate
			N° sterigmata	4	4	4	4	4
	marginal cells		size	16.8 × 5.2	32.4 × 6.9	24.2 × 5.8	26.5 × 6.3	21.5 × 6.6
			shape	poorly differentiated, cylindrical to narrowly clavate, sometimes flexuose	narrowly fusiform to subulate, flexuose	cylindrical to subulate, flexuose	poorly differentiated, cylindrical to narrowly clavate to fusiform, flexuose	undifferentiated, cylindrical to narrowly clavate
Pileipellis	TC margin		size	61.3 × 6.1	57.6 × 5.3	49.3 × 5.8	53.6 × 6.0	61.4 × 6.0
			shape	narrowly cylindrical to subulate, apically attenuated	narrowly cylindrical, apically slightly attenuated	narrowly cylindrical to subulate, apically attenuated	narrowly cylindrical to subulate, apically slightly attenuated	narrowly cylindrical to slightly subulate or narrowly fusiform, apically attenuated
	TC centre		size	57.5 × 3.9	60.9 × 3.7	60.0 × 4.6	59.0 × 5.1	70.5 × 7.4
			subterminal cells	similar in length or larger, rarely shorter, broader, sometimes branched.	similar in length and width, regularly branched	slightly shorter and broader, sometimes branched but deep in the suprapellis, some inflated cells can be observed deeper in the pileipellis	shorter and gradually wider	similar in length and width or slightly wider; containing inflated cells
	PC margin		size	63.2 × 5.6	77.3 × 7.0	68.8 × 7.8	79.6 × 7.0	98–more than 320 × 7.3
			contents	heteromorphous, oily, fragmented in multiple masses	heteromorphous, oily, fragmented in multiple masses	few, heteromorphous, oily, fragmented in multiple masses	very little, heteromorphous, oily content , fragmented in multiple masses to needle-like crystalline	heteromorphous, oily, fragmented in multiple crystalline-like masses or more granulose
			a= appendages b= bifurcations	a=67%, b=11%	a=50%, b=0%	a=0%, b=0%	a=0%, b=30%	
			density	moderately numerous	rare	extremely rare	extremely rare	numerous
	PC centre		size	49.8 × 5.3	50.3 × 5.2	61.6 × 5.3	PC absent	117.4 × 8.4
			contents	heteromorphous, oily, fragmented in multiple masses	heteromorphous, oily, fragmented in multiple masses	few, heteromorphous, oily, fragmented in multiple masses	PC absent	heteromorphous, oily, fragmented in multiple crystalline-like masses or more granulose
			a= appendages b= bifurcations	a=96%, b=0%	a=73%, b=0%	PC absent	a=21.4%, b=14.3%	
			density	numerous	rare to widely dispersed	dispersed	PC absent	numerous
			depth	110–300	100–150	75–125	250–300	200–275
			structure	clearly delimited from trama, subpellis not delimited from suprapellis, dense near trama, gradually less dense to intermediate towards surface, parallel and horizontal near trama, irregular near surface, some gelatinous matter can be present	intermediately delimited from trama, subpellis not delimited from suprapellis, dense near trama and surface, intermediately dense to loose in between, more parallel and horizontal near trama and surface, irregularly oriented in between, some gelatinous matter can be present	gradually passing in trama, subpellis not delimited from suprapellis, intermediately dense, irregularly oriented	not sharply delimited, subpellis not delimited from suprapellis, dense near surface and near trama, loose in intermediate zone, irregularly oriented	not sharply delimited from trama, subpellis not delimited from suprapellis, more dense near surface and near trama, irregularly oriented, more parallel and horizontal near trama
			pigmentation	throughout the pileipellis	throughout the pileipellis	throughout the pileipellis	throughout the pileipellis	only in the upper part
trama			cystidioid hyphae	present	present	present	absent	present
			oleiferous hyphae	present	present	present	present	present

Fig. S5 (cont.)

			R. acrifolia	*R. adusta*	*R. albonigra*	*R. ambusta*	*R. anthracina*	*R. atramentosa*
macromorphology	context	reddening	light to moderately	very faintly (sometimes locally)	no clear reddening or only slightly	no reddening	no reddening or at most weakly, localised	no clear reddening, at most faintly
		blackening	greying, slowly blackening	greying	strong	strong	strong, but slow	greying/blackening
		surface	strongly reddening, blackening	slightly reddening	some reddening possible, strongly blackening	strongly blackening	(strongly) blackeing	strongly and quickly blackening
		$FeSO_4$	green (possibly first orange)	green (possibly first orange)	orange	?	orange	green (possibly first orange)
	lamellae	thickness	narrow to medium	narrow to medium	narrow	narrow	narrow	narrow (to medium)
		density	moderately distant to moderately dense	moderately distant to dense	moderately distant to moderately dense	dense	dense to very dense	dense
		additional	pinkish tinge	slightly pinkish tinge	strongly blackening	strongly blackening	strongly blackening, pinkish tinge possible	strongly blackening, pinkish tinge possible (can be strong)
	odour		fruity, slightly musty when old	musty with fruity component, like old wine barrels	weak of apples	indistinct	indistinct, somewhat musty, with slightly fruity component	fruity, when strong it can resemble apple or ripe pear, with musty component
	taste		acrid to strongly acrid	mild	mild, slightly like mint (refreshing) in the lamellae	first mild, then quickly somewhat cooling with menthol component, never acrid	mild or only slightly acrid in the context, in the lamellae acrid/peppery	mild, possibly slightly refreshing or slightly acrid in the lamellae
		pileus cuticle	shiny, viscid when moist	shiny, viscid when moist	dry, matt	dry matt, viscid when moist	dry matt, viscid when moist	dry, matt

			R. densifolia	*R. densissima*	*R. marxmuelleriana*	*R. nigricans*	*R. nigrifacta*
macromorphology	context	reddening	clear, moderately to strong	no clear reddening	slowly, hardly to only slightly	clear, very strong	no reddening
		blackening	greying/blackening	first greying then blackening	medium to strong	strong	strong
		surface	reddening, blackening	blackening	slightly reddening is possible, browning	strongly reddening, strongly blackening	some reddening possible, strongly blackening
		$FeSO_4$	green (possibly first orange)	?	orange	green (possibly first orange)	green
	lamellae	thickness	very narrow	very narrow to narrow	medium	thick to very thick	narrow
		density	very dense	dense to very dense	moderately distant	widely spaced	dense
		additional	reddening, blackening	edge blackening	pinkish tinge possible	reddening, blackening, pinkish tinge possible (rarely), edge blackening	strongly blackening
	odour		indistinct, slightly fruity, slightly musty	indistinct	indistinct, musty or somewhat bread-like	indistinct, musty, sometimes somwhat unagreeable (sweaty feet), when young there can be a slightly fruity component	fruity, sweet
	taste		mild, or slightly to moderately acrid in the lamellae	mild in the context, in the lamellae acrid	mild	mild	mild to slightly refreshing
		pileus cuticle	dry matt, viscid when moist	rather shiny, viscid when moist	dry, matt	dry	dry matt, viscid when moist

			R. picrophylla	*R. roseonigra*	*R. thuringiaca*	*R. ustulata*	***R*. sp. 1**
macromorphology	context	reddening	clear, moderately to strong	slowly, up to moderately	slowly, weakly	no reddening, at most very faintly	no reddening
		blackening	greying/blackening	first greying then slowly blackening	greying or greying/blackening	strong	strong
		surface	reddening	reddening	slightly reddening is possible on stipe	strongly blackening	strongly blackening
		$FeSO_4$	green	orange	variable	green	orange
	lamellae	thickness	narrow to medium	narrow	medium to thick	thin	thin
		density	moderately distant to dense	moderately distant to moderately dense	rather distant to moderately distant	moderately distant	moderately distant
		additional	pinkish tinge	reddening	very strong salmon tinge	strongly blackening	strongly blackening
	odour		fruity	slightly fruity	indistinct	indistinct	indistinct
	taste		very acrid (burning acrid)	slightly acrid, stronger in the lamellae	mild in the context, in the lamellae mild or slightly to moderately acrid	mild but unagreeable, musty, slightly menthol-like in the lamellae	mild
		pileus cuticle	shiny, viscid when moist	dry matt, viscid when moist	greasy, shiny	dry, shiny	dry, matt

Fig. S5 (cont.)

			+	++	+++	*R. acrifolia*	*R. adusta*	*R. albonigra*	*R. ambusta*	*R. anthracina*	*R. atramentosa*	*R. densifolia*	*R. densissima*	*R. marxmuelleriana*	*R. nigricans*	*R. nigrifacta*	*R. picrophylla*	*R. roseonigra*	*R. thuringiaca*	*R. ustulata*	*R.* sp. 1
spores	ornamentation	Q-value	up to 1.25	1.25-1.29	more than 1.3	+	+	++	+++	++	+	+	+	+++	+	+++	+	+	++	+++	++
		hight	up to 0.3	up to 0.5	higher than 0.6	++	+	++	+	++	+++	++	++	++	++	++	+++	+++	++	+	+
		warts	up to 10	10-12	more than 12	+++	+++	+	++	++	+	++	++	++	++	+	++	+++	++	+++	++
		lines	up to 4	4-7	mote than 7	+++	+++	+	++	++	++	+++	++	++	++	+	++	++	+	+++	+++
hymenium	hymenial cystidia at lamellae sides	width	up to 7	7-8.5	more than 8.5	+	++	++	+++	++	++	++	++	++	+	+++	++	++	+	+++	+++
		contents	almost optically empty	oily distinct	crystalline present	+++	+++	++	++	+	+	++	++	+++	+++	+++	+++	+++	+++	+++	+++
		SV reaction	not reacting	greying	blackening	+++	++	+	+	+++	+	++	++	++	+++	+	++	+++	+++	+	+
		shape	obtuse, often no appendage	subacute	acute, often moniliform	+++	+	+	++	++	+++	+++	+++	+	++	+	++	++	+	++	++
			base inflated	cylindrical or fusiform	top inflated	++	++	++	+++	+++	+	++	+	++	+++	++	++	++	++	++	++
Pileipellis	TC margin	width	up to 6	6-8	more than 8	+	+	++	+	++	+++	+++	+	+	+	+	++	+	+	++	++
		length	up to 40	40-65	more than 65	++	++	+++	+++	++	+++	+	+	++	++	+++	++	++	++	++	++
		shape	base inflated	base inflated or cylindrical	cylindical	+++	++	+	+++	++	+	+	+++	++	++	+++	++	++	++	++	++
		subterminal cells	equal	shorter	shorter and/or wider	+	++	+++	++	++	+	++	+	++	+++	+	++	+	++	+++	++
	PC margin	width	up to 6	6-7	more than 7	+	+++	++	+++	+	+++	++	++	++	+	++	+	++	+++	++	+++
		length	up to 60	60-90	more than 90	++	++	++	+++	++	++	+	++	++	+	+++	++	++	++	++	+++
		contents	almost optically empty	oily distinct	crystalline present	+++	+++	++	+++	+++	+	+	++	++	+	++	++	++	++	+	+++
		bifurcations	up to 10%	10-30%	more than 30%	+	+++	++	+	+	+	+	+	+	+	+	+++	++	+	+	+++
		density	rare	dispersed	numerous	+	+	+	+	+	+	+++	+	+	+	+	++	+	+	+	+++
macromorphology	context	reddening	weak	moderate	strong	++	+	++	+	+	+	++	+	+	+++	+	+++	++	+	+	+
		blackening	weak	moderate	strong	++	+	+++	+++	+++	+++	++	++	++	+++	+++	++	++	++	+++	+++
	lamellae density		dense	moderatately distant	distant	++	++	++	+	+	+	+	+	++	+++	+	++	++	+++	++	++
	taste		mild	weakly acrid	strongly acrid	+++	+	+	+	++	+	++	++	+	+	+	+++	++	++	+	+
	pileus cuticle		dry, matt	in between	viscid, shiny	+++	+++	+	++	++	+	++	+++	+	+	++	+++	++	+++	++	+